

RESEARCH ARTICLE

Effects of environmental temperature on the growth performance of a tropical *Oreochromis esculentus* (Graham, 1928). Implications for the species conservation

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Funding information

The research was funded by the Swedish International Development Agency (SIDA) under Makerere University SIDA Grant Contribution No: 5180060 towards PhD studies for Jane.

Abstract

Climate variability and change are currently recognised global challenges. However, the impacts of rising temperatures may be greatest on tropical freshwater fish, which already exist in warm environments and may be living close to their critical thermal maximum. However, there is limited species-specific information on tropical species' adaptive capacity to increased temperature. This study examined various growth attributes in juvenile populations (farmed, L. Kacheera and L. Nabisojjo) of a critically endangered tropical *Oreochromis esculentus* to determine its adaptive potential. Fish were acclimated at 25, 28, 31 and 34°C for 28 days. Overall, survival rates were high. Growth coefficient *b* was not significantly different from three ($b = 3$) in all treatments, implying isometric growth. The specific growth rates (SGRs), body condition *K*, and hepato-somatic indices (*h*) declined as the acclimation temperatures increased. Although SGR showed significant variations only among populations, the highest in L. Nabisojjo, *K* and *HSI* showed significant variations among treatments. Overall, the growth attributes declined at higher acclimation temperatures, but remained within acceptable ranges, implying that the species may attain normal growth at elevated temperatures experienced in outdoor aquaculture systems, despite its warm environmental background. Hence, we recommend selective breeding for temperature resilience and species introduction into aquaculture using broodstock from L. Nabisojjo.

KEYWORDS

conservation, growth, *Oreochromis esculentus*, temperature

RÉSUMÉ

La variabilité et l'évolution du climat sont actuellement considérées comme des défis à l'échelle mondiale. Cependant, les effets de la hausse des températures affectent tout particulièrement les poissons tropicaux d'eau douce, dont l'habitat a déjà atteint un niveau thermique maximal. Il existe toutefois peu de renseignements spécifiques sur la capacité d'adaptation des espèces tropicales à l'augmentation de la température. Cette étude a examiné diverses caractéristiques de croissance chez des populations juvéniles (d'élevage - L. Kacheera et L. Nabisojjo) de l'espèce *Oreochromis esculentus* gravement menacée, afin de déterminer son potentiel d'adaptation. Les poissons

ont été acclimatés à des températures de 25, 28, 31 et 34°C pendant 28 jours. Dans l'ensemble, les taux de survie étaient élevés. Le coefficient de croissance **b** ne présentait pas de différence significative par rapport au coefficient de régression ($b = 3$) dans tous les traitements, ce qui sous-entend une croissance isométrique. Les taux de croissance spécifiques (TCS), la condition corporelle K et les indices hépatosomatiques (his) ont diminué à mesure que les températures d'acclimation augmentaient. Bien que des variations significatives en matière de TCS uniquement aient été constatées parmi les populations, les variations les plus importantes entre les traitements sont apparues concernant L. Nabisojjo, K et HIS. Dans l'ensemble, les caractéristiques de croissance ont diminué à des températures d'acclimation plus élevées, mais sont restées dans des plages acceptables, ce qui laisse supposer que l'espèce peut atteindre une croissance normale à des températures élevées rencontrées dans les systèmes d'aquaculture en plein air, malgré un environnement chaud. Par conséquent, nous recommandons un élevage sélectif aux fins de résistance aux températures et l'introduction des espèces en aquaculture à l'aide de géniteurs provenant de L. Nabisojjo.

1 | INTRODUCTION

The overall effects of climate change on aquatic ecosystems will likely be an increase in water temperature, which consequently decreases dissolved oxygen levels and increases the toxicity of pollutants (Ficke et al., 2007). Water temperature is also known as a major determinant for fish growth, metabolism and locomotion performance (Pang et al., 2011). According to Pörtner and Farrell (2008), the observable effects of increased temperature are fatal cutbacks in the performance of organisms as an adaptation to limit maintenance costs.

The predicted global atmospheric temperature increase of 1–7°C by the end of the 21st Century (IPCC, 2007) will be followed by an increase in lakes' surface equilibrium temperature, though at a lower rate of 70% to 85% (Schmid et al., 2014). Implying that water temperature may rise to approximately 6°C, which is higher than the level (1–2°C) stipulated to sufficiently affect fish's adaptive capacity to sub-lethal levels (Logue et al., 1995; Sunday et al., 2010). Similarly, Foden et al. (2013) postulated that 2–3°C temperature increase may drive almost 20%–30% of the world's species into extinction. Therefore, it is urgently required that management strategies be formulated to prevent the predicted effects of global warming on biodiversity.

