



Effects of thermal regime variability on adult rainbow trout (*Oncorhynchus mykiss*) mortality in Afromontane river systems

Blessing Mugaviri · Alton Aliko · Bianca Nyamupingidza · Tongayi Mwedzi · Beaven Utete · Taurai Bere

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Abstract Water temperature variability in river systems is a significant environmental concern. This study aimed to assess the effects of thermal regime variability on adult *Oncorhynchus mykiss* mortality in Afromontane river systems; using time series data spanning from 1994 to 2024. The objectives of the study were to analyze temporal and seasonal trends in water temperature (1994–2024) in Nyanga National Park, Zimbabwe, evaluate how temperature variability relates to adult *O. mykiss* mortality, and identify critical thermal thresholds that increase mortality.

The research used both secondary and primary data. Time series approach with a 5-year moving average analyzed temperature trends, while correlation and regression assessed the relationship between water temperature and rainbow trout mortality, and threshold analysis identified critical temperature limits increasing adult *O. mykiss* mortality. Seasonal comparisons revealed marked differences in both water temperature and mortality of *O. mykiss*. Mean water temperature was significantly higher in summer (20.13 ± 0.10 °C) than in winter (13.30 ± 0.13 °C; Welch's *t*-test, $t = 17.91$, $p < 0.01$; $n = 93$ per season). Similarly, mean mortality was substantially greater during summer (1272 ± 44) compared to winter (229 ± 27), with this difference also highly significant (Welch's *t*-test, $t = 13.17$, $p < 0.001$). Correlation and regression analyses revealed a strong positive association between temperature anomalies and mortality anomalies ($\rho = 0.713$; $R^2 = 0.453$) indicating that nearly half of the variability in mortality anomalies is explained by temperature. The positive regression slope (134.1 fish per 1 °C anomaly) highlights the biological sensitivity of the population to even modest warming departures from baseline conditions. A critical thermal threshold of 15.20 °C was identified where *O. mykiss* mortality increased disproportionately above this threshold. Although mean temperatures have not shifted significantly, intra-seasonal variability acts as a primary driver of mortality. Implementing strategies that mitigate the effect of water temperature changes on rainbow trout mortality

B. Mugaviri (✉) · A. Aliko · B. Nyamupingidza · T. Mwedzi · B. Utete · T. Bere
Department of Wildlife Ecology and Conservation,
Chinhoyi University of Technology, Chinhoyi, Zimbabwe
e-mail: mugaviriblessing@gmail.com

A. Aliko
e-mail: altonaliki181@gmail.com

B. Nyamupingidza
e-mail: bnyamupingidza@cut.ac.zw

T. Mwedzi
e-mail: tmwedzi@cut.ac.zw

B. Utete
e-mail: butete@cut.ac.zw

T. Bere
e-mail: there@cut.ac.zw

B. Mugaviri
Zimbabwe Parks and Wildlife Management Authority,
Corner Borrowdale Road, Sandringham Drive, P.O. Box
CY 140, Causeway, Harare, Zimbabwe

is imperative to support economic growth and food security.

Keywords Fish mortality · Water temperature variability · Critical thermal threshold · Eastern Highlands · Afromontane

Introduction

Rising temperatures and unpredictable thermal fluctuations if left uncontrolled can stress fish, reduce growth, and increase disease susceptibility and mortality (Islam et al., 2022). This has become more important in the face of climate change which has led to frequent and unpredictable thermal variability in water bodies (De Silva & Soto, 2009). It has indeed disrupted the aquaculture industry, especially for temperature-sensitive groups like salmonids (Islam et al., 2022).

Globally, stream warming has intensified risks to salmonid aquaculture (Mantua et al., 2010). Studies showed that 1–3 °C stream warming in North America and Europe has led to 20–50% population declines, reduced growth, and increased disease outbreaks in trout farms (Marcos-López et al., 2010; Jonsson, 2023). In subtropical and highland regions, water temperature increase exacerbates hypoxic conditions and pathogen proliferation, compressing cold-water niches, fragmenting habitats, and shifting species distributions (Rolls et al., 2017).

Trout aquaculture in Africa is confined to Afromontane regions, where elevations provide cooler streams (12–18 °C), suitable for the culture of *Oncorhynchus mykiss*. However, erratic rainfall and El Niño-Southern Oscillation (ENSO) events cause acute water temperature spikes up to 22 °C (Gore et al., 2020), increasing disease susceptibility and mortality in trout aquaculture (Kadye et al., 2013; Mabika & Utete, 2024). In Zimbabwe, it is cultured in the Eastern Highlands with cool temperate climate and oligotrophic water bodies (Nhiwatiwa, 2017).

Hypoxic water and elevated water temperatures (>18 °C) are major stressing factors which affect the survival rate, feeding and growth rate, fecundity rate, swimming behavior, and respiration of *Oncorhynchus mykiss* (Jiang et al., 2021). However, below 13 °C, it thrives with reduced metabolic processes (Jiang et al., 2021). Chronic exposure to slightly below or

above optimal thermal range allows for its adaptability while exposure to lethal temperatures (lower lethal temperatures and upper lethal temperatures) results in altered metabolism, causing high mortality of *O. mykiss* (Rosenfeld & Lee, 2022; Strowbridge et al., 2021). Temperature and dissolved oxygen (DO) are crucial parameters to be regulated to ensure minimum *O. mykiss* mortality (Jiang et al., 2021). For trout aquaculture operations in Afromontane regions, key gaps include lack of research on the environmental impacts on *O. mykiss* and the interaction of the species with climate change in Afromontane systems, the scarcity of subtropical data on limno-chemical fluctuation-driven mortality mechanisms, overreliance on temperate models, and limited integration of local factors like stocking density and feeds for predictive tools (Mapfumo, 2022). This hinders aquaculture adaptive strategies to maximize production in developing nations such as Zimbabwe (Mabika & Utete, 2024).

