
**Vulnerability and adaptability of Africa's inland fisheries to climate change:
An interdisciplinary approach to a multi-dimensional conservation challenge**

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Abstract

The unprecedented rate of contemporary climate warming is affecting ecosystems globally; and inland waters are predicted to be among the most vulnerable as they are already heavily exploited by humans for numerous ecosystem services. My doctoral research examined the effects of climate change on the inland fisheries of continental Africa, with a special focus on the ecological and social consequences for the Lake Victoria basin of East Africa. First, I used a trait-based climate-change vulnerability assessment (CCVA) of African freshwater fishes to document biogeographical patterns of climate change threats across the continent. By integrating species traits with projected climatic changes, I identified regions and species that are most at risk, and demonstrated that nearly 40% of African freshwater fish species are highly vulnerable to climate change. This study was also important in highlighting several cases where classic conservation approaches have overlooked species and regions of climate change concern. In the remainder of this dissertation, I focused on the Lake Victoria basin of East Africa, a region that emerged as highly threatened in the CCVA. In a suite of short- and long-term acclimation experiments, I tested the capacity of a commercially harvested species (the Nile perch, *Lates niloticus*), to cope with climate change stresses through physiological adjustments of their thermal tolerance limits. I acclimated Nile perch to a wide range of temperatures over various exposure times (3-days, 3-weeks, 3-months), and measured changes to upper thermal tolerance, metabolic performance, growth, and organ development among temperatures and acclimation times. I found that Nile perch showed evidence for compensation in upper thermal tolerance and metabolic rate over all exposure times, and demonstrated that temperature-induced cardiac remodelling influenced aerobic function in this species. The key findings of this work challenge long-held assumptions that tropical species have limited thermal plasticity for coping with climate change-related stressors. Finally, I investigated vulnerability and resilience of fishery-based social-ecological systems in the Lake Victoria basin. Household surveys, focus group discussions, and key informant interviews were conducted in five villages ranging from low to high-dependence of fishing to determine how

households and communities are affected by and respond to climate-mediated changes in the fishery. I found that climate change is highly disruptive to fishery-based livelihoods, causing social-ecological feedbacks that tend to entrench households and communities into a singular dependence on an already threatened and declining resource. However, fishers' growing awareness of these interactions can lead to adaptive actions that improve resilience to the ongoing changes in this ecosystem. Overall this thesis provides critical insight into climate change vulnerability of Africa's inland aquatic environments, and highlights several mechanisms that may underlie resilience in fish species and the human communities that rely on them.

Résumé

Le réchauffement climatique contemporain procède à un rythme sans précédent et affecte les écosystèmes à une échelle mondiale. Les eaux intérieures (lacs et rivières) sont parmi les écosystèmes les plus vulnérables de par leur forte exploitation par l'homme pour de nombreux services écologiques. Ma recherche de doctorat porte sur les effets des changements climatiques sur les pêcheries en Afrique continentale, mettant l'emphasis sur les conséquences écologiques et sociales de ces changements dans le bassin du lac Victoria en Afrique de l'Est. En utilisant une approche dite « par traits », j'ai d'abord complété une évaluation de la vulnérabilité aux changements climatiques (EVCC) chez les poissons d'eau douce africains pour documenter les patrons biogéographiques de la menace liée au changement climatique à travers ce continent. En combinant une base de données de traits des espèces et des cartes de changements climatiques prévus, j'ai identifié les régions et les espèces les plus à risque et j'ai démontré que près de 40% des espèces de poissons d'eau douce africains sont très vulnérables aux changements climatiques. Cette étude a par ailleurs mis en évidence plusieurs cas où les approches de priorisation traditionnelles en conservation ont omis certaines espèces ou régions à risque. Pour les autres chapitres de cette thèse, je me suis concentrée sur le bassin du lac Victoria en Afrique de l'Est, une région identifiée comme étant fortement à risque dans l'EVCC. Dans une série d'expériences d'acclimatation à court et à long terme avec une espèce pêchée commercialement dans la région (la perche du Nil : *Lates niloticus*), j'ai d'abord testé la capacité d'adaptation de cette espèce aux changements climatiques via un ajustement physiologique de la tolérance thermique. Des perches du Nil ont été acclimatées à diverses températures et pour différentes durées d'exposition (3 jours, 3 semaines ou 3 mois), pour ensuite prendre des mesures de tolérance thermique supérieure, de performance métabolique, du taux de croissance et des taux de développement des organes. J'ai observé une compensation de la tolérance thermique supérieure et du taux métabolique en réponse au réchauffement peu importe la durée d'exposition, et j'ai démontré que le remodelage cardiaque induit par le réchauffement influençait la performance aérobique chez cette espèce. Les résultats principaux

