Aquatic Invasions 2024 Volume 19, Issue 4: 431–443

Research Article

Rapid growth of a locally-endemic tilapia may enable persistence in an African lake invaded by Nile tilapia

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Abstract

The introduction of non-native species can lead to competition with native species for key resources, driving the decline and extinction of endemic biodiversity. Recently, a newly discovered and evolutionarily distinct lineage of Korogwe tilapia (*Oreochromis korogwe*) was reported from small lakes in southern Tanzania. This small-bodied lineage is potentially threatened by introduced Nile tilapia (*Oreochromis niloticus*), an invasive large-bodied congeneric with a pan-tropical non-native distribution. Nile tilapia is known to dominate ecologically-similar native tilapia in competitive interactions, preventing access to resources such as food and shelter. We therefore hypothesised that competition between Nile tilapia and Korogwe tilapia could limit access to resources by the native species and hence reduce their growth rate, a key determinant of fitness. In this study, tilapia were collected from Lake Rutamba in two field seasons, and individuals were classified using microsatellite DNA genotypes as *O. niloticus*, *O. korogwe* or interspecific hybrids. Recent growth rate of these individuals was determined by measuring the distance between scale circuli. In contrast to expectations, we found that native *O. korogwe* overall had a faster growth rate than the invasive *O. niloticus*, with hybrids showing growth rates more similar to *O. korogwe*. We propose that in Lake Rutamba the persistence of *O. korogwe* could be partially enabled by a faster growth rate than the large-bodied invasive *O. niloticus*. Based on these results, we suggest that predictions of the effects of invasive species on native biodiversity may benefit from information on relative fitness, in addition to ecological niche overlap.

Key words: Cichlid fish, freshwater habitats, interspecific competition, ecological displacement, growth

OPEN ACCESS

Academic editor: Takudzwa Madzivanzira
Received: 5 April 2024
Accepted: 29 July 2024
Published: 10 December 2024

Citation: Champneys T, Matiku P, Saxon AD, Shechonge AH, Blackwell T, Ngatunga BP, Ioannou CC, Genner MJ (2024) Rapid growth of a locally-endemic tilapia may enable persistence in an African lake invaded by Nile tilapia. Aquatic Invasions 19(4): 431–443. https://doi.org/10.3391/ai.2024.19.4.136691

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Introduction

Fish populations are typically subject to high mortality rates at juvenile stages, with relatively few individuals surviving to breeding age (Sogard 1997). Factors affecting the fitness of fish species at juvenile stages are therefore especially important

in determining population dynamics. Often, key resources necessary for juvenile survival such as food and shelter are limited, and interspecific competition can determine access to these resources (Chase et al. 2016). Thus, individuals which are at a disadvantage in either exploitative or interference competition will have restricted access to food or shelter, increasing the likelihood of predation, starvation and reduced growth rate (Martin et al. 2010).

The introduction of non-native species can increase competition for key resources, especially when the introduced species occupies a similar niche to native species (Britton et al. 2011; Pacioglu et al. 2019). Many studies have highlighted how competition with non-native species can result in the decline and in some cases extinction of native populations (Human and Gordon 1996; Case et al. 2016). The theoretical principle of competitive exclusion predicts that inferior competitors will go extinct if they are unable to shift niches to avoid competition with the superior species (Hardin 1960; Bøhn et al. 2008). Competition with non-native species, therefore, poses a severe potential threat to native fish populations.

Nile tilapia *Oreochromis niloticus* is a freshwater cichlid fish, with a pan-tropical non-native distribution. Declines in native species following the introduction of Nile tilapia have been reported in many ecosystems, however the mechanisms that drive these declines are not always known (Canonico et al. 2005). The vast majority of non-native Nile tilapia populations are descendants of fish selected for aquaculture or capture fisheries improvement, and are therefore likely to possess phenotypes leading to high production yields, including fast growth rates and large body sizes. It is often predicted that introduced Nile tilapia may outcompete native species, limiting their access to resources (Canonico et al. 2005). Studies have demonstrated that under experimental conditions Nile tilapia forage more efficiently than native species (Gu et al. 2015), including other tilapia (Wing et al. 2021). Such competitive advantages of Nile tilapia over shared food resources could result in a reduced growth rate of native species, which is a crucial determinant of fitness. Additionally, Nile tilapia has been shown to dominate aggressive interactions (Chifamba and Mauru 2017), including outcompeting native cichlids over access to shelter (Martin et al. 2010; Champneys et al. 2021). This could increase the likelihood of predation on native species *in situ*, resulting in a lower survival rate, and a reduced opportunity to reach breeding age. Male-male interference competition over lekking spaces could also reduce breeding output in subordinate species, with further consequences for population fitness. Given the current evidence of competition-induced effects by Nile tilapia on native populations *in situ* (Chifamba and Videler 2014; Bradbeer et al. 2020), research into their impact on potentially affected species appears warranted.

