The effects of climate change on freshwater fauna in the lower Olifants River, South Africa

by

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THE EFFECTS OF CLIMATE CHANGE ON FRESHWATER FAUNA IN THE LOWER OLIFANTS RIVER, SOUTH AFRICA

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GENERAL ABSTRACT

Freshwater rivers are under threat worldwide from anthropogenic disturbances including climate change. Climate change will increase air temperature and, consequently, water temperature in rivers. The survival of aquatic fauna is closely tethered to water temperature, therefore, the increase in water temperature will influence freshwater fauna at both population and community levels. The ecologically and economically important lower Olifants River, in the Kruger National Park (KNP), South Africa was investigated as it is already negatively affected by anthropogenic disturbances, with the aim of validating a statistical model to predict future water temperatures. The study validated a water temperature model for the Olifants River, with Nash Sutcliffe efficiency values of >0.9 for monthly and >0.75 for daily timesteps, indicating the robustness of this model. The model was further validated using the upper

Klaserie River. This statistical model was then used to predict average water temperatures (WT_{avg}) from projected air temperatures to predict monthly and daily WT_{avg} under the Representative Concentration Pathway (RCP) 8.5 scenario using 16 General Circulation Models (GCMs) to 2100 CE. The results showed that monthly WT_{avg} will increase by 3.7° C, and maximum WT_{avg} will reach 33.6° C by 2100 CE. The daily results showed a similar increase of 3.9° C, with some extreme days reaching 42-44° C, and maximum WT_{avg} will increase to 41.1° C by 2100 CE. These predictions were compared to the thermal tolerances of fauna present in the Olifants River to extrapolate which taxa may be vulnerable to the effects of climate change. The investigation used WT_{avg} of 33.6° C and 41.1° C as the thresholds for chronic and acute heat stress, respectively. It was found that 12 fish species and 11 macroinvertebrate families will be susceptible to acute heat stress while five fish species and five macroinvertebrate families will be vulnerable to chronic heat stress. Although statistical modelling approaches are instrumental in modelling climate change as a driver of water flow and temperature over time, they do not extend beyond these parameters to address climate change impact-related questions on ecological functioning, such as trophic ecology. This study used stable isotope analysis (SIA) to extrapolate what the loss of these fish and macroinvertebrates could have on the trophic dynamics under the RCP 8.5 scenario. The results showed that the apex predator is vulnerable, along with other predators, algivores and insectivores. This will ultimately lead to top-down effects and over-proliferation of prey, plants, and algae. While this study is based on a single river, it represents a novel approach that combines: 1) a mechanistic approach of statistical modelling future water temperature; 2) the evaluation of thermal tolerances; and 3) the assessment of trophic cascades using SIA and applying them to evaluate faunal changes at both population and community levels in a river system. This study has implications at a global level on how climate change may affect not only freshwater water temperatures, fish, and macroinvertebrates, but also with ecological, economic, and human health implications in similarly data-deficient river systems globally.

RESEARCH OUTPUTS

Journal articles

ADLAM, A. L., CHIMIMBA, C. T., RETIEF, D. C. H. & WOODBORNE, S. 2022. Modelling water temperature in the lower Olifants River and the implications for climate change. *South African Journal of Science* 118:4–9.

Conference presentations

Oral presentations

ADLAM, A. L., CHIMIMBA, C. T. & WOODBORNE, S. 2023. In hot water: consequences of climate change on freshwater ecosystems. Joint Geography, Geoinformatics & Meteorology and Zoology & Entomology Postgraduate symposium

Poster presentations

ADLAM, A. L., CHIMIMBA, C. T., RETIEF, D. C. H. & WOODBORNE, S. 2022. In hot water: The fate of freshwater fauna under climate change scenarios. 11th Oppenheimer Research Conference

DECLARATION

I, Amanda Laura Adlam, declare that the dissertation/thesis, which I hereby submit for the degree of Doctor of Philosophy at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

DISCLAIMER

This thesis consists of a series of chapters that have been prepared as stand-alone manuscripts for subsequent submission for publication purposes. Consequently, unavoidable overlaps and/or repetitions may occur between chapters.

ETHICS STATEMENT

The author, whose name appears on the title page of this dissertation/thesis, has obtained, for the research described in this work, the applicable research ethics approval.

The author declares that s/he has observed the ethical standards required in terms of the University of Pretoria's Code of Ethics for Researchers and the Policy guidelines for responsible research.

Signature:

Date: 14/12/2023

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The flower that
blooms in adversity
Is the rarest and
most beautiful of all

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Chapter 1

General Introduction

Climate change in freshwater systems

Freshwater systems cover 0.8% of the earth's surface, while hosting 6% of all the species, with an estimated one third of vertebrate species including fish, amphibians, mammals and reptiles being restricted to freshwater environments (Dudgeon *et al*. 2006). Freshwater systems, however, are believed to be the most endangered ecosystems due to anthropogenic effects such as over-exploitation, habitat degradation, species introductions, water flow regime modification, pollution, deforestation, mining, changes in river morphology, and climate change (Kaufman 1992, Lodge *et al*. 1998, Collares-Pereira & Cowx 2004, Dudgeon *et al*. 2006, Moss *et al*. 2010a, Woodward *et al*. 2010a, Friberg *et al*. 2011, Griffiths *et al*. 2015, Pont *et al*. 2015). The effects of climate change on freshwater systems are numerous and include altering air and water temperatures, precipitation, wind and hydrological regimes, nutrients, primary productivity, acidification, salinization and eutrophication (Heino *et al*. 2009, Rolls *et al*. 2017). Many of the world's freshwater systems are particularly vulnerable, enduring both anthropogenic and climate change impacts (Comte & Olden 2017). The Millennium Ecosystem Assessment (2005) listed freshwater systems as one of the most vulnerable ecosystems due to increases in five categories of negative impacts, namely habitat change, climate change, invasive species, over-exploitation, and pollution. These impacts will likely occur simultaneously, causing compounding, interactive impacts that may be worse than the sum of the single effects (Liu *et al*. 2015, Jackson *et al*. 2016, Segurado *et al*. 2016). With the freshwater ecosystem facing such severe impacts, there is an increasing urgency for research, conservation, education and to inform policy, as well as to create initiatives for collaboration (Darwall *et al*. 2018).

The human population closely relies on the persistence of freshwater for drinking, agriculture, and sanitation (Moss *et al*. 2010a). Inland waters also produce ~40% of the world's fish for consumption, providing billions of people with protein, as well as millions for livelihoods (Jackson *et al*. 2016, Lynch *et al*. 2016, Segurado *et al*. 2016). Aquaculture is considered the fastest growing industry globally for food production (De Silva *et al*. 2009). Freshwater fish provide the equivalent of all dietary protein for 158 million people and livelihoods for 820 million people (McIntyre *et al*. 2016, Ainsworth *et al*. 2023). An estimated 81% of people dependant on these fish for nutrition occur in impoverished nations with Gross Domestic Products (GDPs) below the global average (McIntyre *et al*. 2016). While Africa produces the second largest inland fisheries catch globally, nine countries within southern Africa including Zimbabwe, Zambia, Angola, Malawi, and Mozambique have inland fisheries which are vulnerable to climate change (Jackson *et al*. 2016, Ainsworth *et al*. 2023). Freshwater systems are particularly vulnerable to the effects of climate change due to three reasons highlighted by Woodward *et al*. (2010), namely: 1) They are isolated and fragmented within the terrestrial landscape making dispersal and migration of species difficult, and whereas terrestrial animals can track climate to find suitable habitats, this is virtually impossible for freshwater species; 2) Water temperature and water availability, including rainfall, is climate-dependant. Climate change is set to bring about higher water temperatures and its associated reduced water flow. Along with this predicted reduction in water flow, an increase in stochastic events such as floods as warming increases is expected (Mohammed *et al*. 2017); and 3). Freshwater systems are already experiencing a myriad of other anthropogenic disturbances such as pollution, over- abstraction and habitat change.

The sixth assessment report of the Intergovernmental Panel on Climate Change (IPCC) under the "*business as usual*" Representative Concentration Pathway (RCP) 8.5 scenario for southern Africa forecasts a mean annual air temperature rise of 4-7° C, and the maximum annual air temperature will rise by 4-8° C by 2100 CE (Gutiérrez *et al*. 2021, IPCC 2021). Engelbrecht *et al.* (2015) found that global simulations of annual average near-surface temperature will rise by 4-6º C in subtropical Africa by 2100 CE, which is also supported by other studies (Hulme *et al*. 2001). There is a prediction of up to 40% less summer rainfall in southern Africa (Engelbrecht *et al*. 2011). This will not only affect human health (Garland *et al*. 2015), but also have an effect on the rainfall that rivers will receive and therefore will alter the flow regime of the systems. It is also predicted that water quality will decrease and water temperatures will increase (Schulze 2011). Along with these factors is the increase in human demand for freshwater resources. Within the southern African subregion, effective rainfall is low because of low annual average rainfall (675 mm) and high temperatures causing high evaporation rates of up to 65% (Marshall 2011). The highly seasonal climate, along with frequent drought events, cause river systems to experience drastic changes in flow which can lead to intermittent streams and/or temporary pools during extreme dry-up events (Chabwela 1994, Marshall 2011). It is therefore critical to gain insights into the future effects of climate change on these systems and model the changes that temperature and rainfall will have on the rivers.

Historically, there have been few to no studies on climate change and thermal vulnerability within freshwater systems in southern Africa. Recently however, this has changed with the few pioneering studies, mainly within South Africa (Ramulifho *et al*. 2018). These studies include a framework to calculate the thermal resilience of entire catchments by illustrating how to quantify connectivity and thermal vulnerability of a system and to use these parameters to estimate the risk to cold water-adapted macroinvertebrate families within the system (Ramulifho *et al*. 2018).

The South African Water Research Commission (WRC) recently released a report which outlined guidelines for screening and evaluating water temperature within perennial rivers in South Africa to first determine whether the water temperature of a river is of potential concern and includes the following three key questions (Dallas & Rivers-Moore 2019): 1) How resilient is a river to changes in water temperature which can be addressed by considering aspects such as stream order, geomorphological zone, and water yield? 2) What are the hydrological, physico-chemical and habitat aspects that could exacerbate or subtract from thermal impacts such as whether the flow regime is natural or transformed, the presence of impoundments, water quality problems and potential algal blooms? and 3) What is the sensitivity of the organisms within the river by assessing whether there are any *International Union for Conservation of Nature* (IUCN) red-listed species and what is the ecological state and importance of the site using the Ecological Category based on South African Scoring System (SASS) version 5 rapid bioassessment method for rivers (Dickens & Graham 2002)? Once these questions have been addressed, and it has been established that environmental water temperature must be monitored, a risk assessment on the thermal regime of the river can then be undertaken (Dallas & Rivers-Moore 2019). This process is undertaken in two steps: 1) Establishing the thermal metrics of the river under consideration by obtaining water temperature data using electronic data loggers and creating a reference thermograph; and 2) Assessing differences between data gathered and reference data and thermographs (Dallas &

Rivers-Moore 2019). This generates invaluable data that allow insights into river thermal metrics and the potential vulnerability of rivers in southern Africa (Dallas & Rivers-Moore 2019). However, an aspect not taken into consideration in this process is climate change, and the impact this may have on rivers. While higher order rivers are considered to be more resilient to thermal stress (Dallas & Rivers-Moore 2019), these larger perennial rivers can be found in regions with the highest predicted future warming scenarios.

In southern Africa, climate change has already translated into an increase in extreme warm indices and a decrease in cold indices, increased heat waves and lower rainfall (Nkhonjera 2017). In South Africa for example, temperature forecasting for the Olifants River basin has showed an increase of up to 4.6° C by 2100 (Singh *et al*. 2014). Studies conducted for precipitation on the Olifants River basin showed that seasonality would change with a decrease in summer rainfall and an increase in winter rainfall (Cullis *et al*. 2011, Singh *et al*. 2014). In the Olifants River basin, a climate change risk assessment was conducted and it was found that by 2050 climate change and population growth will increase water demand in the river (Cullis *et al*. 2011).

Lake thermodynamics have also been studied in Africa, such as Lake Volta in Ghana by Darko *et al*. (2019) who used modelling techniques to predict the effects of climate change (a 4° C increase in air temperature), and found that this increase would alter the ecological functioning of the lake through an increase in stratification through an ~1 m upward shift in thermocline depth, together with a reduction in oxygen levels. Many of the fish species inhabiting the lake are riverine species and live in the top 3 m of the water, therefore, disruption of this top layer can lead to detrimental effects on the fishes and a reduction of suitable habitat (Dankwa *et al*. 2011, Darko *et al*. 2019). Cohen *et al*. (2016) used the palaeoecological records of Lake Tanganyika to link declining populations of freshwater fish and molluscs to climate warming and increased stratification leading to reduced oxygenation, and also found a decrease in primary productivity, specifically diatoms, which are vital to the diet of many cichlids. A study on Lake Kariba, bordering Zimbabwe and Zambia, showed that although the lake had warmed by 0.7° C between 1986 and 2011, thermal stratification had weakened, in contrast to the above-cited studies (Mahere *et al*. 2014). Instead they found a downward transfer in heat in the lake, reducing thermal stability and oxygenation to lower water levels (Mahere *et al*. 2014). These factors, along with decreased rainfall (6.3 mm per decade), fluctuating water levels, and a 15-25% increase in water loss due to evaporation, have caused declines in fishery catches (Ndebele-Murisa *et al*. 2011). There is a possibility that large embayments may have thermodynamic properties similar to those of a lake. Furthermore, the above-cited studies include fish similar to those within the Olifants River system in the Kruger National Park in South Africa such as species of the genera *Hydrocynus*, *Clarias*, *Tilapia*, *Oreochromis*, *Mormyrus*, and *Labeo* (Dankwa *et al*. 2011) that may represent ideal examples of what may happen within bays of the river or in areas or periods of slow flow under climate change scenarios.

Effects of climate change on freshwater communities

Climate change studies have mainly focused on individual species, while the effects on trophic cascades and the communities within the ecosystem as a whole have been neglected (Hogg *et al*. 1995, Woodward *et al*. 2010b). Given that species within these systems are predominantly ectotherms, changes in water temperature will have profound effects on metabolic rates and foraging behaviour of individuals, which will ultimately affect trophic interdependencies (Woodward *et al*. 2010b). As water becomes warmer, there is also a risk of oxygen depletion as well as changes in the phenology, such as breeding times and lifespan of organisms which could also lead to disruptions in trophic dynamics (Jeppesen *et al*. 2010). There is evidence showing that fish have altered their migration timing in accordance with changing climates, and this earlier migration and rising temperatures have a negative effect on fish abundances (Kuczynski *et al*. 2017). Many vertebrates that utilise freshwater systems are terrestrial, however, fish are ill-adapted to drought conditions, and need to migrate through aquatic systems to survive (Moss *et al*. 2010a). This is becoming an increasing concern as dams and reservoirs block migration routes (Pelicice *et al*. 2015), and the rising temperatures of climate change may cause these systems to become intermittently disconnected. There is evidence that these stressors that are related to climate change may cause phenotypic changes and ultimately adaptations within freshwater fish populations and this may involve epigenetic mechanisms (Jeremias *et al*. 2018).

Changes in hydrology and temperature of freshwater systems can also affect the salinity of the system, especially in coastal lakes (Jeppesen *et al*. 2015), and due to climate change mediated changes in flow and temperature, this problem could increase upstream further into freshwater rivers. With declines in water levels due to climate change, the concentrations of nutrients within these lakes will increase and result in eutrophic conditions (Jeppesen *et al*. 2015). Lower water levels and increased eutrophication will also affect the thermal refugia of freshwater fish, and shallow habitats and the species that feed or spawn in those areas may be lost, while the changing conditions may favour eutrophic-adapted species displacing other species (Jeppesen *et al*. 2015). It has been found that freshwater fish are more tolerant to changes in salinity, followed by macro- and microinvertebrates (Castillo *et al*. 2018a). Different functional feeding groups of insects such as scrapers, gatherers, and filter-feeders are more sensitive to salinization than those at a higher trophic level such as omnivores and predators (Castillo *et al*. 2018a). This evidence shows increased salinity in freshwater systems will have an effect on the ecosystem functioning and trophic interdependencies (Jeppesen *et al*. 2015, Castillo *et al*. 2018a).

A microcosm experiment by Petchey *et al*. (1999) illustrated the effects of warming on foodweb structure in aquatic systems. The study showed that warming caused up to 40% loss in species richness, with high extinction rates of predators and herbivores and little effect on primary producers and bacterivores (Petchey *et al*. 1999). They also found that species diversity within a community did not affect extinction frequencies, and more diverse communities retained functional groups only because of their higher biodiversity (Petchey *et al*. 1999). Primary productivity, including algal biomass and other macrophytes, increased with higher temperatures (Petchey 2000, Friberg *et al*. 2009). This had an effect on the feeding groups within the trophic structure, as filter-feeders, scrapers, and bacterivores increased with more available food (Petchey 2000, Friberg *et al*. 2009). Decomposition rates of leaf litter have also been found to increase with rising temperatures (Petchey 2000, Bärlocher *et al*. 2008, Friberg *et al*. 2009). This decreases the substrate availability for aquatic hyphomycetes (aquatic moulds or fungi) (Bärlocher *et al*. 2008) and could also lead to losses of detritivores. Within southern Africa, shredders which feed on coarse organic matter and scrapers which feed on algae, have the lowest diversity and biomass (Addo-Bediako 2021, 2022, Makgoale *et al*. 2022). It has also been found that these feeding groups are sensitive to disturbances (Addo-Bediako 2021, 2022, Makgoale *et al*. 2022), which may make them particularly vulnerable to the effects of climate change.

Friberg *et al*. (2009) showed that overall macroinvertebrate density increases with higher temperatures. However, this was attributed to higher densities of only a few dominant filter-feeding species, and species diversity within the macroinvertebrate community decreased, i.e. there was a significant decrease in evenness and species overlap with an increase in temperature (Friberg *et al*. 2009). A field experiment by Hogg *et al*. (1995) in which stream temperatures were raised by 2-3.5° C showed that macroinvertebrate species density decreased and growth patterns of species changed. However, this study only assessed two species and is not representative of the entire macroinvertebrate community, but it nevertheless highlights the importance of maintaining habitats with a range of thermal regimes as this may aid in conserving the genetic diversity within populations.

A more recent study by O’Gorman *et al*. (2023) using manipulative field experiments to determine whether warming would have an effect on freshwater ecosystems showed that experimental treatment with predators present in the warmed stream suppressed invertebrate biomass and in turn increased algae biomass. Decomposition rates were also higher in warmer streams (O’Gorman *et al*. 2023). The warmed streams had lower mean trophic levels and less connectivity which could lead to invasions, loss of diversity, loss of predators and top- down control and potentially local extinctions (O’Gorman *et al*. 2023). This field study further supports and adds to the growing knowledge of the consequences of warming in freshwater communities (Petchey *et al*. 1999, Friberg *et al*. 2009, O’Gorman *et al*. 2023).

There is also evidence to suggest that climate warming could alter species richness, distributions, diversity, body size structure, and densities within freshwater communities, towards small-sized individuals at higher densities (Meerhoff *et al*. 2007, Friberg *et al*. 2011, Dallas & Ross-Gillespie 2015, Ruiz-Navarro *et al*. 2016). In macroinvertebrates, larger body size and a high fecundity is found at cooler temperatures, therefore fecundity decreases at higher temperatures (Dallas & Ross-Gillespie 2015). Friberg *et al*. (2009) found that densities of the predatory brown trout (*Salmo trutta*) were higher in warmer streams but lowest in the warmest stream due to the species being a cold-water specialist. This, together with other studies, supports the idea that predators have relatively slower growth rates than species at a lower trophic level and are negatively affected by high temperatures and losses in thermal habitats (Petchey *et al*. 1999, Friberg *et al*. 2009, Santiago *et al*. 2017, Chevalier *et al*. 2018). A study by Ruiz-Navarro *et al*. (2016) on five cyprinid fish species in the United Kingdom also showed that four of the species shifted to faster growth rates and decreased body sizes under climate change scenarios.

Global trends of various taxa show that species are tracking climate change through changes in their distribution; this typically being a poleward movement or moving to higher elevations and therefore towards cooler temperatures (Parmesan & Yohe 2003, Parmesan 2006a, Thuiller 2007, Chen *et al*. 2011). A study in France by Comte & Grenouillet (2013) illustrated that freshwater fish species shift their distributional ranges to higher elevations (13.7 m per decade) and upstream (0.6 km per decade). While fish species distribution ranges increased upstream, their downstream range contracted substantially which shows the effects that climate change has on fish species distributions (Comte & Grenouillet 2013). Although the distribution range shifts of these fish species are substantial, it is estimated that temperatures will shift upstream by up to 140 km using a projected air temperature increase of 2° C under climate change by 2050 CE, and therefore freshwater fish will not be able to keep up with the rapid change in temperature (Isaak & Rieman 2013). The study by Comte & Grenouillet (2013) also showed that fish species with larger population sizes may better buffer the effects of climate change and that individual fish species traits such as dispersal ability, trophic level, and habitat preferences will also influence their response to climate change. Comte *et al*. (2016) also found evidence that fish species with larger body sizes may be better suited to track climate change.

Invasive species and climate change

Conditions for the establishment of alien species in freshwater environments are cold temperatures, winter hypoxia, flow regime and low salinity (Rahel & Olden 2008). Under climate change, these conditions could be altered to warmer temperatures, reduced hypoxia, changes in flow regime, changes in food web structure, increased algal blooms, higher salinity, and reservoir habitats such as dams and lakes (Rahel & Olden 2008, Záhorská 2016). These conditions will increase the likelihood of cold water species leaving their native habitats or becoming locally extinct and being replaced by warmer water-adapted fish species (Rahel & Olden 2008, Moyle *et al*. 2013, Segurado *et al*. 2016, Záhorská 2016, Rolls *et al*. 2017). This has already been found in sub-Arctic regions, where the poleward shift of cyprinids, percids, and centrarchids have displaced the existing freshwater fish species (Rolls *et al*. 2017). In already invaded rivers, indigenous fish species are more likely to become extinct before their alien counterparts (Moyle *et al*. 2013, Shelton *et al*. 2018a). It has also been found that invasive species can spread to new waters through flooding events, and such incidents are increasing with climate change (Záhorská 2016).

Not all distribution ranges of invasive species will increase with climate change as shown by the example of the cold water-adapted rainbow trout (*Oncorhynchus mykiss*) which has established in headwater streams in South Africa (Shelton *et al*. 2018b). Its distribution range contracts during summer to cooler water and that, with the further onset of climate change and the warming of the water in these regions, the distribution and population sizes of this species will decrease (Shelton *et al*. 2018b). While the effects described by the results of the study by Shelton *et al*. (2018b) may be beneficial to the indigenous fish species within invaded rivers, it could potentially open a niche to warmer water-adapted fish species to establish such as the invasive black bass (*Micropterus* spp.) or the native Mozambique tilapia (*Oreochromis mossambicus*) to establish extralimital populations (van Wilgen *et al*. 2014). Black bass, particularly the Florida bass (*Micropterus floridanus*), have been found to increase predatory capacity at higher temperatures suggesting that warmer waters may lead to more deleterious effects to native species such as redfin minnows and outcompeting native predators (van Wilgen *et al*. 2014). Other species of concern within South Africa are the invasive crayfish *Cherax quadricarinatus* and *Procambarus clarkii* which are known to compete with the native crab species *Potamonautes perlatus* (van Wilgen *et al*. 2014). It has been found that at higher temperatures, *P. perlatus* decreases feeding capacity, while *P. clarkii* increases feeding capacity and *C. quadricarinatus* remains unchanged, implying that climate change could positively affect *P. clarkii* (van Wilgen *et al*. 2014).

Pests and diseases in freshwater systems

Disrupted ecosystems, which includes the future altered states caused by climate change, are more susceptible to the impacts of diseases (Riley *et al*. 2008). Rivers are a medium for water-borne diseases such as cholera, as well as for vectors of diseases such as malaria (Johnson & Paull 2011). Fish also act as hosts to a range of zoonotic diseases which include bacteria (e.g., botulism and bacterial kidney disease), viruses, parasites (e.g., nematodes, trematodes, and cestodes) and fungi (Ziarati *et al*. 2022). Ecosystems that have been disrupted are more likely to facilitate the transmission of diseases than those that are healthy, and changes in community structure or in energy flow within the system may contribute to such disruptions (Riley *et al*. 2008). It is therefore likely that the disruptions predicted in the trophic cascades in the current study would contribute to an increase in disease prevalence within the system, and there is already evidence of this increase within freshwater taxa (Johnson & Paull 2011). Within the Olifants River catchment, diseases such as diarrhoea, dysentery, cholera, bilharzia, and typhoid are known to occur, with consumption of fish and water being the major risk factors (Garland *et al*. 2014). This highlights the need for not only good water management, but for a healthy ecosystem and trophic dynamics within the system.

Mosquitoes are known for transmitting diseases in southern Africa, negatively affecting human and animal health (World Health Organization 2020). There are a number of disease-causing genera in South Africa, namely *Aedes*, *Culex*, and *Anopheles*, which act as vectors for diseases such as dengue fever, West Nile virus, and malaria (Sule *et al*. 2018, World Health Organization 2020). There were ~215 million cases of malaria with 386 000 deaths reported in Africa in 2019 (World Health Organization 2020). While global efforts to prevent malaria are focused on prevention, such as insecticide-treated mosquito nets, there are predators of mosquito larvae within aquatic ecosystems that control populations naturally. For example, there are aquatic insects and fish that have been found to feed on and control mosquito populations such as dragonfly (Odonata) larvae from the families Gomphidae, Libellulidae and Coenogrionidae, saucer bugs from the families Naucoridae and Notonectidae, *O. niloticus*, *O. mossambicus*, mosquito fish (*Gambusia affinis*), the common guppy (*Poecilia reticulate*), and larvivorous family Cyprinidae (Howard *et al*. 2007, Quiroz-Martinez & Rodríguez-Castro 2007, Kamatchi *et al*. 2016, Noreen *et al*. 2017, Vatandoost 2021). A disease within the river that is particularly detrimental to the crocodile population, but also occurs in fish, is pansteatitis (Woodborne *et al*. 2012). There have been models developed to predict the potential impact of climate change on pest species, such as the one used by Rivers-Moore *et al*. (2008b) on blackflies (*Simulium chutteri*). This model used water temperature and flow predictions to forecast outbreaks of the blackfly (Rivers-Moore *et al*. 2008b). Diseases and pests are not necessarily the primary focus of the present study, but due to the implications of climate change on pest, disease host and disease suppressor species will also be taken into account.

Thermal tolerance studies

Fish are poikilotherms where their body temperature is similar to that of their environment and they are therefore sensitive to temperature changes (Wagner *et al*. 2023). Using behavioural mechanisms, fish segregate into habitats with preferred temperatures and these are referred to as their thermal niche (Magnuson *et al*. 1979). There are typically three categories of freshwater fish species according to their thermal niche preference, namely: 1) Warm-water (27-31° C); 2) Cool-water (21-25° C); and 3) Cold-water species (11-15° C) (Magnuson *et al*. 1979, Heino *et al*. 2009). The thermal tolerance or upper thermal limit of freshwater fish species is often very similar to the temperatures at which they live, making them indicators of climate as well as making them more susceptible to the consequences of climate change (Comte & Olden 2017, Wagner *et al*. 2023). The critical thermal maxima (CT_{max}) of fish species will not evolve fast enough to track the changes climate warming is predicted to bring (Comte & Olden 2017). It is therefore likely that many fish species will lose habitats, become more range-restricted and locally extinct at the edge of their distributional ranges (Comte *et al*. 2016). Comte *et al*. (2021) found that thermally sensitive communities are experiencing high rates of reorganisation, with an increase in species in warm water species. These changes may be particularly detrimental to specialist species, while opening up opportunities for invasive species (Segurado *et al*. 2016). A study in the United States of America found that cold-water species are vulnerable under climate change scenarios and may be replaced by warmer-water species (Jones *et al*. 2013) which has been supported by other studies (Knouft & Ficklin 2017). As the study by Jones *et al*. (2013) focused mainly on recreational fish species, they estimated a loss of up to US$6.4 billion by 2100 CE from the freshwater recreational fishing industry.

The warming tolerance of freshwater fish, defined as the difference between CT_{max} and the mean temperature of the warmest month experienced by the species within its distribution range ($Thab_{max}$), is considered to decrease with an increase in latitude under climate change projections (Comte & Olden 2017). If this prediction is correct, then fish species within southern Africa may have a relatively good tolerance to climate warming. Fish species, as well as other aquatic organisms such as macroinvertebrates, are also known to use behavioural mechanisms to avoid temperatures exceeding their CT_{max} by utilizing thermal refugia (Dallas & Ross-Gillespie 2015, Dallas & Rivers-Moore 2018). However, this behaviour depends on the thermal heterogeneity of the environment and available microclimates (Dallas & Ross-

Gillespie 2015), and this may not be possible in ephemeral streams. A study on the CT_{max} of eight freshwater fish species in the Cape Fold Ecoregion in South Africa illustrated the importance of thermal and evolutionary histories in the thermal tolerance of fish species (Reizenberg *et al*. 2019). More significant was the finding that the western study site, which was a perennial stream, had more thermally-sensitive fish species than the eastern study site which was a more ephemeral stream (Reizenberg *et al*. 2019). This suggests that the water flow and stream order should be taken into account when studying thermal sensitivity of a system. A similar study on aquatic invertebrates indicated the importance of the evolutionary history of individual species, thermal tolerance, and acclimation ability (Dallas & Rivers-Moore 2018).

A sudden rise in environmental temperatures can cause thermal extremes in aquatic systems and if the rise in temperature exceeds the thermal tolerance of fishes within the system, mass mortality events can occur (Lamberti *et al*. 2020). A study by Till *et al*. (2019) in the United States of America predicted that by 2050 CE, annual die-offs of fish during summer will double to about 10 mass mortality events per year and by 2100 CE, this will increase to ~17 mortality events during summer. These die-offs are likely to accelerate the predicted changes in fish communities such as an overall decrease in body size and invasion by warm-water species (Till *et al*. 2019).

Water temperature modelling

Water temperature is vital in the functioning of fauna in freshwater environments (Rivers-Moore & Lorentz 2004, Yearsley 2009). Water temperature changes can be observed over hourly, daily, monthly and yearly timescales and, therefore, prediction methods are often scalable in space and time (Rivers-Moore & Lorentz 2004, Yearsley 2009). Due to global scenarios of rising air, and therefore water temperatures, along with growing water demand, water modelling methods are required (Yearsley 2012), Various water temperature models have been developed, and these mainly include physical and statistical models (Marce & Armengol 2008, Rivers-Moore *et al*. 2008a, Yearsley 2009, Brennan 2015, Ouellet-Proulx *et al*. 2017). Physical models use heat transfer and physical characteristics such as humidity, soil type, elevation, land cover, precipitation, solar radiation, and flow, and are therefore data-intensive (Yearsley 2009, 2012, Brennan 2015). An example of such a model is the River Basin

Model which is a semi-Lagrangian approach developed by Yearsley (2009), which was later integrated with the Variable Infiltration Capacity (VIC) hydrologic model (Yearsley 2012).

Statistical water models use historical data such as air temperature and statistical relationships with water temperature to model current or future water temperature (Mohseni *et al*. 1998). These statistical models can be either linear or non-linear and more importantly, require fewer data inputs than physical models (Smith 1981, Mohseni *et al*. 1998), which is particularly useful in data-deficient regions. Linear models are considered to be more accurate and produce a better fit (Morrill *et al*. 2005), and statistical linear regression models have been developed to simulate water temperature for South African rivers rather than those developed for northern-hemisphere rivers (Rivers-Moore *et al*. 2005, 2008a). Simple regression models are more parsimonious with fewer parameters and adding variables lowers the predictive value (Rivers-Moore *et al*. 2008a). While these models include parameters such as air temperature, flow, and relative humidity, it was found that the inclusion of flow and relative humidity reduce model accuracy (Rivers-Moore *et al*. 2008a) and, therefore, air temperature is the largest driver of water temperature. Although water temperature statistical modelling approaches are instrumental in modelling climate change as a driver of water flow and temperature over time, they do not extend beyond these parameters. There is therefore a critical need to address climate change impact-related questions on ecological functioning, such as in trophic ecology, that can be appropriately be evaluated using stable isotope analysis (SIA; Frye 1991, Jardine *et al*. 2003).

Stable isotope analysis (SIA)

Stable isotope analysis (SIA) of carbon (C) and nitrogen (N) has been used in aquatic research to identify the feeding ecology of species, as well as the trophic cascade or food web of a system (Frye 1991, Jardine *et al*. 2003, Layman *et al*. 2007, Woodborne *et al*. 2012). However, little is known of the effects of climate change and increasing temperatures on freshwater fauna. Friberg *et al*. (2009) studied the stable isotope ratios of carbon (δ^{13}C) and nitrogen (δ^{15}N) of fish species in ten streams in a geothermal active area in Iceland of differing temperatures and found that δ^{15}N increased across trophic levels with an increase in temperature, but there was no correlation between temperature and δ^{13}C. The relationship between temperature and δ^{15}N could be due to enriched food resources or through changes in growth rates (Friberg *et al*.

2009). Increasing temperature can increase growth rate of individuals, which has been shown to increase the incorporation of dietary $\delta^{15}N$ in fish species (Friberg *et al*. 2009). Nitrogen isotopes are also indicators of anthropogenic disturbances such as pollution (Lake *et al*. 2001).

Problem statement and rationale

While the consequences of climate change such as changes in water flow and air temperature have been explicitly considered, the ecological impacts in river systems have not been studied. It is important to consider the impacts of such changes on fish species and macroinvertebrates. Changes in temperature will ultimately have an impact on species distributions and the available habitat. Modelling techniques will be important to forecast these water temperature changes. In addition, trophic interactions between species may change, due to the possible loss of some species or increased competition for resources. The present study is therefore directed at elucidating these relationships using statistical linear regression water temperature models and SIA to predict changes in trophic structure under the "*business as usual*" Representative Concentration Pathway (RCP) 8.5 scenario, in order to serve as a novel example of the effects of climate change at both individual and community levels, with implications on a global scale.