There is already evidence that species' vulnerability to climate change may greatly differ among species and subspecies based on their physiological sensitivity and adaptability to temperature change (Deutsch et al., 2008; Pörtner, 2002) and evolutionary history (Fangue et al., 2006; Pörtner & Farrell, 2008; Stillman, 2003). The vulnerability may even differ among populations of the same species (FAO, 2012). However, the tropical inland species are presumably at a greater risk to the impacts of climate change than their temperate counterparts (Ficke, 2005; Sunday et al., 2010;

Walters et al., 2012). Based on their existence in relatively warmer temperatures, moreover, with minimum seasonal variations, it suggests that the tropical species may already be close to their critical thermal maximum and have limited capacity to adapt to any further increase in the environmental temperature and extreme weather events (Lapointe et al., 2018; Stillman, 2003; Tewksbury et al., 2008).

Furthermore, the vulnerability of tropical aquatic species to global warming may be exacerbated by the nature of their habitats which are mostly shallow (FAO, 2018), so they tend to warm more rapidly with higher surface water temperature than the deep-water bodies which have a greater heat storage capacity (Oswald & Rouse, 2004).

However, our understanding of the effects of global climate change on tropical freshwater fish species is insufficiently developed due to the wide-ranging research bias towards the temperate marine species (Comte et al., 2013; FAO, 2018; Musa et al., 2017), yet management strategic actions need to be guided by empirical evidence. Therefore, more research is urgently needed to guide the development of conservation strategies for tropical aquatic species (Dawson et al., 2011). Hence, this study was conducted to assess the impacts of elevated environmental temperatures on a tropical species and predict the effects of global warming on *Oreochromis esculentus*.

We hypothesised a normal growth potential of *O. esculentus* at higher temperatures in semi-controlled conditions of aquaculture system. The study objectives were to examine the effect of increased temperature on the survival, growth, body condition and hepato-somatic indices at the stipulated higher temperatures, as predicted by IPCC (2007), and to inform both *ex situ* and *in situ* fish management and conservation decisions geared towards species stock improvement, availability and suitability for aquaculture.

Growth is the general increase in the body size, constituted by the sizes of the various body organs that reflect habitat quality and ecosystem status (Heath, 1995; Le Cren, 1951; Lugert et al., 2014). Growth encompasses many metabolic and biochemical processes which are greatly influenced by environmental temperatures. Whereby, for every 10°C temperature variation, growth variation is doubled or tripled, termed as temperature coefficient (Q_{10}) (Boyd, 2018).

Growth data are generated through biometric valuations, and it is used to deliver information on fish species biomass (Zargar et al., 2012), which is important in fisheries science and management due to its direct economic bearing (Beer et al., 2010). It is also used in predicting the effects of environmental perturbations on the species fitness and survival.

There is already clear indication of environmental perturbation of lakes in Uganda due to climate change. These are evidenced by the changing weather patterns, drop in water levels, and increased frequency of extreme weather events like floods, as well as droughts, whose social economic impacts make communities very vulnerable (Hepworth & Goulden, 2008). For instance, the water surface of L. Kawi and L. Wamala has reportedly shrunk due to rising temperatures (NaFFIRI, 2012). The consequences on the indigenous fish species in these lakes can be enormous because of the isolation and lack of inter-connectivity with other lake systems, as well as destruction of the fish breeding and nursery grounds.

Oreochromis esculentus is an indigenous tilapiine fish species of Africa, endemic only to the Victoria and Kyoga basins. Before it became virtually extinct from the two main water bodies, Lake Victoria and Kyoga, *O. esculentus* constituted the main component of the commercial fishery in Uganda throughout the first half of the 20th century (Ogutu-Ohwayo, 1993). Currently, its populations are fragmented in some minor lakes, within its natural range (Nagayi et al., 2006; Ogutu-Ohwayo, 1993) and it is critically endangered (IUCN, 2020–3). Despite its critical conservation state, the species is still a delicacy and sought after for its superior flesh (Graham, 1929; Mwanja et al., 2017).

Therefore, it is necessary to alleviate the pressure on the wild fishery of *O. esculentus* and to aid its conservation particularly at such a period when there is worldwide decline in wild fishery production and massive extinction of biodiversity due to global warming.