The highly biodiverse freshwater habitats of Tanzania are home to a large number of tilapia species of the genus *Oreochromis*, many of which are endemic to the region (Darwall et al. 2015; Shechonge et al. 2019). Native tilapia play important roles in capture fisheries (Lind et al. 2012) and ecosystem functioning (Lévêque 1995), as well as providing valuable genetic resources from which novel strains for aquaculture could be developed (Eknath and Hulata 2009; Lind et al. 2012). Thus, the preservation of these species has been highlighted as an important conservation goal (Lind et al. 2012). Between 2013 and 2016, an evolutionarily unique lineage of a small-bodied species, the Korogwe tilapia *Oreochromis korogwe*, was discovered in the Rutamba lakes (Lakes Rutamba, Nambawala and Mitupa) near Lindi in Southern Tanzania (Fig. 1; Blackwell et al. 2021). Living in sympatry with the Korogwe tilapia is an introduced population of non-native large-bodied Nile tilapia, and the two species are known to be hybridizing (Blackwell et al. 2021).

Hybridization with invasive species can have irreversible impacts on the genetic diversity of native species, but the extent of the threat depends in part on the relative fitness of these hybrids compared to parental species (Dudgeon et al. 2006). Nile tilapia is known to hybridize with a number of other *Oreochromis* species across its introduced range, and investigating the outcome of hybridization in the Rutamba lakes could help to more clearly define its impact as an invasive species (Blackwell et al. 2021).

Nile tilapia and Korogwe tilapia are closely related, fully sympatric and both are omnivorous, feeding primarily on macrophytes, phytoplankton, and detritus of vegetation (M. Genner pers. obs.). We therefore hypothesised that this ecological similarity may drive competition between the two species, causing a discrepancy in access to food and shelter. To test our hypothesis, we collected individuals from both species in Lake Rutamba, the largest of the three lakes in which they are known to co-occur. Specimens were genotyped using microsatellite DNA markers, enabling classification of individuals as Nile tilapia, Korogwe tilapia, or one of their hybrids. We then measured the recent growth rate of specimens using data from scale circuli. Growth rate is a crucial determinant of fitness in fish and reduced individual growth rate can provide evidence of competition-induced restrictions on available food resources (Diehl and Eklov 1995; Bøhn et al. 2008). Our comparisons of differences in growth rate between species, and between purebreds and hybrids, provide insight into the relative fitness of the populations. The results of this study are discussed with reference to mechanisms that may enable the small-bodied native Korogwe tilapia to persist in Lake Rutamba, despite hybridizing and sharing trophic resources with the large-bodied *O. niloticus*.

Methods

Study site and sample collection

Sampling was conducted at Lake Rutamba (10°01'52"S, 39°27'44"E; Fig. 1) near Lindi in Tanzania during two field sampling events (22–24 October 2016; 1–2 November 2019). Lake Rutamba is a turbid vegetation-rich shallow lake, measuring approximately 2 km × 1 km, with an approximate maximum depth of 2.5 m. Reed beds surround the lake but during the summer months the water level drops and recedes away from the reeds reducing the potential for fish to shelter in vegetation. Predators of fishes observed to be associated with the lake include sharptooth catfish *Clarias gariepinus*, Nile crocodile *Crocodylus niloticus* and birds (*Mycteria ibis*, *Microcarbo africanus*, *Ardea alba*). The lake is exploited as a capture fishery, with approximately 25 active gill net fishers being recorded daily during the 2019 sampling season.

O. niloticus, *O. korogwe* and their hybrids were purchased from local fishers using gill nets (in 2016 and 2019) or collected using a survey seine net (used three times in 2019; dimensions 30 m × 1.5 m, 25.4 mm mesh, fine mesh cod-end). The individuals retained from surveying were selected based on phenotypic characteristics and all individuals retained were greater than 35 mm (Table 1). We aimed to collect a sample enabling comparisons *O. niloticus* and *O. korogwe* specimens, rather than a sample that reflected the relative population size of each species within Lake Rutamba. Samples collected using the survey seine net were euthanised using an overdose of anaesthetic (clove oil). Specimens were pinned to a polystyrene board, photographed, labelled, and stored individually in 100% ethanol before transport. Long-term storage was in 70% ethanol.