de ces études remettent en question l'hypothèse classique stipulant que les espèces tropicales ne possèdent qu'une capacité de plasticité thermique limitée pour faire face aux changements climatiques. Finalement, j'ai aussi étudié la vulnérabilité et la résilience des systèmes socio-écologiques basés sur la pêche dans le bassin du lac Victoria. Pour déterminer si les fluctuations dans les pêcheries liées au changement climatique ont un impact sur les communautés de pêcheurs, des enquêtes auprès des ménages, des groupes de discussion et des entretiens avec des informateurs clés ont été réalisés dans cinq villages variant dans leur dépendance à la pêche. J'ai constaté que le changement climatique perturbe fortement les activités économiques liées à la pêche et qu'il induit des boucles de rétroaction socio-écologiques amenant les ménages et les communautés vers une dépendance accrue à une ressource déjà menacée et en déclin. Néanmoins, la sensibilisation croissante des pêcheurs à ces enjeux entraîne parfois des actions adaptatives qui améliorent la résilience aux changements opérant dans l'écosystème local. Dans son ensemble, cette thèse améliore notre compréhension de la vulnérabilité au changement climatique aux sein des environnements dulcicoles Africains et elle identifie plusieurs mécanismes pouvant améliorer la résilience des espèces de poissons et des communautés humaines qui en dépendent.

Preface

Thesis format

This thesis is presented in a manuscript-based format, with each chapter (1 – 4) consisting of an individual manuscript published or intended for publication in a peer-reviewed, academic journal, with myself as the lead author. This thesis opens with a general introduction to the key topics covered in this work. Chapters are linked by brief statements (prefaces) that summarize the key findings of the previous chapter and introduce concepts and questions explored in the following chapter. This thesis closes with a general conclusion that summarizes the main contributions of this work, and suggests productive avenues for future research. Four appendices provide supplementary information for each chapter. I followed the referencing format of the *Journal of Experimental Biology* for all chapters.

Chapter 1: Nyboer, E.A., Liang, C. and Chapman, L.J. (submitted to *Biological Conservation*). Assessing the vulnerability of Africa's freshwater fishes to climate change: a continent-wide trait-based analysis

Chapter 2: Nyboer, E.A. and Chapman, L.J. Elevated temperature and acclimation time affect metabolic performance in the heavily exploited Nile perch of Lake Victoria. *Journal of Experimental Biology*.

Chapter 3: Nyboer, E.A. and Chapman, L.J. Cardiac plasticity influences aerobic performance and thermal tolerance in a tropical, freshwater fish at elevated temperatures. *Journal of Experimental Biology*.

Chapter 4: Nyboer, E.A. and Chapman, L.J. (in preparation for *Ecology and Society*). Assessing the vulnerability and adaptive capacity of fishing communities to climate change in the Lake Victoria basin of East Africa.

Contribution of authors

All manuscripts included in this thesis are primarily the product of my own original work. As the leading researcher on each project, I was the principal person to develop the research questions, design and carry out experiments, perform the data collection and statistical analysis, and write the manuscripts. My advisor, Dr. Lauren Chapman, contributed substantially to all manuscripts by providing scientific guidance in conceptualizing each project, logistical support for fieldwork and experiments, and critical feedback on experimental design, data analysis and interpretation, and manuscript revision. For Chapter 1, another collaborator contributed expertise in mapping, and is therefore included as a co-author on this manuscript. In addition, Ugandan scientists employed by the National Fisheries Resources Research Institute (NaFIRRI) and the Aquaculture Research and Development Center (ARDC) of Uganda, and skilled personnel employed by the Lake Nabugabo Field Station (Uganda) run by Lauren and Colin Chapman contributed to data collection for Chapters 2 – 4.

Chapter 1: This manuscript is co-authored with Chris Liang and Lauren Chapman. Chris Liang is an undergraduate student in McGill's School of Environment. Chris Liang performed many of the calculations of climate change projections, produced refined species ranges for spatial analysis and mapping, and wrote the related sections of the supplementary materials. Lauren Chapman assisted with manuscript development, provided advice on analysis, and provided feedback the manuscript. I conceived of the project, gathered data from online databases and literature review, analyzed the data, produced the final maps and figures, and wrote the main draft of the manuscript.