Fortunately, there is already evidence that the species can easily adapt to artificial feeds (Mwanja et al., 2017) and can easily breed in captivity (Ssekyewa, 3/10/2018 personal communication). Therefore, its domestication can be considered. However, no data ascertain the species ability to flourish at high climate change-driven temperatures associated with shallow water bodies (FAO, 2018), as would be in outdoor earthen ponds.

2 | MATERIALS AND METHODS

The study procedures for the animal care and experimentation used in this study were approved by the Uganda National Council for

Science and Technology, UNCST Ref No. NS103ES. We followed the UNCST's guidelines in the collection, rearing and handling of the experimental objects.

2.1 | Collection of fish stock for the experiment and rearing conditions

Juveniles of *Oreochromis esculentus* (10–16 cm TL) were collected from three (3) populations, that is, Lake Kacheera (Lake Victoria basin), Lake Nabisojjo (Lake Kyoga basin) and a fish farm (in Masaka District), to compare and evaluate the importance of ecological background in determining species' environmental adaptability. The farm population was a composite mixture from lakes Mburo, Kijanebalola and Kacheera, which had existed in captivity for five (5) years.

Live fish from lakes Kacheera and Nabisojjo were captured using boat seines. However, the farmed fish were harvested by partially draining the ponds and then picking them with a scoop net. The captured fish were left in the same water bodies (confined in hap-pas) overnight to overcome capture stress and decrease stomach fullness. This aimed to minimise water quality deterioration due to metabolic wastes and food regurgitation during transportation and ensure desirable survival rates.

The fish were transported early morning (5:00 am) the following day, when the temperature is low and the fish are less active, in a 500-litre circular plastic tank to Kajjansi Aquaculture Research and Development Centre KARDC, Uganda. At KARDC, the fish were first kept in separate outdoor concrete tanks (6 × 10 × 1 m) for two (2) weeks, before the commencement of the temperature acclimation experiment. The outdoor concrete tanks provided transient environmental conditions between the wild (extensive space with only natural food supply and less human interference) and the fully controlled (smaller space with added artificial feed supply and more human interference) experimental setting, to minimise shock. We assumed that two weeks were long enough for healing of the injuries sustained during capture and transportation, and for fish to get familiar with the artificial feeds which they would be given during the experiment.

2.2 | Experimental design

The experiment encompassed three (3) treatments (T1 = 28°C, T2 = 31°C and T3 = 34°C) and a control (25°C), replicated into three (3). The choice of the experimental temperatures was determined based on the current average lower temperature of 25°C within the Victoria and Kyoga lake basins (Witte & Van Densen, 1995) and the predicted 1–7°C global temperature increase by the end of the 21st century (IPCC, 2007). According to Schmid et al. (2014), water temperature will increase following air temperature rise though at a relatively lower rate of about 70% to 85%. The experimental setup was indoors, in 300-litre circular plastic tanks supplied with immersed Thermostat (W1209®) regulated electric water heaters.

2.3 | Stocking

A total of eighty-four (84) fish per population were transferred to the indoor experimental tanks. First, the fish were anaesthetised in 40 ppm olive oil, for easy handling. Their initial total length TL and the standard length SL were then recorded using a calibrated measuring board. Their initial weight (g) was recorded using a digital electronic scale (Hanchen Precise Analytical Balance®). All individuals of a population were marked with a unique colour of the visible implant elastomer tags (just under the skin). Each fish was tagged in one of the seven different areas of the body, that is, anal, caudal-dorsal, caudal-ventral, pelvic, ventral and dorsal-anterior and dorsal-posterior. Finally, they were systematically distributed, ensuring that each replicate tank is stocked with a mixed set of seven uniquely tagged fish from each of the three populations, making a total of 21 fish per tank, and an overall total of 252 fish for the entire experiment. The fish were mixed for the purpose of uniformity. The tagging was aimed to facilitate identification and record of mortalities, replacements and integration of the individual's initial and final biometric data.

After stocking, the thermal regulated immersed water heaters were switched on and temperature started rising at 1°C per hour, to the desired level (± 0.5 of 25, 28, 31 and 34°C) and was maintained there for a total of 28 days (4 weeks).

The fish mortalities encountered within the first two (2) days of the experiment were removed immediately and replaced; however, any subsequent deaths were only recorded. For proper growth, the fish were reared in approximately 12-h light and 12-h dark cycle which imitated the natural photoperiod in their original habitat. We also ensured that there was continuous aeration in the experimental water tanks for sustained supply of dissolved oxygen and the fish were fed to satiation twice a day (9:00 AM and 5:00 PM) on floating pellets (28% crude protein). The tanks were cleaned twice a day (around 10:00 AM and around 6:00 PM following the feeding sessions), by scooping food remains from the water surface and syphoning the solid metabolic wastes from the bottom, and then replacing the water in the experimental tanks with up to ten percent (10%) of fresh water from the supply tank.