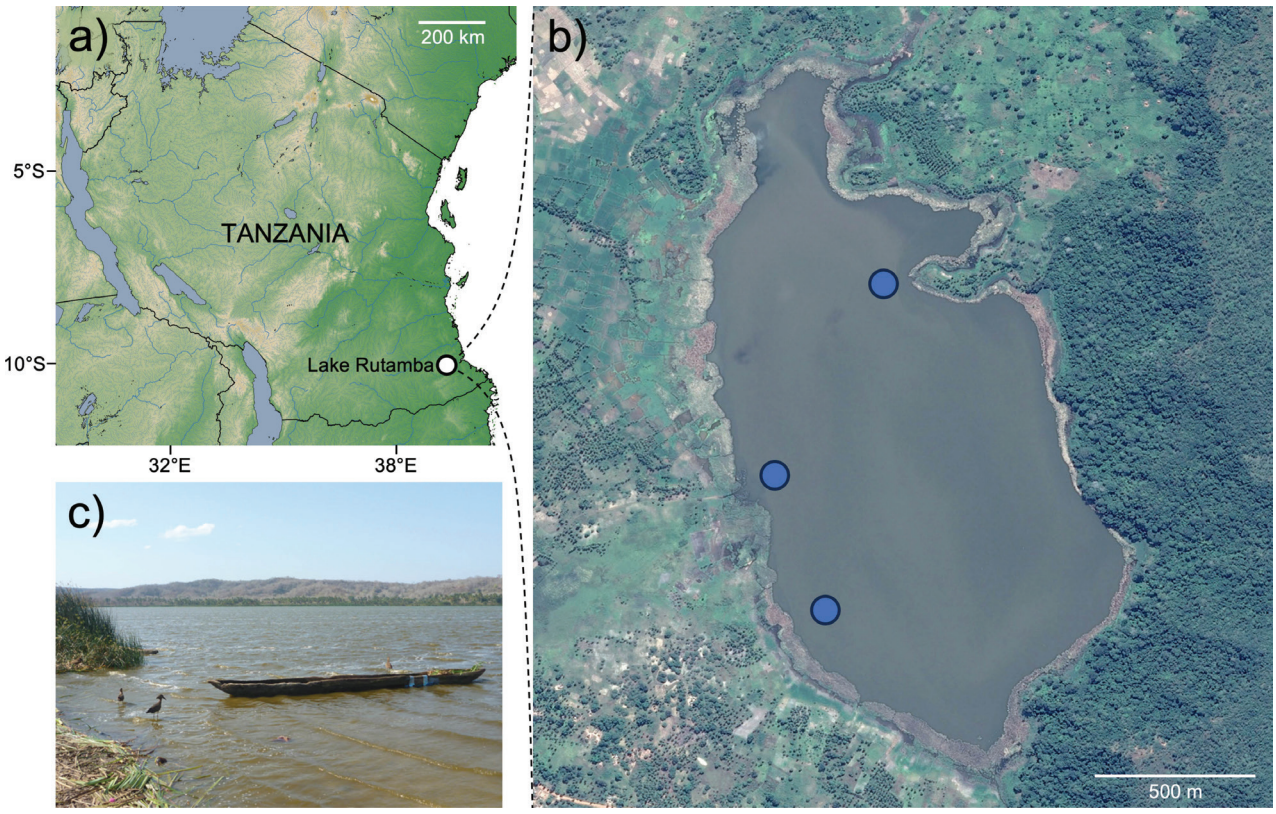

Figure 1. **a)** Location of Lake Rutamba in southeast Tanzania; **b)** Satellite image of Lake Rutamba, Google Earth Pro v. 7.3.6.9345, 3 June 2017, CNES/Airbus 2024; **c)** Lake Rutamba, 14 August 2013, A. Smith, blue circles represent 2019 seine sampling locations.

Table 1. Sampling dates and samples sizes of each species used in the final analyses. The assignment of individuals to the three groups was achieved using microsatellite genotypes.

Sampling date	*O. korogwe*	Hybrid	*O. niloticus*
22/10/2016	17	1	10
23/10/2016	11	2	8
24/10/2016	10	2	0
01/11/2019	4	4	12
02/11/2019	27	4	19
Total	87	13	49

Microsatellite DNA genotyping

We determined the genetic composition of sampled individuals using microsatellite genotypes. DNA was extracted from fin clips following the Wizard Genomic DNA Purification Kit protocol (Promega, Madison, WI). DNA concentrations were measured using an N60 Touch NanoPhotometer (Implen, München, Germany), and diluted to 50 ng/µl. For the assay we selected six microsatellite loci (OMO219, OMO229, OMO391, OMO337, OMO129, OMO043) from Saju et al. (2010) and Liu et al. (2013), previously used to classify individuals as *O. korogwe*, *O. niloticus* or their hybrids (Blackwell et al. 2021). Polymerase chain reactions were performed using 10 µl solutions comprised of: 1 µl DNA, 0.2 µl of the six forward primers (each 10 µM), 0.2 µl of the six reverse primers (each 10 µM), 5 µl of Multiplex PCR Master Mix (Qiagen, Hilden, Germany) and 1.6 µl of distilled water. PCR conditions were an initial denaturation at 95 °C for 60s, followed by 35 cycles of 94 °C for 30s, 57 °C for 90s and 72 °C for 60s,