Chapter 2: This manuscript is co-authored with Lauren Chapman. Lauren Chapman coordinated access to facilities and collaborators at the ARDC (Kajjansi, Uganda) and contributed substantially to experimental design, methodological approach, data analysis, and manuscript writing. I conceived of the project, conducted the experiment with the help of Dominique Lapointe (HotFish research program) and Stephen Kimera, my research assistant at ARDC, performed all analyses, and wrote the main draft of the manuscript.

Chapter 3: This manuscript was co-authored by Lauren Chapman. Lauren Chapman contributed to project development, experimental design, methodological approach, statistical analysis, and manuscript writing. She also coordinated access to facilities and collaborators at the ARDC (Kajjansi, Uganda) and provided essential support for the laboratory component of the work conducted at McGill University. I conceived of the project, developed the experimental design and methodological approach, designed and engineered the rearing infra-structure with the help of Stephen Kimera, my research assistant at the ARDC, conducted the experiment with the help of Stephen Kimera, performed organ measurements (with the help of Luisa Trujillo), performed all analyses, and wrote the main draft of the manuscript.

Chapter 4: This manuscript was co-authored with Lauren Chapman. Lauren Chapman provided advice on survey question development, provided support in developing and negotiating essential collaborations at NaFIRRI, and contributed to manuscript development. I conceived of and designed the research, developed research tools (surveys, focus group discussions, interviews) and sampling methodology, managed the research team and budget, collected and oversaw interpretation and translation of all field data, performed all analyses, and wrote the main draft of the manuscript.

Statement of originality

This thesis takes a cross-disciplinary approach employing both quantitative and qualitative methodologies to integrate social and ecological data for a holistic understanding of the vulnerability of Africa's freshwater fisheries to climate change. This thesis is comprised of three major sections: the first (Chapter 1) uses a meta-analytical approach to predict vulnerability of Africa's exploited freshwater fishes based on species traits and predicted climate change exposure. The second section (Chapters 2 and 3) employs an experimental approach to test the ability of the Nile perch, a commercially harvested fish species in the Lake Victoria basin of East Africa, to physiologically adjust thermal tolerance limits to increased water temperatures. The final section, (Chapter 4), investigates how fishing-dependent

communities adjust to climate-mediated changes in the ecosystem with the aim to determine vulnerability and resilience of stakeholder communities to projected changes in the fishery.

Chapter 1 provides the first comprehensive vulnerability assessment of African freshwater fishes to climate change, offering essential, updated knowledge on conservation priorities for regions and species across the continent. For this chapter, I produced the first thorough dataset documenting current knowledge on African freshwater fish species' ecological traits, highlighting data gaps, and identifying research areas that are necessary for improving conservation of freshwater resources. This analysis allowed me to conclude with quantitative support that African freshwater fish are highly vulnerable to climate change, and showed that incorporating the slow-onset stress of climate change into conservation planning can emphasize regions and species that might otherwise be overlooked under classical conservation schemes.

Chapter 2 provides the first thermal acclimation study with short- and long-term exposures on Nile perch (*Lates niloticus*), and provides insight into this species' capacity to cope with increasing water temperature, improving our ability to predict how the Nile perch may fare under future climate warming scenarios. This study also tests a number of key hypotheses derived from current eco-physiology theory challenging assumptions that thermal plasticity is limited in stenothermal tropical fishes (as compared to eurythermal, temperate fishes), and that changes in metabolic rate are fundamentally connected to fitness-related traits such as growth rate. Both of these topics are currently widely discussed in the ecophysiology and climate change literature (Seebacher et al., 2015; Jutfelt et al., 2018), making this work a timely and important contribution to these ongoing debates.

Chapter 3 builds on the findings of Chapter 2 by evaluating the responses of Nile perch to elevated water temperatures over longer (developmental) timescales. I used an innovative Nile perch rearing infrastructure to conduct the first study to rear Nile perch for an extended length of time (three months) under two rearing temperatures to investigate effects of long term exposure to elevated temperature on metabolic rate and organ (heart, gill and brain)

development. This study is the first to experimentally test the effects of elevated temperature on the heart structure of a tropical fish, and to show that cardiac plasticity plays a role in metabolic compensation. The role of cardiac plasticity in metabolic compensation under high temperature is an active area of research, and this finding is likely to generate further interest in this field.