For proper water quality management, monitoring was done through daily measurements of the water temperature (°C), hydrogen potential pH, electrical conductivity EC and dissolved oxygen DO, using a multi-probe water meter (H19146-Hana instruments®). Nitrite NO₂ and total ammonia NH₃ were measured bi-weekly using a freshwater aquaculture outfit kit (Model AQ-2).

Value ranges of the water temperature (24.5–34.5°C), pH (7.1–7.8), EC (84–150 μ S/cm), dissolved oxygen (4.38–7.6 mg/L), nitrite (0.0 mg/L) and total ammonia (0.7–1.0 mg/L) were recorded and all were within the acceptable range for proper fish growth.

2.4 | Data collection and analysis

Feeding the fish stopped 24 h prior to the commencement of data collection to minimise interference with the total wet fish weight. The surviving fish were transferred to an anaesthetic solution of

40 ppm clove oil till they lost swimming equilibrium. They were measured and weighed to record their final lengths (cm) and weights (g). The fish were dissected to obtain the liver and record its weight. The fish length and weight data were used to determine the specific growth rate, length-weight relationship and fish condition factor and the liver weight used to determine the hepato-somatic index.

2.5 | Details of the performed calculations

2.5.1 | SGR of the fish

Specific growth rate was calculated using natural log (ln) as a percentage of the difference between the final and initial total body weights divided by the rearing period (days) according to Lugert et al. (2014) as shown (Equation 1):

$$SGR = \frac{\log(W_2) - \log(W_1) \times 100}{\text{rearing period}} \quad (1)$$

where W_2 = final weight (g) and W_1 = initial weight (g), respectively.

2.5.2 | Length-weight relationship (LWR)

The length-weight relationship, LWR, was estimated using the following equation: $W = aL^b$ as described by Le Cren, (1951), where W = the total wet weight (g) of the fish, L = total length (cm) of the fish, a = Exponent describing the rate of change of weight with length (= the intercept of the regression line on the Y axis) and b = the slope of the regression line also referred to as the regression coefficient or allometric coefficient.

The linear transformations of the length weight equation were made using base₁₀ logarithm and the intercept 'a' and regression coefficient (slope) 'b' were computed according to Lugert et al. (2014) (Equation 2),

$$\log W = b \log L + \log a \quad (2)$$

2.5.3 | Condition factor K

The condition factor of the fish was calculated according to Lugert et al. (2014), as shown (Equation 3),

$$\text{Fulton's } K = \frac{100 W}{L^3} \quad (3)$$

where K , condition factor, W , the wet body weight (g) of the fish and L , the total length (cm) of the fish.

2.5.4 | Hepato-somatic index (HSI)

The hepato-somatic index, HSI, was calculated as percentage of the liver weight to the total fish weight (Equation 4),

TABLE 1 Summary of survival rates (%) of the fish during the acclimation experiment by population and treatment

Treatment (°C)	Species populations			Overall (%)
	Farmed (%)	Kacheera (%)	Nabisojjo (%)	
25	85.71	80.95	95.24	87.30
28	90.48	85.71	95.24	90.48
31	100.00	85.71	100.00	95.24
34	90.48	80.95	85.71	85.71
Overall	91.67	83.33	94.05	

Note: The total number at the onset of the experiment was 252 fish which comprised of 21 individuals from each population per treatment and 226 fish survived to the end. The overall values were generated as percentages of the sums of the survivors in a given column or row against the overall total (survivors + mortalities) in the column or row.

$$HSI = \frac{WI}{Wb} \times 100, \quad (4)$$

where WI, liver weight and Wb, fish wet body weight.

2.6 | Statistical analysis

The data were verified to be normal after testing using Shapiro-Wilks test according to Zar (1999). Data analyses were performed in R studio and R software to generate the descriptive values of the parameters. Analyses for variation of the SGR, the b values of the LWR, the condition factor and hepato-somatic indices were done using a one-way analysis of variance, ANOVA at 5%. However, the student t-tests were performed to determine if the b value for each temperature regime was significantly different from three ($b = 3$), which is the predicted value for isometric growth (Yilmaz et al., 2012).