The *O. mykiss* was intentionally introduced in Zimbabwe in the early twentieth century, initially for recreational fly-fishing (Chapinduka et al., 2022; Kadye et al., 2013). The government then established trout hatcheries in the Nyanga National Park to stock the Nyangani streams (Chapinduka et al., 2022). The species was later adopted for commercial aquaculture at stations like Claremont, Nyanga Trout Farm, Rugarara, and Troutbeck that had oligotrophic waters favorable for its proliferation (Nhiwatiwa, 2017; Chapinduka et al., 2022). Its value as a hard-fighting game fish and tasty meal has led to its introduction worldwide. The successful introduction of *O. mykiss* in the headwaters of the Odzi River marked a pivotal achievement ecologically and economically, through increased biodiversity, recreational fly-fishing to support tourism, aquaculture production to generate income, employment, and food security (Kadye et al., 2013; Mabika & Utete, 2024). Its culture in the region is greatly benefiting local communities through employment and food security contributing to poverty alleviation (Kadye et al., 2013; Mabika & Utete, 2024). However, water temperature variations are hindering *O. mykiss* aquaculture production and causing local population declines and range shifts of the species in the Nyangani streams (Wenger et al., 2011). Rainbow trout also serves as a valuable biological model for studying thermal physiology and environmental stressors in salmonids (Behnke, 2010).

Historical water temperature trends offer insights on the effects of thermal variability on *O. mykiss* mortality (Behnke, 2010). Conducting a comprehensive assessment of water temperature-mortality correlation is imperative (Chapinduka et al., 2022). Mitigation of adult *O. mykiss* mortality requires understanding of the species' thermal tolerance to develop effective strategies for increasing survival rates, reducing mortality, and addressing albinism issues caused by thermal variation, ultimately enhancing aquaculture sustainability (Chen et al., 2015).

Trout farms in the Eastern Highlands of Zimbabwe are encountering increased fluctuations in rainbow trout mortality due to suspected thermal variability (Chapinduka et al., 2022). Trout mortality affects the flow of income, viability of the aquaculture, and tourism businesses (D'Agaro et al., 2022); and this may lead to low food security, low-income generation, and minimized recreational fly-fishing. There is need for a better understanding of the cause of mortality in *O. mykiss*. However, it has been of concern since some of the rainbow trout before death were reported to have signs related to hypoxia, e.g., lack of energy and reduced feeding. This study aimed to assess the relationship of thermal regime variability on adult *O. mykiss* mortality in the Afromontane Nyanga Trout Research Centre, Eastern Highlands of Zimbabwe, and abet development of strategies for rainbow trout to adapt to the fluctuating water temperatures. The objectives of the study are to determine the temporal and seasonal trends in water temperature from 1994 to 2024 in Nyanga National Park, Zimbabwe, to assess the relationship between water temperature variability and adult *O. mykiss* mortality in the Nyanga National Park, Zimbabwe, and to identify critical thermal thresholds beyond which water temperature changes increase adult *O. mykiss* mortality.

Methods and materials

Study area

The study was carried out at Trout Research Centre in Nyanga National Park (Fig. 1). The area is located in Nyanga District, the Northern Eastern Highlands classified within region 1 of the agroecological regions in Zimbabwe (Kadye et al., 2013). It is characterized by highest altitude > 1500 m above

sea level (a.s.l.), cool temperate climate with mean annual rainfall > 1200 mm and mean annual temperature range of 20–25 °C (Chapinduka et al., 2022). The region has very cold winters with a thermal range of 10–16 °C; however, in some cases, it goes far below the range. Lentic and lotic water near-pristine state from the Nyangani Mountains with little or no anthropogenic pollution is found in the region favoring the culture of rainbow trout (Nhwatiwa, 2017). The fish ponds at NTRC were built in a natural river, and the ponds do not alter the flowing of the water hence best for rainbow trout farming (Chapinduka et al., 2022). Eutrophication in inland water sources is minimized by the geochemistry of the watershed, thus maintaining the oligotrophic state of the reservoirs (Nhwatiwa, 2017).

Quantitative research approach was used, with average monthly water temperatures and monthly mortality data from 1994 to 2024. A total of 120,000 rainbow trout were being monitored during the time under study. A time series analysis approach was used for this study. The approach enables the analysis of temperature and mortality data over the period to determine temporal and seasonal trends, correlations between these two variables, and critical thermal threshold. A multiple regression model was used to capture how the relationship between water temperature and rainbow trout mortality changes across different seasons. Purposive sampling was used to opt for Nyanga Trout Research Centre (NTRC) as the focal site due to data accessibility and consistent trout production. Purposive sampling is appropriate when a certain unit has special relevance to the research question (Campbell et al., 2020). The sample size from NTRC was used; it includes 31 years of recorded water temperature and mortality data (1994–2024), constituting monthly averages for water temperature and corresponding monthly mortality for adult *O. mykiss*. The study relies on both secondary and primary data. Secondary data was accessed from physical records and institutional databases maintained at the NTRC. Water temperature data include daily pond temperature readings captured manually using six thermometers. Mortality data include recorded losses of adult *O. mykiss* at NTRC.

Standard data extraction sheets designed to capture mean monthly water temperatures and monthly mortality for a 31-year period were used to retrieve data (Nagurney et al., 2005). Historical data records from