Aims and objectives of the study

The aims and objectives of this study were to develop, calibrate, and validate a statistical model for water temperature in the heavily polluted and over-abstracted, but ecologically and economically important, lower Olifants River in the Kruger National Park (KNP), Limpopo Province, South Africa under the RCP 8.5 scenario. This model can be used in conjunction with air temperature projections for the region to forecast water temperature by 2100 CE to give an indication of the potential impacts climate change may have on water temperature on a monthly and daily timescale for the river. The implications of these changes on the aquatic fauna can then be assessed. Given that freshwater fish and macroinvertebrates have thermal tolerances, in the present study, these are compared against the predicted rise in temperature to assess whether species will be vulnerable to the effects of climate change. Species vulnerable to climate change may have an effect on the food web and may have cascading trophic effects on the system, and this is assessed using SIA and by observing predator-prey relationships within the river. Ultimately, the aim and objectives of this study are to evaluate the effects of climate change on the water temperature, and thermal tolerances, and trophic niches of fishes and macroinvertebrates in the lower Olifants River, in order to serve as a model study to extrapolate to potential similarly impacted data-deficient rivers globally. The present study represents a novel approach that combines: 1) a mechanistic approach of statistical modelling of future water temperature; 2) the evaluation of thermal tolerances; and 3) and the assessment of trophic cascades using SIA and applies them to evaluate faunal changes at both the population and community levels.

Study area

South Africa is divided into six freshwater ecoregions namely the Cape Fold, Southern Temperate Highveld, Karoo, Zambezian Lowveld, Amatolo-Winterberg Highlands and Drakensburg- Maluti Highlands (Abell *et al*. 2008, Darwall *et al*. 2009). The study area is in the Olifants River Basin (Figure 1.1), which is ~75 000 km^2, extending across South Africa and Mozambique in the Southern Temperate Highveld freshwater ecoregion (Darwall *et al.* 2009, Singh *et al*. 2014). This ecoregion mainly consists of savanna-dry forest rivers, and bioregionally it is defined as of outstanding biological distinctiveness, and its conservation status is categorized as an endangered (EN) (Thieme *et al*. 2005, Darwall *et al*. 2009). The region is described as “The South African interior plateaux subregion of the highveld aquatic ecoregion, fauna with mixed tropical and temperate affinities, sharing species with Limpopo and Zambezi systems” (Thieme *et al*. 2005, Darwall *et al*. 2009).

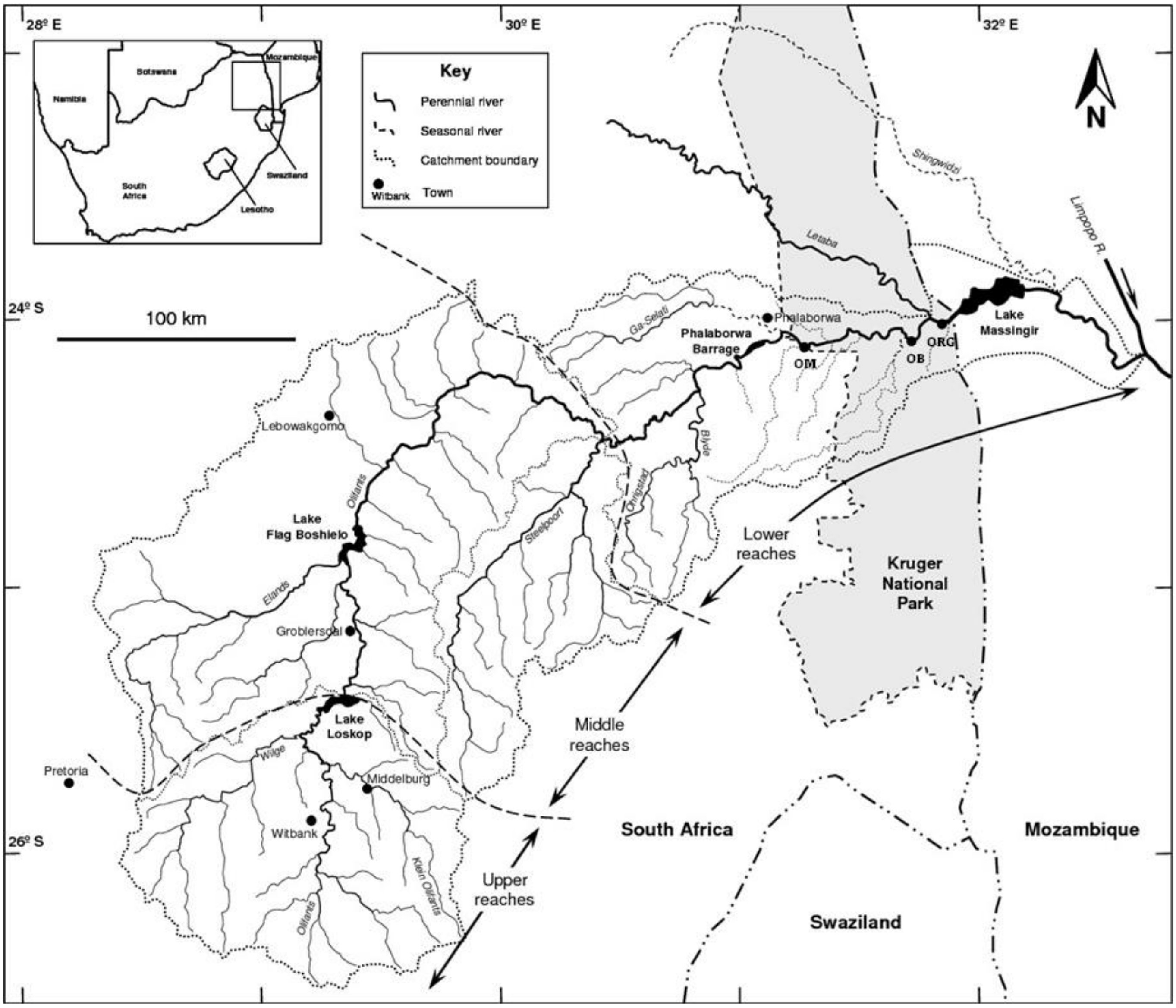

Figure 1.1: Map showing the Olifants River catchment (with an insert of South Africa), including impoundments, and the three study sites within the Kruger National Park, lower Olifants River. OM = Mamba Weir; OB = Balule Weir; ORG = Olifants River Gorge. This map has been adapted from Ashton (2010).

Rainfall in the Olifant River catchment occurs during the austral summer months, from October to April and is usually between 500-800 mm (Mccartney & Arranz 2007).The catchment supports an estimated human population of 3.2 million; represents ~6% of South Africa’s gross domestic product (GDP), and supports multiple industries such as mining, commercial and subsistence agriculture, forestry, power generation and commercial and subsistence fisheries (Mccartney & Arranz 2007). As such, the catchment has been over-abstracted and over-exploited (Ashton & Dabrowski 2011). The catchment is divided into the upper, middle, and lower regions and our study site is located on the lower Olifants River which flows through the KNP into Mozambique (Mccartney & Arranz 2007, Figure 1.1). There are three large impoundments along the Olifants River- two above the study sites namely Lake Loskop and Lake Flag Boshielo, and one below the study sites situated in Mozambique, Lake Massingir (Mccartney & Arranz 2007, Figure 1.1). It is a higher order, perennial river that not only supports a large human population in South Africa and Mozambique, but also the ecological and economic functioning of the KNP (Mccartney & Arranz 2007). The KNP is a large protected area in South Africa and supports ecotourism, receiving more than one million visitors per year (Roux & Nel 2013, Riddell *et al*. 2019). The Olifants River in the KNP also experiences negative impacts of pollution from upsteam and this affects water management within the park (Riddell *et al*. 2019).

Freshwater fish that are known to occur in the lower Olifants River include the redeye labeo (*Labeo cylindricus*), leaden labeo (*L. molybdinus*), purple labeo (*L. congoro*), rednose labeo, (*L. rosae*), sharp tooth catfish (*Clarias gariepinus*), Mozambique tilapia (*Oreochromis mossambicus*), southern mouthbrooder (*Pseudocrenilabrus philander*), threespot barb (*Enteromius trimaculatus*), bowstripe barb (*E. viviparus*), redbreast bream (*Coptodon rendalli*), sawfin rock catlet (*Chiloglanis paratus*), Imberi (*Brycinus imberi*), tigerfish (*Hydrocynus vittatus*), lowveld largescale yellowfish (*Labeobarbus marequensis*), and tank goby (*Glossogobius giuris*) (Woodborne *et al*. 2012, Myburgh 2016, 2019, Kaiser 2019). Macroinvertebrates known to occur in the river are families Baetidae (mayflies), Coenagrionidae (damselflies), Elmidae (riffle beetles), Gyrinidae (water beetles), Heptageniidae (mayflies), Hydropsychidae (caddisflies), Leptoceridae (caddisflies), Libellulidae, Naucoridae (saucer bugs), Notonectidae (saucer bugs), Simuliidae (black flies), Teloganodidae (mayflies), Thiaridae (trumpet snails) and Tricorythidae (mayflies) (Woodborne *et al.* 2012, Myburgh 2016, 2019, Kaiser 2019).

Research questions and predictions

The following research questions (and their associated predictions) were addressed:

1. How does air temperature affect water temperature in the lower Olifants River? It is predicted that air temperature will be an important driver of water temperature (Morrill *et al*. 2005, Rivers-Moore *et al*. 2005, Santiago *et al*. 2017);

2. How will future air temperatures affect water temperature in the lower Olifants River, and can this be simulated? It is predicted that water temperature will rise with rising air temperatures, and can be simulated using Generalised Circulation Models and a simple regression model (Morrill *et al*. 2005, Rivers-Moore *et al*. 2005, Santiago *et al*. 2017);

3. Do future water temperatures exceed thermal maxima of aquatic fauna in the lower Olifants River? It is predicted that there may be fish or macroinvertebrates within the river that have low thermal tolerances and will be vulnerable to climate change (Comte & Olden 2017, Till *et al*. 2019);

4. What are the effects of species losses on the trophic cascade in the lower Olifants River? It is predicted that the loss of vulnerable species will negatively affect the food web of the river (Hogg *et al*. 1995, Petchey 2000, Friberg *et al*. 2009);

5. Are there top-down or bottom-up effects due to losses of taxa within the lower Olifants River? It is predicted that there will be cascading effects due to any potential loss of species, especially of top predators (Petchey *et al*. 1999, Petchey 2000); and

6. Are there species that will occupy open niches, including potential invasive species in the lower Olifants River? It is predicted that there will be invasion potential for non-native or extralimital species should there be open niches available (Rahel & Olden 2008, Moyle *et al*. 2013, Segurado *et al*. 2016, Záhorská 2016, Rolls *et al*. 2017).

Research hypotheses

The following research hypotheses were tested in the four data chapters in this study:

Hypothesis 1 (Chapter 2):
Null hypothesis (H_o): Temperature in the Olifants River is driven by many variables and is too computationally complex to provide reasonable, biologically relevant predictions of water temperature; and
Alternative hypothesis (H_a): Water temperature of the Olifants River is closely linked to air temperature of the region and this relationship can be validated using statistical modelling.

Hypothesis 2 (Chapter 3):
H_o: Climate change and associated rise in air temperature will have no effect on the Olifants River; and
H_a: Climate change will fundamentally alter the temperature regime of the Olifants River, and this can be observed in future projections of water temperature.

Hypothesis 3 (Chapter 4):
H_o: Climate change will have no effect on the thermal niches of fauna in the Olifants River; and
H_a: Climate change-induced variation in water temperature will exceed thermal maxima of aquatic organisms and cause extinctions and mass die-offs of species within the Olifants River.

Hypothesis 4 (Chapter 5):
H_o: Climate change will not affect the trophic structure within the Olifants River; and
H_a: The warming of water will lead to extinctions within the Olifants system and disruptions in its trophic interdependencies.

Study approach

The first part of the study investigated the relationship between air and water temperature by evaluating whether the water temperature of the Olifants River is closely linked to the air temperature of the region and if this relationship can be validated using statistical modelling in order to forecast water temperature from air temperature. This was followed by evaluating whether climate change will fundamentally alter the temperature regime of the Olifants River, and if this can be observed in future projections of water temperature by using the statistical model from the first part of the study through the predictions of air temperature to forecast water temperature for 2100 CE. The next part of the study investigated the thermal limits (CT_{max}) data of aquatic fauna (fish and macroinvertebrates) in the lower Olifants River to assess whether climate change-induced variation in water temperature predicted in the preceding part of the study will exceed the thermal maxima of these organisms for them to be vulnerable and potentially leading to mass die-offs and their extinctions. The final part of the study used the CT_{max} data from the preceding part of the study and SIA to investigate whether there will be: 1) Either top-down or bottom-up effects of the potential loss of vulnerable species (especially top predators) on the trophic cascade leading to negative effects on the food web of the river; 2) Potential invasions of non-native or extralimital species should there be open niches available for them to occupy; and 3) Extinctions and disruptions in trophic interdependencies due to the effects of climate change.

Thesis outline

This thesis comprises five chapters, a General introduction (Chapter 1), four data chapters (Chapters 2, 3, 4 and 5), and a General discussion (Chapter 6). Chapter 1 provides an overview of climate change and its impacts on freshwater systems and associated fauna. Chapter 2 investigated the relationship between air temperature and water temperature. Chapter 3 made predictions on future water temperature under climate change scenarios. Chapter 4 evaluated the effects of climate change on the thermal limits of freshwater fauna. Chapter 5 focused on the effects of climate change on trophic cascades. Chapter 6 concludes the study with a General discussion highlighting the overall findings of the four data chapters.

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Chapter 2

Modelling water temperature in the lower Olifants River and the implications for climate change

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Abstract

Freshwater systems in southern Africa are under threat of climate change, not only from altered flow regimes as rainfall patterns change, but also from biologically significant increases in water temperature. Statistical models can predict water temperatures from air temperatures, and air temperatures may rise by up to 7° C by 2100. Statistical water temperature models require less data input than physical models, which is particularly useful in data-deficient regions. This study validates a statistical water temperature model in the lower Olifants River, South Africa, and verifies its spatial applicability in the upper Klaserie River. Monthly and daily temporal scale calibrations and validations were conducted. The results show that simulated water temperatures in all cases closely mimicked those of the observed data for both temporal resolutions and across sites (NSE > 0.75 for the Olifants River and NSE > 0.8 for the Klaserie). Overall, the model performed better at a monthly than a daily scale, while generally under-estimating from the observed (indicated by negative PBIAS values). The statistical models can be used to predict water temperature variance using air temperature and this can have implications for future climate projections and the effects climate change will have on aquatic species.

Keywords

Climate change, freshwater rivers, statistical models, water temperature, modelling

Introduction

Freshwater systems face compound effects of direct anthropogenic disturbances and climate change, making them among the most vulnerable ecosystems (Kaufman 1992, Dudgeon *et al*. 2006, Woodward *et al*. 2010b, Liu *et al*. 2015, Comte & Olden 2017). Climate change and the consequential rising of water temperatures has had many adverse effects on freshwater fish communities including disrupting trophic inter-dependencies, changing phenology, losses in species richness and diversity, mass mortality events, and extinctions (Petchey *et al*. 1999, Petchey 2000, Jeppesen *et al*. 2010, Comte & Olden 2017, Kuczynski *et al*. 2017, Till *et al*. 2019). In subtropical southern Africa, warming is predicted to occur at more than double that of the global rate, and annual-average near-surface temperatures are predicted to rise by 6° C by 2100 (Engelbrecht *et al*. 2015). The intergovernmental panel on climate change (IPCC) released a sixth assessment report under the RCP8.5 scenario to predict future temperature changes, and a mean air temperature rise of 4-7°C is anticipated, while the maximum air temperatures are predicted to rise by 4-8 °C in southern Africa by the end of the century (Gutiérrez *et al*. 2021). This is compounded with the forecast of up to 40% less summer rainfall in southern Africa (Engelbrecht *et al*., 2011). Higher temperatures and lower rainfall, in conjunction with an increase in associated extreme weather events, along with increasing demand for fresh water from a growing human population is a concern for the persistence of freshwater ecosystems and their associated fauna (Engelbrecht *et al*. 2015, IPCC 2021). For example, freshwater fish inhabit the upper limits of their thermal tolerance and will not be able to move or evolve fast enough to track climate change therefore the effects of rising temperatures will be detrimental to these taxa (Comte & Olden 2017).

Forecasts of water temperature in freshwater rivers and streams have assimilated physical, statistical, and ensemble water temperature models (Marce & Armengol 2008, Rivers-Moore *et al*. 2008a, Yearsley 2009, 2012, Brennan 2015, Ouellet-Proulx *et al*. 2017). An example of a physical model is the semi-Lagrangian River Basin Model (RIC) developed by Yearsley (2009) to solve time-dependant equations for the thermal energy budget in rivers. It can model climate change in rivers and integrate a macro-scale hydraulic model called variable infiltration capacity (VIC) (Yearsley 2012). The RIC and VIC models require large amounts of data and many parameters that include solar and long-wavelength radiation, humidity, soil type, elevation, land cover, precipitation and various river channel parameters, making them data-intensive and constrained by model parameter availability (Yearsley 2009, 2012, Brennan 2015). Statistical water temperature models use variables such as air temperature to estimate current and/or future water temperatures. Although both linear and non-linear regression models have been developed in the pursuit of modelling water temperature using air temperature (Smith 1981, Mohseni *et al*. 1998), linear models are said to be more accurate and produce a better fit (Morrill *et al*. 2005). These types of statistical models require less data input than physical models and are easier to execute (Brennan 2015).

The aim of this study is to use statistical models based on historical data to calibrate and validate water temperature models in the lower Olifants River, South Africa. The lower Olifants River is a higher order river that runs through South Africa’s largest national park, the Kruger Nation Park (KNP), and supplies water to both South Africa and Mozambique (Roux & Nel 2013). Southern African rivers have unique thermal and morphological characteristics and the use of statistical models developed on northern-hemisphere rivers is problematic (Rivers-Moore *et al*. 2005). We follow the framework of a statistical linear regression model developed by Rivers-Moore *et al*. (2008), which has been used to simulate water temperature in four other freshwater rivers in South Africa. The framework uses four options, with varying parameters: 1) air temperature parameters only, 2) air temperature parameters and flow, 3) air temperature parameters and relative humidity, and 4) air temperature parameters, flow, and relative humidity. The previous applications of this approach found that air temperature had the most significant influence, and that flow and relative humidity reduced model accuracy (Rivers-Moore *et al*. 2008a). We will be validating the model using a second river within the Olifants River basin; the upper Klaserie River. This site is at a higher altitude and observed data are predicted to be lower than that of the Olifants River. We aim to test whether the statistical model is equal in efficiency on the Olifants and Klaserie Rivers and predict that the simulated outputs will be similar for both rivers.

Materials and Methods

Hourly air temperature data was obtained from weather stations of the South African Weather Service (SAWS) at Phalaborwa (station number 0681266E6, -23.94 31.17), Hoedspruit (0638081_1, -24.35 31.05), and Giyani (0724318_9, -23.31 30.68), in Limpopo Province, South Africa (Figure 2.1). Hourly water temperature data was collected from a depth of ~1 m in the Olifants River at Mamba Weir (24°3’59.86” S, 31°14’33.6” E, Figure 2.1) from 7 August 2015 to 6 February 2020 using an Aqua TROLL 200 logger (In-Situ Inc., Fort Collins, Colorado, USA). To further validate the model, data from a second river, the upper Klaserie River (24°35’16.46” S, 30°52’48.80” E, Figure 2.1) within the Olifants River system was used. Hourly water temperature data was collected just above the river bed using a HOBO pendant temperature logger (Onset Computer Corporation, Cape Cod, Massachusetts, USA).

Calibrating the model

The air temperature data from the Hoedspruit weather station were primarily used and supplemented by data from Phalaborwa and Giyani. Mean daily, mean monthly, minimum monthly, and minimum daily temperatures were calculated. The general regression model from Rivers-Moore *et al*. (2008) based on correlations between minimum and average air temperatures and the average water temperature (Equation 2.1) was adapted for this study:

$$WT_{max} = \left(AT_{avg} * a\right) + \left(AT_{min} * b\right) + c \qquad \text{[Equation 2.1]}$$

where WT_{max} = maximum water temperature,
AT_{avg} = mean air temperature,
AT_{min} = minimum air temperature,
a = mean air temperature coefficient,
b = minimum air temperature coefficient, and
c = regression constant.

Both monthly and daily datasets were calibrated using August 2015 to November 2017 and validated using December 2017 to February 2020 water temperature data from Mamba Weir. Periods without observed data were deleted to create the best model fit. The parameters were deduced by keeping b and c constant while changing the value of a, and then repeating this process with b and c. Parameter a relates mean air temperature to mean water temperature while b reduces the effects of high diurnal air temperatures (minimum and maximum) on WT_{max}. The set of constants were chosen based on the appearance of the hydrothermograph, the calculated residuals (i.e., the difference between simulated and observed water temperature) and the highest Nash-Sutcliffe efficiency (NSE) that represents an indicator of how well the observed *versus* the simulated data fit the 1:1 line (Nash & Sutcliffe 1970).

Model evaluation statistics

The ~~s~~tatistical analyses of Moriasi *et al*. (2007) were used in addition to the hydrothermographs to evaluate the model performance. These statistical analyses included: the NSE (Equation 2.2); the coefficient of determination (R^2) showing the degree of variance between the simulated and observed datasets and ranges between 0 and 1 (Equation 2.3); the percentage bias (PBIAS) which measures the average likelihood for the simulated data to be higher or lower than the observed data (Equation 2.4); the root mean square error (RMSE; Equation 2.5) which is used to calculate the observations standard deviation ratio (RSR; Equation 2.6) and combines error index statistics and scaling factors by standardizing the RMSE using the standard deviation of the observed data as follows:

$$NSE = 1 - \frac{\sum_{\mathrm{i=1}}^{\mathrm{n}}\left(\mathrm{Y_{obs,i}} - \mathrm{Y_{sim,i}}\right)^2}{\sum_{\mathrm{i=1}}^{\mathrm{n}}\left(\mathrm{Y_{obs,i}} - \mathrm{Y_{obs,mean}}\right)^2} \quad [Equation\ 2.2];$$

$$R^2 = \left(\frac{\sum_{i=1}^{n}\left(Y_{obs,i} - Y_{obs,mean}\right)\left(Y_{sim,i} - Y_{sim,mean}\right)^2}{(\sum_{i=1}^{n}\left(Y_{obs,i} - Y_{obs,mean}\right)^2\big)^{0.5})(\sum_{i=1}^{n}\left(Y_{sim,i} - Y_{sim,mean}\right)^2\big)^{0.5}}\right)^2 \quad [Equation\ 2.3];$$

$$PBIAS = \frac{\sum_{\mathrm{i=1}}^{\mathrm{n}}\left(\mathrm{Y_{obs,i}} - \mathrm{Y_{sim,i}}\right)\times 100}{\sum_{\mathrm{i=1}}^{\mathrm{n}}\left(\mathrm{Y_{obs,i}}\right)} \quad [Equation\ 2.4];$$

$$RMSE = \sqrt{\frac{\sum_{i=1}^{n}\left(Y_{sim,i} - Y_{obs,i}\right)^2}{n-4}} \quad [Equation\ 2.5];$$

$$RSR = \frac{\mathrm{RMSE}}{\mathrm{STDEV_{obs}}} = \frac{\sqrt{\sum_{i=1}^{n}\left(Y_{obs,i} - Y_{sim,i}\right)^2}}{\sqrt{\sum_{i=1}^{n}\left(Y_{obs,i} - Y_{mean}\right)^2}} \quad [Equation\ 2.6]$$

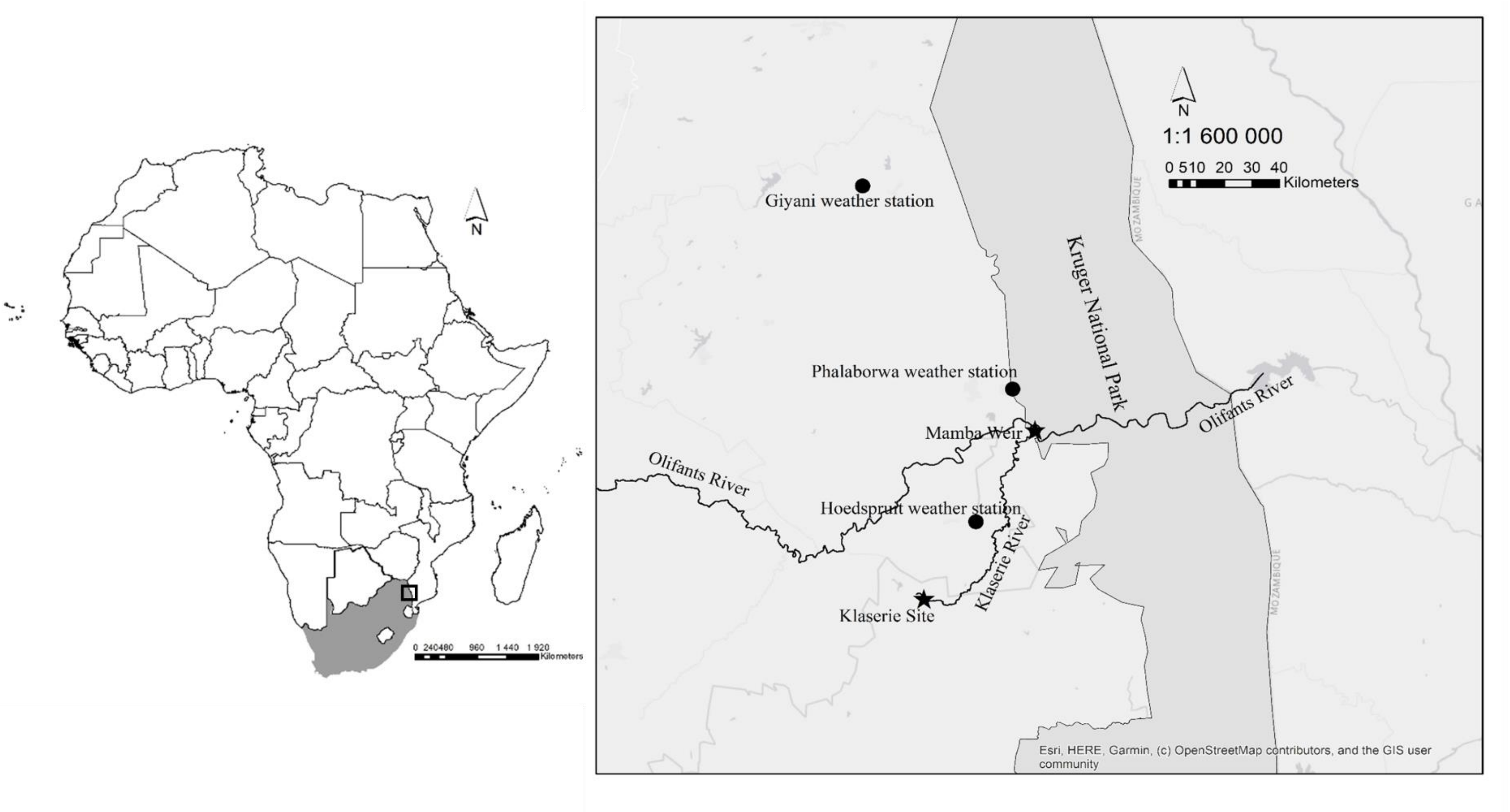

Figure 2.1: Map of study site (with an insert of Africa highlighting South Africa) showing Mamba Weir in the lower Olifants River in Kruger National Park, Limpopo Province; the Klaserie site in the upper Klaserie River, Mpumalanga Province; and three weather stations (Hoedspruit, Phalaborwa, and Giyani), across Limpopo Province and where air temperature measurements were taken for the study.

where Y_{obs} = the observed temperature,

Y_{sim} = the simulated temperature,

$Y_{obs,mean}$ = the mean of observed data for the constituent being evaluated,

$Y_{sim,mean}$ = the mean of the simulated data for the constituent being evaluated,

and n = the total number of observations

Results

Hydrothermographs were generated for calibration and validation data for daily and monthly timescales for Mamba Weir (Figure2.2 A-D) using Equation 2.1 and the following constants: a = 0.900 b = 0.132, and c = 1.600, and for daily and monthly timescales for Klaserie River (Figure2.2 A-B) using the model Equation 2.1 that generated the following constants: a = 0.600 b = 0.132, and c = 1.700.

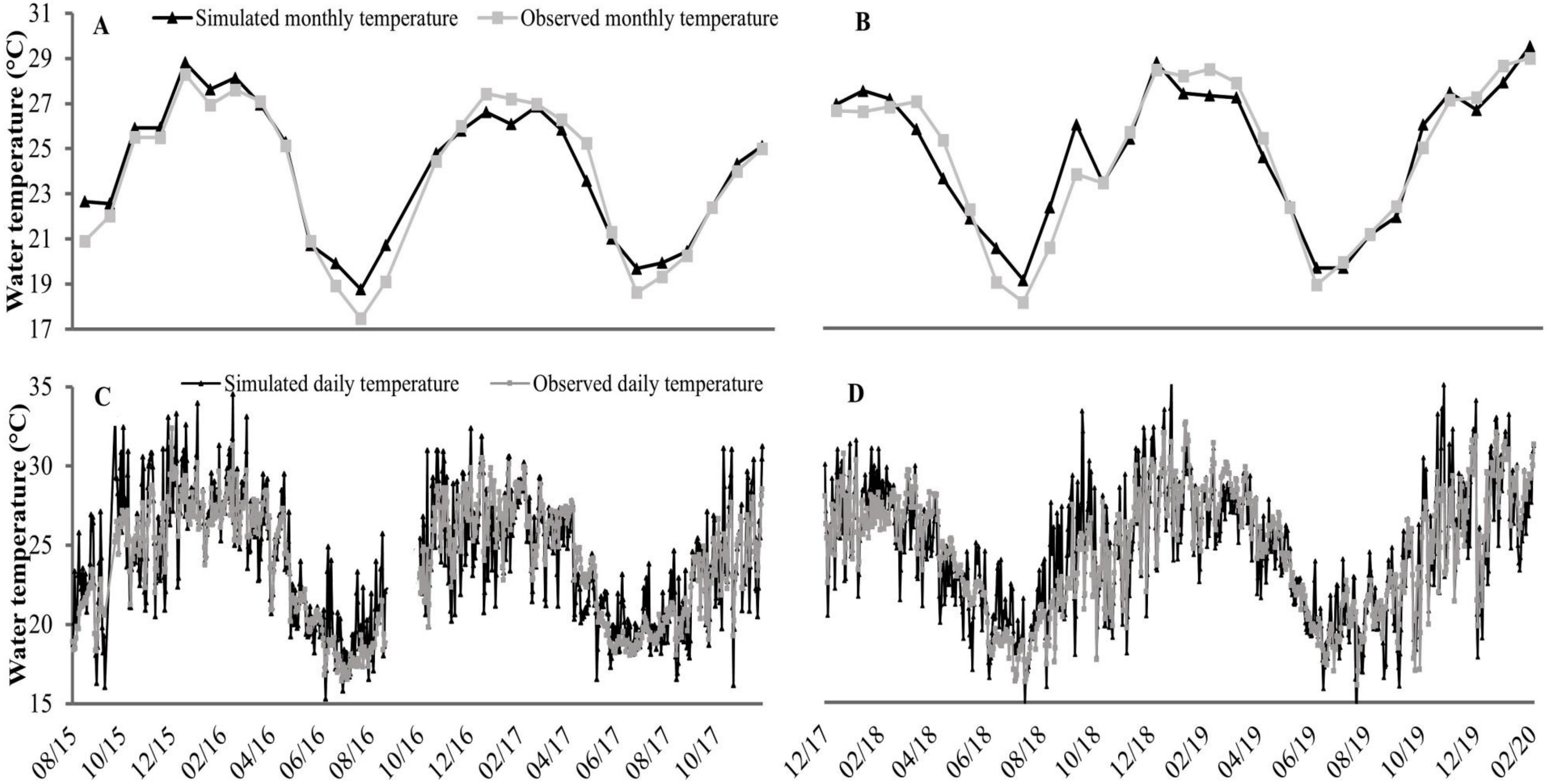

Figure 2.2: Hydrothermographs of: Monthly model calibration (**A**) and daily model calibration (**C**) for August 2015 to November 2017, and monthly model validation (**B**) and daily model validation (**D**) for December 2017 to February 2020 for both simulated (shown in black) and observed (shown in grey) water temperatures for Mamba Weir, Olifants River, South Africa. The gap in **C** is due to 13 days of missing observational data during September 2016.

Figure 2.2A shows the calibration hydrothermograph for Mamba Weir using monthly mean water temperature from August 2015 to November 2017. The mean observed water temperature was 23.70 ± 3.32° C, while the mean simulated water temperature was 23.95 ± 2.96° C. Both observed and simulated hydrographs produce a strong seasonal water temperature pattern (Figure 2.2A). The model evaluation statistics performed for each model (Table 2.1) show that the residuals for monthly mean water temperature from August 2015 to November 2017 are on average 0.25 ± 0.77 °C. The NSE and R^2 are *very good* at 0.94 and 0.95 respectively (Table 2.1). PBIAS is -1.04% (Table 2.1) indicating simulated data is on average below that of the observed, which can also be seen in the Figure 2.2A. The RMSE and RSR values are low at 0.79 and 0.24 respectively (Table 2.1).

Table 2.1: Evaluation statistics for calibration and validation models of monthly and daily water temperatures at Mamba Weir. Statistics shown are Nash-Sutcliffe efficiency (NSE), the coefficient of determination (R^2), the percentage bias (PBIAS), the root mean square error (RMSE) and the observations standard deviation ratio (RSR).

Model	**Model evaluation statistics**						
	n	NSE	R^2	PBIAS	RMSE	RSR	Residuals
Mamba Weir							
Monthly Calibration	27	0.94	0.95	-1.04	0.79	0.24	0.25 ± 0.77
Monthly Validation	27	0.92	0.92	-0.30	0.93	0.28	0.07 ± 0.95
Daily Calibration	796	0.76	0.80	-1.05	1.77	0.49	0.03 ± 1.75
Daily Validation	794	0.78	0.80	-0.17	1.75	0.47	0.04 ± 1.75
Klaserie River							
Monthly	23	0.95	0.96	-1.18	0.59	0.21	0.19 ± 0.57
Daily	592	0.81	0.83	-2.05	1.27	0.44	0.32 ± 1.23

Figure 2.2B shows the hydrothermograph for Mamba Weir using monthly mean and simulated water temperatures for the validation period December 2017 to February 2020. Mean observed water temperature was 24.68 ± 3.38° C, while mean simulated water temperature was 24.75 ± 3.09° C. As expected, both observed and simulated hydrographs produce a strong

seasonal pattern in water temperature with higher temperatures during summer than winter. The model evaluation statistics (Table 2.1) show that the residuals for monthly mean and simulated water temperatures for the validation period December 2017 to February 2020 are low, averaging 0.07 ± 0.95° C (Table 2.1). The simulated temperature is higher than the observed during winter and lower than the observed during summer months indicating some underestimation of the extremes, however, the PBIAS is very low at -0.30%, indicating that the simulated is closely linked to the observed (Table 2.1). The NSE and R^2 are both high at 0.92 and 0.92, respectively, while the RSR is low at 0.28 (Table 2.1).