Chapter 4 is one of three existing studies examining the socio-ecological impacts of contemporary climate variability and change on fishing communities in the Lake Victoria basin in Uganda, and the first to investigate patterns across a range of community sizes from large industrial landing sites to small communities. This work is also the first to apply the concept of social-ecological traps to the Lake Victoria fishery as a framework for both assessing vulnerability of communities to climate change and identifying adaptive strategies that may be successful for escaping these traps.

Ethics statement

All research included in this thesis was conducted under the Animal Care and Use Committee of McGill University (Animal Use Protocol 5029), and the McGill Research Ethics Board I under the Certificate of Ethical Acceptability of Research Involving Humans (REB file number 285-1215). Permission to conduct research in Uganda as granted by the Uganda National Council for Science and Technology (Reference number NS 308), and authorization to export samples from Uganda to was provided by the Ugandan Commissioner for Fisheries.

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Introduction

The unprecedented rate of contemporary climate warming is disrupting ecosystem stability and altering species distributions across the globe (Parmesan and Yohe, 2003; Parmesan, 2006; Watson et al., 2013; Pecl et al., 2017). Recent assessments of the earth's surface temperature indicate warming of 0.72 – 0.85°C since the late 1800s (IPCC, 2014); and despite numerous attempts to reduce greenhouse gas emissions, temperatures have increased at a rate of ~0.116°C per decade (Karl et al., 2015), and are likely to exceed 2 - 4°C above baseline levels by the end of the 21st century (Stocker et al., 2013). Persistent temperature increases, and their associated environmental impacts, have resulted in well-documented alterations in species distributions in terrestrial, marine, and freshwater habitats (reviewed in Cahill et al., 2014; Lenoir and Svenning, 2015), and have disrupted life-cycle phenologies, inter- and intra-specific interactions, biological community composition, and ecosystem function (Walther, 2010; Yang and Rudolf, 2010; Bates et al., 2008; Brown et al., 2016; Scranton and Amarasekare, 2017). Such alterations to the earth's natural systems can pose substantial threats to human society, primarily through changes in the distribution and productivity of natural resources and the availability of ecosystem services (Staudt et al., 2013; Pecl et al., 2017). The responses of human communities to such changes can add novel and potentially synergistic sources of stress to these systems (Staudt et al., 2013). For example, reductions in water levels coincident with climate change (e.g., decreases in precipitation; higher rates of evaporation) can affect availability of freshwater fish resources (Postel and Richter, 2003). This can lead to increased fishing effort and further reductions in water availability owing to human-caused withdrawals (e.g., for crop irrigation) exacerbating reductions in fish abundance (Xenopolous et al., 2005). Understanding impacts of climate change on ecosystems and resources therefore requires integration of direct measures of species' responses to environmental change with knowledge of human reactions to these changes.

My doctoral research explores this conservation challenge by applying an interdisciplinary approach to understand effects of climate change on inland aquatic ecosystems in Africa, with a particular focus on the fisheries of the Lake Victoria basin. I first present a continent-wide climate change vulnerability assessment of freshwater fish species in Africa integrating species' traits and distributions with projected climatic changes. I then focus on one species of high commercial importance in the Lake Victoria basin, the Nile perch (*Lates niloticus*), using an eco-physiological approach to test their capacity to cope with elevated water temperatures. Finally, I investigate how fishing-dependent communities in the Lake Victoria basin respond to climate-mediated changes in the environment to understand perceptions and behaviours of stakeholders. Below, I briefly review our present state of knowledge on impacts of climate change on freshwater fish and fisheries, outline current approaches to understanding effects of elevated temperature on fishes, and discuss knowledge gaps in the literature.