3 | RESULTS

The fish total length (cm) ranged from 11.4 cm to 16.9 cm, and the wet body weight (g) ranged from 22.2 to 79.0 g.

3.1 | Survival rates

The study recorded a high survival rate of 89.68% overall, at the conclusion of the acclimation period. Fish survival rate was highest at 31°C and lowest at 34°C (Table 1). Although not investigated in detail, the prevalence of fungal infections on the fish skin was high in the control group. We managed it by immersing the infested fish in a solution of sodium chloride for approximately 6 h and then returning to the acclimation tank. Although Lake Nabisojjo was observed to have the highest survival rate (94.05%) and Lake Kacheera the lowest (83.33%), the analysis of variance using one-way ANOVA showed no significant difference ($p < 0.05$) in survival rates among acclimation temperatures.

3.2 | Specific growth rate

There was an overall inverse relationship in the SGR and temperature, whereby the peak value was recorded at 28°C and a steady decline at the higher temperatures (Figure 1). The highest SGR was recorded in L. Nabisojjo population, while the lowest was in L. Kacheera. Statistical analyses showed that the differences in the SGR were highly significant ($p < 0.001$) among populations. However, when compared among treatments, there was no significant difference ($p < 0.05$).

3.3 | Length-weight relationship LWR parameters

We tested the hypothesis that *O. esculentus* from the studied populations would attain isometric growth when nurtured at different temperatures. The values of the regression coefficient b were generally within the predicted normal range of 2.5–3.5, according to Froese (2006). Further statistical analyses using students' t-test showed no

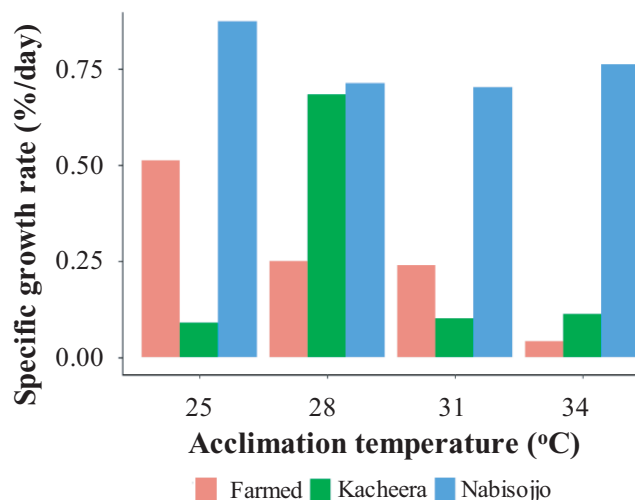


FIGURE 1 Comparing the specific growth rates of *Oreochromis esculentus* in the farmed, L. Kacheera and L. Nabisojjo populations and different acclimation temperatures

TABLE 2 Length-weight relationship of three populations of *Oreochromis esculentus* from farm, L. Kacheera and L. Nabisojjo after acclimation at 25, 28, 31 and 34°C for 28 days

Item	Population			Treatment (°C)			
	Farm	Kacheera	Nabisojjo	25	28	31	34
N	80	70	76	65	64	56	41
a	0.030474	0.013695	0.032563	0.018296	0.01936	0.017845	0.012473
b	2.752724	3.045113	2.749831	2.95718	2.930746	2.954521	3.078029
r ²	0.8988	0.9794	0.8346	0.9296	0.9579	0.8302	0.9265

Abbreviations: a, intercept; b, slope/regression coefficient; N, number of fish; r², coefficient of determination.

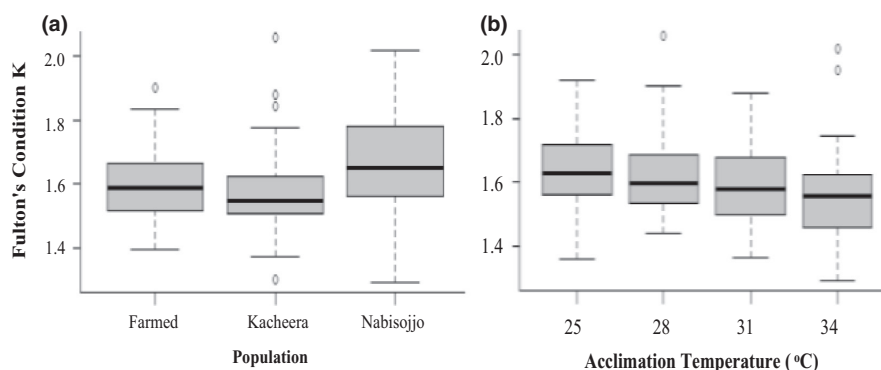


FIGURE 2 Box plot showing comparison of Fulton's condition factor K among three fish populations and the different acclimation temperatures