Figure 2.2C shows the hydrothermographs for average daily observed temperatures and calibration temperatures for Mamba Weir from 7 August 2015 to 3 December 2017. Average observed temperature was 23.77 ± 3.63° C, while the average simulated daily temperature was 24.01 ± 3.87° C. The model evaluation statistics (Table 2.1) for the average daily observed and calibration temperatures for Mamba Weir from 7 August 2015 to 3 December 2017 show that the residuals are on average 0.03 ± 1.75° C. The NSE and R^2 for the monthly calibration are lower than that of the monthly at 0.76 and 0.80, respectively, however, differences are extremely marginal (Table 2.1). PBIAS is -1.05% (Table 2.1) indicating again that simulated data is on average below that of the observed data and the RSR is low at 0.49.

Figure 2.2D shows the hydrothermographs for average daily observed temperatures and simulated temperatures for Mamba Weir for the validation period 4 December 2017 to 6 February 2020. Average observed temperature was 24.53 ± 3.76 °C while average simulated daily temperature was 24.57 ± 3.90° C. The model evaluation statistics (Table 2.1) for the average daily observed temperatures and simulated temperatures for Mamba Weir for the validation period 4 December 2017 to 6 February 2020 show that the residuals were low (0.04 ± 1.75° C). As with the monthly time-step, the graphic representation of the simulated and observed water temperatures are very similar, which is also supported by a low PBIAS -0.17%. There is more variation in daily temperatures of both the simulated and observed temperatures between October and January. Once again, the NSE and R^2 are slightly lower than the monthly time-step at 0.78 and 0.80, respectively, while RSR remains relatively low at 0.47 (Table 2.1).

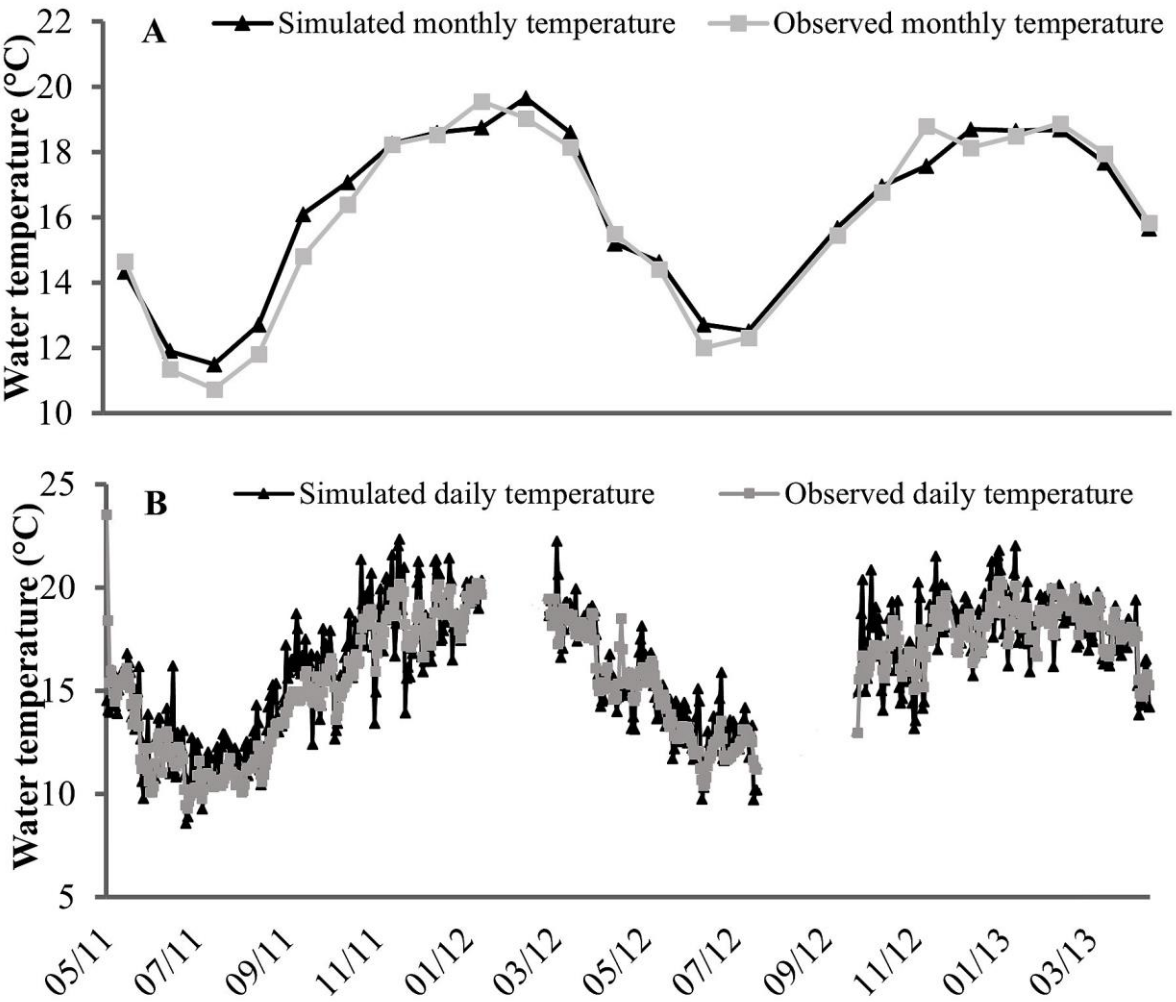

Figure 2.3: Hydrothermographs of: Monthly model (**A**) and daily model (**B**) for March 2011 to April 2013, both simulated (shown in black) and observed (shown in grey) water temperatures for Klaserie River, South Africa. The gaps in **B** are due to periods of missing observational data.

Figure 2.3A shows the hydrothermograph for Klaserie River using monthly mean water temperature from March 2011 to April 2013. The mean observed water temperature was 16.00 ± 2.80° C, while the mean simulated water temperature was 16.18 ± 2.56° C. Both observed and simulated hydrographs produced a strong seasonal water temperature pattern. The residuals for monthly mean water temperature are on average 0.19 ± 0.57° C (Table 2.1). The NSE and R^2 are *very good* at 0.95 and 0.96, respectively (Table 2.1). PBIAS is -1.18% (Table 2.1) indicating simulated data plots below that of the observed, which can also be seen in the Figure 2.3A. The RMSE and RSR values are low at 0.59 and 0.21, respectively (Table 2.1).

Figure 2.3B shows the hydrothermograph for Klaserie River using daily mean water temperature from March 2011 to April 2013. The mean observed water temperature was 16.09 ± 2.95° C, while the mean simulated water temperature was 15.76 ± 2.92° C. Both observed and simulated hydrographs produced a strong seasonal water temperature pattern. The residuals for monthly mean water temperature are on average 0.32 ± 1.23° C (Table 2.1). The NSE and R^2 are 0.81 and 0.83, respectively (Table 2.1). PBIAS is -2.05% (Table 2.1) indicating simulated data is lower that of the observed, which can also be seen in the Figure 2.3A. The RSR value is low at 0.44 (Table 2.1).

Discussion

The model predicts water temperature variance based on air temperature with a degree of accuracy in the seasonal and diurnal time frames that is biologically relevant, for both the Mamba Wier and the upper Klaserie sites. The NSE is one of the most widely used statistic for validating water models, and many studies have found that NSE values of ≥ 0.6 are described as *satisfactory* while values ≥ 0.75 are *very good* (Gupta *et al*. 1999, Motovilov *et al*. 1999, Singh *et al*. 2005, Jones *et al*. 2013, Bello *et al*. 2017, Santiago *et al*. 2017, Olabanji *et al*. 2020). The NSE determines how closely the observed and the simulated data fit the 1:1 line and, similarly, the R^2 measures variance between observed and simulated which indicates the fit of the model (Moriasi *et al*. 2007). Models such as the Hydrological Simulation Program FORTRAN (HSPF) had NSE values of between 0.6 and 0.7 for analysis of monthly water temperatures in tropical rivers of southern Malaysia (Morrill *et al*. 2005). This model produced NSE and R^2 values above 0.75 for both monthly and daily models, with monthly models performing slightly better.

The PBIAS is a measure of how often the simulated data differs from the observed data, and further has the ability to show whether the model is under- or over- estimating simulating temperatures (Gupta *et al*. 1999, Moriasi *et al*. 2007). The results show that the simulations for both daily and monthly datasets resemble the observed data closely. The PBIAS indicates that the model tends to slightly under-estimate the water temperatures, with this being more prevalent during the daily timestep likely due to the model being unable to predict anomalous hot days. Our results estimate between -0.17% and -2% where *satisfactory* PBIAS values lie between ± 25% and *very good* values between ±10%, therefore, our values are almost negligibly under-estimating from the observed (Moriasi *et al*. 2007). RSR incorporates the benefits of error index statistics and includes a scaling/normalization factor (Moriasi *et al*. 2007). A perfect model would have an RSR value of 0 indicating no residual variation and therefore low RSR and RMSE values are considered good indicators of model performance (Singh *et al*. 2005). The RSR values produced are all lower than 0.5 and are considered *very good* (Moriasi *et al*. 2007).

The model had a tendency to under-estimate water temperatures, which must be considered in future projections. While this under-estimation is very small, a conservative model for climate predictions is preferred over a more aggressive model that will give a false representation of the increase in water temperatures. This may be due to the model being over-simplistic and not incorporating variables such as river channel metrics, geology, groundwater metrics, vegetation, humidity, solar radiation, evaporation, and various other parameters that may drive or influence water temperature (Rivers-Moore *et al*. 2005, Dallas & Rivers-Moore 2019). However, it has been demonstrated that the addition of variables such as relative humidity, rainfall, and flow in a multiple regression model had little effect on the model, and in the case of flow, even reducing accuracy (Rivers-Moore *et al*. 2008). While, conversely, air temperature has been shown to be the most important driver of water temperature, and in the absence of additional data, produces a simplistic model that accurately predicts water temperatures (Rivers-Moore *et al*. 2005).

This study also demonstrates that, in the case of the two study river sites, a simple statistical model can simulate water temperature variance with accuracy and precision that is biologically relevant. This is particularly important in data-deficient regions, such as in Africa, where climate change studies on freshwater systems are important given the alarming rising of air temperature (Engelbrecht *et al*. 2015). An important caveat is that, while air temperature is the only input variable to the models, the parameterisation differs between sites. This means that air temperature alone does not account universally for water temperature, and models need site-specific calibration. This shortcoming is perhaps relevant at large spatial or temporal scales, but a critical implication of the models is that diurnal and season *variances* (as opposed to absolute values) in water temperature are strongly driven by variance in air temperature. As a first order approximation of the impact of long-term water temperature drivers, such as climate change, on river biology, this is very useful, and but for a universally applicable solution it is necessary to invoke more complex models.

Complex models, such as multiple regression models, typically have more input parameters, making them susceptible to equifinality. Equifinality is common in hydrological models, and in this context refers to the likelihood that multiple sets of parameters will produce equivalent models (Beven 2001, 2006, Hreiche *et al*. 2002, Lu *et al*. 2009). There are sources of equifinality in models, namely over-parameterization and errors in the observational or input data of parameters (Beven 2006, Lu *et al*. 2009). Errors in observational data not only cause equifinality, but also reduce accuracy (Lu *et al*. 2009), with the more parameters added, the more observer bias or collection errors being added to the model.

The study prediction that the model would successfully simulate water temperature for both rivers was correct, despite the difference in river order and altitude. While Rivers-Moore *et al*., (2008) and this study support the use of simple, linear statistical models in simulating water temperatures using air temperature within South African rivers, this can be applied in other river study sites where there is a deficit of data. Future studies should focus on the effects of global climate change on freshwater systems and include both the physical and biological impacts. Currently, studies on invertebrates and fish within South African rivers are showing the potential impacts of rising water temperatures on species thermal tolerances (Dallas & Ross-Gillespie 2015, Dallas & Rivers-Moore 2018, Shelton *et al*. 2018a, 2018b), however, modelling future water temperature of these rivers is vital towards the understanding of when these impacts will take effect and guide mitigation actions.

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Chapter 3

Climate change in South African rivers: A case study on the Olifants River

Abstract

Freshwater systems are considered one of the most endangered ecosystems, with anthropogenic climate change causing ecological and economic impacts. Increased air temperatures will translate into the warming of rivers, and at the same time climate change will alter flow regimes, increase evaporation, and increase stochastic events. This study used validated statistical water temperature models that predict average water temperatures (WT_{avg}) from air temperature to project monthly and daily WT_{avg} from 2021 to 2100 CE in the heavily polluted and over-abstracted Olifants River, Kruger National Park (KNP), Limpopo Province, South Africa under the "*business as usual*" Representative Concentration Pathway (RCP) 8.5 scenario. The results from 16 General Circulation Models showed that monthly WT_{avg} is likely to increase by 3.7° C and showed summer months reaching up to 34-35° C by 2100 CE. The daily results showed a similar increase of 3.9° C by 2100 CE, with some extreme days reaching 42-44° C. These results support similar research conducted within the Olifants River Basin and add to the limited knowledge of freshwater climate change, especially in Africa. Rising water temperatures in the Olifants River will ultimately change the thermal and physical landscape of the river and this forecast highlights the need for further research on the potential detrimental consequences on freshwater biota such as local extinctions. This study represents part of a much broader novel approach that combines a mechanistic approach of statistical modelling of future water temperature, with the assessment of thermal tolerances and trophic cascades (using stable isotope analysis (SIA)) to evaluate faunal changes at both population and community levels, with implications in similarly heavily polluted and over-abstracted data-deficient river systems globally.

Keywords

Climate change, freshwater rivers, water/air temperatures, General Circulation Models (GCMs), Representative Concentration Pathway (RCP) 8.5 scenario

Introduction

Freshwater systems are under severe pressure from direct and indirect anthropogenic effects that include pollution, habitat degradation, exotic species introductions, over-exploitation, mining, flow regime and river morphology modifications, and climate change (Kaufman 1992, Lodge *et al*. 1998, Collares-Pereira & Cowx 2004, Dudgeon *et al*. 2006, Moss *et al*. 2010a, Woodward *et al*. 2010a, Friberg *et al*. 2011, Griffiths *et al*. 2015, Pont *et al*. 2015, Comte & Olden 2017). These disturbances are occurring in conjunction with each other, and the compounding impacts on freshwater systems can be devastating (Liu *et al*. 2015, Jackson *et al*. 2016, Segurado *et al*. 2016). For example, alterations to the hydrology or river-associated habitats can cause successful species invasions due to changes in habitat and water quality (Ross *et al*. 2001), and land degradation such as deforestation due to mining and agriculture can cause severe flooding during extreme weather events caused by climate change (Douglas *et al*. 2008, Jackson *et al*. 2016).

Due to these cumulative impacts, along with the exponential rise in human population and demand for resources, freshwater systems are considered one of the most vulnerable ecosystems (Millennium Ecosystem Assessment 2005, Moss *et al*. 2010a). Freshwater systems have provided humans with ecosystem services, arguably more than any other ecosystem, but because of their linear nature any transverse or longitudinal disturbance causes cascading effects both up and downstream (Vári *et al*. 2022). In the Danube Basin in Europe, a hydroelectric power plant built to supply energy to south-eastern Europe has modified freshwater ecosystems to such a degree that there are changes in flow regime, habitat and disconnecting floodplains, and with an increase in energy demand due to population growth, these are likely to be exacerbated (ICPDR 2013, Borgwardt *et al*. 2019).

Freshwater systems are particularly vulnerable to the effects of climate change as the systems are fragmented and isolated within terrestrial landscapes, are exposed to anthropogenic stressors, and are also disproportionately exploited considering they cover only 0.8% of the Earth’s surface area (Woodward *et al*. 2010b). The effects of climate change on freshwater systems are not only translated into a rise in water temperature, but also changes in nutrient load and primary productivity, acidification, salinization, eutrophication, flow regime, and more frequent extreme weather events such as flooding (Heino *et al*. 2009, Mohammed *et al*. 2017, Rolls *et al*. 2017).

Rivers in the southern African subregion are likely to be more affected by climate change than those in other regions given that it global mean annual average near-surface temperatures are set to increase by 2-3° C by the end of this century, while mean air temperatures are predicted to rise by 4-7° C (Hulme *et al*. 2001, Engelbrecht *et al*. 2015, IPCC 2021), with maximum air temperatures predicted to increase by 4-8° C by 2100 CE (Gutiérrez *et al*. 2021, IPCC 2021) under low mitigation scenarios. Evaporation rates in southern Africa are as high as 65%, which decreases effective rainfall to a region that is already prone to frequent droughts and will experience a decrease in precipitation in future (Chabwela 1994, Darwall *et al*. 2009, Marshall 2011). Projections of annual reference crop evaporation in South Africa show that by 2100 CE there will be increases of 15-20% in the far interior and 20-25% along the western, southern and eastern borders (Schulze 2012). Along with further water extraction, this can lead to altered flow regimes and even to perennial systems becoming intermittent streams, and to intermittent stream drying up (Chabwela 1994, Darwall *et al*. 2009, Marshall 2011). Freshwater biota, such as fishes and macroinvertebrates, rely on a specific flow regime for breeding and survival, and have very specific thermal niches, and disruptions to these parameters are detrimental to the ecology of freshwater systems (Magnuson *et al*. 1979, Comte & Olden 2017, Darwall *et al*. 2018).

The prediction of future water temperature scenarios in South Africa has previously been based on a statistical linear regression model developed by Rivers-Moore *et al*. (2008). The model established that water temperature can be simulated using air temperature. The model also established that the thermal properties of South African rivers may differ from those of other regions, and a linear regression model was developed and tested on rivers in the country (Rivers-Moore *et al*. 2005, 2008a).

The aim of this study was to simulate future water temperatures from 2021 to 2100 CE and to investigate the effects of future air temperatures on the water temperatures in south-eastern Africa based on the Olifants River in the Kruger National Park (KNP), Limpopo Province South Africa under the “*business as usual*” Representative Concentration Pathway

(RCP) 8.5 scenario as a case study. This river is an example of a freshwater system that is already heavily impacted by pollution and over-abstraction (Ashton *et al*. 2001, Ashton & Dabrowski 2011) and is likely to be even more impacted than those in other regions globally. While there have been studies on future climate change scenarios within the Olifants River Basin, many of these studies were conducted on the entire Olifants Basin, not one particular river and, more importantly, did not take into account the change in water temperature but instead were based on air temperature (Singh *et al*. 2005, Olabanji *et al*. 2020). While water and air temperatures provide an important baseline for the present study, a more focused investigation on water temperature within the river is essential for understanding the ecological impacts on freshwater ecosystems.

The KNP is already facing many challenges of water management due to pollution in its rivers from upstream and other anthropogenic disturbances (Riddell *et al*. 2019). The warming of these rivers, along with decreased run-off, decreased precipitation and increased water-use by humans will lead to the loss of habitat and heat stress which subsequently will result in mass die-offs and extinctions of the aquatic fauna, as well as water stress to the animals within KNP that rely on these rivers as water sources. It is predicted that with a rise in air temperature to the end of the century, both average monthly and daily temperatures of the Olifants River will also increase, and this will ultimately have a negative effect on the aquatic fauna of this river. This study forms part of a much broader novel approach that combines a mechanistic approach of statistical modelling of future water temperature (Chapter 2), with the assessments of thermal tolerances (Chapter 4) and trophic cascades (using stable isotope analysis (SIA)) (Chapter 5) to evaluate faunal changes at both population and community levels, with implications in similarly heavily polluted and over-abstracted data-deficient river systems globally.

Materials and Methods

The study site on the Olifants River is located at Mamba Weir (24°3’59.86” S, 31°14’33.6” E) in the KNP, Limpopo Province, South Africa as a case study site (Figure 3.1). The Olifants Basin is ~75 000 km^2, expanding across South Africa and Mozambique (Singh *et al*. 2014). The Olifants River is a perennial river that runs through the KNP which represents the largest protected area in South Africa and contributes immensely to tourism within the region, while supplying water to both South Africa and Mozambique (Roux & Nel 2013, Riddell *et al*. 2019). It represents approximately 6% of South Africa’s gross domestic product (GDP), contributing to industries such as mining, agriculture and commercial forestry (Mccartney & Arranz 2007). Mamba Weir was selected as a case study site as it is located on the lower Olifants River in the KNP as one of the rivers contributing to the ecological integrity and ultimately the biodiversity of the park, and its proximity to Phalaborwa Weather Station (23°55'48.0"S 31°09'00.0"E) for recording air temperature.

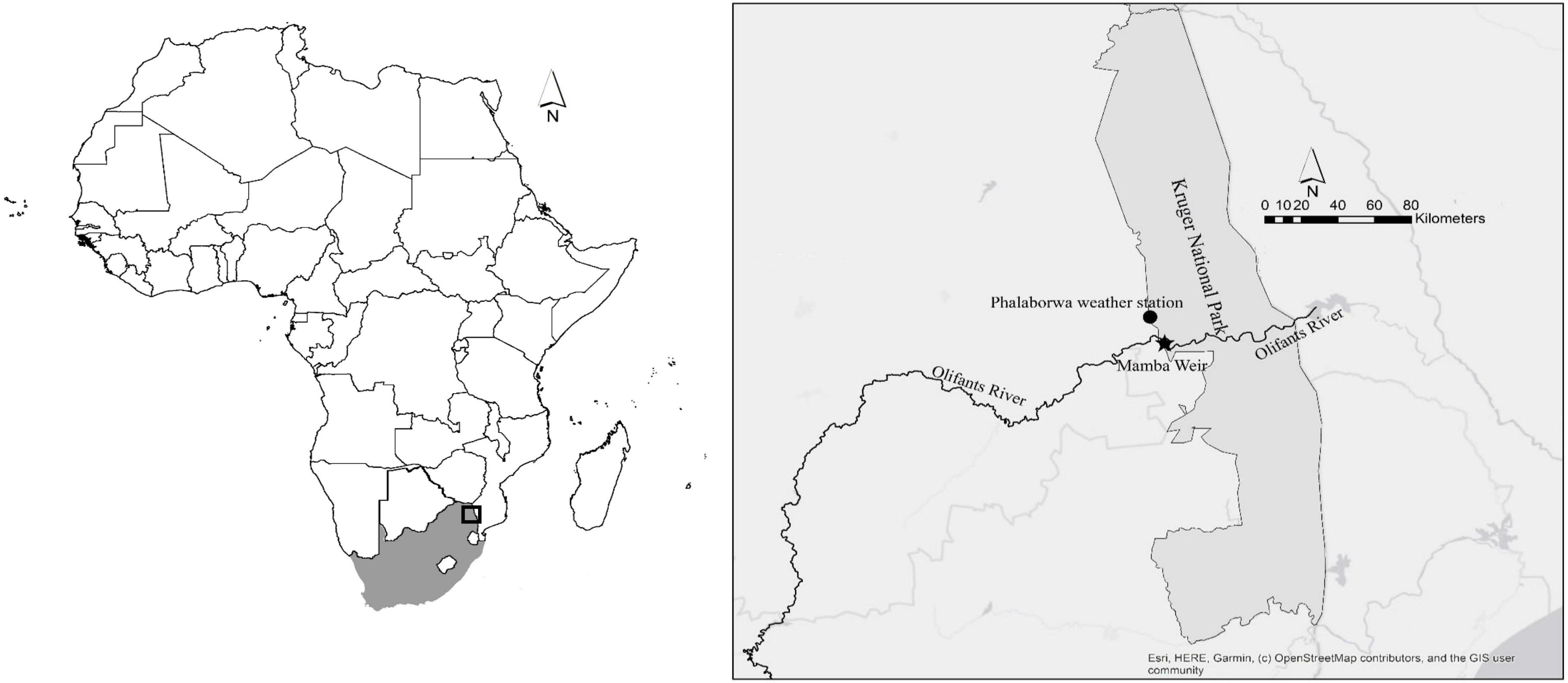

Figure 3.1: Map of the study site (with an insert of Africa highlighting South Africa) showing Mamba Weir in the lower Olifants River in the Kruger National Park (KNP) and Phalaborwa weather station, Limpopo Province, South Africa where air temperature was recorded for the study.

Downscaled localized climate change projections were previously developed for the Olifants River Catchment through a partnership with the Climate Systems Analysis Group (CSAG) for the United States Agency for International Development (USAID): Resilience in the Limpopo Basin Program-Olifants (RESILIM-O) programme implemented by the Association for Water and Rural Development (AWARD) (Clifford Holmes *et al.* 2016, Climate System Analysis Group (CSAG) 2016, Kong *et al*. 2019, Pollard *et al*. 2020b, 2020a). The climate model projections were performed for the Phalaborwa Weather Station and produced down-scaled 25 x 25 km climate projections for 16 General Circulation Models (GCMs)) under the Representative Concentration Pathway (RCP) 8.5 scenario which represents the "*business as usual*" pathway for carbon emission projections in 2100 CE (Moss *et al*., 2010). CSAG used an empirical down-scaling technique, the Self-Organizing Map-based downscaling, which is a statistical approximation of regional scale response based on global scale circulation and historical observed data (Climate System Analysis Group (CSAG) 2016, Kong *et al*. 2019). The climate projections produced air temperature parameters including minimum (AT_{min}) and maximum (AT_{max}) air temperatures from which average daily and average monthly temperatures were calculated.

The general regression model for river water temperature was adapted from Rivers-Moore *et al*. (2008) based on correlations between minimum and average air temperatures, and average water temperature, as shown in Equation 3.1:

$$WT_{max} = \left(AT_{avg} * a\right) + \left(AT_{min} * b\right) + c \qquad [Equation\ 3.1]$$

where WT_{max} = maximum water temperature; AT_{avg} = mean air temperature; AT_{min} = minimum air temperature; a = mean air temperature coefficient; b = minimum air temperature coefficient; c = regression constant.

The constants used were a = 0.900, b = 0.132, and c = 1.600, and the model validated with a Nash-Sutcliffe efficiency (NSE) of 0.92 for the monthly timestep and 0.78 for the daily timestep and had a percentage bias (PBIAS) of -0.3% during the monthly timestep and -0.17% for the daily timestep (Adlam *et al*. 2022).

The validated simple regression model was used, in conjunction with the climate model projections produced by CSAG, to generate predictions of monthly WT_{max} and daily WT_{max} in the Olifants River from 2021 to 2100 for 16 GCMs. Hydrothermographs and box and whisker plots were generated using the WT_{max} projections for both daily and monthly timescales while pairwise *t*- tests were used to test for statistically significant differences in monthly WT_{max} and in daily WT_{max} between 2021 as the beginning of the recording period and 2100 CE as the end of the projected period. Box and whisker plots for the most conservative, least conservative and two other models are shown.

Results

Monthly and daily summary average maximum water temperatures (WT_{avg}) for the 16 GCMs are indicated in Table 3.1, while their generated monthly and daily hydrothermographs are shown in Figures 3.2 and 3.3, respectively, and box and whisker plots for monthly and daily WT_{avg} between 2021 and 2100 are shown in Figures 3.4 and 3.5 respectively, all showing the difference between the beginning of each recording period (2021) and end of the projected period (2100 CE). The results showed an increase in maximum monthly average water temperatures (WT_{avg}) of 3-4° C by the end of the century, while the highest monthly temperature recorded in many models exceeds 33° C (Figures 3.2 and 3.4). The daily WT_{avg} show a similar trend, increasing ~3-4° C by the end of the projected period, with the daily maximum water temperatures reaching up to 44° C (Figures 3.3 and 3.5). Pairwise *t*-tests showed statistically significant differences ($P < 0.01$) in monthly WT_{avg} (Figure 3.4) and daily WT_{avg} (Figure 3.5) in all GCMs indicating that monthly and daily WT_{avg} increases between 2021 and 2100 CE.

Table 3.1: A summary of average maximum water temperatures (WT_{avg}) at monthly and daily timescales for starting and ending temperatures derived from simulated time series from 2021 to 2100 CE for 16 General Circulation Models (GCMs) under the Representative Concentration Pathway (RCP) 8.5 scenario at Mamba Weir, Kruger National Park (KNP), Limpopo Province, South Africa.

Model	Year	Monthly WT_{avg} (°C)	Highest monthly WT_{avg} (°C)	Daily WT_{avg} (°C)	Highest daily WT_{avg} (°C)
bcc-csm1-1	2021	24.2	28.8	28.1	36.7
	2100	25.3	33.30	29.2	41.1
BNU-ESM	2021	24.6	29.3	21.5	32.0
	2100	28.4	34.3	24.9	36.5
CanESM2	2021	25.4	29.2	26.4	36.8
	2100	30.1	34.5	30.9	42.7
CMCC	2021	25.0	29.5	21.7	31.3
	2100	29.9	34.3	26.6	38.1
CNRM-CM5	2021	24.3	29.2	25.2	35.5
	2100	27.3	32.7	28.1	40.3
GFDL-ESM2G	2021	24.9	28.4	26.1	36.1
	2100	28.0	32.8	28.9	42.2
GFDL-ESM2M	2021	25.1	29.4	26.0	36.4
	2100	28.7	34.6	29.6	42.5
HadGEM2-CC	2021	24.9	29.5	25.9	36.4
	2100	29.0	34.4	30.1	41.8
inmcm4	2021	23.1	26.7	23.9	33.0
	2100	26.0	30.5	26.9	38.3
IPSL-CM5A-MR	2021	25.3	29.2	26.3	38.7
	2100	30.3	35.5	31.0	44.3
IPSL-CM5B-LR	2021	24.6	29.3	25.6	36.4
	2100	27.9	33.2	28.9	41.5
MIROC5	2021	24.9	29.9	25.7	36.4
	2100	27.3	32.7	28.1	40.4

MIROC-ESM-CHEM	2021	24.1	29.2	25.0	35.7
	2100	29.3	34.0	30.2	42.0
MIROC-ESM	2021	25.0	29.4	26.0	37.9
	2100	30.2	34.4	31.1	42.6
MPI-ESM-LR	2021	25.0	28.7	26.0	36.4
	2100	28.6	33.7	29.5	41.6
MRI-CGCM3	2021	24.3	28.4	25.3	34.8
	2100	28.4	32.6	29.4	40.9
SUMMARY Averages	2021	24.7	29.0	25.1	35.7
	2100	28.4	33.6	29.0	41.1

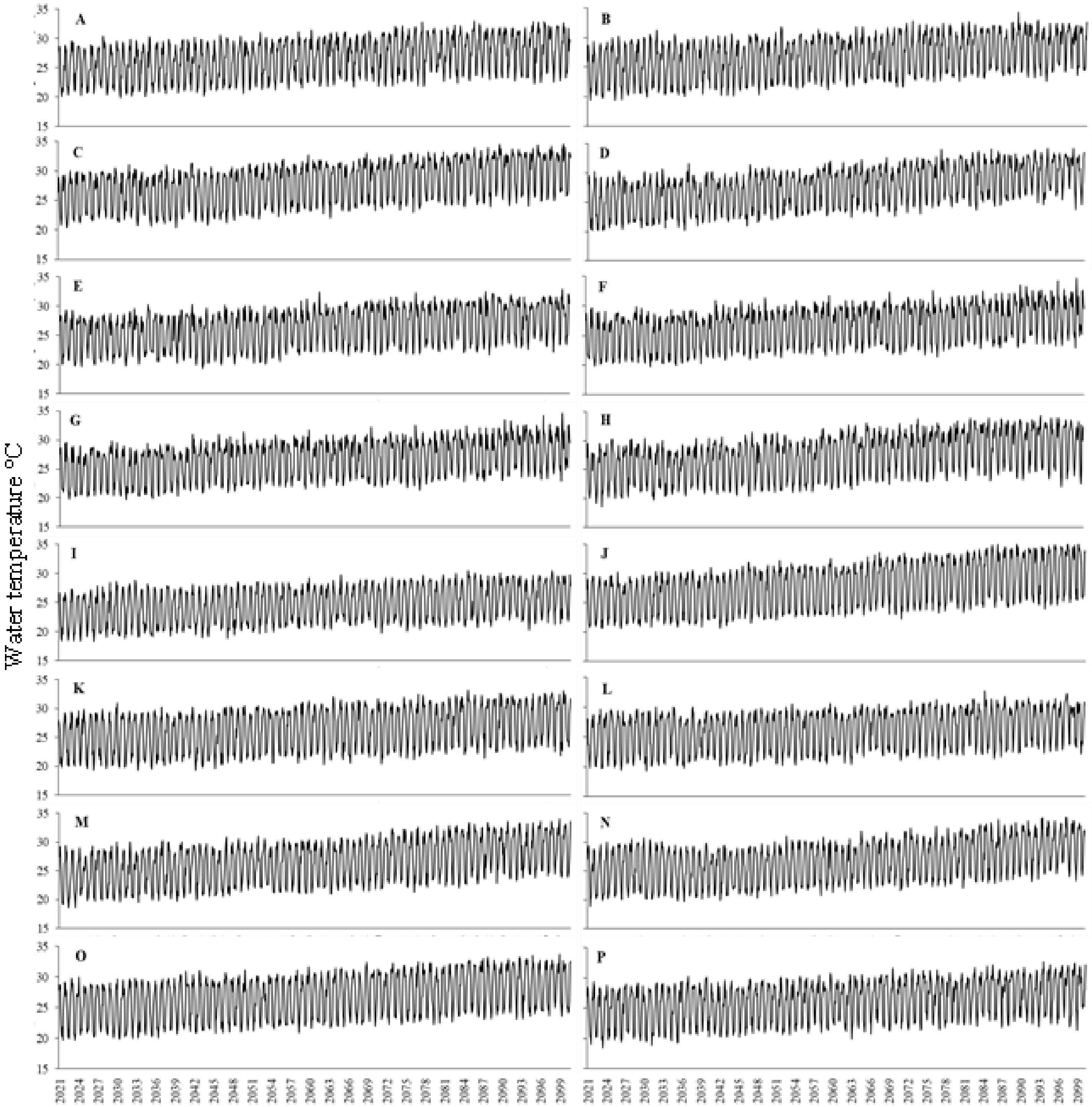

Figure 3.2: Hydrothermographs of monthly maximum water temperature variance projections from 2021 to 2100 CE under the Representative Concentration Pathway (RCP) 8.5 scenario at Mamba Weir, Olifants River, Kruger National Park (KNP), Limpopo Province, South Africa using 16 General Circulation Models (GCMs) as indicated in Table 3.1: **A** = bcc-csm1-1; **B =** BNU-ESM; **C =** CanESM2; **D** = CMCC; **E** = CNRM-CM5; **F =** GFDL-ESM2G; **G =** GFDL-ESM2M; **H** = HadGEM2-CC; **I** = inmcm4; **J** = IPSL-CM5A-MR; **K** = IPSL-CM5B-LR; **L** = MIROC5; **M** = MIROC-ESM-CHEM; **N** = MIROC-ESM; **O** = MPI-ESM-LR; and **P** = MRI-CGCM3.