Effects of climate change on inland aquatic ecosystems

Inland aquatic environments are predicted to be among the most vulnerable ecosystems on the planet (Schindler, 1997; Dudgeon et al., 2006; Heino et al., 2009; Woodward et al., 2010; Comte et al., 2013; Hermoso, 2017; Pletterbauer et al., 2018). They are affected by several anthropogenic stressors including water diversions and extractions, dam construction, influx of wastes, fertilizers, pollutants, and contaminants, widespread land conversion, introduction of invasive species, and over-exploitation of harvested species (Dudgeon et al., 2006; Kundzewicz et al., 2008; Strayer and Dudgeon, 2010; Vörösmarty et al., 2010; Nickus et al., 2010; Hermoso, 2017; Knouft and Ficklin, 2017). Climate change has emerged as a novel but increasingly important threat that is predicted to interact with and exacerbate many of these existing stressors (Mooney et al., 2009; Staudt et al., 2013). Increases in surface water temperature have been documented in numerous lakes, rivers, streams, and wetlands around the world (Livingstone, 2003; O'Reilly et al., 2003; Adrian et al., 2009; Nickus et al., 2010; Knouft and Ficklin, 2017; Pletterbauer et al., 2018), often leading to increased primary production, altered food-web structure, and disrupted nutrient dynamics (Jeppesen et al., 2009; Moss et al.,

2011). Changes in precipitation patterns can modify hydrological cycles and increase discharge into lake and river systems (Jeppesen et al., 2009; Nickus et al., 2010; Knouft and Ficklin, 2017; Taniwaki et al., 2017), which can increase the inputs of solutes, pollutants, and fertilizers to surface waters. Changes in the pattern and intensity of precipitation can also affect water levels in inland systems affecting biogeochemical processes (Nickus et al., 2010; Taniwaki et al., 2017; Pletterbauer et al., 2018), and reducing connectivity in rivers (Woodward et al., 2010). These fundamental alterations to ecosystem structure and function can affect many aspects of the biogeography, life-history, and physiology of freshwater fishes (Myers et al., 2017).

To cope with rapidly changing thermal regimes and other climate-induced alternations, fish populations must either relocate to more suitable habitats or rapidly adjust to novel conditions through genetic adaptation and/or environmentally induced phenotypic plasticity (Poff et al., 2002; Rosset and Oertli, 2011; Huey et al., 2012; Myers et al., 2017). Latitudinal range shifts have already been observed in dozens of marine ectotherms (Perry et al., 2005; Sorte et al., 2010; Poloczanska et al., 2013); however, fishes inhabiting land-locked, inland systems will be limited in the degree to which they can relocate, and will therefore need to adjust to novel conditions *in situ*. In addition, the ability of species to make these adjustments can be limited by selection pressure exerted by fishing. Fishing-induced size-at-age truncation, population shrinkage, and forced redistribution of stocks are predicted to increase the sensitivity of exploited species to climate-change stressors (Hsieh et al., 2006; Ficke et al., 2007; Brander, 2007, 2010). Failing to adapt will lead populations or species to extinction on local or global scales. Therefore, a growing number of studies attempt to predict how climate change might impact fish populations based on ecological, behavioural, and physiological traits (Cadotte et al., 2011; Foden et al., 2013; Pacifici et al., 2015; Hare et al., 2016), and on their ability to adjust those traits through genetic adaptation or phenotypic plasticity (Crozier and Hutchings, 2014).

Temperature effects on fishes

In fishes (and other ectothermic animals) a key physiological trait affecting overall performance is the range of temperatures (thermal window) within which they are able to carry

out vital, life-sustaining functions (Brett, 1971; Huey and Stevenson, 1979; Schulte et al., 2011). In ectotherms, environmental temperature has a profound effect on the rates of physiological processes (e.g., aerobic metabolism). In general, responses of biological rates to temperature can be illustrated by thermal performance curves, with the efficiency of a given physiological function starting at zero at the lower critical thermal limit ($T_{crit,min}$), undergoing a rapid (exponential) increase with temperature, peaking at optimal temperatures (T_{opt}), and then declining to zero at upper critical thermal limits ($T_{crit,max}$; Fig. 1A) (Fry, 1947; Brett, 1971; Huey and Stevenson, 1979; Pörtner, 2010; Schulte, 2015). The range of temperatures containing this curve is generally assumed to comprise the thermal window of the animal (Fig. 1A). In this thesis, I am primarily interested in the forces governing the upper half of this thermal performance curve as climate change is expected to result in overall increases in water temperature in most regions (IPCC, 2014).