significant differences ($p < 0.05$) between the regression coefficient b and the predicted value three ($b = 3$), for isometric growth as reported by Yilmaz et al. (2012). Hence, our results imply isometric growth for the studied populations of *O. esculentus*. Statistical tests using one-way analysis of variance indicated no significant differences among treatments nor the studied populations. Values of the coefficient of determination r^2 were high, ranging from 0.729 in L. Nabisojjo to 0.996 in L. Kacheera at acclimation temperature 28°C, suggesting a high correlation between the acclimation temperature and growth (Table 2).

3.4 | Condition factor K

Generally, the body condition showed an inverse correlation with the acclimation temperature. The condition of the combined fish populations was highest (1.63) at 25°C and lowest (1.52) at 34°C. Comparing populations, fish condition was highest in L. Nabisojjo and lowest in L. Kacheera populations (Figure 2). Statistical tests using one-way analysis of variance ANOVA showed that there were significant differences among populations ($p < 0.001$) as well as among acclimation temperatures ($p < 0.001$).

3.5 | Hepato-somatic indices

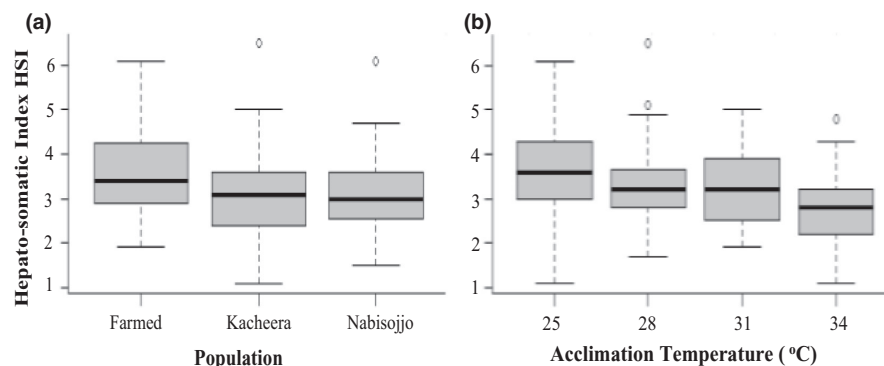
There was an inverse correlation between the HSI and acclimation temperatures. A one-way analysis ANOVA of the hepato-somatic indices HSI revealed significant differences ($p < 0.001$) among

populations and acclimation temperatures. Overall, the farmed populations recorded the highest HSI values, while L. Nabisojjo recorded the lowest values (Figure 3).

4 | DISCUSSIONS AND RECOMMENDATIONS

Fish growth is a fundamental aspect of the fisheries science and management, especially due to its economic bearing (Beer et al., 2010). Although growth occurs throughout the body, the rate at which it happens in the different body parts /organs depends on the external and internal environment as a means of adaptation (Heath, 1995). Therefore, our study examined the predicted effects of increased environmental temperatures, matching the postulations of global warming, on the adaptive potential of an indigenous tropical fish species *Oreochromis esculentus*. The presumptions that any slight increase in environmental temperatures may affect the tropical species to sub-lethal levels were tested at the maximum range (1–7°C) of global warming temperature predictions (IPCC, 2007). Our findings of high survival rates across all treatments were an indication of the species capacity to withstand the predicted high temperature. However, the relatively high mortality levels in the control group coupled with the high prevalence of fungal infections indicated that 25°C is possibly too low for the proper physiological functioning of the body. It is also important to take into consideration that the frequent use of sodium chloride in an effort to control the fungal infections could have impacted on the other tested growth attributes. Since the highest survival rate was recorded in L.

FIGURE 3 A comparison of the hepato-somatic indices among the species populations and the different acclimation temperatures



Nabisojjo population, so we consider L. Nabisojjo population as the most resistant to the predicted higher temperatures.

The SGR and the regression/growth coefficient b in the length-weight relationship LWR which are very important for deriving the species growth were within normal range. Studies of the LWR are used in predicting weight from length measurements in yield assessment (Nehemia et al., 2012; Pauly, 1983). The recorded b values in the current study were very close to three, which denotes isometric growth of the *O. esculentus*. Isometric growth is associated with no change of body shape as an organism grows. Since there were no significant differences among the fish groups acclimated at various temperatures, it is an indication that the species will attain normal growth when exposed to higher climate change-induced temperatures such as those experienced in outdoor aquaculture facilities.