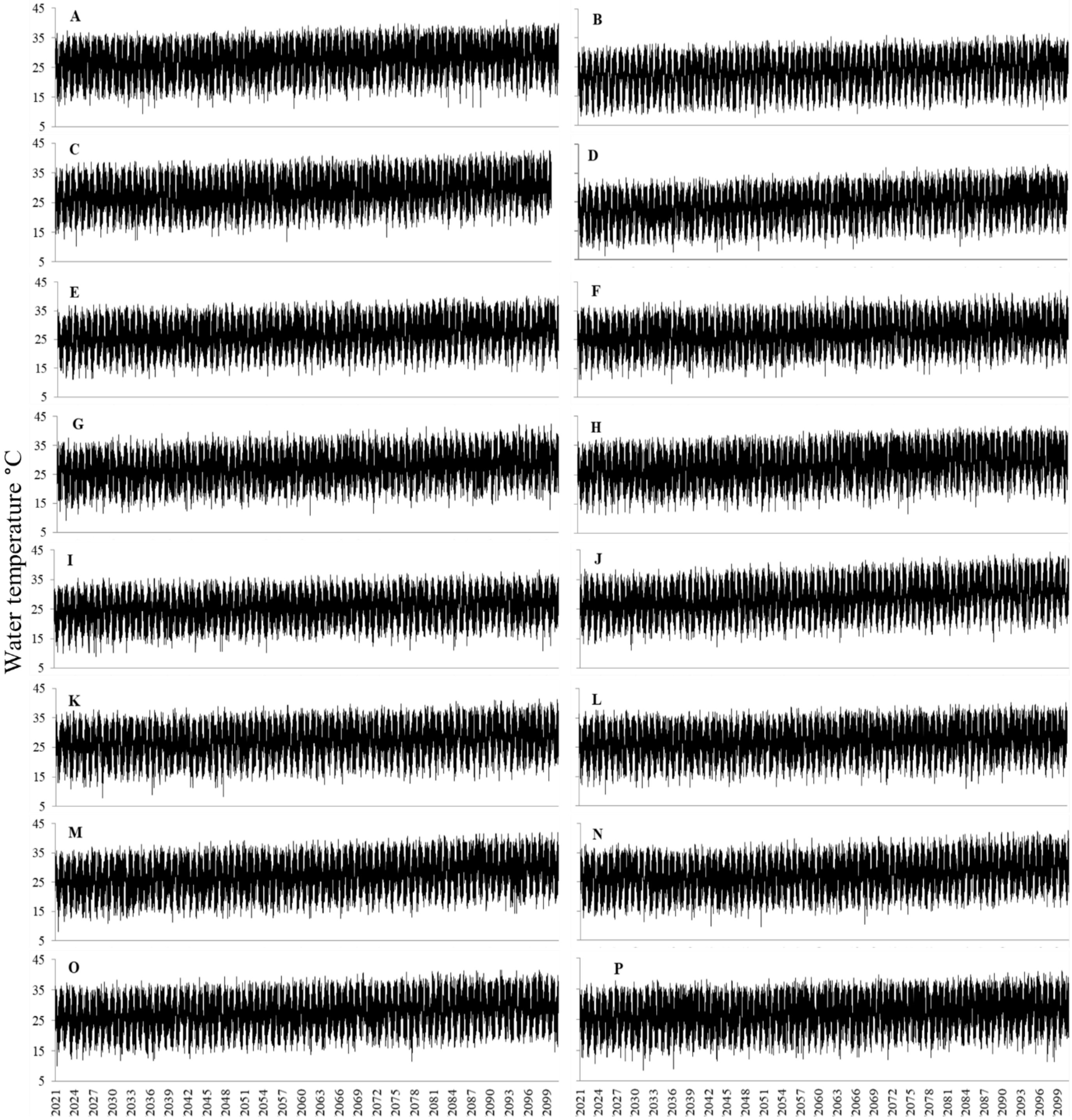

Figure 3.3: Hydrothermographs of daily maximum water temperature variance projections from 2021 to 2100 CE under the Representative Concentration Pathway (RCP) 8.5 scenario at Mamba Weir, Olifants River, Kruger National Park (KNP), Limpopo Province, South Africa using 16 General Circulation Models (GCMs) as indicated in Table 3.1: **A** = bcc-csm1-1; **B** = BNU-ESM; **C** = CanESM2; **D** = CMCC; **E** = CNRM-CM5; **F** = GFDL-ESM2G; **G** = GFDL-ESM2M; **H** = HadGEM2-CC; **I** = inmcm4; **J** = IPSL-CM5A-MR; **K** = IPSL-CM5B-LR; **L** = MIROC5; **M** = MIROC-ESM-CHEM; **N** = MIROC-ESM; **O** = MPI-ESM-LR; and **P** = MRI-CGCM.

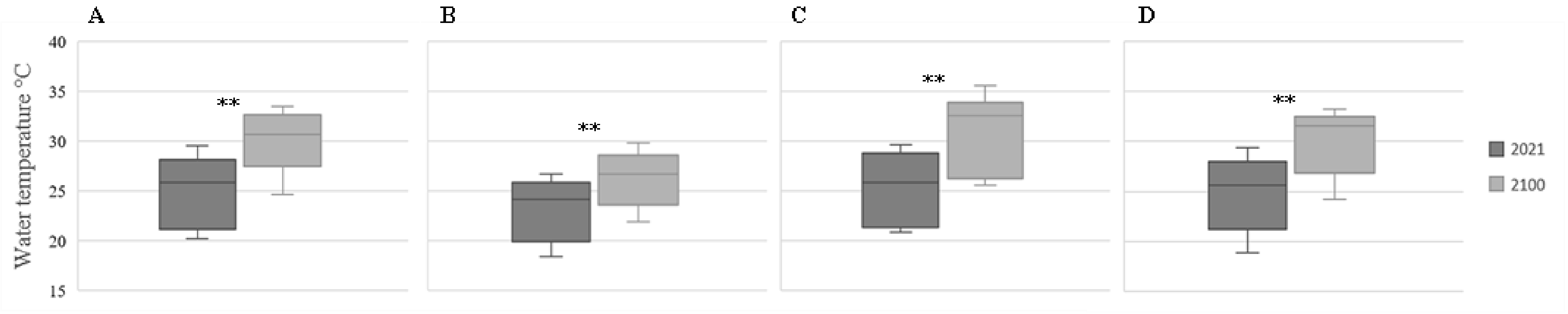

Figure 3.4: Box and whisker plots of monthly water temperature variance projections between 2021 (dark grey) and 2100 (light grey) under the Representative Concentration Pathway (RCP) 8.5 scenario at Mamba Weir, Olifants River, Kruger National Park (KNP), Limpopo Province, South Africa using the following General Circulation Models (GCMs): **A** = CMCC; **B** = inmcm4; **C** = IPSL-CM5A-MR; and **D** = MIROC-ESM. These represent the most conservative, least conservative and two moderate GCMs. ** = $P < 0.01$.

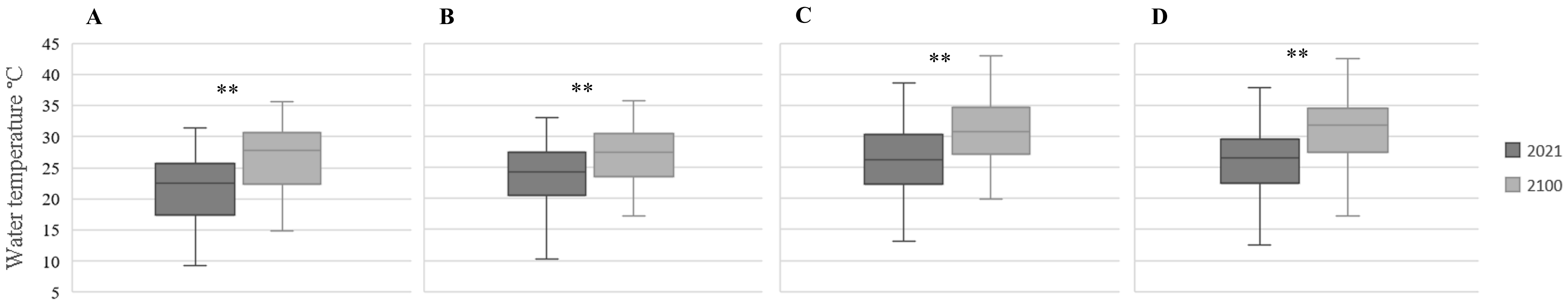

Figure 3.5: Box and whisker plots of daily water temperature variance projections between 2021 (dark grey) and 2100 (light grey) under the Representative Concentration Pathway (RCP) 8.5 scenario at Mamba Weir, Olifants River, Kruger National Park (KNP), Limpopo Province, South Africa using the following General Circulation Models (GCMs): **A** = CMCC; **B** = inmcm4; **C** = IPSL-CM5A-MR; and **D** = MIROC-ESM. These represent the most conservative, least conservative and two moderate GCMs. ** = *P* < 0.01.

The monthly WT_{avg} in 2021 is between 23.1-25.4° C and increases to 25.3-30.3° C by 2100 (Table 3.1), while the highest monthly WT_{avg} increases from 26.7-29.9° C to 30.5-35.5° C by 2100 CE (Table 3.1). The daily timescale shows that between 2021 and 2100 CE, the WT_{avg} increases from 21.5-28.1° C to 24.9-31.1° C among the GCMs. The highest daily WT_{avg} increases from 31.3-38.7° C to 36.5-44.3° C by 2100 CE (Table 3.1).

The averages of the projections from the 16 GCMs show that by 2100 CE, monthly WT_{avg} will increase from 24.7° C to 28.4° C (a 3.7° C increase), while the maximum monthly WT_{avg} will rise from 29° C to 33.6° C (a 4.6° C increase). The daily timescale for air temperature from the 16 GCMs shows a similar trend, with the daily WT_{avg} showing an increase from 25.1° C to 29.0° C to the end of the century (a 3.9° C increase). The maximum WT_{avg} increases from 35.7° C to 41.1° C (a 5.4°C increase). The IPSL-CM5A-MR is shown as the least conservative model for monthly and daily projections (Table 3.1, Figures 3.2J, 3.3J, 3.4C, 3.5C), while the inmcm4 model appears the most conservative (Table 3.1, Figures 3.2I, 3.3I, 3.4B, 3.5B).

Discussion

The simulations in the present study suggest that rising air temperature as a result of climate change will translate into rising water temperature in the Olifants River, with both daily and monthly water temperature variances rising by up to 5° C by 2100 CE. More alarming, monthly water temperatures during summer, rise from 28-29° C in 2021 to 34-35° C by the end of the century while daily temperatures may reach 42-44° C from 36-38° C. These results do not just indicate a large rise in water temperature but allude to the Olifants River undergoing other changes, such as increased evaporative losses and possible changes in flow regime. The river will experience changes in both thermal and physical habitats which has detrimental effects on the survival and breeding of freshwater species which are sensitive to disruptions in flow regime and temperature change (Darwall *et al*. 2009).

Our predictions are similar to those of other studies on the Olifants River Basin. Singh *et al*. (2014) used 10 GCMs to predict air temperatures between the middle-of-century (2046–

2065) and the end-of-century (2081–2100) under two emission scenarios (A2 and B1). The A2 scenario describes a heterogeneous world with a rapidly growing population, while the B1 scenario describes a convergent world with a low population growth (Nakicenovic & Swart 2000). The B1 scenario is broadly comparable to an RCP 6.0 scenario, while the A2 scenario can be compared to an RCP 8.5 scenario (Pachauri & Meyer 2014), which is the scenario that was used in the present study, and therefore its findings can be compared to those of the A2 scenario. Singh *et al*. (2014) predicted that by the end of the century, the mean annual air temperature will increase by 4.6° C, which translates into an increase of 13.6% in potential evapotranspiration (PE). Olabanji *et al*. (2020) used the Water Evaluation and Planning (WEAP) model under the RCP 8.5 scenario and found a mean temperature increase of 1° C between 2010 and 2039, 2° C between 2040 and 2069, and 4° C between 2070 and 2099. The fundemental difference between these studies and the present study is that Singh *et al*. (2005) and Olabanji *et al*. (2020) investigated the entire Olifants Basin rather than a single study site or river, and their projections were based on air temperature rather than on water temperature.

Human-driven climate change will not just impact water temperature, but will most likely translate into a decrease in surface water flow most notably during the dry season and increased water demands for mining, irrigation for agriculture and forestry, and industrial and household use (Mccartney & Arranz 2007). Olabanji *et al*. (2020) reported that the Olifants River Basin will have a 30% decrease in precipitation and a 17% decrease in annual average streamflow. In addition, future scenarios forecast decreased run-off (Singh *et al*. 2014, Engelbrecht *et al*. 2015), suggesting that by the end of the century, unmet water demand could be as high as 80% due to decreased water flow and increased human population and its associated economic activities (Olabanji *et al*. 2020). The Olifants River Basin also relies on groundwater for mining, drinking, agriculture, and to provide thermal buffering in the system (Aston 2000, Shelton *et al*. 2018b). However, the increase in demand for wate due to a growing human population, and consequences of climate change such as chnages in precipitation, land-use and flow rate have altered the rate of groundwater recharge (Nkhonjera 2019). It has been predicted that within the Olifants River Basin, groundwater recharge will decrease by 2100 under RCP4.5 and RCP8.5 scenarios (Nkhonjera 2019), and this is likely to affect thermal buffering in the region.

The Selati River within the lower Olifants catchment is also projected to have increased evaporation and decreased rainfall (Clifford Holmes *et al*. 2016, Climate System Analysis Group (CSAG) 2016). While these findings are bleak, mitigation actions have been taken in the Olifants Basin by the RESILIM-O project (Pollard *et al*. 2020b). This key project run by AWARD identified and responded to three key areas to build the resilience of the river, namely: 1) Reduce climate vulnerability by promoting the adoption of science-based adaptation strategies in priority sub-catchments; 2) Conserved and sustainably managed biodiversity in high-priority ecosystems; and 3) Capacity of stakeholders developed to sustainably manage water resources and biodiversity in priority sub-catchments (Pollard *et al*. 2020b).

While the present study only addresses the effects of climate change on the abiotic factors in the Olifants River, there is a critical need to gain insights into the biotic implications of the warming of the river. For example, Dallas & Rivers-Moore (2012) found that the critical thermal maxima (CT_{max}) of two macroinvertebrate families, the blackflies of the family Simuliidae and the mayflies of the family Baetidae were 31.6° C and 36.7° C, respectively. Given the results of the present study, by the end of the century, the Simuliidae will experience chronic thermal stress (i.e., an impact that will eventually have severe consequences if it occurs often enough and/or at high enough levels) as they will be exposed to long periods above their CT_{max}, and may undergo local extinction events. While the Baetidae may avoid the chronic stress being within the threshold of the maximum monthly temperatures, the family may experience acute stress (i.e., a severe impact over a short duration) as they will be exposed to days above their CT_{max}, and this will likely result in mass die-off events. Although these are only two macroinvertebrate families that will be affected by the rising water temperatures, it is likely that there are many more species, including fishes, other vertebrates and algae that will also be either acutely or chronically affected by climate change. A similar study conducted in Canada on the Fraser River Basin found that summer temperatures during the period 2070-2099 would increase by 1.9° C, exposing salmon to temperatures above 20° C which negatively affects spawning success (Morrison *et al*. 2002). Similarly, a study on the Douro River Basin in Portugal revealed that by 2065, a 2° C increase is to be expected along with a decrease in annual precipitation, which will decrease the distribution of the European eel (*Anguilla anguilla*) and brown trout (*Salmo trutta fario*) (Segurado *et al*. 2016). More alarmingly, a study by Jones *et al*. (2013) across the United States found that there will be a 50% reduction in thermal habitat for coldwater species such as *S. trutta*, which will translate into cumulative economic losses of between $81 million and $6.4 billion by 2100 CE.

Freshwater fauna are predominantly ectotherms, therefore, increases in water temperature will have profound effects on these species (Woodward *et al*. 2010b, Capon *et al*. 2021). Cold water species are vulnerable to extinction and replacement by warmer water species, which also leaves room for biological invasions to occur (Rahel & Olden 2008, Jones *et al*. 2013). Studies have shown that warming can cause up to 40% loss in species richness, with high extinction rates of predators and herbivores (Petchey *et al*. 1999). In addition, the critical thermal maxima (CT_{max}) of fishes will be unable to evolve fast enough to track climate change and increased water temperatures (Comte & Olden 2017). As previously mentioned, southern Africa, including the Olifants River, is predicted to be affected far greater by climate change than the global average (Hulme *et al*. 2001, Engelbrecht *et al*. 2015, IPCC 2021). This likely has more severe implications for the species within these rivers as the consequences of climate change are felt. Given this, and the findings of the present study, it is clear that freshwater ecosystems are threatened at a global scale and further studies are needed on the impacts of the warming of rivers on their aquatic fauna particularly in similarly heavily polluted and over-abstracted data-deficient freshwater systems globally.

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Chapter 4

Thermal tolerance of freshwater fauna in response to climate change: A case scenario based on the Olifants River, South Africa

Abstract

Water temperature influences the fitness, growth and survival of fish and aquatic invertebrates, and some species may be affected by rising water temperature driven by climate change. The case scenario of the heavily polluted and over-abstracted Olifants River, Limpopo Province, South Africa, assesses the effects of future water temperature under the "*business as usual*" Representative Concentration Pathway (RCP) 8.5 scenario on aquatic taxa in a system that is more vulnerable to climate change than most rivers globally. Critical thermal maxima (CT_{max})or thermal tolerances of fishes and invertebrates were compared with maximum monthly and maximum daily water temperature forecast averages for 2100 CE. Future climate change scenario predictions indicated that some fishes and macroinvertebrates will experience chronic (i.e., a cumulative impact that will eventually have severe consequences if it occurs often enough and/or at high enough levels) and acute (i.e., an instantaneous, severe impact over a short duration) stressors. Results showed that 12 fish species and nine macroinvertebrate taxa are vulnerable to the effects of warmer water in the future. This negative climate change impact scenario raises concerns for the future of these taxa, as they are vulnerable to mass die-offs, changes to population structure, local extinction, and biological invasions; a scenario that may have implications for both the individual and community structure in similarly heavily polluted and over-abstracted freshwater systems globally. Fish and macroinvertebrate taxa that provide essential ecosystem services, such as controlling pests and hosts that are responsible for malaria, are under threat. The present study is particularly relevant for fish species in the upper reaches of rivers where movement mitigation of thermal stress is limited. This study represents part of a broader novel approach that combines the assessment of thermal tolerances, with a mechanistic approach of statistical modelling of future water temperature and the evaluation of trophic cascades (using stable isotope analysis (SIA)) to evaluate faunal changes at both population and community levels, with implications in similarly heavily polluted and over-abstracted data-deficient river systems globally.

Keywords

Climate change, freshwater rivers, thermal tolerance, thermal niche, critical thermal maxima (CT_{max}), acute/chronic stressors

Introduction

Water temperature is arguably the most important abiotic factor influencing aquatic biology and it is therefore important to understand the thermal tolerances of aquatic fauna (Dallas 2008). Vannote & Sweeney (1980) conceived the optimum thermal regime, theorising that organisms have a range of temperatures optimal for growth, reproduction, metabolism, emergence, distribution and fitness and conditions outside that range will have negative effects on the individual and community structure. Temperatures above or below the organism's optimum temperature would result in smaller body- sized individuals and a lower reproductive rate, therefore, the optimum thermal regime is to have both optimal adult body size and fecundity (Vannote & Sweeney 1980). Aquatic organisms are mostly ectotherms and changes in water temperature have profound effects on metabolic rates and foraging behaviour (Woodward *et al*. 2010b). The Intergovernmental Panel on Climate Change (IPCC) temperature forecasting models have shown alarming rates of increase in southern Africa, with mean air temperatures predicted to rise by up to 7° C and maximum air temperatures predicted to increase up to 8° C by 2100 CE (Gutiérrez *et al*. 2021, IPCC 2021). This will increase water temperature in rivers and lead to changes in precipitation, primary productivity, eutrophication, and flow regimes (Heino *et al*. 2009, IPCC 2021).

Aquatic fauna are categorized into different thermal classes: (1) cold stenotherms; organisms with narrow tolerance ranges in cold (arctic) regions, (2) warm stenotherms; organisms with narrow tolerance ranges in warm regions in the tropics, and (3) eurytherms; organisms with wide thermal tolerance ranges (Dallas 2008). Chronic thermal stress occurs at temperatures that have severe consequences if they occur often enough, while acute thermal stress occurs at higher temperatures that have a severe impact on an organism over a short duration (Borgwardt *et al*. 2019). Controlled laboratory experiments have been used to determine thermal tolerances for selected species by increasing or decreasing water temperature at a constant rate until an endpoint is reached, which may be sub-lethal or lethal

(Dallas 2008). Lethal effects have been determined by exposing individuals to a range of temperatures until a median lethal time until death (LT_{50}) is reached (Dallas 2008). The LT_{50} represents the duration resulting in 50% mortality at a specific temperature (Dallas 2008).

The Critical Thermal Method (CTM) is commonly used to find the critical thermal maxima (CT_{max}) or critical thermal minima (CT_{min}) (Cowles & Bogert 1944, Becker & Genoway 1979). A sample of organisms can be acclimated to a specific temperature and the temperature is increased or decreased at a constant linear rate until a predefined sub-lethal endpoint (Becker & Genoway 1979). These critical thermal endpoints are the ''*arithmetic mean of collected thermal points at which locomotor activity becomes disorganized to the point at which the organism loses its ability to escape conditions that will promptly lead to its death*" (Beitinger *et al*. 2000). In aquatic invertebrates, this endpoint is considered as the inability of benthic organisms to remain attached to a substrate or increased movement, followed by immobility and no response when stimulated (Dallas & Rivers-Moore 2012). In fish, it manifests as a loss of equilibrium, muscle spasms, flaring of operculars, or non-reaction to prodding (Beitinger *et al*. 2000). *In situ* measurements from field observations can also provide useful insights into species' preferred thermal environment (Beitinger *et al*. 2000). However, these data may not provide an upper or lower thermal tolerance of a species because individuals will avoid extreme temperatures (Beitinger *et al*. 2000).

Fish segregate using behavioural mechanisms into habitats with preferred temperatures and these are referred to their thermal niche (Magnuson *et al*. 1979). There are typically three categories of freshwater fishes according to their thermal niche preference and these include: 1) Warm-water (27-31° C); 2) Cool-water (21-25° C); and 3) Cold-water (11-15° C) species (Magnuson *et al*. 1979, Heino *et al*. 2009). Where freshwater fish species occur near their upper thermal limits, they are vulnerable to the effects of climate change (Comte & Olden 2017). This is because freshwater fish occupy limited latitudinal ranges and therefore their CT_{max} corresponds closely with temperatures that they experience (Comte & Olden 2017). When faced with stressors, fish employ primary responses that are neuroendocrine in nature, including the release of corticosteroid hormones, and secondary responses including eliciting changes in plasma, metabolites, and heat shock proteins (Barton 2002).

Acute stressors (i.e., an instantaneous, severe impact over a short duration) cause physiological and behavioural responses, but this is ineffective where the stressor is prolonged or cannot be avoided (Alfonso *et al*. 2021). Chronic stressors (i.e., a cumulative impact that will eventually have severe consequences if it occurs often enough and/or at high enough levels) cause long-term negative effects on the immune system, growth and reproduction of fishes, and is ultimately detrimental to fish populations by causing mortalities (Alfonso *et al*. 2021, Islam *et al*. 2022). Both acute and chronic exposure to warm water temperatures can alter the cardiac rhythm and coping ability of fishes to further stressors (Alfonso *et al*. 2021). One reason for mass mortality events, or mass die-offs, is when a rise in water temperature exceeds the thermal tolerance of the fishes within the system, and they are unable to employ behavioural mechanisms to escape (Till *et al*. 2019). A study by Till *et al*. (2019) in the United States predicted that annual summer die- off events will double to ~10 per year by 2050 CE, and then increase to ~17 die- off events per year by 2100 CE. These mass-mortality events result in changes in community structure, with a decrease in body size and invasion by warm water species (Till *et al*. 2019).

The Olifants River, Kruger National Park (KNP), Limpopo Province, South Africa, is a freshwater system that is heavily impacted by pollution and over-abstraction (Ashton *et al*. 2001, Ashton & Dabrowski 2011). These factors compounded with high evaporation rates and high projected temperatures in the southern African subregion will result in this river being even more impacted by climate change than most rivers globally (Schulze 2012). We use predictions of future water temperature variances for this river to assess the potential impacts of climate change on freshwater fish and macroinvertebrates under the "*business as usual*" Representative Concentration Pathway (RCP) 8.5 scenario. The CT_{max} of these organisms will be compared to daily and monthly water temperature forecasts for 2100 CE to predict whether they will be at risk due to the thermal impacts of climate change. We predict that these organisms will be at risk to chronic and/or acute heat exposure and will therefore be vulnerable, and that this reflects analogous processes that many occur in many similarly polluted and over-abstracted rivers globally. This study represents part of a broader novel approach that combines the assessment of thermal tolerances, with a mechanistic approach of statistical modelling of future water temperature (Chapters 2 and 3) and the evaluation of trophic cascades (using stable isotope analysis (SIA)) (Chapter 5) to evaluate faunal changes at both population and community levels, with implications in similarly heavily polluted and over-abstracted data-deficient river systems globally.

Materials and Methods

The study site was Mamba Weir on the Olifants River, Limpopo Province, South Africa (24°3'59.86" S, 31°14'33.6" E; Chapters 2 and 3). Mamba Weir is in KNP which is a major protected area within South Africa, and the river affects the associated ecology within the park which contributes immensely to tourism in the country (Mccartney & Arranz 2007). Air temperature projections were obtained from 16 General Circulation Models (GCMs) under the Representative Concentration Pathway (RCP) 8.5 scenario which represents the "*business as usual*" pathway for carbon emission projections in 2100 CE (Moss *et al*., 2010). A general regression model for river water temperature was adapted from Rivers-Moore *et al*. (2008) to obtain future water temperatures (Chapter 2, Adlam *et al*. 2022). These data showed that the averages of the projections to 2100 CE for maximum monthly and maximum daily WT_{avg} were 33.6° C and 41.1° C, respectively (Chapter 3). Therefore, 33.6° C was taken as a threshold of chronic heat stress, as taxa that have thermal tolerances below this temperature are likely to experience long periods, ie at least one month, above their thermal maximum temperatures. A 41.1° C threshold was used as an indicator of acute heat stress, as taxa that have thermal tolerances below this temperature will experience short periods of time above their thermal maximum temperatures. Capture records for freshwater fish and macroinvertebrates within the lower Olifants River were compiled from various studies (Woodborne *et al*. 2012, Myburgh 2016, 2019, Kaiser 2019).

Thermal tolerance temperatures of fish and macroinvertebrates were sourced from the peer-reviewed published literature. Thermal tolerance data were sourced for fish species sharp tooth catfish (*Clarias gariepinus*), Mozambique tilapia (*Oreochromis mossambicus*), redbreast bream (*Coptodon rendalli*), tank goby (*Glossogobius giuris*) and southern mouthbrooder (*Pseudocrenilabrus philander*),and for macroinvertebrate families Baetidae (mayflies), Coenagrionidae (damselflies), Elmidae (riffle beetles), Gyrinidae (water beetles), Heptageniidae (mayflies), Hydropsychidae (caddisflies), Leptoceridae (caddisflies), Libellulidae (skimmers), Naucoridae (saucer bugs), Notonectidae (saucer bugs), Simuliidae (black flies), Teloganodidae (mayflies), Thiaridae (trumpet snails) and Tricorythidae (mayflies), from various published sources. With the exception of Thiaridae (*Tarebia granifera*), adult macroinvertebrates were sampled in rivers in the south- western Cape Province, South Africa and acclimated to 17° C before experimentation began (Dallas & Rivers-Moore 2012). At least 10 individuals from each family, often from different species, were collected and the mean CT_{max} of the individuals was calculated and used for this study (Dallas & Rivers-Moore 2012).

While Nile tilapia (*O. niloticus*) and silver carp (*Hypophthalmichthys molitrix*) have not currently been detected in the river, (*H. molitrix* has been detected in the downstream impoundment Massingir Dam), they were included as examples of a potentially invasive species. Four *Labeo* species the redeye labeo (*Labeo cylindricus*), leaden labeo (*L. molybdinus*), purple labeo (*L. congoro*) and rednose labeo, (*L. rosae*) are found within the Olifants River, but their thermal tolerance temperature data were not available from the published literature. The thermal tolerance temperature of *L. rohita* (a *Labeo* species found in the tropical and sub-tropical zones of Asia and used extensively in aquaculture) was used as a surrogate indicator of the thermal tolerance of the four Olifants River *Labeo* species.

Where no thermal tolerance temperature data were available, thermal preference temperature data were used from published literature, and in the case where these were also unavailable, water temperature recorded at which species were captured during a published study, was used as a proxy for thermal preference data. Thermal preference temperatures and capture data were converted to lethal limit temperature (used as an upper thermal limit temperature) by using the equation (Equation 4.1) from Jobling (1981) that shows the relationship between thermal preference and lethal temperatures in fishes as follows:

$$a = 0.66b + 16.43 \text{ [Equation 4.1]}$$

where a is the lethal temperature and b is the preferred temperature.

Thermal preference data for fish species sawfin rock catlet (*Chiloglanis paratus*), threespot barb (*Enteromius trimaculatus*), bowstripe barb (*E. viviparus*), *Micralestes acutidens*, tigerfish (*Hydrocynus vittatus*), lowveld largescale yellowfish (*Labeobarbus marequensis*) were sourced from published literature.

Results

The upper thermal tolerance temperatures of fish species and macroinvertebrate families found in the lower Olifants River are presented in Tables 4.1 and Table 4.2. *Oreochromis niloticus* and *H. molitrix* were added as potential invasive species.

Table 4.1: Thermal tolerance of fish species in the Olifants River, Kruger National Park (KNP), Limpopo Province, South Africa and their data sources. Values with an asterisk (*) indicate upper thermal limits calculated from thermal preference data.

Fish species	References	Upper thermal tolerance (° C)
Chiloglanis paratus	(Froese & Pauly 2023)	32.3*
Clarias gariepinus	(Babiker 1984)	50.0
Coptodon rendalli	(Whitfield & Blaber 1976)	41.9
Enteromius trimaculatus	(Froese & Pauly 2023)	33.6*
Enteromius viviparus	(Froese & Pauly 2023)	32.3*
Glossogobius giuris	(Koniyo & Juliana 2018)	33.0
Hydrocynus vittatus	(Thorstad *et al*. 2002, Roux *et al*. 2018)	36.6*
Hypophthalmichthys molitrix	(Opuszynski *et al*. 1989, Tripathi 1989)	46.5
Labeo cylindricus, L. molybdinus, L. congoro, L. rosae (from *L. rohita*)	(Chatterjee *et al*. 2004)	40.2
Labeobarbus marequensis	(Froese & Pauly 2023)	34.3*
Micralestes acutidens	(Froese & Pauly 2023)	33.6*
Oreochromis mossambicus	(King & Sardella 2017), (Whitfield & Blaber 1976)	44.5
Oreochromis niloticus	(Whitfield & Blaber 1976)	42.0
Pseudocrenilabrus philander	(Loiselle 1982, Polling *et al*. 1995)	35.6

Table 4.2: Thermal tolerance temperatures of macroinvertebrate species and families in the Olifants River, Kruger National Park (KNP), Limpopo Province, South Africa and their data sources.

Macroinvertebrate species and families	**Reference**	**Upper thermal tolerance (° C)**
Baetidae	(Dallas & Rivers-Moore 2012)	34.6
Coenagrionidae	(Dallas & Rivers-Moore 2012)	40.8
Elmidae	(Dallas & Rivers-Moore 2012)	39.0
Gyrinidae	(Dallas & Rivers-Moore 2012)	42.3
Heptageniidae	(Dallas & Rivers-Moore 2012)	32.5
Hydropsychidae	(Dallas & Rivers-Moore 2012)	32.9
Leptoceridae	(Dallas & Rivers-Moore 2012)	32.0
Libellulidae	(Dallas & Rivers-Moore 2012)	42.2
Naucoridae	(Dallas & Rivers-Moore 2012)	39.9
Notonectidae	(Dallas & Rivers-Moore 2012)	40.7
Simuliidae	(Dallas & Rivers-Moore 2012)	30.3
Teloganodidae	(Dallas & Rivers-Moore 2012)	32.9
Thiaridae (*Tarebia granifera*)	(Miranda *et al*. 2010)	47.5
Tricorythidae	(Dallas & Rivers-Moore 2012)	38.5

Fish and macroinvertebrates that were least susceptible to rising water temperature are the species *C. gariepinus*, *O. mossambicus*, *O. niloticus*, *C. rendalli*, *H. molitrix* and *T. granifera*, and the macroinvertebrate families Gyrinidae and Libellulidae, as they have thermal tolerances above both the acute and chronic exposure thresholds (Figures 4.1, 4.2). Organisms with thermal tolerances lower than 41.1° C are likely to experience temperatures above their thermal maximum temperatures and are vulnerable to acute heat stressors. These include the fish species *Labeo* spp, *P. philander, H. vittatus, L. marequensis, E. trimaculatus, E. viviparus, M. acutidens*, and *G. giuris* (Figure 4.1) and the macroinvertebrate families Simuliidae, Elmidae, Baetidae, Coenagrionidae, Leptoceridae, Naucoridae, Notonectidae, Tricorythidae, Teloganodidae, Heptageniidae, and Hydropsychidae (Figure 4.2). Species that have thermal tolerance temperatures below 33.6° C and are vulnerable to chronic stress, and are therefore, likely to experience long periods above their thermal maximum temperatures, are the fish species *C. paratus*, *E. trimaculatus*, *E. viviparus*, *M. acutidens*, and *G. giuris* (Figure 4.1) and the macroinvertebrate families Simuliidae, Leptoceridae, Teloganodidae, Hydropsychidae and Heptageniidae (Figure 4.2). The fish *E. trimaculatus* and *M. acutidens* have thermal tolerances of 33.6° C, which is on the bordeline of the threshold, and were conservatively allocated to the chronic stress category.