For ectotherms, the shape of their thermal performance curve is thought to be determined by the temperature range in their natural habitat (adaptive background), and their ability to cope physiologically with thermal change (phenotypic plasticity; Huey and Stevenson, 1979; Huey and Kingsolver, 1989; Schulte, 2015). In terms of adaptive background, fishes that encounter a wider range of temperatures in their natural habitat (e.g., temperate species) are hypothesized to be more likely to survive thermal stress events since they have intrinsic mechanisms for coping with a wide range of temperatures (Huey and Hertz, 1984; Bush and Hooghiemstra, 2005; Ghalambor et al., 2006; Hoegh-Guldberg et al., 2007; Tewksbury et al., 2008). Warm-adapted tropical species that inhabit relatively thermo-stable environments are expected to be more sensitive to warming since they are thought to reside near their upper thermal limit, and are thus likely to be driven over $T_{crit,max}$ by even slight temperature increases (Stillman, 2002, 2003; Deutsch et al., 2008; Tewksbury et al., 2008; Nilsson et al., 2009; Wright et al., 2009). Regardless of adaptive background, species that are capable of adjusting optimal temperatures or critical thermal limits through physiological acclimation are more likely to survive extended thermal stress events (Stillman, 2003; Pörtner and Farrell, 2008; Schulte, 2015). Acclimation is a form of plasticity that occurs through the alteration of physiological characteristics to better

suit an environment. Plastic adjustments can counteract fundamental climate-induced changes to fish populations (Hawkins, 1996; Visser, 2008; Nilsson et al., 2009), and can occur over the lifetime of the organism, or as reversible transformations in the adult organism (Fry, 1967; Hazel and Prosser, 1974; Woods and Harrison, 2002; Schaefer and Ryan, 2006; Schulte et al., 2011; Donelson et al., 2012; Grenchik et al., 2013; Schulte, 2015). Given their thermostable backgrounds, tropical species are generally predicted to have less capacity for acclimation; however, several meta-analyses have revealed conflicting evidence for this (Sunday et al., 2011; Seebacher et al., 2015; Gunderson and Stillman, 2015; Comte and Olden, 2017), and currently much less is known about the acclimation responses of tropical, freshwater species relative to temperate, marine animals (Seebacher et al., 2015), so this is a topic of increasing interest in strengthening our ability to predict effects of climate change on inland fishes.

Fish metabolism and temperature

The effect of temperature on metabolic functioning in fishes was first recognized in the early 20th century with the founding research of August Krogh (Krogh, 1916); however, it was not until the 1940s that Frederick Fry proposed a mechanistic explanation for how fish metabolism responded to temperature variation, and how this defined thermal limits in fishes (Fry, 1947). Fry and colleagues suggested that temperature tolerance in fishes could be explained by ‘metabolic scope for activity’, now termed aerobic scope (AS), which is simply the difference between the standard (lowest) and maximum (highest) metabolic rates (SMR and MMR) of fishes (Fry, 1947; Fry and Hart, 1948), and is hypothesized to loosely represent an animal’s capacity for activity over and above base survival (Fry, 1947; Farrell, 2016). As observed by Fry (1947), and quantified in several subsequent studies, SMR increases exponentially with temperature, whereas MMR is predicted to increase initially, and then plateau or decline at the highest temperatures (approaching $T_{crit,max}$), ultimately bringing about declines in AS at high temperatures (Fig. 1BC; Fry, 1947; Frederich and Pörtner, 2000; Lee et al., 2003; Lannig et al., 2004; Farrell, 2009). Essentially, this suggests that variation in AS with temperature follows the classic thermal performance curve described above (Fig. 1BC).