before a final extension stage at 60 °C for 30 minutes. PCRs were conducted on a 3PRIMEX/02 thermal cycler (Techne, Staffordshire, UK). Amplicons were genotyped using a 3500 Genetic Analyser (Applied Biosystems, Waltham, MA) with a LIZ500 size standard, and scoring was conducted using Genemapper 4.1 (Applied Biosystems, MA). Amplification of one locus (OMO043) was unsuccessful, so analyses were conducted on the five remaining loci. Genetic composition of individuals were estimated using the admixture model in Structure v.2.3.4 (Pritchard et al. 2000), assuming two populations (K = 2; *O. korogwe* or *O. niloticus*), in 10 separate runs of 100,000 steps following a 100,000 burn-in. This resulted in an assignment probability of between 0 and 1 for each specimen. Following Blackwell et al. (2019) Individuals with < 0.1 were deemed to be *O. korogwe*, individuals > 0.9 *O. niloticus*, and individuals > 0.1 and < 0.9 to be hybrids.

Growth rate scale measurement

To assess the recent growth rate of the *Oreochromis* specimens we followed an approach developed by Doyle et al. (1986). This method provides an instantaneous measurement of individual growth rate using scale circuli measurements, circumventing the need for the release and recapture of the same individual over a known length of time. Specifically, the authors demonstrated that the distance between marginal scale circuli in *Oreochromis mossambicus* × *O. urolepis* hybrids was significantly correlated with growth rate (Doyle et al. 1986). Experiments further demonstrated that the ratio between body length and the distance between scale circuli can be used to reliably compare the growth rate of different tilapia species and aquacultural strains (Matricia et al. 1989; Talbot and Doyle 1992; Martin 2012). This method has previously been used to compare relative growth of invasive *O. niloticus* and indigenous Tanzanian tilapia species (Bradbeer et al. 2020).

Three scales were collected from the right side of each specimen, from the first scale row dorsal to the lateral line and posterior to the pelvic girdle. To ensure consistency in scale type, scales were removed sequentially until three fully formed scales with tight foci were obtained (Fig. 2a). Scales were submerged in water and excess skin and debris were removed using forceps to ensure individual circuli were visible. Scales were then dried, coated with glycerol on a microscope slide and covered with a glass coverslip. Images of individual scales were then taken using a M205c stereo microscope (Leica Microsystems, Wetzlar, Germany) with a GX-CAM HICHROME MET-M camera attachment (GT Vision, Newmarket, UK). Five measurements were recorded from each scale in micrometres (μm). First, the total width of the scale at its widest point (0.78× magnification), followed by four measurements of the distance between the five outermost circuli on four primary radii (5× magnification; Fig. 2b). Measurements, calibrated using an image of a graticule taken at the same magnification, were made using Image-J v.1.3.3 (Schneider et al. 2012).

Statistical analysis

All analyses were performed in R v.4.1.3 (R Core Team 2022). To investigate variation in growth rate between *O. niloticus*, *O. korogwe* and their hybrids a linear model was constructed with growth increment as the dependent variable, defined as the average distance in μm between the five outer circuli from four primary radii on three separate scales. We included species (*O. korogwe*, *O. niloticus* and *O. korogwe* × *O. niloticus* hybrids) as a fixed factor, alongside mean scale diameter (μm) as a covariable indicator of body size. We also included the interaction term