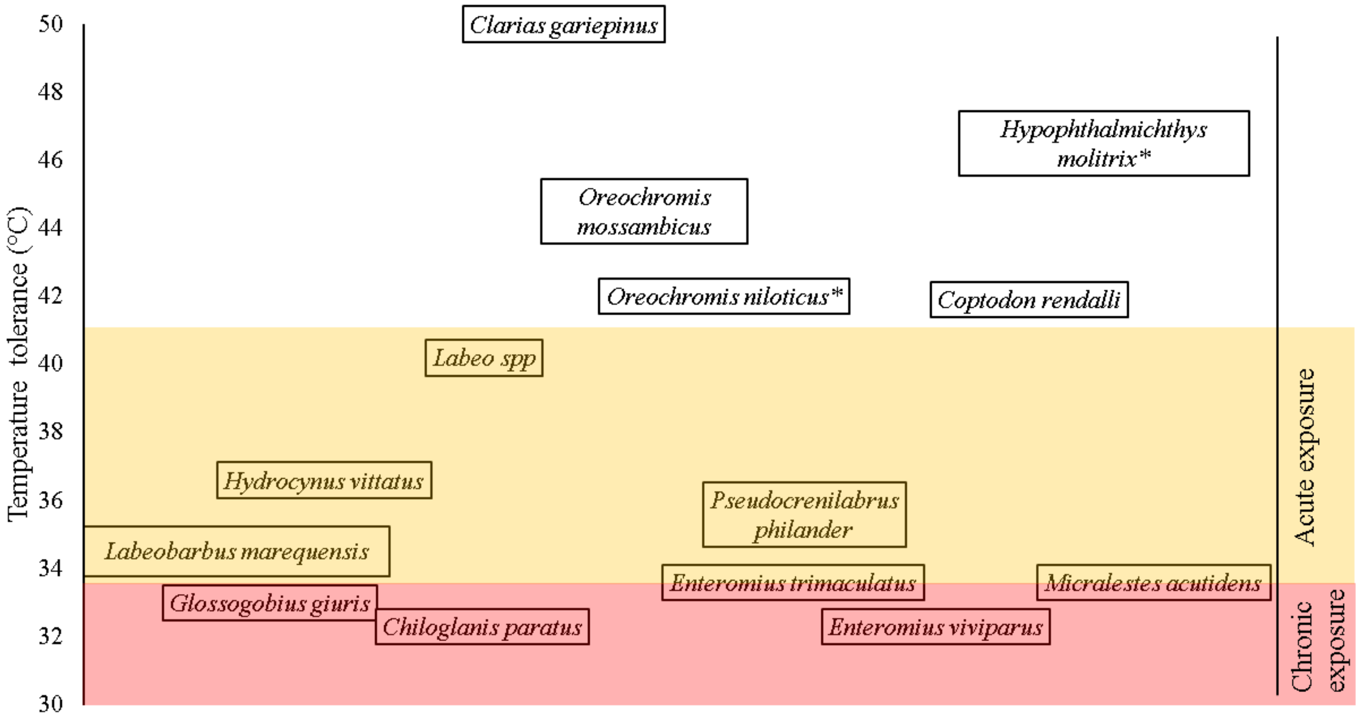

Figure 4.1: Temperature tolerances of fish species in the Olifants River, Kruger National Park (KNP), Limpopo Province, South Africa, and their exposure to acute (orange) and chronic (red) heat exposure in water temperature projections for 2100 CE. Taxa marked with an asterisk (*) are potential invasive species.

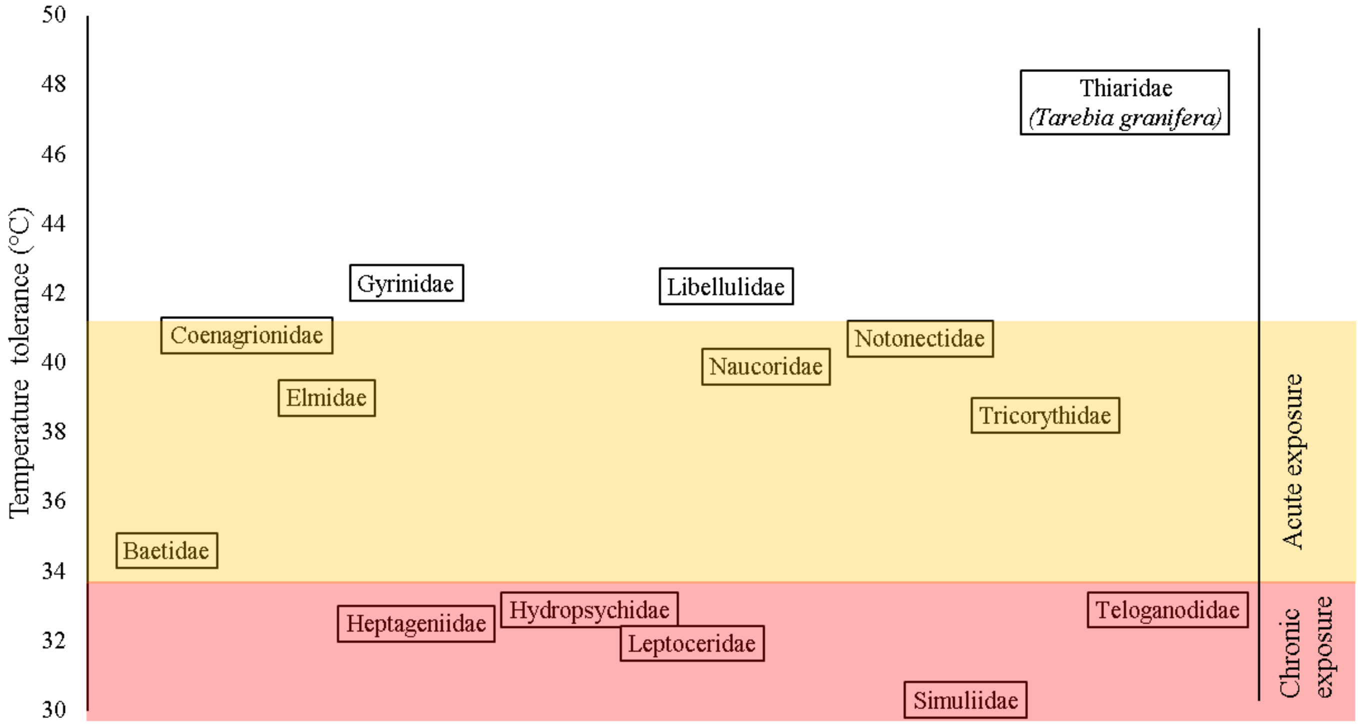

Figure 4.2: Temperature tolerances of macroinvertebrate species and families in the Olifants River, Kruger National Park (LNP), Limpopo Province, South Africa, and their exposure to acute (orange) and chronic (red) heat exposure in water temperature projections for 2100 CE.

Discussion

Freshwater biota have specific flow regimes and thermal niches upon which they rely for survival and breeding, and disruptions to these parameters are detrimental to their survival (Magnuson *et al*. 1979, Comte & Olden 2017, Darwall *et al*. 2018). Global change is not only bringing higher air temperatures, and therefore higher water temperatures, but also will result in extreme climatic events such as droughts, floods, hurricanes, cyclones, and temperature anomalies or heat waves (Moreno & MØller 2011). These events affect populations through the reduction of reproductive success and adult and juvenile survival rates, and mass mortality events (Moreno & MØller 2011). The present study predicts that certain aquatic organisms within the Olifants River will experience such events and extrapolates which populations may be exposed to chronic and/or acute thermal stressors. While a few borderline cases were observed, such as *E. trimaculatus* and Notonectidae, they were conservatively placed in the heat stress category of their upper thermal tolerance. The statistical model used to predict the future water temperatures slightly underestimated temperatures (Adlam *et al*. 2022) which makes the thresholds a conservative estimate.

Twelve of the 15 fish species and 11 of the 14 macroinvertebrate families are likely to experience mass die-off events in the Olifants River if they are unable to find microclimates or thermal refugia or adapt or acclimate from acute heat stress that will be experienced in future. However, it has been found that the CT_{max} of fish species may not evolve fast enough to track climate change (Comte & Olden 2017). Habitat heterogeneity ultimately dictates whether thermal refugia are available; cooler water is often associated with side-channels, alcoves, lateral seeps, and floodplain spring brooks (Ebersole *et al*. 2003, Dallas 2009). It has also been found that riffle and run biotopes generally have warmer water temperatures than pools (Dallas & Rivers-Moore 2011). A shading experiment conducted by Ebersole *et al*. (2003) showed that shaded patches had surface water temperatures 2-4° C cooler than the control areas, indicating the vital importance of riparian vegetation cover as a thermal refuge for aquatic animals. Additionally, while evidence suggests little thermal stratification in more lotic regions of rivers, lentic areas such as pools have been known to have temperature differences: a study found water temperature differences of 1.9° C in a 1.4 m deep pool, while another found no difference in pools less than 0.9m deep but differences up to 4.5° C in pools deeper than 0.9m (Appleton 1976, Dallas 2009, Dallas & Rivers-Moore 2011). These studies show the importance of habitat heterogeneity in order to maintain thermal refugia, which is important within the Olifants River and in many other similar rivers globally.

Loss of species will ultimately cause negative effects within the trophic cascades or food web (Woodward *et al*. 2010b). One of the more concerning impacts within the Olifants River is the potential loss of the apex predator, *H. vittatus* through acute heat stress which will have top-down effects on the trophic cascade (Pace *et al*. 1999, Estes *et al*. 2011). The loss of this top predator may create an open niche for *C. gariepinus* which is an omnivore that can feed on fish (Skelton 2001, Marshall 2011). The concern that *C. gariepinus* shifts to a higher intake of fish is that it coincides with the presence of pansteatitis, an inflammatory disease that can lead to death in many animals including the Nile crocodile (*Crocodylus niloticus*) within the Olifants River (Woodborne *et al*. 2012). It has been shown that *C. gariepinus* that shifted from a herbivorous to a piscivorous diet correlated with a high prevalence of pansteatitis

(Woodborne *et al*. 2012). Another top-down effect of concern will be the loss of algivores and detritivores such as *Labeo* species. This loss, compounded by an already polluted system (Riddell *et al*. 2019), will promote algal blooms as algae diversity and biomass increases with temperature to ~30° C, and above 30° C cyanobacteria dominate (DeNicola 1996, Dallas 2008).

As climate change increases temperatures and changes flow regime and trophic interdependencies, indigenous colder-water species are likely to be replaced by warmer-water species (Rahel & Olden 2008, Záhorská 2016). In the Olifants River, both the indigenous and invasive *Oreochromis* species have similar thermal niches and tolerances, and therefore *O.niloticus* replacing its native counterpart due to climate warming is not a concern. However, *O. niloticus* is a successful invader known to hybridise with other *Oreochromis* species and competitively excludes them as it has a faster growth rate, so this still poses a negative conservation issue (de Moor & Druton 1988, Chifamba & Videler 2014). It has been introduced into many freshwater systems throughout Africa, including South Africa, for its aquacultural importance and for sport fishing (Marshall 2011).

Another invasive species of concern in the Olifants River system is the silver carp, *Hypophthalmichthys molitrix*, which was introduced into South Africa in 1975 to control algal blooms and is known to occur in Lake Flag Boshielo in the middle Olifants River as well as Lake Massingir in the lower Olifants River (Sara *et al*. 2018). It is a generalist feeder that consumes large volumes of zooplankton, phytoplankton, and detritus (Cooke *et al*. 2009, Sara *et al*. 2018), but stomach content analysis shows that it also exploits the benthos when under nutritional stress (Lübcker *et al*. 2016). Along with its adaptive feeding capacity, it can tolerate high water temperatures of 40° C and has an upper lethal limit of 46.5° C (Opuszynski *et al*. 1989, Tripathi 1989). Fish species with lower thermal limits such as *L. cylindricus*, *L. molybdinus*, *P. philander*, *L. marequensis*, *M. acutidens*, *C. paratus*, *E. trimaculatus*, *E. viviparus*, *M. acutidens*, and *G. giuris* are all susceptible to effects of this invasion as they share similar food sources, and ultimately will have consequences on the trophic cascade.

One of the limitations of the present study was the lack of available CT_{max} data for some of the fish species that occur in the Olifants River. Neill (1979) reported that fish use behavioural thermoregulation to maximise temperatures optimal for their physiology and life processes. Fish and aquatic invertebrates, as ectotherms, have thermal tolerances close to their environmental temperatures (Comte & Olden 2017, Capon *et al*. 2021), and therefore their thermal preference is a good indicator of what temperatures they may be able to withstand. Jobling (1981) also found significant correlations between preferred, lethal, and optimal growth temperatures. In the present study it was necessary to use some thermal preference temperature data as a proxy, given the paucity of thermal tolerance temperature data.

Climate change will undoubtedly have a negative effect worldwide on aquatic species; studies on rising temperatures show that aquaculturally important fish, such as the tra catfish (*Pangasianodon hypophthalmus*) (Phuc *et al*. 2017), rainbow trout (*Oncorhynchus mykiss*) (Currie *et al*. 2013) and Mozambique tilapia (*O. mossambicus*) (Basu *et al*. 2001) are threatened by chronic and acute thermal stressors. Two important fish species for both commercial and subsistence fisheries in the current study are *C. gariepinus* and *O. mossambicus*, and given their hardiness not only to warm water temperatures but also to drought conditions and low oxygenation, they are less susceptible to the effects of climate change (Huisman & Richter 1987, Skelton 2001, Marshall 2011, Polacik & Podrabsky 2015). This is positive for aquaculture in southern Africa, and indigenous species such as these should be prioritised for mass rearing initiatives.

A study conducted in the Cape Fold Ecoregion in South Africa examined the CT_{max} of eight freshwater fish species in response to climate warming found that fishes in perennial streams were more thermally-sensitive than those in streams with intermittent flow regimes (Reizenberg *et al*. 2019). This raises a concern for our study as the Olifants River is a perennial river (Ashton & Dabrowski 2011), although this is only through judicious catchment management aimed at curbing over-abstraction to protect the ecological flow reserve in the KNP. Studies are being conducted on mitigation measures to combat the effects of high-water temperatures. An emerging mitigation measure is using nature-based solutions which is defined as “actions to protect, sustainably manage, and restore natural or modified ecosystems, that address societal challenges effectively and adaptively, simultaneously providing human well-being and biodiversity benefits” (IUCN 2016). These are intended to address climate change problems such as decarbonisation and stochastic events, however, they often provide additional benefits including food and water security and biodiversity conservation (Miles *et al*. 2021). In freshwater ecosystems, nature-based solutions are being implemented to address a multitude of climate-change related problems such as river flooding, urban flooding, water scarcity, drought, erosion and water quality deficits (OECD 2020, Albert *et al*. 2021).It has also been found that in fish, poor diet may have a negative impact in higher temperature scenarios, for example, in *C. gariepinus*, diet can play an important role in its health and fitness under thermal stress (Al-Deghayem & Suliman 2019). Similarly, *O. niloticus*, fed diets with white button mushrooms had better antioxidative resistance, immunity, and growth under heat stress, than those on a control diet (Dawood *et al*. 2020). However, such studies are conducted in controlled aquaculture populations, so the realistic implementation of these methods in wild species is difficult to determine.

In agreement with the present study's prediction that organisms are likely to be differentially at risk to chronic and/or acute heat exposure and will therefore be vulnerable, the present study has shown that the Olifants River is highly likely to be biophysically affected by climate change, and this is likely to result in changes in the ecological functioning of the river through shifts in the trophic cascades. The scenario is not unique to the Olifants River, and what emerges is likely to replicate in many other similarly polluted and over-abstracted rivers globally. Various taxa, including animals and plants, are avoiding climate change through range shifts to higher latitudes and/or higher elevations (Parmesan & Yohe 2003, Parmesan 2006b, Chen *et al*. 2011). A study on freshwater fish showed that temperatures will shift upstream more than 100 km, and fish will not be able to track this change fast enough (Comte & Grenouillet 2013). Species with larger populations, large body size and better dispersal ability may be able to respond better to changing climatic conditions (Comte & Grenouillet 2013, Comte *et al*. 2016).

One of the greatest threats to fish movement is the building of impoundments and dams which fragment rivers, alter flow regimes and stop fish from migrating freely (Poff *et al*. 1997, Morita & Yamamoto 2002, Pelicice *et al*. 2015). While there are mitigation measures such as fish ladders and fishways, these are ineffective in some cases (Pelicice *et al*. 2015). It has been illustrated that while species distributions shrink at the lower end, but expand upstream by about 0.6 km per decade (Comte & Grenouillet 2013). The Olifants River has multiple impoundments, and these barriers may mean they cannot migrate or shift their distribution to cooler water temperatures when they are under thermal stress.

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Chapter 5

Implications of climate change impacts on trophic cascades in freshwater rivers: A case scenario based on the Olifants River, South Africa

Abstract

Temperature forecasting has shown that air temperatures will increase in southern Africa by 2100 CE due to climate change and will likely result in ecologically significant warmer water temperatures in freshwater rivers. Apart from modifying water flow regimes due to changes in rainfall patterns, this rate of increase in water temperature may also alter species phenology, distribution, and the trophic dynamics within these systems in the southern African subregion. This is particularly alarming in heavily polluted and over-abstracted rivers such as the Olifants River in the Kruger National Park (KNP), Limpopo Province, South Africa. Although the mechanistic air and water temperature statistical modelling approaches are instrumental in modelling climate change as a driver of temperature over time, they do not extend beyond these parameters to address climate change impact-related questions on ecological functioning, such as in trophic ecology. The present study investigated the impact of future warmer waters on the trophic interdependence in the Olifants River using stable isotope analysis (SIA) of fish species and invertebrate families to elucidate trophic cascades, and to extrapolate possible changes in food-web dynamics under climate change scenarios in 2100 CE under the "*business as usual*" Representative Concentration Pathway (RCP) 8.5 scenario. The results showed top-down effects from the loss of apex predators, predatory omnivores, and insectivores from the system, and that there also may be problems with algal blooms, as algivorous fish are also under threat. Apart from implications on trophic interdependence in impacted freshwater systems, these results highlight the importance of SIA in the assessment of trophic cascades and future impacts under different climate change scenarios and their associated threats due to trophic disruptions on ecosystem services. This study represents part of a broader novel approach that combines the assessment of trophic cascades using SIA, with the use of a mechanistic approach of statistical modelling of future water temperature and the assessment of thermal tolerances to evaluate faunal changes at both the population and community levels, with implications in similarly heavily polluted and over-abstracted data-deficient river systems globally.

Keywords

Stable isotope analysis (SIA), trophic cascades, climate change, freshwater rivers, fish, invertebrates, Olifants River, South Africa

Introduction

Climate change will alter the temperature, precipitation, and hydrology of rivers, which will ultimately affect the distribution, abundance, and phenology of species within these ecosystems (Woodward *et al*. 2010a, Alp & Cucherousset 2022). These changes will in turn alter the trophic dynamics as there will be changes in primary production, predator-prey interactions, species extinctions, and invasions by warm water-adapted species (Dallas 2009, Alp & Cucherousset 2022, Leclerc *et al*. 2023). However, while for example, for temperature--related studies, mechanistic air and water temperature statistical modelling approaches (e.g., Chapters 2 and 3) are important in modelling climate change as a driver of temperature over time, they do not extend beyond these parameters to address climate change impact-related questions on ecological functioning, such as in trophic ecology that is for example, evaluated using stable isotope analysis (SIA; Frye 1991, Jardine *et al*. 2003).

Trophic cascades occur between species or populations within a community, usually between predators and prey (Paine 1966). They occur in terrestrial, marine, and freshwater ecosystems, and at varying complexities (Pace *et al*. 1999, Schmitz *et al*. 2000, Hessen & Kaartvedt 2014, Eger & Baum 2020). Human-mediated extinctions of top-predators or consumers is detrimental and often irreversible in trophic cascades, and is referred to as trophic downgrading (Pace *et al*. 1999, Estes *et al*. 2011). Top-down effects occur when a predator or consumer is removed or disturbed within a system, and this has cascading effects down the trophic levels. An example of this top-down effect in a terrestrial ecosystem is Isle Royale National Park in Michigan, USA; the wolf population reached unprecedented low numbers and with no predators to keep the herbivore population under control, the moose population increased, and this led to the over-consumption and suppression of the balsam fir (McLaren & Peterson 1999). In marine ecosystems, it has been shown that the presence of sea otters limit sea urchin populations (Estes & Duggins 1995). This is critical as sea urchins are herbivores that feed on kelp and when left unregulated over-consume algae leading to destructive grazing (Estes & Duggins 1995). This phenomenon has also been shown in freshwater systems, such as in an Oklahoma (USA) creek, where largemouth and spotted bass as predators control the populations of herbivorous minnows that feed on benthic algae (Power *et al*. 1985). The removal of the predators, indirectly led to the loss of algal biomass (Power *et al*. 1985).

Previous studies have shown that climate change in freshwater systems may alter species richness, species evenness, distribution, diversity, body size structure and densities within affected communities (Meerhoff *et al*. 2007, Friberg *et al*. 2011, Dallas & Ross-Gillespie 2015, Ruiz-Navarro *et al*. 2016). It has been found that at higher temperatures, individuals are less fecund, are smaller body-sized, and occur higher densities (Meerhoff *et al*. 2007, Dallas & Ross-Gillespie 2015). A field experiment by O'Gorman *et al*. (2023) found that warmed streams had lower mean trophic levels and less connectivity which could lead to invasions, loss of diversity, loss of predators and top-down control and potentially local extinctions. These trophic disruptions can be studied using stable isotope analysis (SIA). SIA has advanced ecological studies in freshwater systems in understanding migration patterns, diet, and feeding ecology of species, tracing contaminants, and in determining trophic interdependencies (Peterson & Fry 1987, Post 2002, Layman *et al*. 2007). Carbon (C) and nitrogen (N) stable isotopes are the most important elements for trophic ecological studies as $\delta^{15}N$ value is an indicator of trophic level, while $\delta^{13}C$ value distinguishes between sources of primary producers such as algae, macrophytes, and C_3 and C_4 plants (Frye 1991, Vander Zanden *et al*. 1997, Woodborne *et al*. 2012). $\delta^{15}N$ values increase by ~2.5-3.5‰, while the difference of $\delta^{13}C$ is <1‰ between diet and tissue, making nitrogen the better indicator of trophic levels (Frye 1991).

The diet-to-tissue isotopic discrimination of ^{13}C and ^{15}N results in isotopic enrichment in species or populations at higher trophic levels, distinguishing primary producers, primary consumers such as herbivores, detritivores, omnivores, and predators (Frye 1991, Vander Zanden *et al*. 1997, Post 2002, Jardine *et al*. 2003, Woodborne *et al*. 2012). SIA of aquatic organisms can be used to monitor the effects of climate change on food webs (Friberg *et al*. 2009). It has been shown that there is an increase in $\delta^{15}N$ values across trophic levels with an increase in water temperature, but no correlation between temperature and $\delta^{13}C$ values (Friberg *et al*. 2009). The increase in $\delta^{15}N$ values is caused by either temperature-induced isotope fractionation or mediated through the resource base (Friberg *et al*. 2009). While isotope chemistry may change under climate change, present study uses the trophic relationships in order to assess structural impacts of species vulnerability in the context of food web structures.

The Olifants River in the Kruger National Park (KNP) in South Africa represents a heavily polluted and over-abstracted freshwater system (Ashton *et al*. 2001, Ashton & Dabrowski 2011). These impacts together with high evaporation rates and predicted high water temperatures in the southern African subregion will result in the Olifants River being more significantly impacted by climate change than most rivers globally (Schulze 2012).

Fish

Fish species recorded to occur in the lower Olifants River include the redeye labeo (*Labeo cylindricus*), leaden labeo (*L. molybdinus*), purple labeo (*L. congoro*), sharp tooth catfish (*Clarias gariepinus*), Mozambique tilapia (*Oreochromis mossambicus*), southern mouthbrooder (*Pseudocrenilabrus philander*), threespot barb (*Enteromius trimaculatus*), bowstripe barb (*E. viviparus*), redbreast bream (*Coptodon rendalli*), sawfin rock catlet (*Chiloglanis paratus*), tigerfish (*Hydrocynus vittatus*), lowveld largescale yellowfish (*Labeobarbus marequensis*), and tank goby (*Glossogobius giuris*) (Woodborne *et al*. 2012, Myburgh 2016, 2019, Kaiser 2019).

Fishes have different feeding habits and occupy different niches within their interconnected system (Elton 1927) and therefore the vulnerability of any individual species due to climate change may have implications on the trophic cascade for all the other species in the system. For example, the cichlid species, *O. mossambicus* is microphagous, feeding on algae, diatoms, detritus, zooplankton, and plant material, while *C. rendalli* has similar feeding habits; feeding more on macrophytes (Heeg & Kok 1988, Skelton 2001, Marshall 2011, Griffiths *et al*. 2015). The other cichlid species found within the Olifants River, *P. philander* is omnivorous and feeds on algae, shrimps, crustaceans, invertebrates and small fishes (Mitchell 1976, Mhlanga 2000). The three *Labeo* species are known to feed on algae, organic matter and "*aufwuchs*", the small animals and plants particularly algae and diatoms that adhere to surfaces in freshwater habitats (Bell-Cross & Minshull 1988, Skelton 2001, Marshall 2011).

Similarly, the two cyprinid species of the genus *Enteromius* also feed on similar items which are mostly aquatic insects such as small aquatic fleas of the Order Cladocera (Cambray 1983, Marshall 2011). The other cyprinid species, *L. marequensis,* is omnivorous and feeds on algae, invertebrates, snails and small fishes (Skelton 2001, Marshall 2011, Griffiths *et al*. 2015). Another omnivore in the Olifants River system is *C. gariepinus* which feeds on a wide range of food resources ranging from invertebrates, plant matter to snails, is also known to hunt fish and other organisms in packs (Skelton 2001, Marshall 2011, Griffiths *et al*. 2015).

Chiloglanis paratus and *G. giuris* feed on aquatic insects, with the latter species also being a predator on fish (Skelton 2001, Marshall 2011). The top predator in the Olifants River is *H. vittatus* which feeds exclusively on fish mainly of the family Cichlidae, but also the families Cyprinidae and Clariidae (Kenmuir 1973, Dalu *et al*. 2012). However, the fry of these fish feed on zooplankton and small invertebrates (Marshall 2011, Dalu *et al*. 2012). A species of main concern for invasion because of its warm-water adaptive capacity is the silver carp (*Hypophthalmichthys molitrix*) as it can tolerate water temperatures of up to 45° C, and feed on large volumes of zooplankton, phytoplankton, and detritus (Opuszynski *et al*. 1989, Tripathi 1989, Cooke *et al*. 2009, Sara *et al*. 2018). The warm-water adaptive capacity of *H. molitrix* together with its adaptive feeding capabilities makes it a direct competitor (Cooke *et al*. 2009, Sara *et al*. 2018) with species, such as *O. mossambicus*, *C. rendalli*, and juvenile *H. vittatus.* Chapter 4 showed that *E. trimaculatus*, *E. viviparus*, *C. paratus*, and *G. giuris* will be susceptible to chronic heat stress that will eventually have severe consequences if it occurs often enough and/or at high enough levels as they will experience consecutive days over their upper thermal limits. Similarly, Chapter 4 showed that *P. philander*, *H. vittatus*, *L. marequensis*, *L. cylindricus*, *L. molybdinus*, and *L. congoro* will experience acute heat stress that will have a severe impact over a short duration as they may experience periods around their critical thermal maximum.

Macroinvertebrates

Some of the invertebrate families recorded to occur in the lower Olifants River, are likely to be vulnerable to both acute and chronic heat stressors and include four families from the Order of mayflies (Ephemoroptera) namely, the families Baetidae, Tricorythidae, Heptageniidae and Teloganodidae (Chapter 4). The Ephemoroptera are vital in freshwater ecosystems as primary consumers, and they contribute to nutrient cycling, break-down and remove substances, and filter-feed that purifies water (Jacobus *et al*. 2019). Most families are collector-gatherers and scrapers, feeding on detritus and plant matter making them detritivorous and herbivorous (Shapas & Hilsenhoff 1976, Jacobus *et al*. 2019). Two families of caddisflies of the Order Trichoptera recorded to occur in the lower Olifants River, namely the Leptoceridae and the Hydropsychidae are vulnerable to warm temperatures (Chapter 4). Larvae of the family Leptoceridae are mostly herbivorous and are classified as scrapers and shredders but sometimes are predatory, while members of the family Hydropsychidae are net-spinners, shredders, and filter-feeders, but prey-stalking may also occur (Shapas & Hilsenhoff 1976). Black flies of the family Simuliidae are primarily filter-feeders that use specialized mouthparts, the cephalic fans, to feed on organic matter (Wallace & Merritt 1980). The riffle beetles of the family Elmidae are detritivores being mostly collector-gatherers and scrapers and also sometimes feed on algae (Elliott 2008). Saucer bugs of the family Naucoridae are predatory and feed on aquatic invertebrates and are also considered to be beneficial in controlling mosquito populations, while members of the family Notonectidae are well-known as biocontrol agents for mosquitos (Quiroz-Martinez & Rodríguez-Castro 2007).

Given the importance of feeding ecology on trophic cascades, the present study is aimed at using SIA to assess the potential impacts of local extinctions of fish species and macroinvertebrate families on the food web in the lower Olifants River in KNP, Limpopo Province, South Africa under the "*business as usual*" Representative Concentration Pathway (RCP) 8.5 scenario. As functional feeding groups are important to the persistence of freshwater ecosystems (Petchey *et al*. 1999, Friberg *et al*. 2009, Alexander *et al*. 2015, Castillo *et al*. 2018b), the study assesses the ecosystem changes in terms of both functional and taxa changes. The present study hypothesized that there will be trophic cascades and future impacts under different climate change scenarios and their associated threats due to trophic disruptions on the Olifants River ecosystem that may reflect analogous processes in other similarly impacted freshwater rivers globally. This study represents part of a broader novel approach that combines the assessment of trophic cascades using SIA, with the use of a mechanistic statistical approach of modelling future water temperature (Chapters 2 and 3) and the assessment of thermal tolerances (Chapter 4) to evaluate faunal changes at both population and community levels, with implications in similarly heavily polluted and over-abstracted data-deficient river systems globally.

Materials and Methods

Data collection

Fish and invertebrate sampling was conducted during studies by Woodborne *et al*. (2012), Myburgh (2016, 2019), and Kaiser (2019) in the lower Olifants River, Kruger National Park (KNP), Limpopo Province, South Africa at three locations; Mamba Wier (24°3’59.86” S, 31°14’33.6” E), sampled in June 2019, Balule Wier (24°3’22.5” S, 31°43’13.30” E) sampled in June 2019, and the Olifants River Gorge (23°59’21.8” S, 31°49’35.6” E) sampled during different seasons in 2011, April 2016, March 2017, March and November 2018, and June 2019 (Figure 5.1). This sampling regime accounted for both wet and dry seasons and for both high and low flow. Fish samples were collected by electrofishing (SAMUS725MP electrofisher, Samus Special Electronics, Warsaw, Poland) for one hour and by rod-and-reel angling. Fish were housed in an aerated water bath then identified to species level using the *Guide to the freshwater fishes of Southern Africa* by Skelton (2001), and a small fin clipping from the dorsal fin (0.5 x 0.5 cm or smaller) was taken. Fish were then released. Invertebrates were sampled using the South African Scoring System, version 5 method (SASS5) (Dickens & Graham 2002) with a 30 x 30 cm with 1 mm mesh size sweep net in the current, over sand and rocks, and riparian vegetation. Invertebrates were identified to the family level using *Aquatic invertebrates of South African rivers: Field Guide* by Gerber & Gabriel (2002).

Figure 5.1: Map of study sites (with an insert of Africa highlighting South Africa) showing Mamba Weir, Balule Weir and Olifants River gorge sites in the lower Olifants River in Kruger National Park (KNP), Limpopo Province, South Africa.

SIA

SIA was undertaken in previous studies (Woodborne *et al*. 2012, Myburgh 2016, 2019, Kaiser 2019) and the methods that were used followed protocols outlined by Woodborne *et al*. (2012). Fin-clippings were subjected to lipid extraction using a 2:1 methanol/chloroform solution. Samples of fins and invertebrates were dried in an oven overnight at 70° C. Invertebrate samples were homogenized. Samples were weighed into ~0.5 to 0.6 mg aliquots and placed into tin capsules that were pre-cleaned in toluene for stable light isotope analysis. Every 12th sample was run in duplicate to measure sample inhomogeneity. Isotopic analysis was conducted on a Flash EA 1112 Series coupled to a Delta V Plus stable light isotope ratio mass spectrometer via a ConFlo IV system (all equipment supplied by Thermo Fischer, Bremen, Germany). Two laboratory running standards, Merck Gel ($\delta^{13}C$ = -20.26‰, $\delta^{15}N$ = 7.89‰, C% = 41.28), N% = 15.29) and DL-Valine ($\delta^{13}C$ = -10.57‰, $\delta^{15}N$ = -6.15‰, C% = 50.55, N%= 11.86) and a blank sample was run after every 11 unknown samples.

All results are referenced to Vienna Pee-Dee Belemnite (VPDB) for carbon isotope values, and to air for nitrogen isotope values. Results are expressed in delta notation on a per mille scale using the following standard equation (Equation 5.1):

$$\delta X\ (‰) = [(R_{sample}-R_{standard})/R_{standard}-1] \times 1000\ [\text{Equation 5.1}]$$

where X = ^{15}N or ^{13}C and R represents $^{15}N/^{14}N$ or $^{13}C/^{12}C$, respectively.

Standard ellipses analysis and mean and standard deviation analyses for the three sites were performed in R version 4.2.2 (R Core Team, 2023). Output graphs resulting from the standard ellipses analysis (SEAc) were performed using Stable isotope Bayesian Ellipses in R (SIBER) (Jackson *et al.* 2011). Ellipses represent 40% of the data for all convex hulls (Jackson *et al.* 2011). Niche overlap plots and calculations were also generated using R version 4.2.2 and packages SIBER (Jackson *et al*., 2011), and nicheROVER (Swanson *et al*. 2015). SIBER was used to determine the Total Area (TA), Standard ellipse area (SEA), and sample size-corrected SEA (SEAc). The niche area overlaps and niche sizes were determined through the package nicheROVER which allows the uncovering of overlap directionality where for example, if Species A and Species B) have overlapping niches, it can be determined how large the niche of Species A is relative to Species B and *vice-versa*, as opposed to having one overlap percentage value for both species, which would be obtained from SIBER (Swanson *et al*. 2015). The package nicheRover relies on Bayesian statistics to compute the required SEAb overlaps which have an α value of 95% which was chosen for this study (Swanson *et al*. 2015). The resultant overlap percentage represents the mean value of the 95% credible interval (CI) (Swanson *et al*. 2015). Low overlap ranges from 0 to 29%, medium overlap ranges from 30 to 60%, while high overlap is > 60% (Langton 1982, Golikov *et al*. 2022). Taxa with $n < 3$ samples were excluded from the overlap calculations.