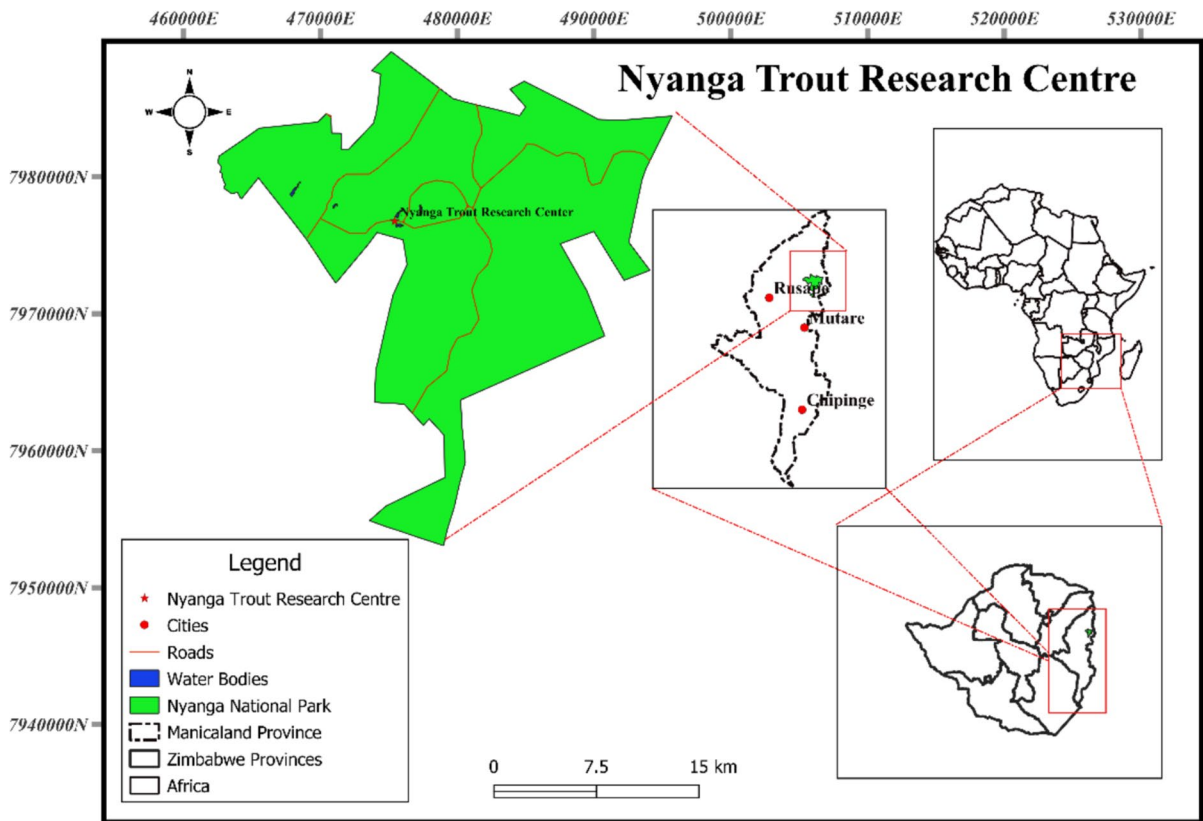


Fig. 1 Map showing NTRC, Eastern Highlands of Zimbabwe

water quality monitoring instruments and farm mortality logbooks form the core sources. The reliability of the findings in this study heavily depends on the quality of the historical data. This long-term reflective dataset was prone to incomplete records, inconsistencies in data entry, and occasional measurement errors. Statistical multiple imputation techniques were used to replace missing data with substituted values to retain dataset integrity. Records were cross-verified between physical logbooks and institutional databases. Implausible water temperature and mortality values were examined cautiously and either corrected through verification with source documents or retained when confirmed as genuine observations.

Data analysis used both descriptive and inferential statistical techniques in R-Studio (v4.5.1). The analytical framework integrated temporal trend assessment, seasonal pattern evaluation, anomaly detection, relationship modeling, and threshold analysis to comprehensively assess thermal regime variability and its effects on *O. mykiss* mortality. The results were

presented through summary tables, time series plots, and statistical test outputs, thereby allowing for both numerical and visual interpretation of the observed trends.

Descriptive statistics were used to summarize the central tendencies and variability of both water temperature and trout mortality from 1994 to 2024. Mean, standard deviation, range, and standard error were calculated to describe the distribution and dispersion of each variable. Seasonal and decadal means (\pm SE) were computed to highlight intra-annual and interdecadal variations in the thermal regime and associated adult *O. mykiss* mortality. The summarized descriptive results provided an illustration of both overall and seasonal patterns before inferential statistical analyses are applied.

Dataset was tested for compliance with statistical assumptions to ensure the validity of parametric tests. The Shapiro–Wilk test was used to assess normality distribution for water temperature and trout mortality data. However, the temperature and mortality

data significantly deviated from a normal distribution ($W=0.94$; $p < 0.001$ and $W=0.92$; $p < 0.001$ respectively), therefore necessitating for the use of non-parametric tests. Welch’s t -test was used to verify the equality of variance between summer and winter. Kruskal–Wallis’ test ($p < 0.05$ significance level) was used to test for significant differences across the three decades (1994–2003, 2004–2013, 2014–2024). These steps ensure that correlation and regression analyses are strong and also the conclusions drawn are based on appropriate statistical grounds.

Seasonal and decadal analyses were conducted to determine the degree of intra-annual and interdecadal variability in water temperature. Seasonal and decadal means (\pm SE) for temperature and mortality were compared between summer and winter using Welch sample t -test to determine significant seasonal differences. Kruskal–Wallis’ test was used to compare decadal means across the three distinctive decades. These analyses provided insight into both seasonal and decadal fluctuations in water temperature and mortality.

Trend and anomaly analyses were conducted to capture temporal variations and deviations from the mean. A 5-year moving average was used to smooth short-term water temperature fluctuations. Temperature and mortality anomalies were calculated using the formula: Anomaly = Observation – Long-term mean.

Linear regression analysis was used to quantify the direction and magnitude of temporal trends in water temperature and mortality anomalies. The regression

model, $Y = \beta_0 + \beta_1 (\text{Time}) + \epsilon$, was used, where Y is the anomaly and β_1 is the rate of change over time. Model significance was tested using the F -test and the t -test to assess the significance of the slope coefficient at $p < 0.05$. Mann–Kendall trend test was used to enhance the reliability of the trend analysis. This statistical test ensured that linear and monotonic trends are detected accurately.

Regression and correlation analyses were used to assess the relationship between water temperature variability and rainbow trout mortality. The Spearman rank correlation (ρ) was used to assess the strength and direction of the linear association between water temperature anomalies and rainbow trout mortality. A simple linear regression model [mortality anomaly = $\beta_0 + \beta_1 (\text{temperature anomaly}) + \epsilon$] was applied to determine the influence of water temperature anomalies on trout mortality.

A multiple linear regression model was created which incorporates month as a categorical variable to account for the impact of seasonality. The interaction term evaluated if the impact of water temperature on trout mortality varies significantly by month. The model significance was estimated at a 95% confidence interval.

Segmented analysis was used to identify critical thermal thresholds that lead to a significant rise in *O. mykiss* mortality. This technique helped determine the exact temperature at which the relationship between temperature and mortality shows a notable change in slope, thus reflecting a physiological limit for *O. mykiss*. The model used was,

$$\text{Mortality} = \beta_0 + \beta_1 (\text{Temperature}) + \beta_2 (\text{Temperature} - \psi) + \epsilon$$

where ψ is the estimated breakpoint. The Davies test assessed the statistical significance of change in slope.

Logistic regression was applied to analyze mortality as a binary outcome (high versus low mortality) across different temperature ranges. It was selected since the data is binary in nature and it can incorporate confounding variables among other reasons. This facilitated the estimation of the likelihood of high mortality at various temperature points. However, there are other variables that were not included in the study, for example, streamflow and water level

variability. The assumption was that all variables remain constant during the study.