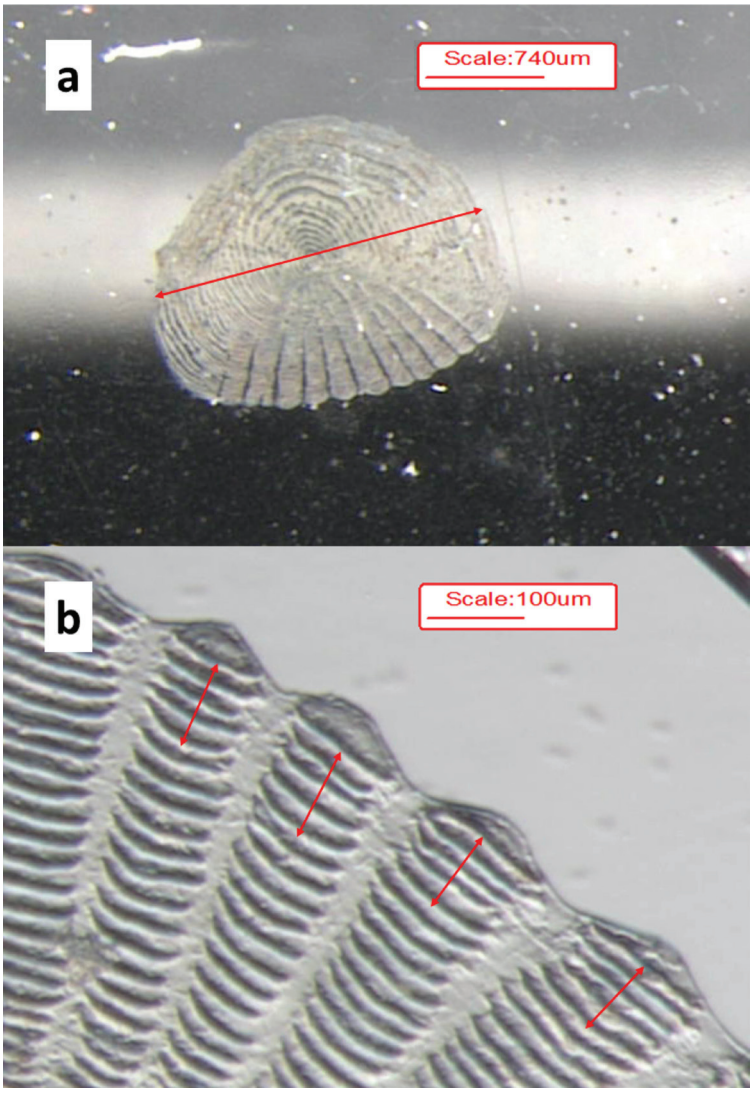

Figure 2. Stereomicroscope images of **a**) whole scale and **b**) outer scale circuli on primary radii. Red arrows represent the measurements made of scales for this study.

of species × mean scale diameter, to investigate whether the association between growth increment and mean scale diameter varied among the groups of individuals. In a second linear model, also including growth increment as the dependent variable, we included species, standard length (SL, another indicator of body size) and an interaction between these variables. The growth rate, mean scale diameter and SL were $\log_{10}$ transformed for analyses. The *simulate.Residuals* function in the package DHARMa v.0.4.6 (Hartig 2020) was used to generate a Q-Q plot of observed vs expected residuals, and a plot of residuals vs fitted values, to ensure normality of residuals and homogeneity of variances. The function *Anova* in the package car v.3.1-2 (Fox et al. 2013) was used to test for the significance of the fixed effects, employing a type II model due to unequal sample sizes across the three groups of individuals. Figures were produced using ggplot2 v.3.4.4 (Wickham 2016).

Results

Across all collections, *O. niloticus* ranged from 42.9 to 107.3 mm SL, *O. korogwe* from 33.6 to 102.3 mm SL, and hybrids from 34.7 to 90 mm SL (Fig. 3a). Using growth increment as the dependent variable, there was a significant interaction