We observed the highest SGR at 28°C followed by 31°C with lower levels in the control group 25 and 34°C, as was the case in the species survival rates. The values were lower in the control group 25°C but increased and plateaued at 28 and 31°C, and then dropped to 34°C. Therefore, our results fit in the normal growth curve with progression at the lower temperature, and then it plateaus after reaching a maximum level at its optimum water temperature and then declining with any further increase in water temperature (Jobling, 1997). Therefore, 28–31°C can be considered as the optimum temperature range for specific growth and survival rates of *O. esculentus*.

The current findings are similar to those reported in a closely related tilapiine species *O. niloticus*, where the highest specific growth rate (0.034 ± 0.055) was observed at 29°C (Lapointe et al., 2018). However, as mentioned earlier, the high fungal infestation could be the cause for the low SGR in the control group. Since the SGR was significantly different in the three populations, it confirms the prediction that climate change responses may differ among populations of the same species depending on their acclimation capacity (FAO, 2012), and the highest values of SGR having been recorded in L. Nabisojjo population, then broodstock for use in aquaculture may be obtained from L. Nabisojjo.

The highest recorded condition factor K (1.64) in the present study was apparently lower than (1.89) the value reported by Nagayi et al., (2006) in seven satellite lakes, which was also lower than (2) in the earlier survey of Lake Victoria (Graham, 1929) in the same fish species. It is reported that the body condition expresses the degree

of wellness of the fish in their habitat (Khristenko & Kotovska, 2017; Lizama & Ambrosio, 2002), whereby the more plump fish imply favourable environmental conditions and ample food availability (Blackwell et al., 2000), and vice versa.

The declined body condition may be a result of changed diet. *O. esculentus* was reported to feed selectively on diatoms, especially *Aulacosira* spp (Payne, 1971). However, due to changes in environmental conditions, eutrophication became apparent in most water bodies, resulting in scarcity of diatoms and dominance of the blue-green algae (Cyanobacteria), especially *microcystis* spp. which are indigestible and toxic to fish (Mugidde, 1993). Such changes could have driven genetic selection of *O. esculentus* towards more flexible feeders, and probably the existing populations of the species are those with poorer growth potential. Additionally, the overall reduction in body condition in our study could be attributed to handling stress and change of diet in the controlled environment. However, the reported differences in the species body condition between satellite lakes populations (Nagayi et al., 2006) and L. Victoria (Graham, 1929) populations may be due to environmental temperature and fishing pressure. Being very small and shallow, the satellite lakes tend to experience higher temperature fluctuations and are also more vulnerable to overfishing compared to the larger deeper L. Victoria which has a higher specific heat capacity, and therefore warms more slowly (Oswald & Rouse, 2004) and may not be easily affected. Such ecological stresses could have led to natural selection for the smaller resilient individual. Therefore, it is increasingly important to protect the heterogeneity of habitats as well as genetic diversity within a species in order to sustain the capacity of a species to adapt (Bellard et al., 2012).

Furthermore, the body condition which is a significant predictor of body energy reserves such as lipids, protein, glycogen and total protein (Chellappa et al., 1995) declined steadily at higher acclimation temperatures in the current study. Similarly, the HSI which depict the metabolic cost on the body showed an inverse relationship with temperature. On the other hand, the declining HSI at higher environmental temperatures may signify a reduction in the digestive capacity and probably the underlying cause for the deteriorating body condition, specific growth and survival rates as the results indicated. Our findings bear a resemblance with the study of largemouth bass *Micropterus salmoides* in which the HSI declined in warmer temperatures (Adams & Mclean, 1984). We, therefore, recommend

detailed studies of tropical species' digestive enzymatic activity at higher temperatures than the current average.

The growth imbalance towards lower levels in our results implies that climate variability and change are likely to affect the production of inland fisheries if they go unchecked. Since fish biomass has a direct economic bearing (Beer et al., 2010), the reduction in body condition will result into significant loss of revenue and household income. However, the poor and marginalised communities who directly depend on fisheries for their livelihood may be affected most, given that they have limited capacity to adapt (Cinner et al., 2011). Apparently, 240 million people in Sub Saharan Africa are poor, with 60%–70% of them depending directly on natural resources, such as fisheries (FAO, 2010). Coupled with the greater vulnerability of tropical inland fish species to the impacts of climate change compared to their temperate marine counterparts (Tewksbury et al., 2008), indeed Africa may be affected the most overall (Allison et al., 2009).