Results

Descriptive statistics and data characteristics

Over the 1994–2024 study period, mean monthly water temperature was 17.44 ± 2.96 °C, ranging from 9.70 to 22.50 °C. Mean monthly mortality of *O. mykiss* was 737 ± 590 individuals, with counts

Table 1 Monthly water temperature and *O. mykiss* mortality from 1994 to 2024

Variable	Mean \pm SD	Minimum	Maximum	Shapiro–Wilk and <i>p</i> value
Water temperature (°C)	17.44 \pm 2.96	9.70	22.50	<i>W</i> =0.94 <i>p</i> <0.01
Trout mortality (count)	737 \pm 590	3	2986	<i>W</i> =0.92 <i>p</i> <0.01

Table 2 Seasonal statistics for water temperature and *O. mykiss* mortality (mean \pm SE)

Group	Season		Welch's <i>t</i> -test and <i>p</i> values
	Summer	Winter	
Mean temp (°C) \pm SE	20.13 \pm 0.10	13.30 \pm 0.13	<i>t</i> =17.91, <i>p</i> <0.01
Mean mortality \pm SE	1272 \pm 44	229 \pm 27	<i>t</i> =13.17, <i>p</i> <0.01
<i>n</i>	93	93	–

varying from 3 to 2986. Shapiro–Wilk tests indicated significant departures from normality for both water temperature ($W=0.94$, $p<0.001$) and mortality ($W=0.92$, $p<0.001$). The relatively high standard deviation observed for mortality reflects death variances between periods, substantial inter-month variability across the 30-year monitoring period. This indicates highly inconsistent mortality patterns over time (Table 1).

Seasonal comparisons revealed marked differences in both water temperature and mortality of *O. mykiss*. Mean water temperature was significantly higher in summer (20.13 \pm 0.10 °C) than in winter (13.30 \pm 0.13 °C; Welch's *t*-test, $t=17.91$, $p<0.01$; $n=93$ per season). Similarly, mean mortality was substantially greater during summer (1272 \pm 44) compared to winter (229 \pm 27), with this difference also highly significant (Welch's *t*-test, $t=13.17$, $p<0.001$). These results demonstrate pronounced seasonal variation, with elevated summer temperatures coinciding with significantly increased mortality (Table 2).

Time series decomposition

There is no statistically significant change in water temperature temporal and seasonal trends from 1994 to 2024 ($t=0.99$; $p=0.32$). The time series decomposition plot (Fig. 2) showed a stable seasonal cycle continuing from 1994 to 2024, with no clear temporal trend visible ($\tau=0.053$, $p=0.133$). Time series decomposition of monthly water temperature (1994–2024) revealed a strong and persistent seasonal

pattern, characterized by regular annual fluctuations of consistent amplitude throughout the study period. The trend component indicated relatively stable temperatures from the mid-1990s to the late 2000s, followed by a marked decline around 2008–2009 and a gradual upward trend thereafter, culminating in higher temperatures toward 2024. The remainder component showed random short-term variability centered around zero, with occasional anomalies but no clear structure. Overall, seasonal variation was the dominant source of variability, superimposed on a modest long-term warming trend (Fig. 2).

There is no statistically significant change in decadal trend identified (1994–2003, 2004–2013, 2014–2024). The Kruskal–Wallis test confirmed no significant differences [$\chi^2(2)=2.04$, $p=0.36$] (Fig. 3). Decadal comparisons of mean water temperature showed relatively small differences among periods. Mean temperature remained similar between 1994–2003 and 2004–2013, with a slight increase observed during 2014–2024. Error bars (\pm SE) were narrow and largely overlapping across decades, indicating limited variability in decadal means. The results suggest a modest upward shift in mean temperature in the most recent decade relative to earlier periods (Fig. 3).

Figures 4 and 5 show average monthly summer anomaly (AMSA) trend and average monthly winter anomaly (AMWA) trend respectively. Additionally, summer anomaly trend (Fig. 4) shows a gradual warming trend from 1994 to 2024 but no statistically significant change ($\tau=0.24$; $p=0.06$). Summer temperature anomalies exhibited substantial

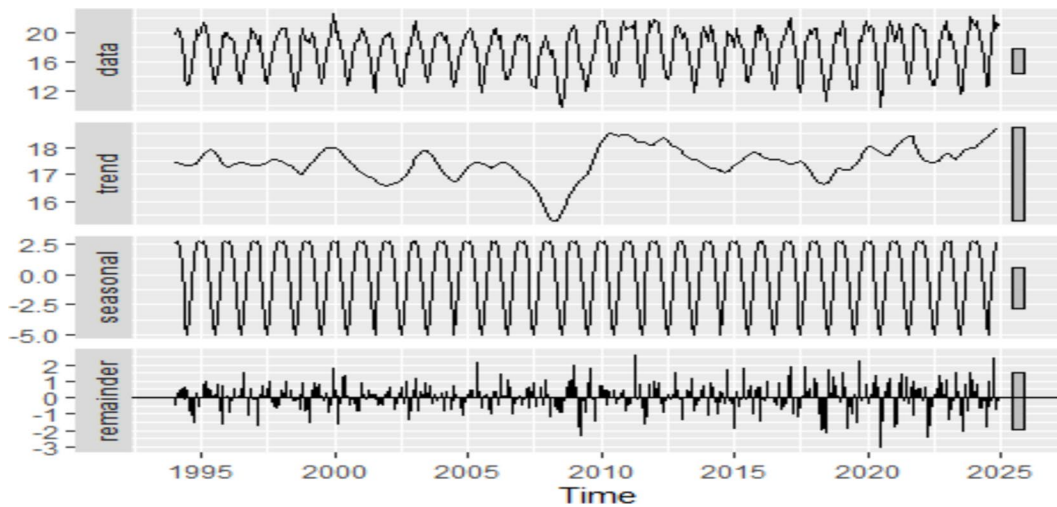


Fig. 2 Time series decomposition

interannual variability over the study period. Negative anomalies dominated the late 1990s and mid-2000s, with a pronounced minimum around 2008. Thereafter, anomalies shifted predominantly positive, particularly from 2010 onward. The 5-year moving average indicated a general upward trend in summer temperature anomalies, with sustained positive deviations after the early 2010s and higher anomaly values in the most recent years. Overall, the results suggest an increasing tendency toward warmer-than-average summer conditions in recent decades (Fig. 4).