Chronic heat stress

Following the results of Chapter 4, this chapter used a threshold of 33.6° C for assessing the vulnerability to chronic heat stress, where taxa with thermal tolerance below this CT_{max} may experience chronic stress. The results showed that the fish species within the Olifants River that are predicted to be vulnerable to chronic stress are all the only exclusive insectivores in the system and include *E. viviparus*, *E. trimaculatus* and *C. paratus* which have thermal tolerances of 32.3° C, 33.6° C, and 32.3° C, respectively (Chapter 4). While *E. trimaculatus* is on the borderline of the threshold, it was conservatively placed in the chronic stress category. *Glossogobius giuris*, an omnivore that feeds on both insects and fish, is also predicted to be under threat given its thermal limit of 33.0° C (Chapter 4). Macroinvertebrate families, Simuliidae Leptoceridae, Teloganodidae, Hydropsychidae and Heptageniidae with CT_{max} values of 31.6° C, 32.0° C, 32.9° C, 32.9° C, 32.5° C, respectively, may also be under threat of chronic heat stress (Chapter 4).

Acute heat stress

Following the results of Chapter 4, this chapter used a threshold of 41.1° C for assessing the vulnerability to acute heat stress, where taxa with thermal tolerance below this CT_{max} may experience acute heat stress. These results showed that seven fish species from the Olifants River are predicted to be vulnerable to acute heat stress, and include four *Labeo* species, namely, *L. cylindricus*, *L. molybdinus*, *L. congoro*, and *L. rosae* which have a thermal tolerance of 40.2° C (Chapter 4). These species represent the only obligate algivores among the fish species in the Olifants River and occupy a unique niche in the food web (Chapter 4). *Hydrocynus vittatus*, with a thermal tolerance of 36.6° C, and the only obligate piscivore is also predicted to be vulnerable to acute heat stress (Chapter 4). *Labeobarbus marequensis*, with a thermal tolerance of 34.3° C, is an omnivore that also feeds on fish is also predicted to be vulnerable to acute heat stress (Chapter 4). As there are only four fish species in the system, *L. marequensis*, *H. vittatus*, *G. giuris* and *C. gariepinus* that feed on fish and the first three are predicted to be vulnerable to either chronic or acute heat stress, the results predict that there will be a large niche open for only *C. gariepinus* to occupy (Chapter 4). The macroinvertebrate families Baetidae, Naucoridae, Elmidae, Coenogrionidae, Notonectidae and the Tricorythidae, with thermal limits of 34.6° C, 39.9° C, 39.0° C, 39.8° C, 40.7° C, and 38.5° C, respectively, are also predicted to be vulnerable to acute heat stress (Chapter 4). While the family Notonectidae is on the border of this threshold, it was conservatively placed in the acute stress category. All these macroinvertebrate families are detritivores and herbivores, except for the Naucoridae, Notonectidae and Coenogrionidae which are insectivorous known to feed on mosquitoes (Chapter 4).

From all the above information, the present study combined all the chronic and acute heat-stressed taxa and represented them as thermally “vulnerable”. It was assumed that the potential loss of thermally vulnerable taxa creates open niches under climate change scenarios.

Results

The highest trophic level at Mamba Weir includes the omnivore fish species *C. gariepinus* and *L. marequensis* and the two algivore *Labeo* species *L. cylindricus* and *L. molybdinus* (Figures 5.2 and 5.4). The fish and invertebrate insectivores overlap their niches and the invertebrate plant feeders have a broad niche (Figure 5.4A). Fish species with the broadest niche are *L. cylindricus* and *O. mossambicus*, followed by the two *Enteromius* species, *L. molybdinus* and, surprisingly, *C. gariepinus* and *L. marequensis* have the least large niche sizes (Figure 5.3). All the invertebrates in Mamba Weir appear to have smaller niche widths than their fish counterparts (Figure 5.3). However, many were excluded from the analyses due to low sample sizes. These results are supported by niche overlap percentage results for Mamba Weir (Table

5.1), where *O. mossambicus* overlaps with multiple fish and macroinvertebrates. The two *Labeo* species overlap with each other, indicating that they occupy a similar niche, different from other species, supported by the fact that they are the only algivores. Two fish species, *L. marequensis* and *C. gariepinus* do not overlap into other niches, indicating that they do not need to compete with other taxa for resources. None of the macroinvertebrates overlap either, however this is likely due to exclusion of many taxa in the analysis due to sample size. All the algivores are vulnerable, potentially leaving a large niche space open under climate change scenarios (Figure 5.4B and 5.4C). The vulnerable *L. marequensis* also has a broad niche as an omnivore, and also *Enteromius* species as insectivores, leaving large gaps in the food web (Figures 5.4B and 5.4C). Many of the invertebrate species that are vulnerable are detritivores, except for the insectivorous families, the Naucoridae, Notonectidae and the Coenogrionidae (Figures 5.4B and 5.4C)

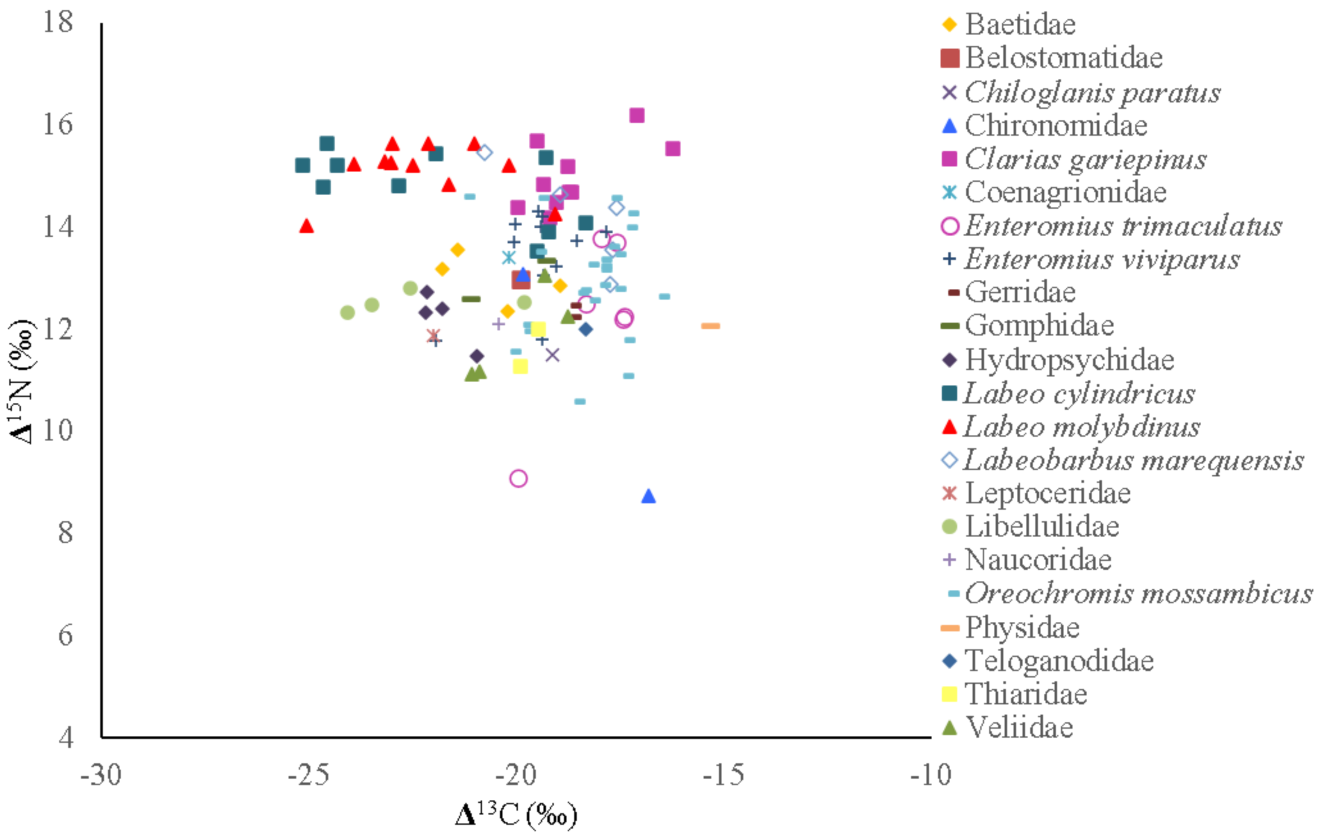

Figure 5.2: Stable isotope bi-plots of carbon (δ^{13}C) and nitrogen (δ^{15}N) of fish species and macroinvertebrate families from Mamba Weir, Kruger National Park (KNP), Limpopo Province, South Africa.

Table 5.1: Niche overlap of taxa at Mamba Weir, Olifants River, South Africa. Percent sample size-corrected standard ellipses area (SEAb % overlap represents the mean value of the 95% credible interval (CI), and the numbers in parentheses representing the range of possible values within the 95% credible interval. Low overlap = 0-29%; medium overlap = 30-60%; and high overlap (shown in bold) = >60% (shown in **bold**). Taxa that had *n* < 3 samples were excluded from the overlap analysis.

SEAb% overlap (α = 0.95% credible interval)	*Clarias gariepinus*	*Enteromius trimaculatus*	*Enteromius viviparus*	*Labeo cylindricus*	*Labeo molybdinus*	*Labeobarbus marequensis*	*Oreochromis mossambicus*	Baetidae	Hydropsychidae	Libellulidae	Veliidae
Clarias gariepinus	**NA**	12 (0-54)	58 (18-94)	58 (23-95)	40 (3-90)	53 (25-87)	**63 (20-95)**	4 (0-22)	0 (0-1)	0 (0-2)	3 (0-24)
Enteromius trimaculatus	7 (0-27)	**NA**	29 (2-76)	18 (0-49)	1 (0-12)	28 (7-62)	**78 (48-99)**	12 (0-44)	0 (0-3)	4 (0-19)	18 (0-60)
Enteromius viviparus	32 (9-71)	20 (2-65)	**NA**	48 (17-86)	11 (0-41)	36 (13-75)	**86 (61-99)**	40 (16-77)	2 (0-8)	14 (1-34)	36 (9-79)
Labeo cylindricus	24 (7-47)	6 (0-18)	23 (7-45)	**NA**	**66 (36-93)**	24 (6-57)	24 (6-50)	6 (0-38)	0 (0-2)	0 (0-3)	2 (0-11)
Labeo molybdinus	15 (2-43)	1 (0-5)	8 (0-31)	**87 (60-100)**	**NA**	19 (2-54)	8 (0-32)	3 (0-24)	0 (0-2)	0 (0-0)	0 (0-2)
Labeobarbus marequensis	46 (17-81)	34 (9-69)	59 (24-90)	**68 (25-98)**	30 (3-76)	**NA**	**78 (40-99)**	4 (0-30)	0 (0-0)	1 (0-11)	12 (0-50)
Oreochromis mossambicus	17 (5-38)	57 (33-85)	58 (34-86)	34 (8-69)	6 (0-27)	42 (20-72)	**NA**	23 (4-57)	0 (0-2)	8 (0-26)	30 (8-63)
Baetidae	9 (0-58)	12 (0-42)	**70 (26-98)**	23 (0-92)	5 (0-36)	5 (0-40)	**60 (17-96)**	**NA**	3 (0-15)	26 (1-70)	27 (3-71)
Hydropsychidae	1 (0-10)	1 (0-13)	34 (0-93)	3 (0-29)	1 (0-9)	0 (0-0)	7 (0-65)	18 (0-86)	**NA**	41 (13-82)	20 (0-71)
Libellulidae	1 (0-17)	4 (0-21)	29 (3-65)	3 (0-34)	0 (0-0)	2 (0-13)	19 (1-56)	30 (2-77)	18 (5-39)	**NA**	11 (0-41)
Veliidae	2 (0-18)	25 (1-82)	**68 (25-99)**	8 (0-40)	0 (0-4)	9 (0-36)	**66 (26-98)**	28 (3-70)	6 (0-22)	11 (0-37)	**NA**

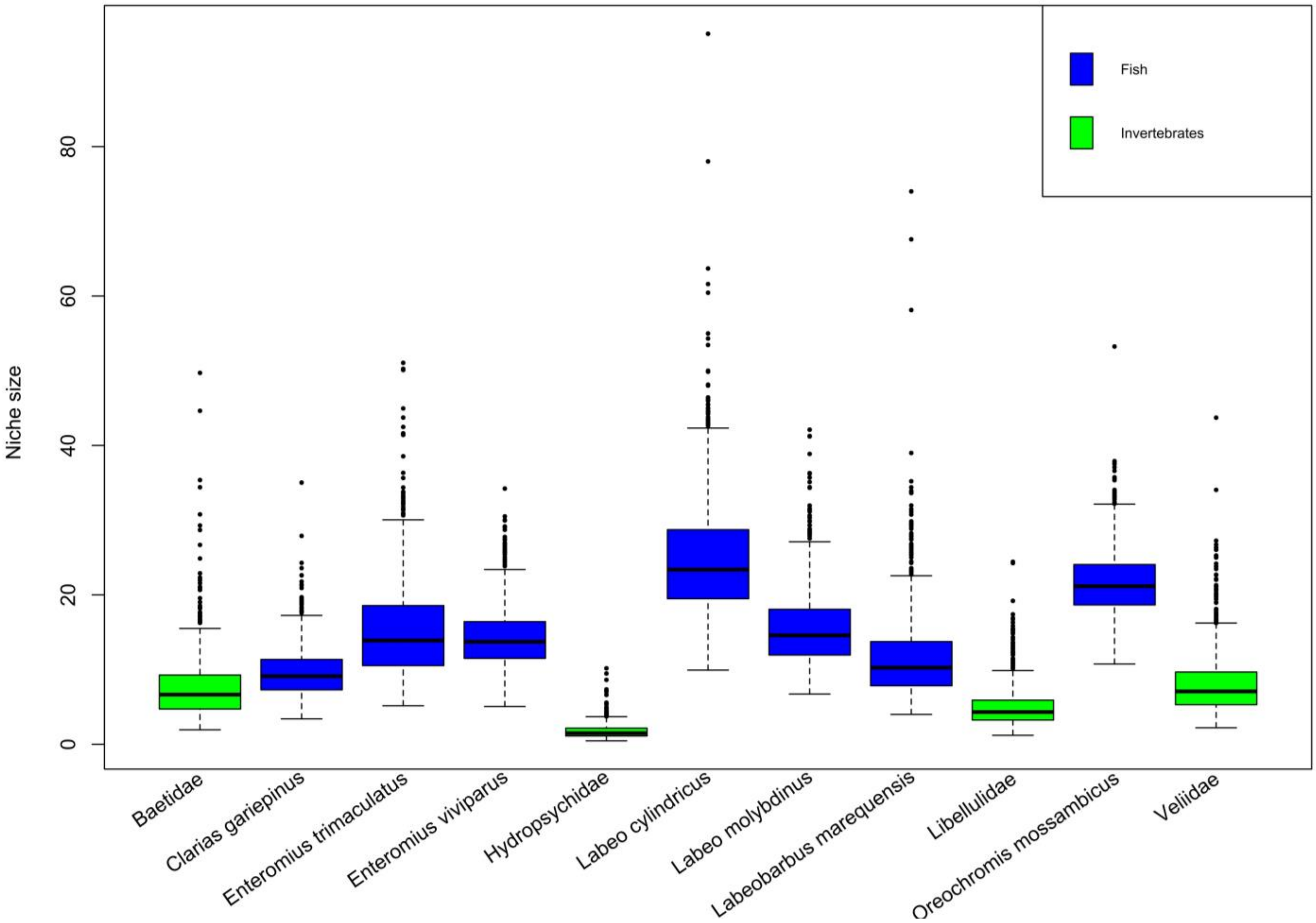

Figure 5.3: Isotopic niche width of freshwater fish and invertebrates in Mamba Weir, Olifants River, South Africa.

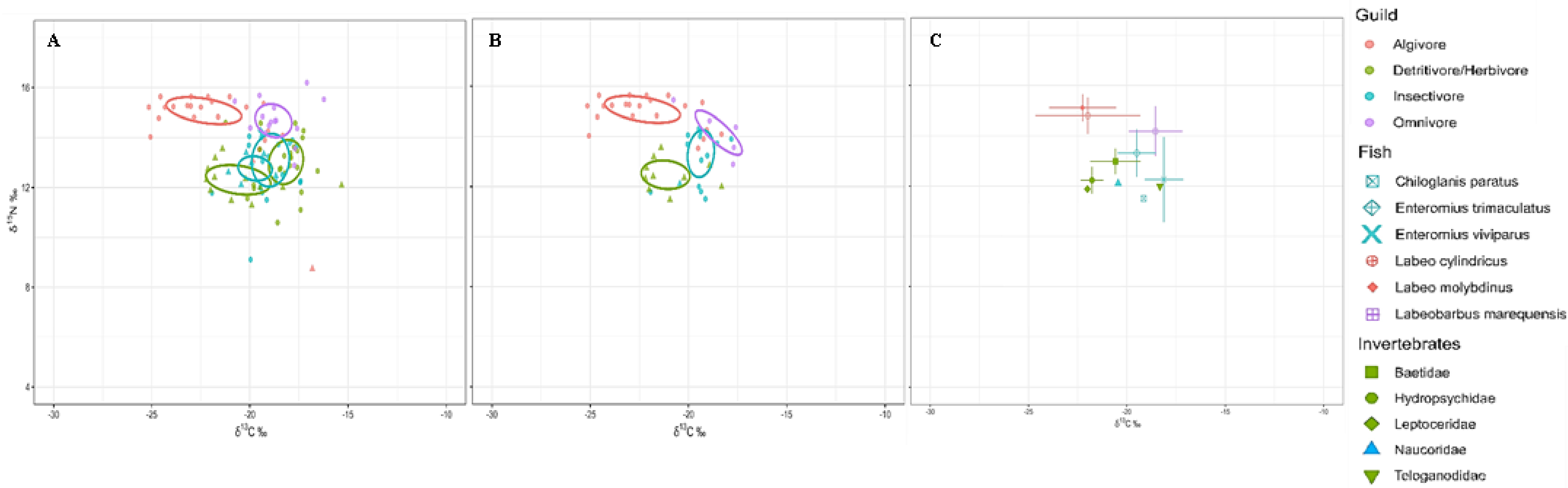

Figure 5.4: Standard ellipses of δ^{13}C and δ^{15}N values for: **A**) Invertebrate and fish guilds; **B**) Vulnerable invertebrate and fish guilds; and **C**) Means and standard deviations of δ^{13}C and δ^{15}N values for vulnerable fish species and invertebrate families from Mamba Weir, Kruger National Park (KNP), Limpopo Province, South Africa. Fish guilds are represented by a circle, while invertebrate guilds are represented by a triangle.

The top of the trophic cascade at Balule Weir is occupied by the omnivores *B. imberi*, *C. gariepinus*, and *L. marequensis* (Figure 5.5 and 5.7A). The insectivore, *E. trimaculatus* is also high up on this food web and to the left (Figure 5.5, Figure 5.7A). Fish detritivores and invertebrate insectivores are lower in the tropic cascade followed by the invertebrate detritivores (Figures 5.5 and 5.7A). In contrast to Mamba Weir, *C. gariepinus* and *L. marequensis* have the largest niche sizes, while the rest of the fish species and macroinvertebrate taxa have narrow niches (Figure 5.6). This is supported by the niche overlap percentages, showing *C. gariepinus* and *L. marequensis* overlapping with other fish species (Table 5.2). As in Mamba Weir, none of the macroinvertebrates overlap, however this is likely due to exclusion of many taxa due to sample size limitations. The vulnerable scenario shows all algivores at this site, *L. cylindricus*, *L. rosae* and *L. congoro* to be at risk (Figure 5.7B and 5.7C). A large number and therefore a wide trophic range of the omnivores and fish insectivores are also vulnerable (Figure 5.7B and 5.7C). Similar to Mamba Weir, most of the invertebrate species that are vulnerable at Balule Weir are detritivores (Figure 5.7B and 5.7C).

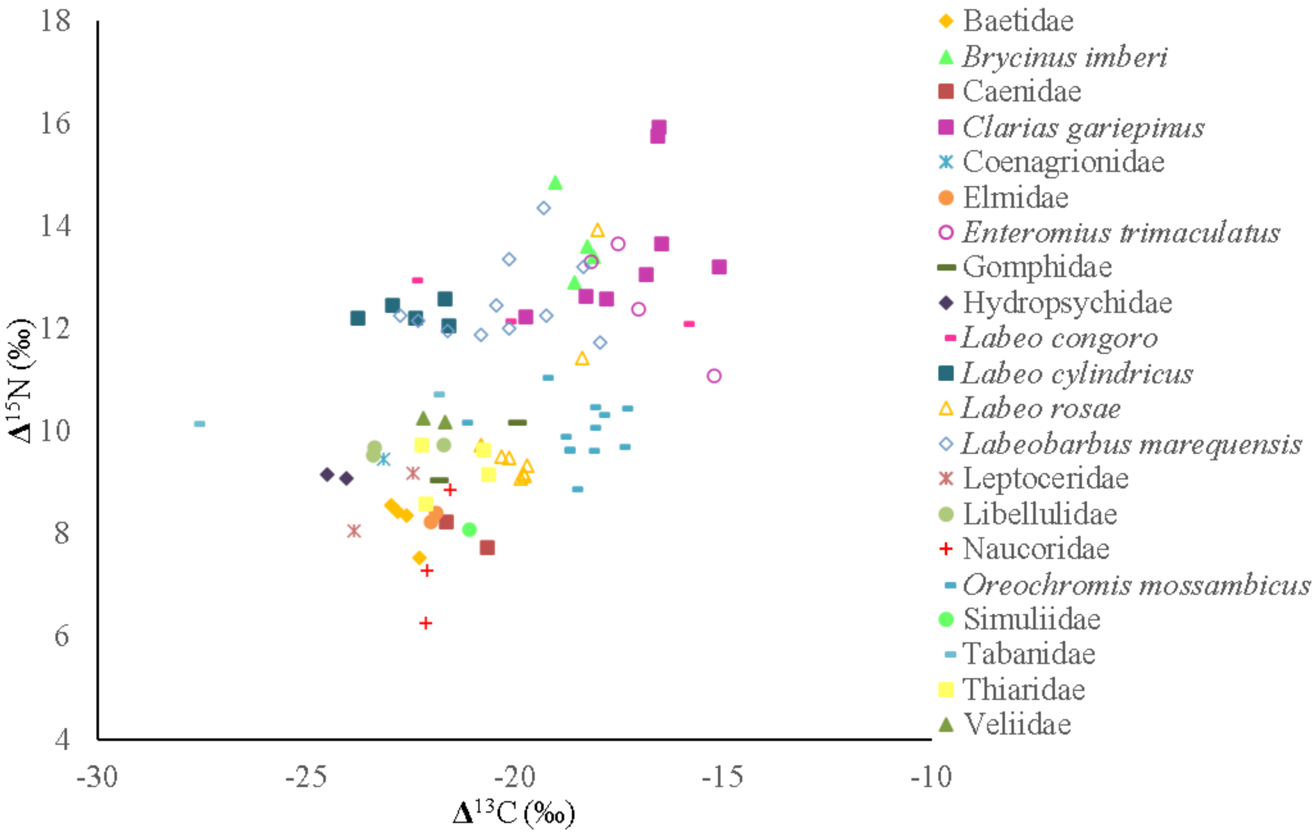

Figure 5.5: Stable isotope bi-plots of carbon (δ^{13}C) and nitrogen (δ^{15}N) of fish species and macroinvertebrate families from Balule Weir, Kruger National Park (KNP), Limpopo Province, South Africa.

Table 5.2: Niche overlap of taxa at Balule Weir, Olifants River, South Africa. Percent sample size-corrected standard ellipses area (SEAb% overlap represents the mean value of the 95% credible interval (CI), and the numbers in parentheses representing the range of possible values within the 95% credible interval. Low overlap = 0-29%; medium overlap = 30-60%; and high overlap (shown in bold) = >60% (shown in **bold**). Taxa that had *n* < 3 samples were excluded from the overlap analysis.

SEAb% overlap (α = 0.95% credible interval)	*Brycinus imberi*	*Clarias gariepinus*	*Enteromius trimaculatus*	*Labeo cylindricus*	*Labeobarbus marequensis*	*Oreochromis mossambicus*	Baetidae	Libellulidae	Naucoridae	Thiaridae
Brycinus imberi	**NA**	**87 (44-100)**	52 (3-96)	0 (0-1)	**68 (11-100)**	1 (0-7)	0	0	0	0 (0)
Clarias gariepinus	13 (3-32)	**NA**	22 (8-44)	1 (0-4)	37 (8-77)	4 (0-15)	0 (0-0)	0	0 (0-1)	1 (0-5)
Enteromius trimaculatus	18 (2-54)	**73 (31-100)**	**NA**	0 (0)	38 (0-85)	0 (0-4)	0	0 (0-0)	0	0 (0-0)
Labeo cylindricus	0 (0-1)	6 (0-60)	0 (0-0)	**NA**	**83 (36-100)**	0 (0-0)	0	0	0 (0-1)	1 (0-0)
Labeobarbus marequensis	8 (1-21)	45 (10-92)	7 (0-22)	15 (3-39)	**NA**	2 (0-13)	0 (0-0)	0 (0-0)	0 (0-4)	1 (0-13)
Oreochromis mossambicus	1 (0-8)	24 (0-91)	0 (0-2)	0 (0-0)	6 (0-46)	**NA**	0	1 (0-7)	0 (0-2)	11 (0-61)
Baetidae	0	1 (0-0)	0	0	0 (0-0)	0	**NA**	0 (0-4)	4 (0-24)	24 (0-95)
Libellulidae	0	2 (0-32)	0	0	3 (0-52)	4 (0-28)	1 (0-12)	**NA**	2 (0-12)	47 (1-100)
Naucoridae	0	1 (0-13)	0	0 (0-1)	2 (0-14)	1 (0-14)	4 (0-22)	1 (0-4)	**NA**	22 (1-69)
Thiaridae	0 (0-0)	6 (0-71)	0 (0-0)	0 (0-0)	3 (0-32)	15 (0-63)	1 (0-7)	6 (0-20)	11 (0-34)	**NA**

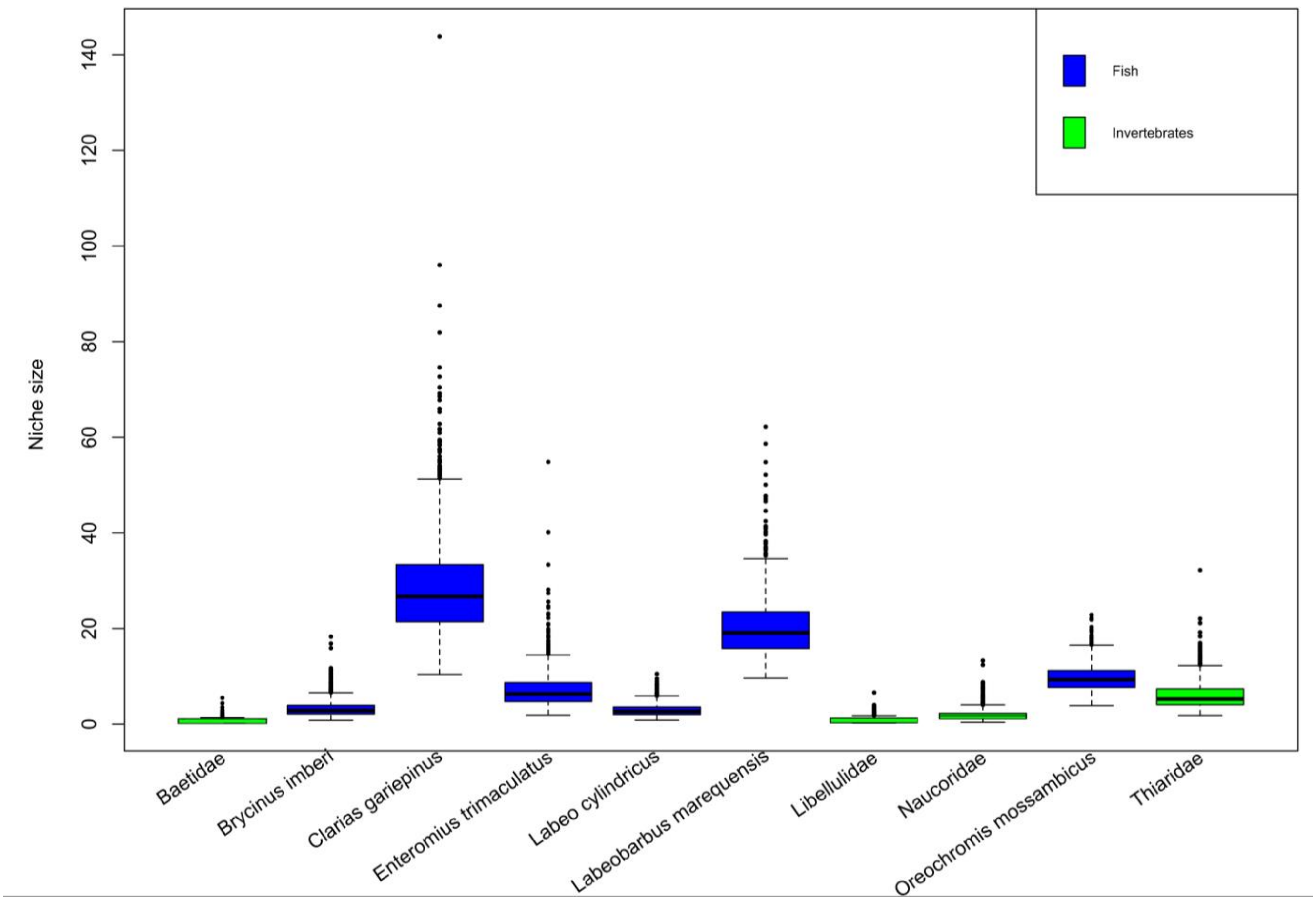

Figure 5.6: Isotopic niche width of freshwater fish and invertebrates in Balule Weir, Olifants River, South Africa.

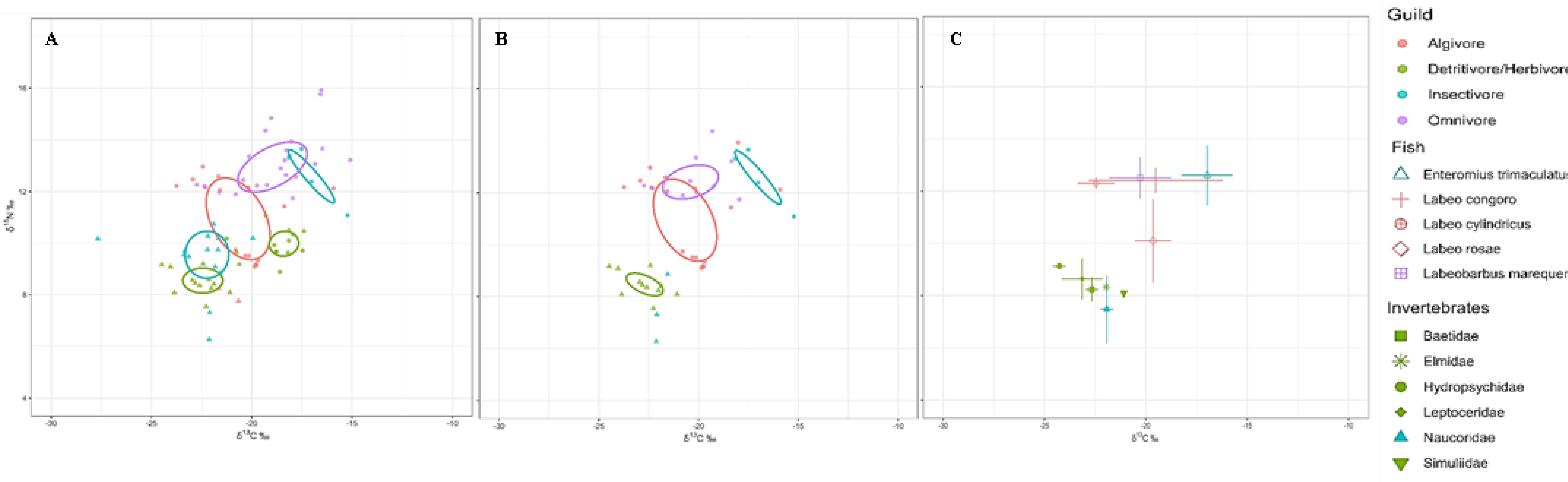

Figure 5.7: Standard ellipses of $\delta^{13}C$ and $\delta^{15}N$ values for: **A**) Invertebrate and fish guilds; **B**) Vulnerable invertebrate and fish guilds; and **C**) Means and standard deviations of $\delta^{13}C$ and $\delta^{15}N$ values for vulnerable fish species and invertebrate families from Balule Weir, Kruger National Park (KNP), Limpopo Province, South Africa. Fish guilds are represented by a circle, while invertebrate guilds are represented by a triangle.