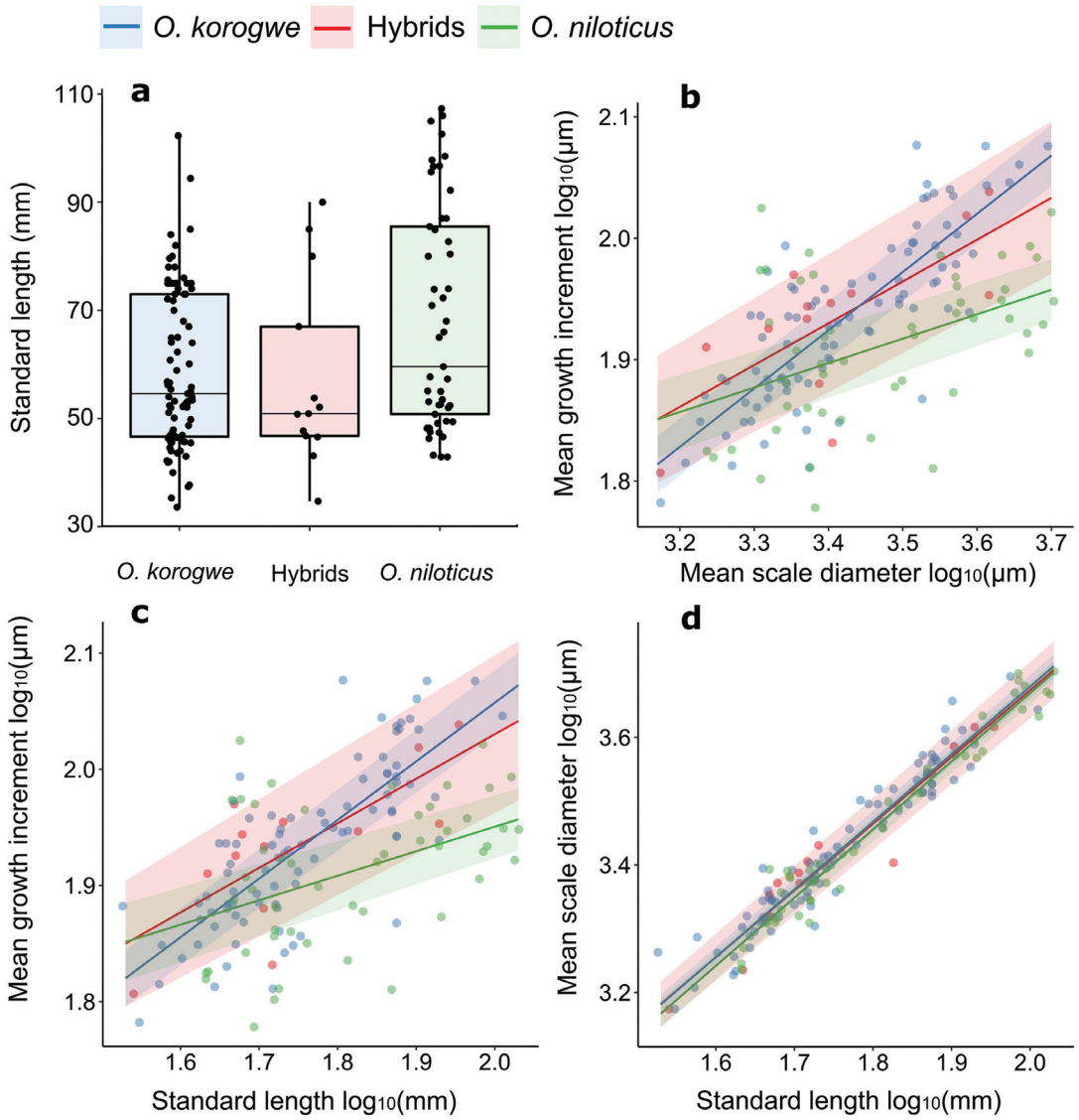

Figure 3. **a**) Standard length of analysed *O. korogwe*, *O. niloticus* and *O. korogwe* × *O. niloticus* hybrids; **b**) Growth increment as a function of mean scale diameter, separated by species group; **c**) Growth increment as a function of standard length, separated by species group; **d**) Mean scale diameter as a function of standard length, separated by species group. In **b–d**, individual data points represent the predicted values from the linear model, fitted lines are calculated from fixed effect estimates and shaded areas represent 95% confidence intervals.

between species and mean scale diameter (Model A, Table 2, Fig. 3b), suggesting that the slope of the association between body size and growth increments differed between the species. The same result was found when mean SL was used rather than mean scale diameter (Model B, Table 2). Scale diameter and standard length were strongly correlated (Fig. 3d). Plots of the predicted values reveal that at small body sizes (33–50 mm SL), there was little difference in growth increments between the species (Fig. 3b, c). By contrast at larger body sizes (50–110 mm SL), *O. korogwe* had considerably larger growth increments than *O. niloticus*. *O. korogwe* × *O. niloticus* hybrids had growth increments closer to *O. korogwe* (Fig. 3b, c).

Discussion

Nile tilapia is a large-bodied tilapia species widely used in aquaculture due to a relatively fast growth rate, and in natural water bodies it has been observed to have higher growth rates than native *Oreochromis* species (Chifamba and Videler 2014;

Table 2. Linear models quantifying variation in growth increments in relation to fish size (measured using scale diameter (model A) and standard length (model B)) and species (*O. korogwe*, *O. niloticus* and interspecific hybrids).

Model	Predictor variables	Sum of squares	d.f.	*F*	*P*
A	$\log_{10}$ mean scale diameter	0.30	1	137.9	<0.001
	species	0.05	2	12.6	<0.001
	$\log_{10}$ mean diameter × Species	0.04	2	9.5	<0.001
	residuals	0.31	143	–	–
B	$\log_{10}$ standard length	0.27	1	117.1	<0.001
	species	0.06	2	13.6	<0.001
	$\log_{10}$ standard length × species	0.04	2	8.1	<0.001
	residuals	0.31	143	–	–

Bradbeer et al. 2020). However, within Lake Rutamba, we found that *O. korogwe* had higher growth rates than *O. niloticus*. This result contrasts with our expectations that the large bodied and fast-growing *O. niloticus* would have a greater growth rate than the native species (Bradbeer et al. 2020). Growth rate is a crucial determinant of fitness in fish as it allows them to quickly bypass the most vulnerable stages of their lifespan where mortality is highest (Sutherland 1996). Thus, we consider that the population dynamics of the tilapia within this lake, and specifically the survival and fitness of *O. korogwe* in the face of *O. niloticus* introduction, could be linked to this relatively high relative growth rate of *O. korogwe*.