Winter temperature anomaly (Fig. 5) trend shows no statistically significant increase ($\tau = -0.17$; $p = 0.2$). Winter temperature anomalies exhibit pronounced interannual variability over the study period, with fluctuations around the climatological mean. The 5-year moving average reveals decadal-scale variability rather than a monotonic long-term trend, characterized by near-neutral conditions in the late 1990s, a marked cold excursion in the mid-2000s, relative warming during the early 2010s, followed by cooling in the mid-to-late 2010s and a partial rebound in the early 2020s. Overall, short-term extremes dominate the record, while the smoothed series highlights alternating warm and cool phases on multi-year timescales (Fig. 5).

Temperature-mortality relationship

Figure 6 shows a relationship between water temperature anomalies and trout mortality indicates positive

association ($\rho = 0.713$, $p < 0.001$). Mortality rates tend to increase with warmer-than-average water temperatures, as reflected by the upward slope of the fitted regression line. Confidence intervals around the regression line indicate that, while the trend is positive, the strength of the relationship is modest.

A linear regression was conducted to test if there was a trend over time and examine whether temperature anomalies significantly predicted mortality anomalies. It showed statistically significant dependence of mortality anomaly based on temperature anomaly ($F = 306.6$; $p < 0.001$; $R^2 = 0.453$). This indicated that 45.3% of the variance in mortality anomalies can be explained by temperature anomalies alone. The model equation is mortality anomaly = $0 + 134.1 * (\text{temperature anomaly})$. The scatterplot shows a positive association between the two variables, with a fitted regression line indicating that increases in temperature anomaly are linked to increases in mortality anomaly. The model suggests that for every 1 °C rise in temperature anomaly, the mortality anomaly increases linearly, implying higher temperatures are associated with elevated mortality levels in the studied population. The distribution of data points exhibits greater dispersion at higher temperature anomalies, indicating potential variability in response at extreme temperatures. Results suggest that unusual high temperature is associated with increased mortality although substantial variability exists across observations (Fig. 7).

A multiple regression model incorporating month and an interaction term between average water temperature and month was also tested. The model was statistically significant ($F=28.5$; $p<0.001$; $R^2=0.653$).

Critical thermal thresholds and breakpoints

The Davies test confirmed a statistically significant change in the slope of the temperature-mortality relationship (best at 15.4 °C; $p=0.00$). A breakpoint was estimated at 15.2 °C ($SE=\pm 0.65$ °C). The model significance was estimated at a 95% confidence interval. Although mortality tends to increase with temperature, the wide spread of observations indicates uncertainty around the exact magnitude of the effect which would be reflected in a wider confidence interval. A segmented model showed a distinct change in water temperature against rainbow trout mortality. Below 15.2 °C, water temperature showed a positive relationship with mortality, although this relationship was not statistically significant ($slope=18.9$, $p=0.67$). This indicates that mortality increased only slightly with rising temperature below the threshold. However, above 15.2 °C, the relationship became markedly stronger, with the slope increasing sharply to 177.9 fish per 1 °C increase in temperature. This means that for every 1 °C rise in temperature beyond 15.2 °C, mortality increased by approximately 178

fish. The abrupt change in slope was highly significant ($t=3.91$, $p<0.001$), confirming the presence of a critical thermal threshold at 15.2 °C. The confidence interval around the breakpoint estimate further supports the reliability of this threshold, indicating that mortality responses intensify substantially once temperatures exceed this level (Fig. 8). This significant change indicates that 15.2 °C marks an essential thermal threshold where the physiological stress on *O. mykiss* increases abruptly and induces mortality. Mortality exhibited a clear positive association with temperature. At lower temperatures (<14 °C), mortality remained consistently low, with relatively limited variability. Between approximately 14–16 °C, mortality began to increase gradually, while variability among observations widened. Above ~16 °C, mortality increased more sharply, with pronounced dispersion and several high-mortality outliers (>2000 individuals), particularly at temperatures exceeding 18 °C. The fitted trend line indicates a nonlinear, temperature-dependent escalation in mortality, with a marked inflection around 16 °C. This pattern suggests the presence of a thermal threshold beyond which mortality risk increases disproportionately. Overall, the results demonstrate that elevated water temperatures are strongly associated with increased mortality in *O. mykiss*, with both the magnitude and variability of mortality intensifying at higher temperatures (Fig. 8).

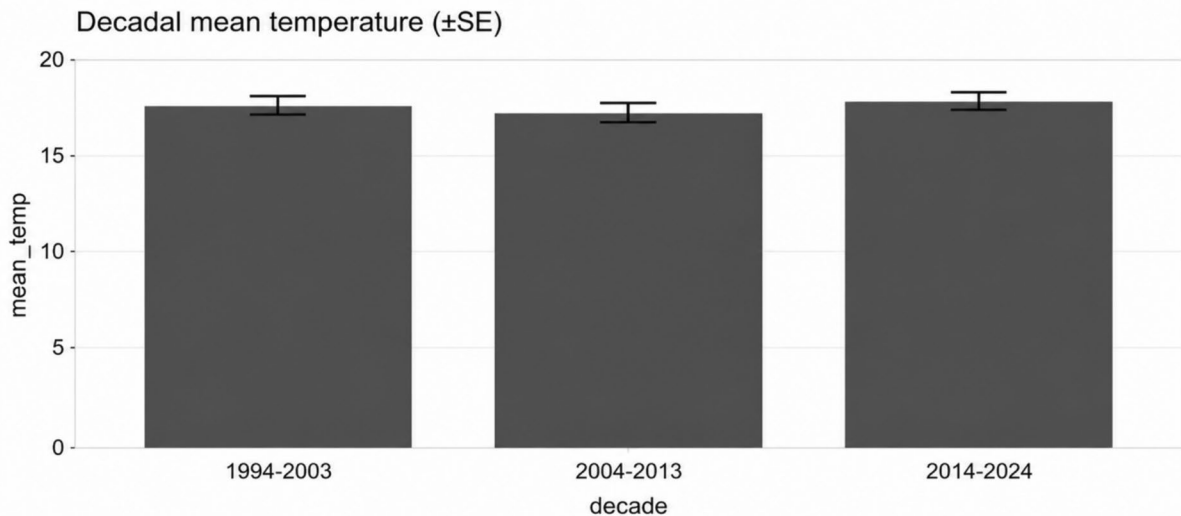


Fig. 3 Decadal decomposition (1994–2003; 2004–2013; 2014–2024)