The top niche at Olifants River Gorge is occupied by the obligate piscivore, *H. vittatus*, followed by the omnivores, *C. gariepinus*, *G. giuris* and *L. marequensis* (Figure 8 and 5.10A). The insectivore, *C. paratus* has a narrow niche (Figure 8 and 5.10A). The algivores, *L. molybdinus*, *L. congoro*, *L. rosae* and *L. cylindricus* are high up the trophic cascade but occupy a unique niche to the left characterised by lower δ^{13}C (Figure 8 and 5.10A). The herbivore, *O. mossambicus* also has a wide niche (Figure 8, Figure 5.9 and 5.10A). Both insectivore and detritivore invertebrates have a broad niche space (Figure 5.9 and 5.10A). The piscivorous fish species, *H. vittatus*, has the largest niche size of all the fish species present in the Olifants River gorge and overlaps niche with many fish species and macroinvertebrate taxa (Figure 5.9, Table 5.3). *Glossogobius giuris* also has a large niche within the fish species, and overlaps niche with many fish species, but no macroinvertebrates (Figure 5.9, Table 5.3). Notonectidae, Naucoridae and Libellulidae have the largest niche sizes within the site and overlap with most fish and other macroinvertebrates (Figure 5. 9, Table 5.3). The fish *C. paratus*, has a very small niche size and no overlap with other species, confirming that it is a specialist species (Figure 9, Table 5.3). Macroinvertebrates Simuliidae, Pleuceridae and Elmidae exhibit a similar pattern. The piscivore, *H. vittatus* is vulnerable to climate change (Figure 5.10B and 5.10C), and while its niche is at the top of the food web, it is noted that the individuals that plot similar to the detritivore/herbivores are likely juveniles (Figure 5.10A and 5.10B). Both *G. giuris* and *L. marequensis* are vulnerable which leaves only *C. gariepinus* to occupy the omnivorous niche and the top of the trophic cascade (Figure 5.10A, 10B and 10C). The insectivorous *C. paratus* is also vulnerable, and its niche is unlikely to be filled as it is a specialist species (Figure 5.10C). No fish detritivore/herbivore is under threat; however, many invertebrate families are likely to be, and these include the families Baetidae, Elmidae, Heptageniidae, Hydropsychidae, Leptoceridae, and Simuliidae (Figure 5.10B and 5.10C). Similar to the Mamba Weir and Balule Weir sampling sites, the invertebrate families that are vulnerable at the Olifants River gorge are detritivores, except for the families for the Naucoridae, Notonectidae and Coenogrionidae which are insectivores (Figure 5.10B and 5.10C).

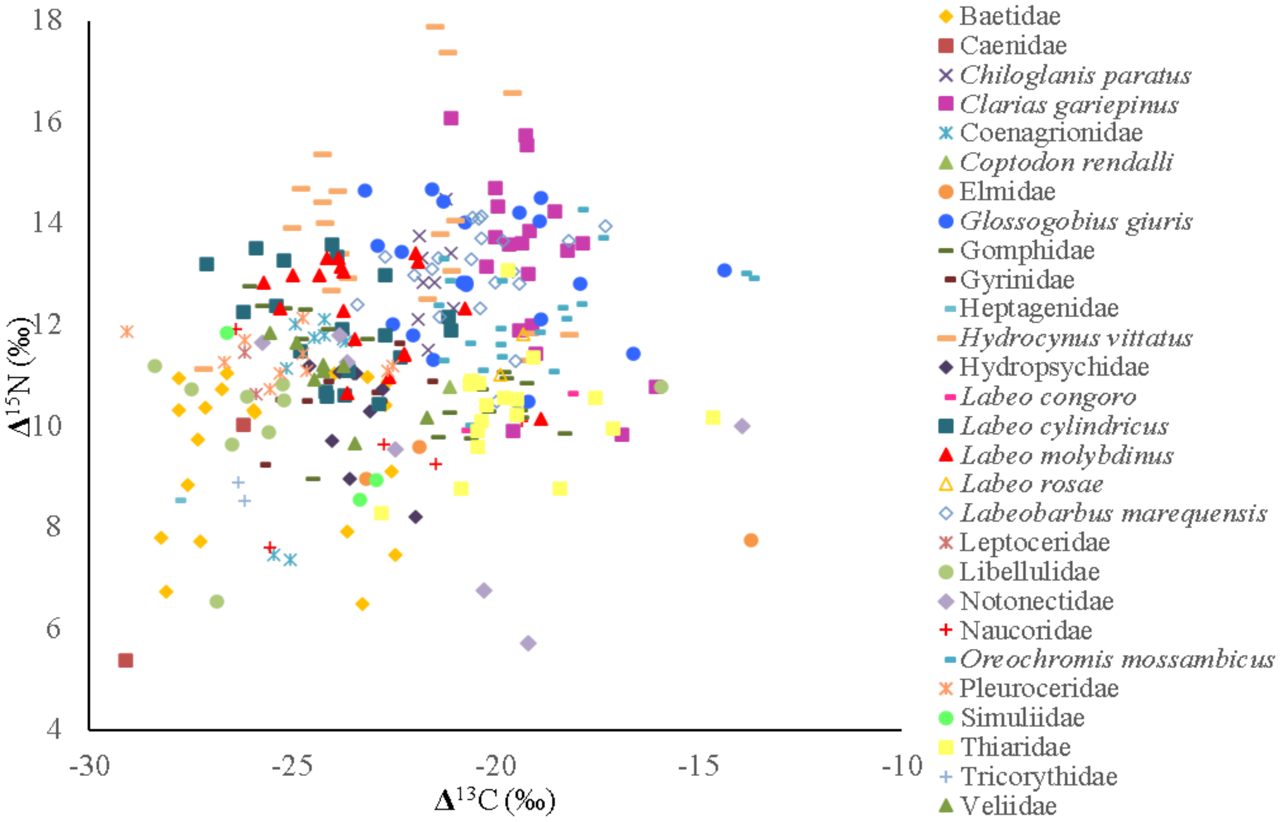

Figure 5.8: Stable isotope bi-plots of carbon (δ^{13}C) and nitrogen (δ^{15}N) of fish species and macroinvertebrate families from Olifants River gorge, Kruger National Park (KNP), Limpopo Province, South Africa.

Table 5.3: Niche overlap of taxa at Oliphants River gorge, Olifants River, South Africa. Percent sample size-corrected standard ellipses area (%SEAb) overlap represents the mean value of the 95% credible interval (CI), and the numbers in parentheses representing the range of possible values within the 95% credible interval. Low overlap = 0-29%; medium overlap = 30-60%; and high overlap (shown in bold) = >60% (shown in **bold**). Taxa that had $n < 3$ samples were excluded from the overlap analysis.

SEAb overlap (α = 0.95% credible interval)	*Chiloglanis paratus*	*Clarias gariepinus*	*Glossogobius giuris*	*Hydrocynus vittatus*	*Labeo cylindricus*	*Labeo molybdinus*	*Labeobarbus marequensis*	*Oreochromis mossambicus*	Baetidae	Coenagrionidae	Elmidae	Gomphidae	Gyrinidae	Hydropsychidae	Libellulidae	Naucoridae	Notonectidae	Pleuroceridae	Simuliidae	Thiaridae	Velidae
Chiloglanis paratus	**NA**	28 (0-91)	**98 (87-100)**	**100 (97-100)**	59 (12-96)	**75 (41-99)**	**95 (77-100)**	**76 (38-99)**	18 (0-83)	0 (0-1)	0 (0-4)	40 (11-79)	15 (0-51)	1 (0-9)	51 (4-99)	40 (0-100)	**76 (18-100)**	6 (0-26)	0 (0-0)	21 (1-70)	1 (0-6)
Clarias gariepinus	3 (0-10)	**NA**	**84 (65-97)**	**83 (53-99)**	3 (0-18)	9 (0-34)	**64 (41-87)**	**66 (45-87)**	2 (0-20)	0 (0-0)	2 (0-7)	17 (3-40)	3 (0-24)	0 (0-0)	35 (1-81)	22 (0-90)	49 (6-99)	1 (0 -7)	0	37 (16-62)	0 (0-0)
Glossogobius giuris	17 (8-30)	59 (39-80)	**NA**	**88 (65-99)**	27 (8-52)	37 (15-66)	**70 (50-88)**	**69 (46-91)**	11 (0-48)	6 (1-16)	1 (0-5)	26 (8-53)	8 (0-28)	3 (0-9)	41 (5-89)	29 (1-93)	**60 (12-99)**	4 (0-14)	0 (0-1)	29 (9-57)	2 (0-7)
Hydrocynus vittatus	12 (6-22)	28 (13-48)	**65 (40-86)**	**NA**	37 (19-60)	41 (23-65)	41 (22-64)	31 (14-55)	19 (4-49)	16 (4-33)	2 (0-8)	28 (12-48)	8 (2-20)	7 (1-20)	32 (9-69)	27 (75-100)	54 (16-95)	9 (2-20)	2 (0-7)	13 (3-31)	6 (1-14)
Labeo cylindricus	7 (1-17)	2 (0-11)	56 (18-93)	**94 (74-100)**	**NA**	**83 (61-98)**	30 (7-65)	41 (13-77)	68 (28-96)	42 (23-67)	5 (0-25)	**83 (61-97)**	29 (12-54)	35 (12-64)	**77 (42-100)**	**65 (17-100)**	**92 (53-100)**	41 (21-68)	7 (1-21)	20 (4-51)	33 (15-60)
Labeo molybdinus	15 (5-29)	7 (0-23)	**75 (41-98)**	**97 (84-100)**	**87 (67-99)**	**NA**	49 (20-80)	53 (24-84)	51 (10-94)	34 (17-57)	2 (0-12)	**77 (52-97)**	24 (8-50)	22 (4-53)	**71 (28-99)**	58 (9-100)	**90 (54-100)**	26 (8-54)	2 (0-7)	26 (6-62)	16 (3-42)
Labeobarbus marequensis	26 (14-43)	**66 (42-91)**	**97 (88-100)**	**97 (86-100)**	31 (9-63)	45 (20-80)	**NA**	**80 (54-98)**	11 (0-50)	3 (0-12)	0 (0-2)	28 (8-57)	10 (1-42)	2 (0-8)	45 (4-97)	32 (1-99)	**65 (12-100)**	4 (0-17)	0 (0-0)	28 (5-65)	1 (0-50)
Oreochromis mossambicus	9 (3-18)	**61 (41-82)**	**87 (67-99)**	**76 (40-98)**	25 (8-50)	35 (14-62)	**61 (39-84)**	**NA**	15 (1-48)	3 (0-9)	2 (0-9)	39 (19-65)	15 (2-44)	5 (1-13)	59 (15-98)	41 (4-97)	**67 (23-99)**	9 (1-27)	1 (0-3)	55 (24-85)	4 (0-12)

Baetidae	1 (0-4)	1 (0-4)	7 (0-22)	30 (6-71)	26 (9-52)	14 (3-32)	3 (0-12)	10 (1-33)	**NA**	30 (16-48)	25 (2-60)	27 (10-53)	26 (11-52)	21 (9-38)	**87 (66-99)**	**74 (41-98)**	**79 (41-100)**	18 (7-35)	16 (7-34)	14 (2-36)	14 (6-29)
Coenagrionidae	0 (0-0)	0 (0-1)	29 (4-67)	**67 (32-97)**	**63 (36-89)**	47 (20-76)	8 (0-35)	18 (0-66)	84 (56-99)	**NA**	19 (0-52)	56 (30-82)	41 (19-67)	42 (13-76)	**82 (53-99)**	**77 (39-100)**	**90 (62-100)**	34 (16-59)	21 (8-44)	6 (0-48)	34 (17-58)
Elmidae	0 (0-2)	5 (0-27)	1 (0-17)	14 (0-58)	9 (0-44)	3 (0-22)	0 (0-2)	4 (0-66)	40 (7-78)	8 (0-21)	**NA**	37 (2-86)	10 (0-31)	16 (3-37)	59 (15-97)	**60 (19-98)**	**84 (43-100)**	2 (0-17)	9 (1-24)	47 (16-83)	6 (0-27)
Gomphidae	8 (1-20)	15 (3-35)	48 (13-85)	**75 (41-97)**	**65 (42-86)**	**63 (39-88)**	26 (6-57)	56 (28-82)	59 (25-90)	19 (9-33)	13 (1-55)	**NA**	33 (16-57)	27 (13-47)	**88 (64-99)**	**78 (42-99)**	**96 (80-100)**	37 (16-65)	5 (0-15)	**60 (38-84)**	27 (13-52)
Gyrinidae	6 (0 - 22)	3 (0-18)	30 (3-81)	**77 (25-100)**	**77 (44-98)**	54 (20-89)	20 (1-63)	52 (10-96)	**92 (65-100)**	47 (22-77)	23 (0-78)	**78 (47-98)**	**NA**	56 (28-86)	**99 (90-100)**	**95 (68-100)**	**98 (83-100)**	51 (15-88)	21 (7-50)	38 (3-86)	49 (24-79)
Hydropsychidae	0 (0-4)	0 (0-0)	18 (0-72)	**68 (16-100)**	**70 (34-97)**	45 (12-84)	7 (0-43)	36 (0-88)	**97 (83-100)**	40 (11-78)	37 (7-82)	**75 (40-98)**	55 (29-85)	**NA**	**97 (82-100)**	**96 (75-100)**	**99 (94-100)**	38 (14-73)	23 (4-67)	46 (3-93)	59 (30-89)
Libellulidae	3 (0-8)	8 (1-20)	19 (3-44)	40 (11-76)	32 (12-58)	23 (7-45)	10 (1-27)	24 (6-52)	**72 (45-94)**	20 (10-35)	24 (4-61)	42 (20-69)	27 (11-52)	21 (9-38)	**NA**	**68 (36-96)**	**77 (43-99)**	20 (7-41)	12 (4-27)	30 (10-54)	17 (7-33)
Naucoridae	3 (0-12)	7 (0-27)	19 (1-54)	43 (6-86)	35 (7-69)	25 (4-58)	10 (0-35)	26 (3-63)	**72 (36-98)**	21 (8-43)	31 (8-71)	49 (18-84)	26 (8-55)	29 (11-55)	**83 (45-100)**	**NA**	**90 (55-100)**	17 (2-41)	15 (4-38)	44 (14-78)	19 (5-43)
Notonectidae	3 (0-9)	11 (1-28)	21 (4-48)	37 (10-71)	27 (9-51)	23 (7-48)	12 (2-28)	23 (6-47)	44 (17-74)	12 (4-23)	24 (9-52)	43 (19-71)	15 (5-30)	16 (6-34)	**60 (25-91)**	**58 (28-91)**	**NA**	13 (3-30)	9 (2-22)	39 (16-68)	12 (4-26)
Pleuroceridae	2 (0-10)	1 (0-9)	23 (0-74)	**78 (31-100)**	**80 (50-98)**	55 (19-89)	11 (0-42)	30 (4-75)	**92 (68-100)**	38 (19-61)	5 (0-58)	**82 (53-100)**	37 (11-71)	37 (16-63)	**96 (74-100)**	**78 (20-100)**	**93 (52-100)**	**NA**	23 (3-56)	15 (1-48)	53 (28-84)
Simuliidae	0 (0-0)	0	2 (0-24)	42 (0-97)	40 (2-85)	8 (0-49)	0 (0-0)	6 (0-49)	**85 (42-100)**	36 (11-69)	35 (1-84)	40 (2-89)	33 (9-66)	43 (8-85)	**82 (36-100)**	**81 (34-100)**	**93 (55-100)**	25 (4-58)	**NA**	18 (0-71)	17 (0-67)
Thiaridae	3 (0-10)	42 (18-72)	45 (15-85)	48 (7-93)	21 (3-57)	28 (5-64)	19 (3-47)	55 (25-85)	28 (4-75)	1 (0-6)	24 (7-60)	**77 (56-95)**	10 (1-34)	8 (1-24)	**83 (40-100)**	**73 (27-100)**	**94 (72-100)**	8 (0-35)	2 (0-8)	**NA**	7 (0-22)
Veliidae	1 (0-6)	0 (0-0)	21 (0-92)	**89 (35-100)**	**93 (71-100)**	**69 (17-99)**	6 (0-49)	41 (0-93)	**97 (81-100)**	55 (28-86)	14 (0-77)	**97 (79-100)**	**60 (31-91)**	**73 (40-96)**	**97 (82-100)**	**90 (50-100)**	**98 (84-100)**	71 (42-97)	12 (0-53)	31 (2-76)	**NA**

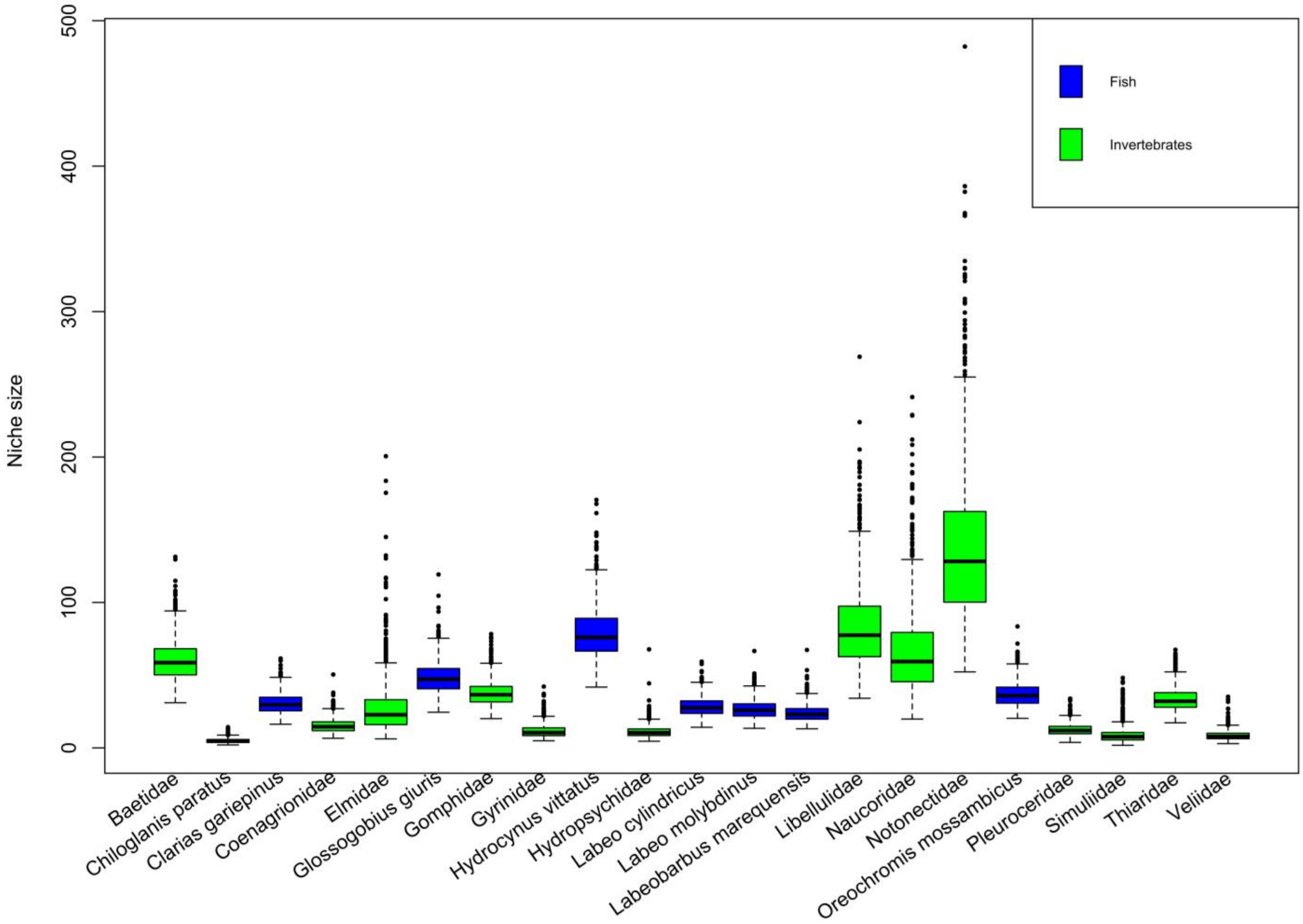

Figure 5. 9: Isotopic niche width of freshwater fish and invertebrates in Olifants River gorge, Olifants River, South Africa.

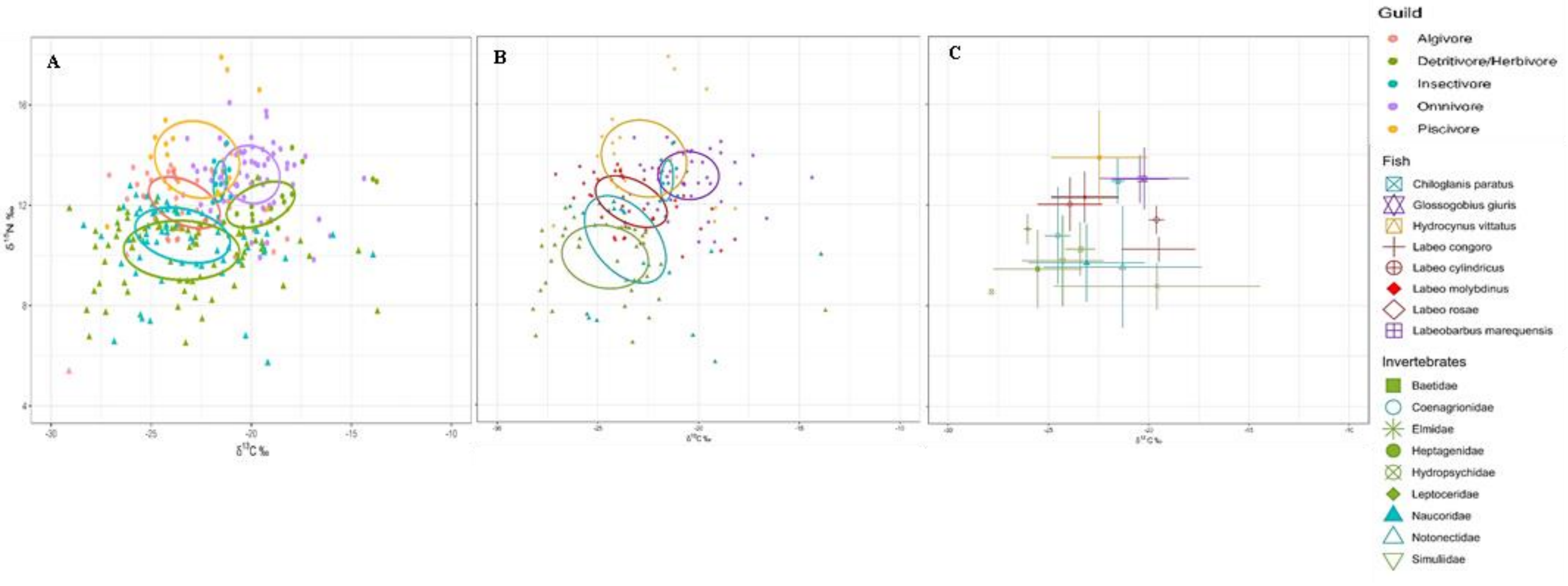

Figure 5.10: Standard ellipses of δ^{13}C and δ^{15}N values for: **A**) Invertebrate and fish guilds; **B**) Vulnerable invertebrate and fish guilds; and **C**) Means and standard deviations of δ^{13}C and δ^{15}N values for vulnerable fish species and invertebrate families from Olifants River Gorge, Kruger National Park (KNP), Limpopo Province, South Africa. Fish guilds are represented by a circle, while invertebrate guilds are represented by a triangle.

Throughout all three sampling sites, the results show that all algivorous and insectivorous fish are vulnerable. This includes all four *Labeo* species, two *Enteromius* species and *C. paratus*. The single obligate piscivore, *H. vittatus*, is found on only one site but is vulnerable. Of the omnivorous fish species, all but one were found to be vulnerable. However, the one that is not vulnerable, *C. gariepinus*, is found in all three sampling sites and is abundant. The only herbivorous/detritivorous fish sampled, *O. mossambicus*, was found in all three sites and is not vulnerable. No macroinvertebrate algivores were found to be vulnerable, however there were only two samples from each site indicating a low abundance of this functional group. Detritivorous/herbivorous macroinvertebrates are affected disproportionately more than the insectivorous guild. The larger number of unaffected detritivorous macroinvertebrates in the Olifants River gorge sampling site is due to the high number of freshwater snails (the Thiaridae and the Pleuroceridae) sampled.

Discussion

The present study adds a novel approach in using future water projections to predict community level changes using SIA, rather than in previous studies on impacts of warming often conducted under laboratory conditions (Petchey *et al*. 1999, Dallas 2008). While Friberg *et al*. (2009) showed the importance of SIA with increased temperature, functional feeding ecology or individual vulnerability was not taken into account to assess the effect of climate change on the trophic cascade.

A study by Petchey *et al*. (1999) on warming in aquatic communities showed that an increase in water temperature leads to ~30-40% decrease in species diversity and high extinction rates of predators and herbivores while having little effect on producers and bacterivores. While this study was conducted on aquatic microbes, the current study showed similar results, where it is predicted that within the fish populations, a large number of predators, predatory omnivores, and insectivores will be more affected by climate warming than the detritivores. This is supported by other research such as Jackson *et al*. (2020), that found that increased temperature lowered functional diversity and food chain length. Food webs may become less diverse due to losses of predators (Jackson *et al*. 2020), and in the current study, the apex predator, *H. vittatus*, is predicted to be under threat of extinction. This exerts pressure on piscivorous omnivores to control lower trophic levels, however, *L. marequensis* and *G. giuris*, are also predicted to be under the same threats. Three of the fish insectivores in the Olifants River were predicted to be under threat of chronic heat stress, and y*et al*so control macroinvertebrate populations from over-grazing primary producers. In addition, many of the fish and invertebrates that are predicted to not be under threat are herbivores and detritivores, which exerts pressure on primary producers and may result in the depletion in plant biomass in future.

Within the invertebrate community, predators are predicted to be less affected than detritivores and herbivores. The Ephemoroptera which includes the families Baetidae, Tricorythidae, Heptageniidae, and Teloganodidae are all predicted to be vulnerable to heat stress and this is of particular concern as the Baetidae are abundant within the Olifants River and a large food source for fish. Mayflies are generally known for the breaking down and cycling of nutrients, and filtering water (Jacobus *et al*. 2019). Loss of these invertebrate families may disrupt the overall balance and functioning of aquatic ecosystems. Primary productivity has also been found to increase with an increase in temperature, and this includes algal biomass (Petchey 2000, Friberg *et al*. 2009). Algal diversity and biomass increases with temperature to ~30° C as different classes of algae dominate at varying temperatures (DeNicola 1996, Dallas 2008). This succession is from the family Bacillariophyceae (diatoms) (< 20° C) to the Chlorophyceae (green algae) (15-30° C), to the Cyanophyceae (blue- green algae) (> 30° C), and above 30° C, a few Cyanobacteria dominate (DeNicola 1996). Within the Olifants River, the algivorous *Labeo* species are all predicted to be vulnerable to the effects of climate warming. As this system already suffers from eutrophication due to high phosphate levels and is prone to algal blooms (Retief & Pollard 2020), loss of species that help regulate algae populations will likely exacerbate this situation.

Habitat loss, pollution, and climate change have been shown to influence disease transmission in freshwater systems (Riley *et al*. 2008, Johnson & Paull 2011, Cable *et al*. 2017). Within the Olifants River, diseases such as diarrhoea, dysentery, cholera, bilharzia, and typhoid are known to occur, with consumption of fish and water being major risk factors (Garland *et al*. 2014). This highlights the need for not only good water management, but for a healthy ecosystem and trophic dynamics within the system. Mosquitoes are known for transmitting diseases in southern Africa, negatively affecting human and animal health, with malaria being of main concern (World Health Organization 2020). Rivers harbour natural predators for mosquito larvae as a form of population control namely: dragonfly (Odonata) larvae from the families Gomphidae, Coenogrionidae and Libellulidae, saucer bugs from the families Naucoridae and Notonectidae, *O. niloticus*, *O. mossambicus*, mosquito fish (*Gambusia affinis*), the common guppy (*Poecilia reticulate*), and the larvivorous family Cyprinidae (Howard *et al*. 2007, Quiroz-Martinez & Rodríguez-Castro 2007, Kamatchi *et al*. 2016, Noreen *et al*. 2017, Vatandoost 2021). The current study showed that the cyprinids such as *E. trimaculatus* and *E. viviparus*, and the families Naucoridae, Notonectidae and Coenogrionidae are under threat from climate warming which is particularly alarming as they are known mosquito predators. Only *O. mossambicus* may not be affected by warmer water conditions. This highlights the need to maintain functional diversity within the system in order to maintain ecosystem services and aid disease suppression and in turn serve as an example of how a disruption in the trophic cascade may not only lead to ecological consequences, such as the top-down effects mentioned previously, but also has wider human health implications.

Another disease of concern within the Olifants River is pansteatitis, which is an inflammatory disease that led to mass-mortalities in Nile crocodiles (*Crocodylus niloticus*) and fish (Woodborne *et al*. 2012). Pansteatitis prevalence in *C. gariepinus*, increases as the fish feed on more fish than vegetation (Woodborne *et al*. 2012). With the predicted potential loss of the apex predator, *H. vittatus*, the niche of a piscivore will be occupied by *C. gariepinus*, therefore increasing the likelihood of spreading pansteatitis within the Olifants River. Furthermore, *C. gariepinus* is harvested both commercially and for subsistence which leads to concerns about food security.

The hypothesis in this study that there will be trophic cascades and future impacts under different climate change scenarios, and their associated threats due to trophic disruptions on the Olifants River ecosystem is not rejected, as the current study has shown that changes in community structure will have detrimental effects on the overall ecosystem functioning. The limitations of this study are that two of the study sites were only sampled during winter, however, many of the species recorded to occur in the Olifants River (Skelton 2001) were sampled. The current study also shows the importance of well-curated samples from previous studies lending to monitoring effects of climate change studies (Woodborne *et al*. 2012, Myburgh 2016, 2019, Kaiser 2019). The present study showed that stable isotopes are an effective method to show the impacts climate change will have on trophic interdependencies within the system. Warmer water will affect predator-prey interactions which will disrupt food web dynamics and ultimately negatively affect ecosystem services. These may lead to negative impacts on food security and an increase in disease prevalence, which has implications on human health.

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Chapter 6

General discussion

Anthropogenic disturbances including climate change are affecting freshwater systems globally. While these effects are often studied as changes in temperature, the ecological impacts on fish species and macroinvertebrates in river systems need to be considered. A statistical air-water temperature regression model was calibrated and validated for the lower Olifants River, Limpopo Province South Africa, and verified in its tributary, the upper Klaserie River. The two rivers, while geographically similar, differ in altitude, depth, flow, water volume and stream order. The results showed that at both a monthly and daily temporal scale, simulated water temperatures closely mirrored the observed data. The Nash-Sutcliffe efficiency (NSE) index is a widely used statistic for validating water models, and studies have found that NSE values of ≥ 0.75 are considered *very good* (Moriasi *et al*. 2007). Our NSE values for the Olifants River water temperature model were > 0.9 for monthly and > 0.75 for daily timesteps, indicating the robustness of this model.

The validated model was then used to predict average water temperatures (WT_{avg}) from air temperature to project monthly and daily WT_{avg} from 2021 to 2100 CE in the Olifants River under the Representative Concentration Pathway (RCP) 8.5 scenario using 16 General Circulation Models (GCMs) (Moss *et al*. 2010b). The results showed that monthly WT_{avg} will increase by 3.7° C, and maximum WT_{avg} will reach 33.6° C by 2100 CE. The daily results showed a similar increase of 3.9° C, with some extreme days reaching 42-44° C, and maximum WT_{avg} increases to 41.1° C by 2100 CE.

Given these rises in monthly and daily temperatures, the study then assessed the effect such temperatures could have on fish and macroinvertebrate communities in the Olifants River under chronic (i.e., an impact that will eventually have severe consequences if it occurs often enough and/or at high enough levels) and acute (i.e., a severe impact over a short duration) stressors (Borgwardt *et al*. 2019). The study found that 12 of the 15 fish species and 11 of the 14 macroinvertebrate families will be susceptible to acute thermal stress and are at risk to mass die-off events while five fish species and one macroinvertebrate family will be vulnerable to extinction. The loss of these species will have effects on the trophic cascade and was investigated using SIA (Pace *et al*. 1999). This study extrapolates that the dynamics will change within the river; top-down effects will occur with the loss of predators and insectivores, leading to over-proliferation of prey and plants. As all algivorous fish are under threat, this also may cause populations of algae to increase exponentially.

The status of research hypotheses tested in the present study

The following are the research hypotheses tested in the four data chapters in this study and their status:

Hypothesis 1 (Chapter 2):

Null hypothesis (H_o): Temperature in the Olifants River is driven by many variables and is too computationally complex to provide reasonable, biologically relevant predictions of water temperature; and

Alternative hypothesis (H_a): Water temperature of the Olifants River is closely linked to air temperature of the region and this relationship can be validated using statistical modelling.

Status: Statistical modelling was used to calibrate and validate a water temperature model for the lower Olifants River at both monthly and daily timescales (NSE > 0.75). The model was further validated using the Klaserie River (NSE > 0.80) to assess the applicability in other rivers. Therefore, the null hypothesis rejected in favour of the alternative hypothesis.

Hypothesis 2 (Chapter 3):

H_o: Climate change and associated rise in air temperature will have no effect on the Olifants River; and

H_a: Climate change will fundamentally alter the temperature regime of the Olifants River, and this can be observed in future projections of water temperature.

Status: Projections of WT_{avg} from 16 GCMs showed monthly WT_{avg} will increase by 3.7° C, and daily WT_{avg} will increase by 3.9° C to 2100 CE. There is also evidence that monthly and daily maxima will increase, suggesting that the temperature regimes of the Olifants River will change and the null hypothesis was rejected in favour of the alternative hypothesis.

Hypothesis 3 (Chapter 4):

H_o: Climate change will have no effect on the thermal niches of fauna in the Olifants River;

H_a: Climate change-induced variation in water temperature will exceed thermal maxima of aquatic organisms and cause extinctions and mass die-offs of species within the Olifants River.

Status: With predicted maximum daily and monthly WT_{avg} reaching 33.6° C and 41.1° C respectively, the results showed that 12 fish species and nine macroinvertebrate families are potentially under threat of mass mortality events and/or local extinctions. The null hypothesis, therefore, is rejected in favour of the alternative hypothesis.

Hypothesis 4 (Chapter 5):

H_o: Climate change will not affect the trophic structure within the Olifants River;

H_a: The warming of water will lead to extinctions within the Olifants system and disruptions in its trophic interdependencies.

Status: Results from SIA of fish and macroinvertebrates within the Olifants River show the possible trophic disruptions by 2100 CE which include top-down effects from loss of predators and insectivores and major impacts on the algae populations due to loss of algivores. These results favour the alternative hypothesis and therefore, the null hypothesis was rejected.

Implications from the present study

The present study contributes to the growing body of knowledge on the effects of climate change within freshwater ecosystems. The statistical model used shows that simple methods can be used to model current and future water temperatures within rivers. While there may be other factors that affect water temperature, this simplistic approach can be applied in data-deficient regions, where temperature monitoring has not been undertaken. Previous studies have shown that models driven by air temperature parameters accurately predict water temperature, while adding additional variables can reduce accuracy and lead to equifinality (Beven 2001, 2006, Hreiche *et al*. 2002, Rivers-Moore *et al*. 2008a, Lu *et al*. 2009). The use of future water temperature projections on observing the effects of climate change at an individual level, by comparison of the critical thermal maximum of taxa, and at a community level, by SIA, appears a novel mechanistic approach. Previous studies have been conducted on the potential impact of warm water on invertebrates and fish, this is often undertaken under laboratory conditions (Dallas 2008) and/or only focuses on one or a few of the taxa present within the river, and not the entire community. Petchey *et al*. (1999) illustrated community level change was, and while this is an important study in this field, it was also conducted on aquatic microbes under laboratory conditions. Additionally, the SIA approach in the present study of observing changes in food web dynamics under climate changes scenarios is novel. Friberg *et al*. (2009) used SIA to identify a $\delta^{15}N$ increase across trophic levels with an increase in temperature but did not observe functional of community changes in their study.