However, despite the declining body condition at higher temperatures, there is a possibility of conserving the species through aquaculture based on the recorded body condition values which were higher than one (1). According to Ayode (2011) in the study of the African Carp *Labeo ogunensis*, a value of fish body condition higher than one is desirable in fish farming. Additionally, the species attained normal growth at higher water temperature similar to the outdoor aquaculture systems. Finally, the species can easily adapt to artificial feeds (Mwanja et al., 2017). Therefore, this provides hope that tropical freshwater fishes may persist in the face of rising temperatures over the following decades, particularly through *ex situ* interventions. We, therefore, recommend the introduction of *O. esculentus* for aquaculture. Culturing the species will not only improve the stocks and accessibility of a fishery resource which is so highly desired (Graham, 1929; Mwanja et al., 2017; Trewavas, 1983), but will also conserve the already critically endangered species (IUCN, 2020). Most importantly, introduction of *O. esculentus* in aquaculture will diversify the culture fish species, thus improving the economic well-being of the people in the region.

Although most growth attributes did not differ significantly among the studied populations of *O. esculentus*, L. Nabisojjo population displayed the highest adaptive potential to increased environmental temperature, and L. Kacheera the lowest, implying that the latter will be affected earliest by global warming. Since L. Nabisojjo recorded the highest tolerance to increased temperature, we recommend that broodstocks for future research and management interventions such as species selective breeding for temperature tolerance, aquaculture, restocking of the natural water bodies and storage of gametes in genetic banks should be obtained from there.

Furthermore, management interventions should be directed towards designing reserve networks that protect biodiversity *in situ* (Bellard et al., 2012). In the case of *O. esculentus*, improving law enforcement to control fishing effort through the co-management policies in the natural water bodies where remnants of the species survive may be highly useful for its conservation.

However, when global warming increases and persists, the plastic phenotypic responses observed in our study of declining somatic

growth, body condition and HIS which symbolise the species' adaptation to minimise maintenance costs (Pörtner & Farrell, 2008) will reach a physiological limit at which they cannot decrease indefinitely under sustained environmental change (Chevin et al., 2010). At such levels, species extinctions may result (Dawson et al., 2011) as a power function of the expected global warming (Hansen et al., 2010).

Our results also illustrate the importance of attempting to limit the magnitude of temperature rise. Actions towards minimising global warming and other global change drivers should be prioritised in conservation sciences, in order to increase the overall resilience of biodiversity in the face of climate change (Bellard et al., 2012; Hughes et al., 2003), and there is global need to drastically reduce greenhouse gas emissions.

ACKNOWLEDGEMENTS

The authors are grateful to the Swedish International Development Agency (SIDA) and Makerere University under SIDA Grant Contribution No: 5180060 for funding the PhD studies for the first author. The data were collected during the PhD study entitled 'Physiological response of *Oreochromis esculentus*' (Graham, 1929) to different temperature regimes. The authors are also indebted to the management of Gulu University, the employing University of the first author for granting her study leave during her PhD studies at the Department of Zoology, Entomology and Fisheries Sciences, School of Biological Sciences, College of Natural Sciences, Makerere University, Uganda. We are also thankful to the management and staff of Kajjansi Aquaculture Research and Development Centre, KARDC, where the study experiment was conducted, for their support, advice and assistance, especially to Ms. Ganda E., Mr. Kityo the farm manager, to Michael and Mr. Okello. Thanks so much for all the assistance.

CONFLICT OF INTEREST

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could cause any competing interests.

AUTHOR CONTRIBUTIONS

Conceptualisation (Jane, Matthew, Joseph and Juliet), methodology (Jane, Matthew, Joseph and Juliet), validation (Jane, Matthew and Alfonse), data analysis (Jane), writing original draft (Jane), editing draft (Alfonse, Matthew and Joseph), supervision (Matthew and Joseph) and funding acquisition (Jane).

DATA AVAILABILITY STATEMENT

The data are available at Mendeley Data, V1, <https://doi.org/10.17632/gznmk99838.1> (<https://dx.doi.org/10.17632/gznmk99838.1>).

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How to cite this article: Nagayi, J. K. Y., Kisakye, J. J., Mwanja, M. T., Nattabi, J., & Opio, A. (2022). Effects of environmental temperature on the growth performance of a tropical *Oreochromis esculentus* (Graham, 1928). Implications for the species conservation. *African Journal of Ecology*, 60, 581–590. <https://doi.org/10.1111/aje.12939>