Fig. 4 Average monthly summer anomaly (AMSA) trend

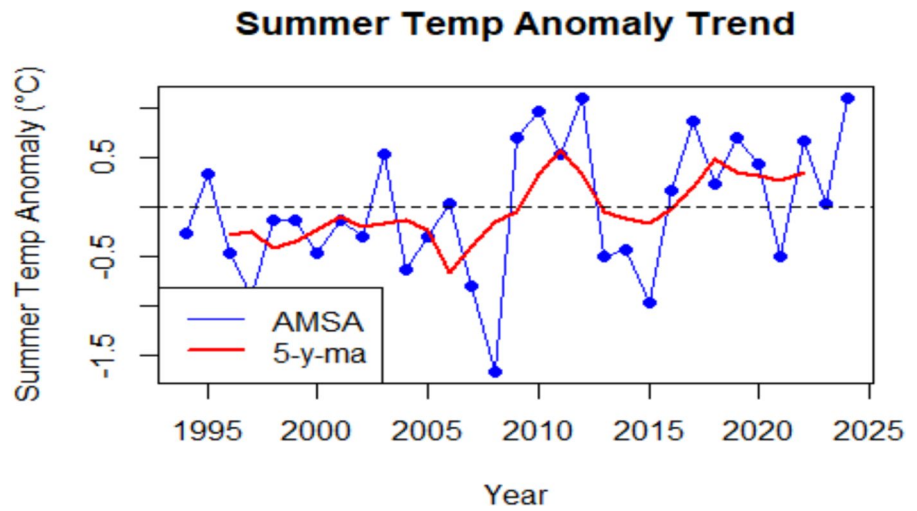
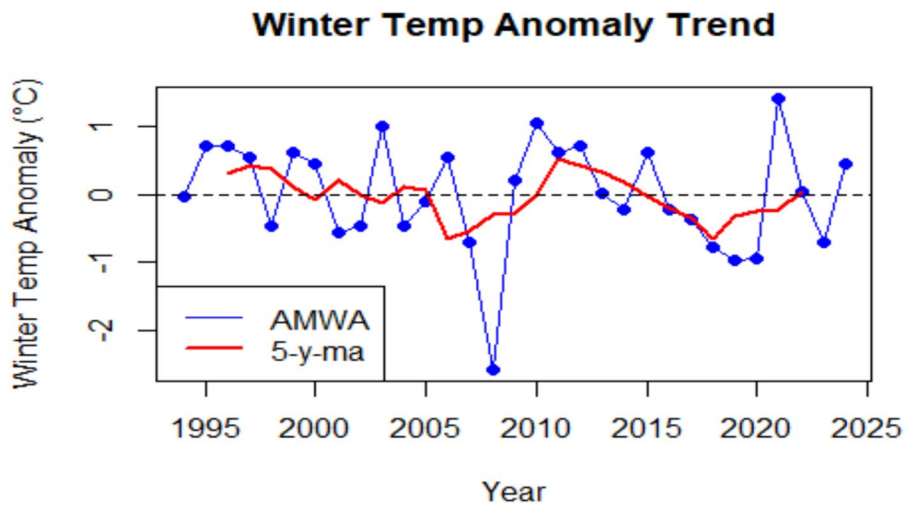


Fig. 5 Average monthly winter anomaly (AMWA) trend



Logistic regression was used to model the outcome of high mortality occurred as a function of water temperature. The model was highly significant [$\chi^2(1)=108, p<0.001$]. The positive coefficient for temperature ($\beta=0.640, p<0.001$) showed that the probability of high mortality increases with temperature. Figure 9 shows a classic S-curve, where the probability of high mortality remains low at colder temperatures and then rises sharply, approaching nearly 100% as temperatures exceed approximately 20 °C. This supports the finding from the segmented analysis, indicating a critical temperature zone after 15.2 °C where the mortality escalates rapidly. At lower temperatures (<13

°C), the predicted probability of high mortality was close to zero. Between approximately 14–17 °C, the probability increased progressively, with the steepest rise occurring around 16–18 °C. The model’s inflection point appears near ~17 °C, where the predicted probability approaches 0.5, indicating a threshold at which high-mortality events become as likely as low-mortality events. Above 19–20 °C, the predicted probability exceeded 0.8 and approached unity at the highest observed temperatures, suggesting that high mortality becomes highly probable under elevated thermal conditions. The logistic regression demonstrates a clear thermal threshold effect, with the likelihood of high

Fig. 6 Scatter plot showing a strong linear relationship between temperature and mortality anomalies

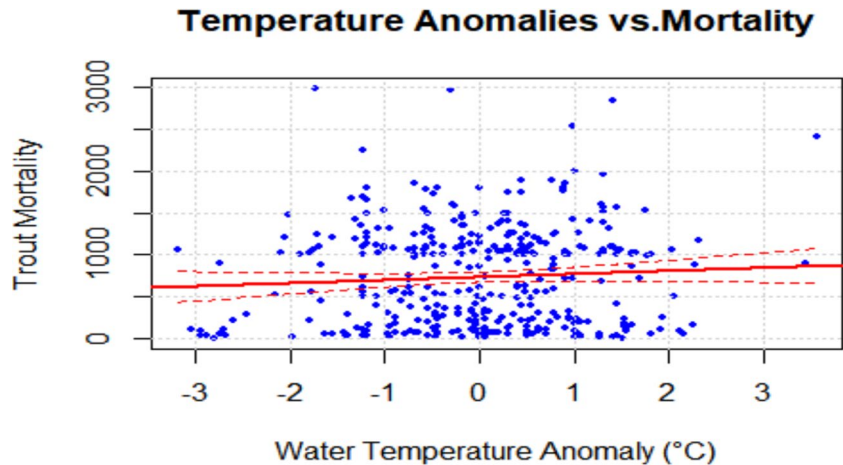
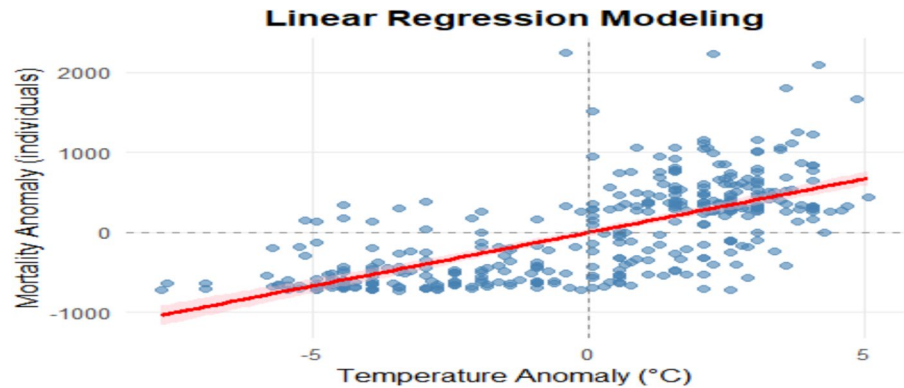


Fig. 7 Linear regression modeling of anomalies



mortality increasing sharply beyond approximately 16–17 °C. These results provide strong evidence that elevated water temperatures substantially elevate the risk of high-magnitude mortality events in *O. mykiss* (Fig. 9).