The use of future water temperature projections on observing the effects of climate change at an individual level (by comparing critical thermal maximum of taxa) and at a community level (by SIA) appears to be a novel mechanistic approach. While this study was conducted at a single locality, it was anticipated that this approach can be duplicated in rivers worldwide, particularly in similarly heavily polluted and over-abstracted data-deficient freshwater systems. As climate change and rising water temperatures becomes an increasing issue in freshwater ecosystems, compounded with other anthropogenic effects, the need for this kind of simple method that ranges from air temperature to future water temperature to the implications on freshwater fauna is ideal.

Previous studies on impacts of warming have often been conducted under laboratory conditions (Petchey *et al*. 1999, Dallas 2008). While Friberg *et al*. (2009) showed the importance of SIA with increased temperature, functional feeding ecology or individual vulnerability was not taken into account to assess the effect of climate change on the trophic cascade. The three-pronged approach in this study that combines: 1) a mechanistic approach of statistical modelling of future water temperature; 2) the evaluation of thermal tolerances; and 3) and the assessment of trophic cascades using SIA and applies them to evaluate faunal changes at both the population and community levels is novel and is ideal for future studies that could also consider the inclusion of additional approaches to be considered.

A global perspective

The present study shows the consequences of climate change scenarios on freshwater fauna, but the effects of the changes in water temperature will not be limited to the taxa studied in this study. For example, a study in South Africa which included mammals, birds, and terrestrial reptiles and invertebrates under a 2.5-3° C change by 2050 showed 78% of species will contract their distributional ranges, mostly in an easterly direction, suggestion that the KNP may lose up to 66% of the species within the study area (Erasmus *et al*. 2002). However, this study does not include aquatic or semi aquatic species, which will undoubtedly make the number of species lost in the KNP even higher.

Human health and persistence are likely to be greatly affected in future as the United Nations International Children's Emergency Fund (UNICEF) (UNICEF 2023) reported that "*a change in climate is felt primarily through a change in water*". The organization reported that climate change is increasing the intensity and frequency of water-related natural disasters, increasing risk of contaminants, pathogens and diseases, exacerbates water stress and increases salinization of fresh water sources (UNICEF 2023). Research supports this, showing increases in extreme weather events (Moreno & MØller 2011), increase in salinization causing trophic disruptions (Castillo *et al*. 2018b, Iglesias 2020) and increase in disease transmission (Riley *et al*. 2008, Johnson & Paull 2011, Cable *et al*. 2017) in freshwater systems under threat of climate change. While the present study does not directly address the above issues, modelling water temperatures represents the first critical step in understanding these issues, and such monitoring needs to be implemented worldwide.

Globally, it is estimated that 126 000 plant and animal species rely on freshwater habitats (Schmutz & Sendzimir 2018). Animals that utilize freshwater ecosystems are not limited to fish, but also include amphibians, water birds, and reptiles, and these are predicted to be five times more vulnerable to extinctions than terrestrial species (Revenga *et al*. 2000). Freshwater fish have an estimated 35-37% of species at risk and are one of the most vulnerable groups facing extinction (Kaufman 1992, Collares-Pereira & Cowx 2004, Helfman *et al*. 2009, Hoffmann *et al*. 2010, Griffiths *et al*. 2015). However, many studies show that the group most under threat are amphibians with up to 44% of species vulnerable to climate change (Foden *et al*. 2013). Although some salt-tolerant species have been identified, these organisms rely exclusively on freshwater aquatic systems for their reproduction and survival (Hopkins & Brodie 2015). Crocodilians, which are reptilian predators, are also under threat (Maciejewski 2006, Fukuda *et al*. 2022). These threats include sea level rises, climate change-induced temperature increases, human conflict, loss of habitat and prey and increase in disease prevalence (Maciejewski 2006, Utete 2021, Fukuda *et al*. 2022). One of the greatest threats to Crocodilians is the sex of the hatchlings is determined by the incubation temperature of the eggs and with rising temperatures due to climate change, there could be a skewed sex ratio as well as affect the survival of eggs and hatchlings (Maciejewski 2006, Fukuda *et al*. 2022). What has not been investigated, is the potential effects of warmer water on these semi- aquatic reptiles. Crocodiles, such as the Nile crocodile (*Crocodylus niloticus*) which occurs throughout Africa, is an ectotherm that relies on environmental temperature to maintain an optimal body temperature (Viljoen *et al*. 2023). It employs behaviours such as basking, gaping, burrowing and shuttling to water as thermoregulatory mechanisms (Downs *et al*. 2008, Viljoen *et al*. 2023). Previous studies found that *C. niloticus* attains maximum body temperatures of between 26.9 and 29.2° C and average back temperatures of 30.4° C (Downs *et al*. 2008, Viljoen *et al*. 2023). As the maximum temperatures are reached, it is assumed *C. niloticus* would shuttle to water to cool off, but as some of the climate change predictions in the present study are showing maximum monthly temperatures of 33.6° C which is above these reptiles' maximum body temperature, this could be a new challenge facing the species.

Study limitations

There are some limitations of this study: (1) The simple statistical model assumed that air temperature is the sole driver of water temperature (Adlam *et al*. 2022). While the present study found that it is a significant factor affecting water temperature, there are other factors that differentially influence water temperature such as flow, humidity, evaporation, and channel characteristics (Rivers-Moore *et al*. 2005, Dallas & Rivers-Moore 2019). (2) There was only one study site (Mamba Weir) on the Olifants River where the present study was able to obtain temperature data, and so the study was unable to compare temperature between sampling sites, or between different rivers such as conducted by Friberg *et al*. (2009). Such data are scarce across all the rivers in Africa, and this limitation is likely to be ubiquitous, but the impact of climate change on ecosystem services offered by rivers that is highlighted in this study also motivates for further instrumentation of rivers. For example, as temperature increases, the concentration of dissolved oxygen in water decreases and there is less oxygen available for aquatic organisms to utilise (Dallas 2008, Bello *et al*. 2017). Morrill *et al*. (2005) showed that sites on a river that had low dissolved oxygen would fall into the critically low range with future increase in water temperatures. This highlights the need to monitor a range of physical and chemical characteristics of water in order to understand and mitigate the effects of climate change. Additionally, studies of thermal maximum for fishes and macroinvertebrates are scarce, which resulted in some taxa being excluded from the present study. The studies found on macroinvertebrates also only use adult individuals, and so the impact on young individuals is unknown. Furthermore, fish sampling methods such as electrofishing often only yields smaller body sized individuals, giving body size bias to populations. Given the difficulty of sampling within the Olifants River due to rapid water and the presence of dangerous wild animals, it is also possible that some taxa have been missed during sampling initiatives, resulting in an incomplete trophic web structure. (3) There is also the unavoidable impact of COVID-19 on the present study as research activities were suspended due to the pandemic and field studies were impossible during the study period. The impacts of COVID-19 were experienced worldwide by researchers (Radecki & Schonfeld 2020, Gao *et al*. 2021).

Recommendations

Algal blooms

The Olifants River is polluted, and high phosphate levels have caused eutrophication in the system which has led to algal blooms (Retief & Pollard 2020). Given that primary production, algae diversity and biomass increases with increasing temperatures (Petchey 2000, Friberg *et al*. 2009), the frequency and intensity of algal blooms is likely to increase. This is compounded by the potential loss of the four algivorous *Labeo* fish species which may have aided in alleviating this issue. While this is an example at a single locality, this may be an issue worldwide as river ecosystems are already threatened by pollution and this problem will increase as the human population increase, exacerbated by climate change, this will make algal blooms within freshwater rivers in South Africa a significant problem. The invasive planktivorous silver carp (*Hypophthalmichthys molitrix*) was introduced into South Africa to control such algal blooms and occurs in Lake Massingir downstream from the lower Olifants River (Lübcker *et al*. 2016, Sara *et al*. 2018). However, chemical analyses on these algae have proven to be toxic, and this fish species does not occur in the Olifants River, only in its impoundments.

As algal blooms are caused by eutrophication and trophic disruptions within the river system (Jeppesen *et al*. 2010, Schmutz & Sendzimir 2018), the mitigation for such a problem can only be to monitor pollutants that enter the river. This would require baseline water quality studies of the river and then monitoring of microbial and nutrient contaminants that may enter the river system. Additionally, efforts should be initiated to monitor and conserve our indigenous algivorous species.

Disease

Disturbed ecosystems or disrupted trophic cascades are likely to be negatively impacted by diseases (Riley *et al*. 2008). Within the Olifants River, this is already being observed with the prevalence of pansteatitis in Nile crocodiles and fish (Woodborne *et al*. 2012). This disease may become a challenge as its most prevalent in fish, *C. gariepinus*, becomes more predatory with the loss of *H. vittatus* within the river and spread the disease further (Woodborne *et al*. 2012). There is also the threat of out-breaks of pest species such as blackflies as ecological communities are disturbed (Rivers-Moore *et al*. 2008b). In addition, the potential impacts on human health as invertebrate and fish taxa that are known for controlling malaria and other vector-borne diseases are under threat of climate change (Howard *et al*. 2007, Quiroz-Martinez & Rodríguez-Castro 2007, Kamatchi *et al*. 2016, Noreen *et al*. 2017, Vatandoost 2021). While this may not be an immediate threat in this region, it represents a global example of the importance of ecosystem health. As malaria and other vector-borne diseases spread with the warming of regions, maintaining their natural predators as biological control is imperative.

Invasive species

With the increase of water temperatures, colder water species that are unable to adapt will be replaced by warmer water species (Rahel & Olden 2008, Záhorská 2016). Within the Olifants River, the invasive *H. molitrix* is a concern as it is shown to have a high thermal limit and may invade reaches of the river in which it has yet to be recorded (Woodborne *et al*. 2012). This species was introduced to control algae populations (Lübcker *et al.* 2016), and as recommended above, this can be avoided by the monitoring of rivers as well as maintaining the naturally-occurring algivores such as the *Labeo* species.

Fish species are also often introduced for their aquacultural importance and then out-compete the native species and disrupt ecosystems, such as *O. niloticus* (Marshall 2011). This species has a high thermal tolerance which also makes it an ideal aquacultural model in warm regions, however, indigenous species such as *C. gariepinus* and *O. mossambicus* also have high thermal tolerances, and are less susceptible to low oxygenation and drought conditions (Huisman & Richter 1987, Skelton 2001, Marshall 2011, Polacik & Podrabsky 2015). Therefore, to avoid further invasive species being introduced due to the aquaculture industry, management initiatives need to refer to studies on native species alternatives that can be mass-reared and withstand current and future warm water conditions.

This concern is not limited to non-native species as water temperature rises, species may shift thermal habitats and establish extra-limital distributions which may also have an impact on the trophic interdependencies of the system. However, this is unavoidable as it is being observed in various taxa worldwide with organisms moving either pole-wards or to higher elevations (Parmesan & Yohe 2003, Parmesan 2006a, Thuiller 2007, Chen *et al*. 2011). While this has been observed in fish species (Comte & Grenouillet 2013), it is unlikely that they will be able to track the rapid rate of climate change (Isaak & Rieman 2013). The loss of species due to climate change and biological invasions may lead to homogenization of ecosystems and resultant loss of Beta-diversity between systems (Socolar *et al*. 2016). Beta-diversity is the component of regional biodiversity that accumulates due to inter-site differences between local species assemblages (Socolar *et al*. 2016). A study on future climate change predictions within the Adour- Garonne River Basin, France, showed fish assemblages would be modified to more similar, homogenized composition (Tisseuil *et al*. 2012), thus decreasing the overall Beta- diversity. A similar study conducted in France by Buisson & Grenouillet (2009) found similar results, and predicted that climate change could lead to both taxonomic and functional homogenization in fish assemblages. This is also a concern in the current study, as extinctions and invasions may cause homogenization of the Olifants River fish diversity.

Further studies

Thermal variability within rivers has not been considered in the context of how freshwater fauna may use thermal refugia during heat stress. It is implied that water temperature is uniform, however further studies on the change in temperature with depth for example, will elucidate whether species can shift thermal habitats within a river environment in order to escape warm temperatures. This kind of research can allow better insights into how freshwater fauna utilise thermal niches and partition these spatially and temporally, and what mechanisms are employed during extreme temperatures. This could provide an understanding of the “thermal landscape” of freshwater systems. There is also a critical need for more data collection within southern Africa. For example, higher temperature is known to decrease concentration of dissolved oxygen which also negatively effects freshwater fauna. The consequences of increased temperatures and reduced flow may also translate into the receding of ephemeral headwater streams. These streams have been established as refugia for threatened species and therefore the impacts of losing these pristine waters also need to be investigated. The two possible scenarios are that the headwaters recede, and the vulnerable species are lost, or that they successfully colonise downstream sites.

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Appendix

Stable Isotopes

Mamba Weir

Taxa	δ^{15}N	δ^{13}C
Baetidae	12,9	-18,9
Baetidae	13,6	-21,4
Baetidae	13,2	-21,8
Baetidae	12,4	-20,2
Belostomatidae	13,0	-19,9
Chiloglanis paratus	11,5	-19,1
Chironomidae	8,7	-16,8
Chironomidae	13,1	-19,8
Clarias gariepinus	14,7	-18,7
Clarias gariepinus	14,8	-19,3
Clarias gariepinus	16,2	-17,1
Clarias gariepinus	14,2	-19,2
Clarias gariepinus	14,4	-20,0
Clarias gariepinus	14,5	-19,0
Clarias gariepinus	14,7	-18,7
Clarias gariepinus	15,2	-18,8
Clarias gariepinus	15,5	-16,2
Clarias gariepinus	15,7	-19,5
Coenagrionidae	13,4	-20,2
Enteromius trimaculatus	9,1	-20,0
Enteromius trimaculatus	12,2	-17,4
Enteromius trimaculatus	12,3	-17,4
Enteromius trimaculatus	12,5	-18,3
Enteromius trimaculatus	13,8	-18,0
Enteromius trimaculatus	13,7	-17,6
Enteromius viviparus	13,9	-17,8
Enteromius viviparus	13,7	-18,5
Enteromius viviparus	11,8	-21,9
Enteromius viviparus	13,2	-19,0
Enteromius viviparus	13,1	-19,3
Enteromius viviparus	14,3	-19,5
Enteromius viviparus	11,8	-19,4
Enteromius viviparus	12,0	-19,5
Enteromius viviparus	13,7	-20,1
Enteromius viviparus	14,2	-19,4
Enteromius viviparus	14,0	-19,4
Enteromius viviparus	14,1	-20,0
Gerridae	12,5	-18,7
Gerridae	12,3	-18,7
Gomphidae	12,6	-21,1
Gomphidae	13,3	-19,3
Hydropsychidae	11,5	-20,9
Hydropsychidae	12,4	-21,8
Hydropsychidae	12,3	-22,2
Hydropsychidae	12,7	-22,1
Labeo cylindricus	14,8	-24,6
Labeo cylindricus	13,5	-19,5
Labeo cylindricus	15,4	-21,9
Labeo cylindricus	15,4	-19,3
Labeo cylindricus	14,8	-22,8
Labeo cylindricus	15,2	-25,1
Labeo cylindricus	15,2	-24,3
Labeo cylindricus	15,6	-24,6
Labeo cylindricus	14,1	-18,3
Labeo cylindricus	13,9	-19,2
Labeo molybdinus	15,2	-20,2
Labeo molybdinus	14,3	-19,1
Labeo molybdinus	15,2	-22,5
Labeo molybdinus	15,3	-23,2
Labeo molybdinus	14,8	-21,6
Labeo molybdinus	15,3	-23,0
Labeo molybdinus	15,2	-23,9
Labeo molybdinus	15,6	-23,0
Labeo molybdinus	15,6	-22,1
Labeo molybdinus	14,0	-25,1
Labeo molybdinus	15,6	-21,0
Labeobarbus marequensis	14,6	-18,9
Labeobarbus marequensis	13,6	-17,7
Labeobarbus marequensis	14,4	-17,6
Labeobarbus marequensis	15,5	-20,8

Labeobarbus marequensis	12,9	-17,7
Leptoceridae	11,9	-22,0
Libellulidae	12,5	-19,8
Libellulidae	12,3	-24,1
Libellulidae	12,5	-23,5
Libellulidae	12,8	-22,5
Naucoridae	12,1	-20,4
Oreochromis mossambicus	13,5	-17,6
Oreochromis mossambicus	11,1	-17,4
Oreochromis mossambicus	12,0	-19,8
Oreochromis mossambicus	13,5	-19,5
Oreochromis mossambicus	13,6	-17,7
Oreochromis mossambicus	11,6	-20,1
Oreochromis mossambicus	12,1	-19,8
Oreochromis mossambicus	12,8	-17,6
Oreochromis mossambicus	13,3	-18,2
Oreochromis mossambicus	12,9	-18,0
Oreochromis mossambicus	12,6	-18,2
Oreochromis mossambicus	14,6	-17,7
Oreochromis mossambicus	14,3	-17,3
Oreochromis mossambicus	12,7	-16,5
Oreochromis mossambicus	11,8	-17,4
Oreochromis mossambicus	14,0	-17,3
Oreochromis mossambicus	14,6	-21,2
Oreochromis mossambicus	13,4	-17,9
Oreochromis mossambicus	12,7	-18,5
Oreochromis mossambicus	12,8	-18,4
Oreochromis mossambicus	14,6	-19,4
Oreochromis mossambicus	13,2	-17,9
Oreochromis mossambicus	13,2	-17,9
Oreochromis mossambicus	10,6	-18,6
Physidae	12,1	-15,3
Teloganodidae	12,0	-18,3
Thiaridae	11,3	-19,9
Thiaridae	12,0	-19,5
Veliidae	11,1	-21,1
Veliidae	12,2	-18,7
Veliidae	13,1	-19,3

Balule Weir

Baetidae	8,4	-22,6
Baetidae	7,5	-22,3
Baetidae	8,6	-23,0
Baetidae	8,5	-22,8
Brycinus imberi	13,6	-18,3
Brycinus imberi	12,9	-18,6
Brycinus imberi	13,4	-18,1
Brycinus imberi	14,9	-19,0
Caenidae	8,2	-21,6
Caenidae	7,8	-20,7
Clarias gariepinus	13,1	-16,8
Clarias gariepinus	15,9	-16,5
Clarias gariepinus	13,2	-15,1
Clarias gariepinus	13,7	-16,5
Clarias gariepinus	12,2	-19,7
Clarias gariepinus	12,6	-18,3
Clarias gariepinus	12,6	-17,8
Clarias gariepinus	15,8	-16,6
Coenagrionidae	9,5	-23,1
Elmidae	8,2	-22,0
Elmidae	8,4	-21,9
Enteromius trimaculatus	13,7	-17,5
Enteromius trimaculatus	12,4	-17,0
Enteromius trimaculatus	11,1	-15,2
Enteromius trimaculatus	13,3	-18,2
Gomphidae	10,2	-19,9
Gomphidae	9,1	-21,8
Hydropsychidae	9,1	-24,0
Hydropsychidae	9,2	-24,5
Labeo congoro	12,2	-20,2
Labeo congoro	12,1	-15,9
Labeo congoro	13,0	-22,4
Labeo cylindricus	12,1	-21,6
Labeo cylindricus	12,2	-22,4
Labeo cylindricus	12,6	-21,7
Labeo cylindricus	12,2	-23,8
Labeo cylindricus	12,5	-22,9
Labeo rosae	9,1	-19,9
Labeo rosae	9,3	-19,7
Labeo rosae	9,1	-19,8
Labeo rosae	9,2	-19,8
Labeo rosae	9,5	-20,3
Labeo rosae	9,5	-20,1
Labeo rosae	9,7	-20,8
Labeo rosae	13,9	-18,0

Labeo rosae	11,4	-18,4
Labeobarbus marequensis	12,3	-22,7
Labeobarbus marequensis	12,5	-20,4
Labeobarbus marequensis	13,4	-20,1
Labeobarbus marequensis	12,2	-22,3
Labeobarbus marequensis	12,0	-21,6
Labeobarbus marequensis	11,9	-20,8
Labeobarbus marequensis	12,0	-20,1
Labeobarbus marequensis	12,3	-19,2
Labeobarbus marequensis	11,7	-18,0
Labeobarbus marequensis	13,2	-18,3
Labeobarbus marequensis	14,4	-19,3
Leptoceridae	8,1	-23,9
Leptoceridae	9,2	-22,4
Libellulidae	9,7	-23,3
Libellulidae	9,7	-21,7
Libellulidae	9,6	-23,4
Naucoridae	8,9	-21,6
Naucoridae	7,3	-22,1
Naucoridae	6,3	-22,1
Oreochromis mossambicus	9,7	-17,5
Oreochromis mossambicus	9,7	-18,8
Oreochromis mossambicus	10,5	-18,1
Oreochromis mossambicus	9,9	-18,9
Oreochromis mossambicus	10,1	-18,2
Oreochromis mossambicus	10,2	-21,2
Oreochromis mossambicus	8,9	-18,6
Oreochromis mossambicus	10,3	-17,9
Oreochromis mossambicus	9,6	-18,2
Oreochromis mossambicus	10,5	-17,4
Oreochromis mossambicus	9,6	-18,8
Oreochromis mossambicus	11,1	-19,3
Simuliidae	8,1	-21,1
Tabanidae	10,2	-27,7
Tabanidae	10,7	-21,9
Thiaridae	9,7	-22,2
Thiaridae	9,7	-20,8
Thiaridae	8,6	-22,1
Thiaridae	9,2	-20,6
Veliidae	10,2	-21,7
Veliidae	10,3	-22,2

Olifants River Gorge

Baetidae	7,5	-22,5
Baetidae	10,3	-27,8
Baetidae	10,3	-26,0
Baetidae	9,7	-27,3
Baetidae	11,0	-23,2
Baetidae	11,0	-24,0
Baetidae	10,9	-22,6
Baetidae	10,4	-22,7
Baetidae	10,7	-26,7
Baetidae	10,9	-27,8
Baetidae	7,8	-28,2
Baetidae	6,7	-28,1
Baetidae	8,9	-27,6
Baetidae	10,3	-25,9
Baetidae	11,0	-26,6
Baetidae	7,7	-27,3
Baetidae	7,9	-23,7
Baetidae	10,4	-27,1
Baetidae	6,5	-23,3
Baetidae	9,1	-22,6
Caenidae	10,0	-26,2
Caenidae	5,4	-29,1
Chiloglanis paratus	13,4	-21,1
Chiloglanis paratus	14,5	-21,2
Chiloglanis paratus	13,3	-21,8
Chiloglanis paratus	12,3	-21,0
Chiloglanis paratus	12,8	-21,8
Chiloglanis paratus	12,8	-21,5
Chiloglanis paratus	13,8	-21,9
Chiloglanis paratus	11,5	-21,6
Chiloglanis paratus	12,1	-21,9
Clarias gariepinus	15,5	-19,2
Clarias gariepinus	16,1	-21,1
Clarias gariepinus	15,8	-19,3
Clarias gariepinus	13,5	-18,2
Clarias gariepinus	13,6	-17,9
Clarias gariepinus	13,6	-19,3
Clarias gariepinus	13,7	-20,0
Clarias gariepinus	14,2	-18,5
Clarias gariepinus	13,2	-20,2
Clarias gariepinus	11,9	-19,4
Clarias gariepinus	12,0	-19,1

Clarias gariepinus	14,7	-20,0
Clarias gariepinus	13,0	-19,2
Clarias gariepinus	9,9	-19,6
Clarias gariepinus	13,8	-19,2
Clarias gariepinus	11,4	-19,0
Clarias gariepinus	14,3	-19,9
Clarias gariepinus	13,6	-19,7
Clarias gariepinus	10,8	-16,1
Clarias gariepinus	9,8	-16,9
Coenagrionidae	7,5	-25,5
Coenagrionidae	7,4	-25,0
Coenagrionidae	11,7	-23,7
Coenagrionidae	12,0	-24,9
Coenagrionidae	12,1	-24,2
Coenagrionidae	11,2	-25,2
Coenagrionidae	11,8	-24,2
Coenagrionidae	11,7	-24,5
Coenagrionidae	11,7	-23,7
Coptodon rendalli	10,8	-21,1
Elmidae	9,6	-21,9
Elmidae	7,8	-13,7
Elmidae	9,0	-23,2
Glossogobius giuris	14,5	-18,9
Glossogobius giuris	14,2	-19,4
Glossogobius giuris	12,8	-20,7
Glossogobius giuris	12,8	-20,8
Glossogobius giuris	12,8	-20,7
Glossogobius giuris	11,8	-22,0
Glossogobius giuris	13,6	-22,9
Glossogobius giuris	13,5	-22,3
Glossogobius giuris	14,7	-23,2
Glossogobius giuris	14,1	-18,9
Glossogobius giuris	13,1	-14,4
Glossogobius giuris	12,1	-18,9
Glossogobius giuris	10,5	-19,2
Glossogobius giuris	11,4	-16,6
Glossogobius giuris	12,8	-17,9
Glossogobius giuris	14,0	-20,8
Glossogobius giuris	14,7	-21,6
Glossogobius giuris	14,4	-21,3
Glossogobius giuris	11,3	-21,5
Glossogobius giuris	12,0	-22,5
Gomphidae	9,9	-18,3

Gomphidae	9,0	-24,5
Gomphidae	11,7	-23,1
Gomphidae	12,3	-25,2
Gomphidae	12,4	-25,8
Gomphidae	11,9	-24,1
Gomphidae	12,3	-24,7
Gomphidae	11,7	-24,8
Gomphidae	12,8	-26,0
Gomphidae	10,7	-20,4
Gomphidae	11,1	-19,8
Gomphidae	10,9	-19,7
Gomphidae	10,3	-20,2
Gomphidae	9,8	-21,4
Gomphidae	9,8	-20,6
Gomphidae	10,3	-21,1
Gomphidae	10,3	-19,4
Gomphidae	10,2	-19,3
Gomphidae	10,8	-19,2
Gyrinidae	9,3	-25,8
Gyrinidae	10,5	-25,4
Gyrinidae	10,9	-24,2
Gyrinidae	10,5	-24,7
Gyrinidae	11,6	-22,5
Gyrinidae	10,5	-22,9
Gyrinidae	10,7	-23,0
Gyrinidae	10,9	-21,7
Heptagenidae	8,6	-27,8
Hydrocynus vittatus	14,1	-21,0
Hydrocynus vittatus	14,7	-24,8
Hydrocynus vittatus	12,7	-24,1
Hydrocynus vittatus	11,9	-19,2
Hydrocynus vittatus	12,5	-21,7
Hydrocynus vittatus	11,1	-27,2
Hydrocynus vittatus	13,1	-21,1
Hydrocynus vittatus	13,4	-23,9
Hydrocynus vittatus	12,9	-23,7
Hydrocynus vittatus	11,3	-19,2
Hydrocynus vittatus	13,8	-21,4
Hydrocynus vittatus	13,9	-25,0
Hydrocynus vittatus	14,0	-24,2
Hydrocynus vittatus	14,7	-23,9
Hydrocynus vittatus	14,4	-24,3
Hydrocynus vittatus	15,4	-24,3

Hydrocynus vittatus	11,8	-18,2
Hydrocynus vittatus	17,9	-21,5
Hydrocynus vittatus	16,6	-19,6
Hydrocynus vittatus	17,4	-21,2
Hydropsychidae	9,7	-24,0
Hydropsychidae	8,2	-22,0
Hydropsychidae	11,0	-23,4
Hydropsychidae	10,7	-22,8
Hydropsychidae	11,1	-23,5
Hydropsychidae	11,1	-23,8
Hydropsychidae	11,2	-24,6
Hydropsychidae	9,0	-23,6
Hydropsychidae	10,3	-23,1
Labeo congoro	9,9	-20,8
Labeo congoro	10,6	-18,2
Labeo cylindricus	13,6	-24,0
Labeo cylindricus	11,1	-23,6
Labeo cylindricus	13,4	-23,9
Labeo cylindricus	11,8	-22,7
Labeo cylindricus	11,9	-23,8
Labeo cylindricus	12,2	-21,2
Labeo cylindricus	11,4	-22,3
Labeo cylindricus	10,4	-22,9
Labeo cylindricus	11,9	-21,1
Labeo cylindricus	11,5	-24,8
Labeo cylindricus	10,6	-23,7
Labeo cylindricus	10,7	-24,2
Labeo cylindricus	10,6	-24,1
Labeo cylindricus	13,3	-25,2
Labeo cylindricus	12,3	-26,2
Labeo cylindricus	12,4	-25,4
Labeo cylindricus	13,2	-27,1
Labeo cylindricus	13,5	-25,9
Labeo cylindricus	13,0	-22,7
Labeo molybdinus	11,7	-23,4
Labeo molybdinus	13,4	-22,0
Labeo molybdinus	11,4	-22,3
Labeo molybdinus	13,0	-24,3
Labeo molybdinus	13,3	-23,9
Labeo molybdinus	13,2	-23,8
Labeo molybdinus	10,1	-18,9
Labeo molybdinus	12,3	-20,7
Labeo molybdinus	13,3	-24,1

Labeo molybdinus	13,1	-23,8
Labeo molybdinus	12,3	-23,8
Labeo molybdinus	11,4	-22,3
Labeo molybdinus	11,0	-22,6
Labeo molybdinus	10,7	-23,7
Labeo molybdinus	12,8	-25,7
Labeo molybdinus	12,3	-25,3
Labeo molybdinus	13,3	-21,9
Labeo molybdinus	13,0	-25,0
Labeo rosae	11,0	-19,9
Labeo rosae	11,8	-19,3
Labeobarbus marequensis	11,3	-19,5
Labeobarbus marequensis	12,3	-20,4
Labeobarbus marequensis	12,8	-19,4
Labeobarbus marequensis	10,5	-20,0
Labeobarbus marequensis	13,1	-19,6
Labeobarbus marequensis	14,1	-20,4
Labeobarbus marequensis	14,1	-20,6
Labeobarbus marequensis	12,8	-20,0
Labeobarbus marequensis	13,7	-20,3
Labeobarbus marequensis	13,7	-19,8
Labeobarbus marequensis	14,1	-20,3
Labeobarbus marequensis	13,1	-21,6
Labeobarbus marequensis	12,2	-21,4
Labeobarbus marequensis	13,4	-22,7
Labeobarbus marequensis	13,0	-22,0
Labeobarbus marequensis	12,4	-23,4
Labeobarbus marequensis	13,3	-20,6
Labeobarbus marequensis	13,3	-21,4
Labeobarbus marequensis	13,7	-18,2
Labeobarbus marequensis	14,0	-17,3
Leptoceridae	10,6	-25,9
Leptoceridae	11,5	-26,2
Libellulidae	10,8	-15,9
Libellulidae	10,5	-19,5
Libellulidae	6,6	-26,8
Libellulidae	11,2	-28,4
Libellulidae	10,6	-26,1
Libellulidae	10,5	-25,2
Libellulidae	9,9	-25,6
Libellulidae	9,6	-26,5
Libellulidae	10,7	-27,5
Libellulidae	10,8	-25,2

Naucoridae	7,6	-25,5
Naucoridae	11,9	-26,4
Naucoridae	10,1	-19,4
Naucoridae	9,6	-22,7
Naucoridae	9,3	-21,5
Notonectidae	5,7	-19,2
Notonectidae	6,8	-20,3
Notonectidae	10,0	-13,9
Notonectidae	9,6	-22,5
Notonectidae	11,8	-23,8
Notonectidae	11,3	-23,6
Notonectidae	11,6	-25,7
Oreochromis mossambicus	12,4	-18,0
Oreochromis mossambicus	13,0	-13,9
Oreochromis mossambicus	12,9	-13,7
Oreochromis mossambicus	13,3	-21,4
Oreochromis mossambicus	13,7	-17,4
Oreochromis mossambicus	14,3	-18,0
Oreochromis mossambicus	10,0	-20,7
Oreochromis mossambicus	12,4	-18,4
Oreochromis mossambicus	11,9	-19,0
Oreochromis mossambicus	12,1	-18,4
Oreochromis mossambicus	11,1	-18,7
Oreochromis mossambicus	11,1	-20,4
Oreochromis mossambicus	11,6	-20,0
Oreochromis mossambicus	12,0	-20,0
Oreochromis mossambicus	12,4	-21,5
Oreochromis mossambicus	12,9	-21,2
Oreochromis mossambicus	11,6	-20,7
Oreochromis mossambicus	11,4	-19,9
Oreochromis mossambicus	11,3	-21,4
Oreochromis mossambicus	12,9	-20,0
Pleuroceridae	12,1	-24,8
Pleuroceridae	11,9	-29,1
Pleuroceridae	10,7	-25,6
Pleuroceridae	11,0	-25,3
Pleuroceridae	11,1	-22,6
Pleuroceridae	11,3	-26,7
Pleuroceridae	11,1	-24,6
Pleuroceridae	11,7	-26,2

Pleuroceridae	11,2	-22,5
Pleuroceridae	11,4	-24,7
Simuliidae	8,9	-22,9
Simuliidae	11,9	-26,6
Simuliidae	8,5	-23,3
Thiaridae	9,9	-20,4
Thiaridae	13,1	-19,7
Thiaridae	10,4	-20,2
Thiaridae	8,8	-20,9
Thiaridae	10,9	-20,6
Thiaridae	10,6	-19,8
Thiaridae	10,5	-19,5
Thiaridae	10,8	-20,6
Thiaridae	9,6	-20,4
Thiaridae	11,4	-19,1
Thiaridae	10,1	-20,4
Thiaridae	10,8	-20,4
Thiaridae	10,2	-19,5
Thiaridae	10,6	-17,5
Thiaridae	10,2	-14,6
Thiaridae	10,0	-17,1
Thiaridae	8,8	-18,4
Thiaridae	8,3	-22,8
Tricorythidae	8,9	-26,3
Tricorythidae	8,5	-26,2
Veliidae	11,1	-24,3
Veliidae	11,2	-23,7
Veliidae	11,8	-25,6
Veliidae	11,6	-24,9
Veliidae	10,9	-24,5
Veliidae	11,2	-24,2
Veliidae	10,2	-21,7
Veliidae	9,7	-23,5