How might *O. korogwe* persist in the face of invasion by a large-bodied competitor?

Nile tilapia has been widely introduced to natural water bodies across Tanzania since the 1950s, but the precise timing of the introduction into Lake Rutamba is unclear. We know that *O. niloticus* was fully established in the lake in 2013 (Blackwell et al. 2021). We also know that samples of *O. korogwe* from Lake Rutamba were accessioned to the Natural History Museum in London in 1982 (as *Sarotherodon ruvumae*), alongside *Coptodon rendalli* (as *Tilapia rendalli*), but no *O. niloticus* individuals were accessioned alongside them, suggesting Nile tilapia were absent at the time of collection (presumed to be early 1980s). We therefore estimate that *O. niloticus* was introduced to the lake between the early 1980s and the early 2010s. Evidence of the negative effects of *O. niloticus* across its native range (Canonico et al. 2005), including the extinction of a native tilapia species from the Hombolo reservoir in Tanzania (Turner et al. 2019), implies that *O. niloticus* may pose a major threat to native tilapia in East African freshwaters. Thus, the ability of *O. korogwe* to persist in the face of *O. niloticus* introduction for numerous generations is contrary to expectation and suggests that this species may possess traits which predispose them for resilience to *O. niloticus* invasion.

Higher growth rates leading to increased body size are linked to several competitive advantages. These include performance during interference competition for shelter, greater efficiency during exploitative competition for food resources, increased reproductive output in mature females, and an enhanced probability of success during interference competition for lekking spaces in males (Chifamba and Videler 2014; Barneche et al. 2018; Bradbeer et al. 2020). Previous studies have shown that *O. niloticus* is an aggressive competitor that can dominate competitive interactions and prevent access to shelter in subordinate species (Martin et al. 2010; Champneys et al. 2021). Typically, fish are most vulnerable to predation during juvenile stages (Sogard 1997), and in Lake Rutamba, survival is likely to depend on access to shelter

resources such as the large reed beds located in the littoral regions. Elevated growth rates leading to increased body size could enable *O. korogwe* to avoid competitive dominance by *O. niloticus* and access shelter resources and preferred habitats despite competition. During sampling in 2019, *O. niloticus* and *O. korogwe* were both found in all three seine locations in the littoral areas of the lake (Fig. 1), suggesting strong habitat overlap and likely competition over preferred habitats. However, more accurate information about the habitat use and niche overlap of the two species within the lake would lead to more precise predictions about the likely prevalence and outcomes of competition between the species over shared resources.

How does *O. korogwe* achieve higher growth rates than *O. niloticus*?

Since introduced *O. niloticus* are typically descendants of fish selected for high production yields, including fast growth rates, the increased growth rate observed in the native *O. korogwe* contrasts with our expectations. One explanation is that introduced *O. niloticus* are relatively poorly adapted to the local environment in comparison to the native *O. korogwe*. Unlike native species, which have had a long evolutionary timeframe in which to adapt to environmental conditions, introduced species are faced with novel conditions to which they must rapidly adapt to become established (Flores-Moreno et al. 2015). Studies have shown that introduced species can be successful through rapid adaptation to novel environments via behavioural, phenological and morphological changes (Thompson 1998; Lambrinos 2004). However, such rapid adaptation is not ubiquitous, and slow rates of phenotypic evolution following introduction are also reported (Mooney and Cleland 2001; Sakai et al. 2008). Growth rate is crucially influenced by access to food resources and a relatively poor ability to locate and consume food items could result in the relatively higher growth rates in *O. korogwe*, which may be better adapted to exploiting these resources.

Given that the relatively high growth rate of *O. korogwe* was most exaggerated in larger individuals, it is possible that *O. korogwe* and *O. niloticus* diverge in their feeding strategy as they grow. Fish commonly shift their diet upon reaching larger sizes (Juncos et al. 2015), and while both species are microphagous generalists (M. Genner pers obs.), resources in offshore habitats may enable the species to diverge into planktivorous and detritivorous feeding strategy, with one providing nutrition which facilitates higher growth rates. Such a separation of dietary niches may not be feasible in inshore nursery habitats, and this could explain the size-dependent differences in growth rate between the two species. Further investigation into ontogenetic dietary overlap of the two species using gut content or stable isotope analysis may help to clarify trophic niches of these species, while surveys of distributions of the species in the lake will provide corresponding insight into any differences in habitat use.