Discussion

The assessment demonstrates that water temperature is a major driver of *O. mykiss* mortality, primarily through seasonal thermal extremes and short-term temperature anomalies rather than gradual long-term warming. Mortality varied markedly throughout the study period, individuals with variability exceeding the mean, indicating episodic die-offs rather than stable background mortality. The non-normal distribution of both temperature and mortality suggests that acute thermal stress during high-risk periods

triggered these mortality events, likely through physiological stress, reduced dissolved oxygen availability, and impaired metabolic performance, as commonly reported in salmonids exposed to extreme thermal conditions (Fullerton et al., 2010).

Seasonal patterns emerged as one of the strongest predictors of mortality. Summer months experienced significantly higher water temperatures and mortality rates compared with winter, with mortality increasing from 229 ± 27 individuals in winter to 1272 ± 44 individuals in summer. This temporal synchrony strongly suggests that elevated summer temperatures exceed the optimal thermal tolerance of *O. mykiss*, increasing physiological stress. As a cold-water species, *O. mykiss* is particularly vulnerable to elevated temperatures because warming increases metabolic demands while simultaneously reducing dissolved oxygen availability and impairing immune responses (Chen et al., 2015). These findings indicate that seasonal thermal peaks

may be more ecologically important than annual mean temperatures when assessing population vulnerability.

Although long-term trend analyses did not detect statistically significant monotonic warming across the full study period, temporal decomposition revealed modest warming in more recent years, particularly after 2010. Similarly, summer anomaly analyses indicated a greater frequency of positive temperature anomalies during the last decade, despite these patterns not reaching conventional levels of statistical significance. These findings suggest that subtle changes in mean temperature may obscure biologically important increases in the frequency of short-term warming events. This aligns with projections from Intergovernmental Panel on Climate Change indicating that climate change may increasingly manifest through greater variability and more frequent extreme temperature events rather than uniform warming trends (Fullerton et al., 2010).

Regression analyses further demonstrated the biological significance of short-term thermal anomalies. A strong positive relationship was observed between temperature anomalies and mortality anomalies ($\rho=0.713$; $R^2=0.453$), indicating that temperature alone explained nearly half of the variation in mortality. Specifically, mortality increased by approximately 134.1 fish for every 1 °C increase in temperature anomaly.

This highlights the sensitivity of *O. mykiss* populations to relatively small deviations from normal

thermal conditions. However, the increasing dispersion in mortality at higher temperatures suggests that thermal stress may interact with additional environmental pressures such as hypoxia, disease outbreaks, and density-dependent stress (Jacobsen, 2008).

The multiple regression model further strengthened this interpretation by incorporating seasonal effects through month and interaction terms, increasing explanatory power from $R^2=0.453$ to $R^2=0.653$. This demonstrates that mortality responses to temperature are context-dependent and vary seasonally. Identical temperatures may therefore produce different mortality outcomes depending on factors such as seasonal acclimation, life-history stage, and cumulative exposure to prior stressors (Woltemade, 2017).

Overall, these findings suggest that future conservation strategies for *O. mykiss* should focus less on gradual warming trends and more on mitigating seasonal thermal extremes and acute warming events. Management actions such as preserving riparian vegetation, improving stream shading, maintaining flow regimes, and protecting cold-water refugia may help buffer populations against increasingly frequent thermal stress events under future climate change scenarios.

Segmented regression and the Davies test identified a statistically significant breakpoint at approximately 15.2 °C. A range between 15 and 17 °C is reported globally; therefore, this is within the range (Latour et al., 2017; McCormick et al., 2013). Below

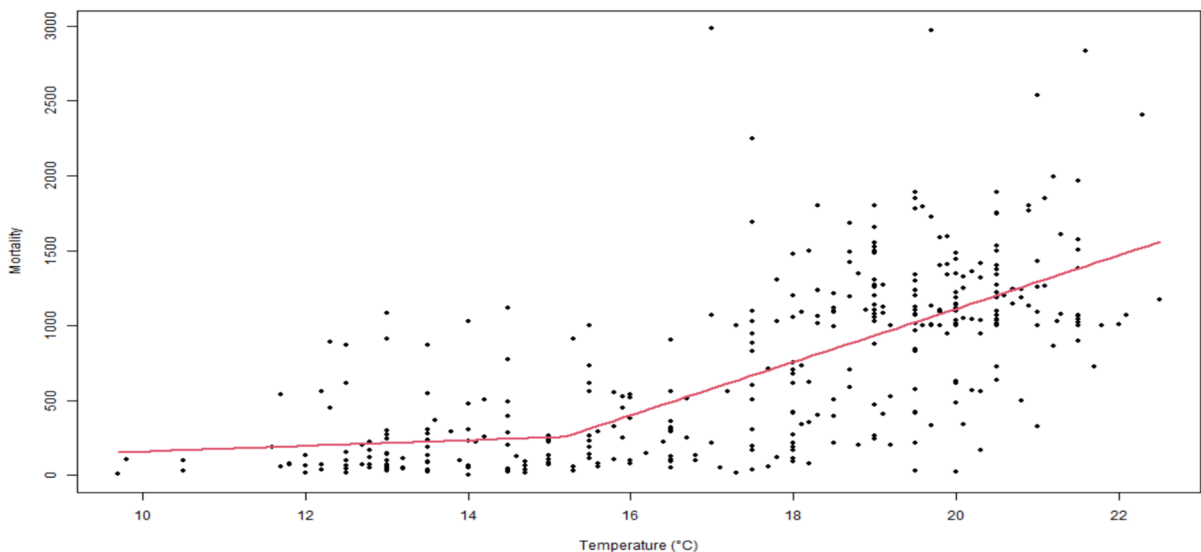


Fig. 8 Segmented plot showing critical thermal thresholds

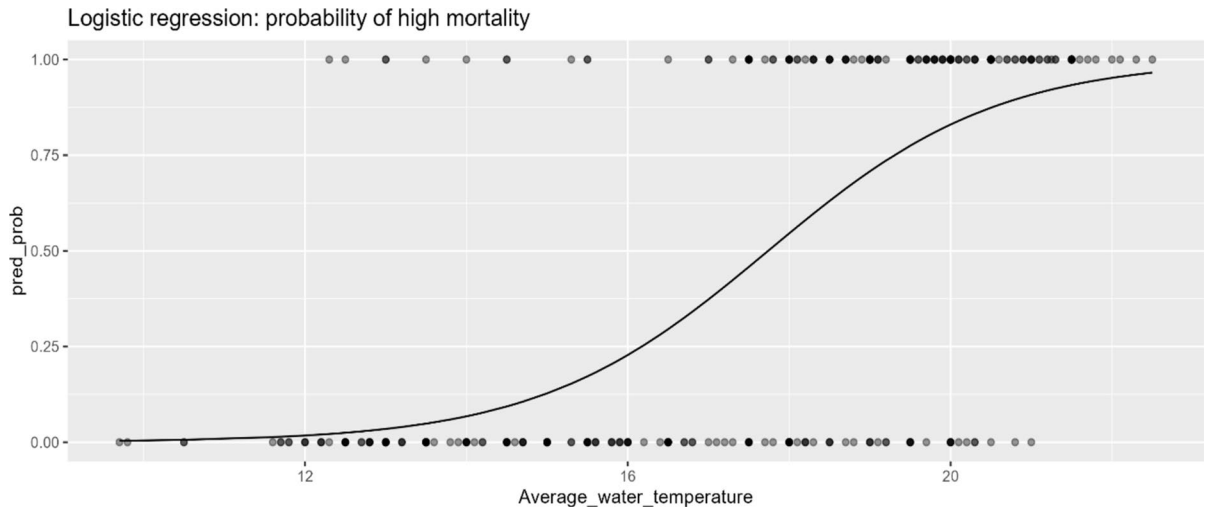


Fig. 9 Logistic curve showing probability of high mortality

this threshold, temperature had little effect on mortality; above it, mortality increased sharply (~178 additional fish per 1 °C). Logistic regression further supported this nonlinear response, with the probability of high mortality rising steeply beyond 16–17 °C and approaching certainty above 20 °C.

These findings indicate that mortality risk is not linearly proportional to temperature but is instead governed by a critical thermal zone. Once temperatures exceed approximately 15–16 °C, physiological stress likely surpasses compensatory capacity, leading to disproportionately high mortality. Such threshold dynamics are particularly concerning under climate change scenarios, where increased frequency and duration of warm events may push temperatures repeatedly beyond biologically critical limits (McCormick et al., 2013).

Although long-term warming trends were modest and statistically non-significant in some analyses, the presence of clear mortality thresholds indicates that ecological impacts can occur even without strong linear warming trends (McCormick et al., 2013). Once critical thresholds are exceeded, relatively small increases in mean temperature or the frequency of thermal anomalies may trigger disproportionate increases in mortality (Latour et al., 2017). This suggests that ecological vulnerability in *O. mykiss* is driven more by extreme thermal events than by gradual changes in average temperature. Collectively, these findings demonstrate that water temperature is a dominant predictor

of mortality, acting through seasonal thermal amplification and nonlinear threshold responses. The recent increase in positive summer temperature anomalies may therefore elevate the likelihood of recurrent high-mortality events if warming persists.

To reduce thermal-related mortality, management strategies should prioritize continuous high-resolution temperature monitoring, particularly during summer months. Threshold-based early warning systems should be implemented, with approximately 15 °C serving as an alert threshold and 17–18 °C representing a high-risk level for mortality. Integrating temperature forecasting into management frameworks would improve the ability to anticipate periods of elevated mortality risk. Additional mitigation measures should include restoration and protection of riparian vegetation to enhance shading and reduce solar heating, conservation of groundwater-fed tributaries and deep pools that function as thermal refugia, and improved flow management during critical summer periods where feasible (McCormick et al., 2013).

The identified thermal thresholds should also be incorporated into long-term conservation and aquaculture planning. Future climate scenario modeling is needed to estimate the frequency and intensity of threshold exceedance under projected warming conditions and to identify habitats likely to remain below critical thermal limits. Such information would support the prioritization of climate-resilient refugia and targeted conservation interventions.

Further research should investigate the interactive effects of additional environmental stressors, including dissolved oxygen, pathogens, and flow variability, to improve predictive mortality models (Islam et al., 2022). Experimental studies on *O. mykiss* hatching and early developmental stages are also necessary to identify strategies for reducing mortality and improving production efficiency. In addition, longitudinal genomic studies could provide insight into adaptive traits associated with thermal tolerance in highland trout populations. Comparative studies across Afromontane ecosystems, supported through collaboration with regional stakeholders, would further strengthen understanding of climate resilience within trout aquaculture systems. Ultimately, these efforts will contribute to improved sustainability, reduced economic losses, and enhanced ecological understanding of rainbow trout production under changing climatic conditions.

Conclusion

This study evaluated the effects of thermal variability on adult *O. mykiss* mortality in Nyanga National Park, Zimbabwe, from 1994 to 2024. The findings revealed a relatively stable long-term thermal regime with strong seasonal variability and no significant evidence of decadal warming. However, short-term temperature fluctuations emerged as a major driver of mortality, with mortality increasing sharply when water temperatures exceeded a critical threshold of approximately 15.2 °C.

The positive relationship between temperature anomalies and mortality highlights those acute warming events, rather than gradual climate warming, pose the greatest risk to *O. mykiss* populations in this Afromontane system. These thermal spikes may increase physiological stress, disease susceptibility, and mortality, although other factors such as water quality, stocking density, feed quality, and genetic variation may also contribute to mortality patterns.

A key contribution of this study is the identification of a relatively low thermal threshold for tropical highland *O. mykiss*, suggesting heightened vulnerability to short-term heat stress. The long-term dataset also demonstrates that stable average temperatures can mask significant mortality risks associated with seasonal extremes.

To reduce future mortality, management should prioritize continuous temperature monitoring, early warning systems for thermal thresholds, habitat cooling strategies such as riparian shading and aeration, and long-term climate adaptation measures. These findings provide important insights for sustainable trout management in Afromontane ecosystems under increasing climate variability.

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Declarations

Ethics approval The research presented in this article was approved by the directorate at the authors' organization.

Competing interests The authors declare no competing interests.

Clinical trial number Not applicable.

Authors' declaration All authors have read, understood, and have complied as applicable with the statement on "Ethical responsibilities of Authors" as found in the Instructions for Authors.

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