The effect of fishing pressure and predation on the impacts of invasive *O. niloticus* in Lake Rutamba

Fishing pressure is high within Lake Rutamba, with at least 25 fishers active during the 2019 sampling period. Fishers were using gill nets which target larger individuals in the central areas of the lake. During both sampling periods, catches were observed to be dominated by *O. niloticus*, which suggests that fishing pressure may be reducing the population of *O. niloticus* disproportionately relative *O. korogwe*, potentially removing breeding adults from the population. This pattern was evident within our sampling, where the largest *O. niloticus* was only 23 cm total length — roughly half the maximum size of *O. niloticus* observed in Tanzania

(~45 cm total length; Genner et al. 2018). By reducing population sizes of *O. niloticus*, fishing likely reduces competition for resources, and in turn potentially prevents the formation of interspecific dominance hierarchies over shared resources.

Predation is likely to have a strong effect on the population sizes of both *O. niloticus* and *O. korogwe* within Lake Rutamba, especially during summer months when the water level recedes from littoral vegetation, reducing the availability of shelter. Predation by sharptooth catfish *Clarias gariepinus*, Nile crocodile *Crocodylus niloticus* and piscivorous birds (*Mycteria ibis*, *Microcarbo africanus*, *Ardea alba*) could disproportionately affect introduced *O. niloticus* due to poorer anti-predatory adaptations within the introduced species resulting from generations of selection in aquaculture, or a poorer adaptation to the local environment. Evidence of the dietary composition of predator populations within Lake Rutamba would be necessary to expand on this hypothesis.

When ecosystems are affected by multiple stressors there can be antagonistic interactions between them, with one stressor offsetting the other (Berlarde et al. 2016). Few studies have considered how other stressors, such as fishing pressure, can interact with the impacts of invasive species to exacerbate or reduce their negative effects. Further research may be able to able to confirm if there is an antagonistic interaction between fishing pressure and the invasive *O. niloticus* that may contribute to the persistence of the relative fast-growing *O. korogwe* in a heavily modified environment.

Hybridization and growth rate

We found clear evidence of hybridization between *O. korogwe* and *O. niloticus* in our samples, in accordance with the findings of Blackwell et al. (2021). The hybrid individuals within our sample were of a range of body sizes and showed a growth rate closer to the faster growing *O. korogwe*. This result suggests that there is no strong ecological selection against hybrid genotypes, and hybrids may persist within the population. Considering our findings, it is possible that hybrids possessing a faster growing phenotype may have competitive advantages over the parental species, if the elevated growth rates of *O. korogwe* are combined with traits which may benefit *O. niloticus* such as a maximum large body size. Parental species are thought to be most threatened when hybrids possess fitness advantages. Where such heterosis is present, genetic swamping can lead to the formation of hybrid swarms (Hwang et al. 2012). Further work is needed to establish the reproductive preferences of parental species and their hybrids within Lake Rutamba, which is important given genomic evidence of fertile hybrids and introgression between the species (Blackwell et al. 2021). Moreover, information on the abundance and habitat use of purebreds and hybrids within this population would be useful for accurate prediction of the consequences of hybridization for these fish populations.

Author contributions

Conceptualization: MJG, CCI, TC; methodology: TC, MJG, CCI, TB, AHS; formal analysis: TC, MJG, TB; data curation: TC, TB, PM, AHA, ADS; writing - original draft: TC; writing - review and editing: MJG, CCI; supervision: MJG, CCI; funding acquisition: MJG, CCI, TC, BPN.

Funding declaration

This project was funded by a NERC GW4+ FRESH CDT PhD studentship awarded to TC (NE/R011524/1). Fieldwork was supported by Royal Society-Leverhulme Trust Africa Awards AA100023 and AA130107.

Ethics and Permits

Permits to undertake fieldwork were granted by the Tanzania Commission for Science and Technology (COSTECH) to TC (2019-551-NA-2019-356) and TB (2016-303-NA-2011_103).

Data availability

The data and code used in this study are available to access via the following link: https://zenodo.org/doi/10.5281/zenodo.12740930.

Acknowledgements

We thank the Tanzania Commission for Science and Technology (COSTECH) for fieldwork approval and permits, and staff of the Tanzania Fisheries Research Institute (TAFIRI) for contributions to fieldwork. We are grateful to Cosmass Conrade and Seif for their contributions to fieldwork data collection. We thank Jane Coghill and Christy Waterfall from the Bristol Genomics Facility for their assistance with specimen genotyping. We are grateful to Will Hurley and the staff of the University of Bristol Life Sciences Teaching Lab for assistance with microscopy. We are thankful to the GW4 FRESH Centre for Doctoral Training in Freshwater Biosciences and Sustainability for their support of this project. We thank George Turner and Andrew Radford for valuable comments on the manuscript. We thank the reviewers of this manuscript for their time and valuable comments on the manuscript.

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