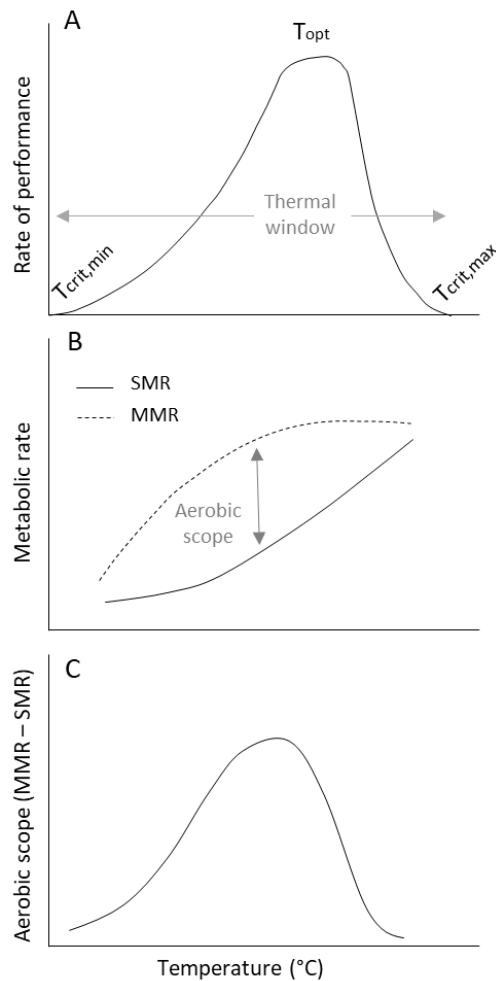


Figure 1. Illustrations adapted from Schulte (2015) depicting temperature effects on rates of performance and metabolic function. A) A classic thermal performance curve (TPC) summarizing the effects of temperature on biological rates including an initial rapid increase, the thermal optimum (T_{opt}), and the thermal window extending between minimum and maximum critical thermal limits ($T_{crit,min}$ and $T_{crit,max}$). B) A depiction of how SMR (standard metabolic rate) and MMR (maximum metabolic rate) vary with temperature assuming that MMR is limited by oxygen supply. C) The aerobic scope curve (approximately matching the TPC) resulting from hypothetical data presented in B.

The effect of temperature on fish physiology has continued to be an active area of research, and AS has emerged as a key measure of metabolic performance in fishes (Farrell, 2016; Pörtner et al., 2017; Jutfelt et al., 2018). Over the past decade, measurements of metabolic rate (operationalized as oxygen consumption rate, Mo_2) have been incorporated into predictions of how climate change will impact fishes (Pörtner and Knust, 2007; Pörtner and Farrell, 2008; Nilsson et al., 2009; Donelson et al., 2011, 2014; Eliason et al. 2011; Neuheimer et al., 2011; Donelson and Munday, 2012; Comte and Grenouillet, 2013), largely owing to theoretical developments relating Fry's aerobic scope curve to whole-animal performance and fitness through a process known as oxygen- and capacity-limited thermal tolerance (OCLTT) (Pörtner and Knust, 2007; Pörtner and Farrell, 2008; Farrell et al., 2009; Pörtner, 2010; Pörtner and Peck, 2010; Clark et al., 2011; Farrell, 2016; Pörtner et al., 2017). According to the OCLTT concept, declines in performance (i.e., AS) at high temperatures are predicted because the cardiorespiratory system cannot keep pace with oxygen demands in respiring tissues as increasing temperatures elevate metabolic demands (Pörtner and Knust, 2007; Pörtner and Farrell, 2008; Pörtner, 2010; Pörtner et al., 2017). Mismatches between oxygen supply and demand (manifesting in

reductions in AS) are therefore thought to define thermal limits in teleost fishes. OCLTT further predicts that AS is closely linked to fitness-related performance traits such as growth and reproductive success, implying that declines in AS may have negative fitness consequences for aquatic ectotherms (Pörtner and Knust, 2007; Pörtner and Farrell, 2008; Pörtner, 2010).

Although OCLTT provides a useful conceptual framework for predicting how ectotherms may respond to thermal stress (Pörtner and Farrell, 2008; Farrell et al., 2008, 2009; Pörtner, 2010), the majority of support for this hypothesis comes from studies on species inhabiting open oceans for at least part of their life cycle (Frederich and Pörtner, 2000; Lee et al., 2003; Lannig et al., 2004; Pörtner and Knust, 2007; Farrell, 2009), with few examples from tropical, inland fishes. And, numerous recent studies have shown that declines in performance at high temperatures may be driven by mechanisms other than a mismatch between oxygen supply and demand, providing convincing evidence that optimal temperatures for AS do not necessarily elicit maximal performance in other fitness-related measures (Healy and Schulte, 2012; Clark et al., 2013; Gräns et al., 2014; Norin et al., 2014; Wang et al., 2014; Brijs et al., 2015; Ern et al., 2016). In addition, the maximum oxygen uptake curves of many species lack meaningful temperature optima, with MMR and AS increasing with temperature to near-lethal limits (Gräns et al., 2014; Norin et al., 2014; Ern et al., 2016), raising questions about the broad applicability of the OCLTT framework (Jutfelt et al., 2018). Several recent studies on tropical, inland fishes have shown a diversity of responses to temperature variation, some of which counter core predictions of OCLTT (McDonnell and Chapman, 2015; Chrétien and Chapman, 2016; Lapointe et al., in press). There are many pathways for fish to respond to oxygen limitation, scaling from whole-body to cellular levels (Pörtner, 2002; Angilletta, 2009; Biro and Stamps, 2010), and alterations at any stage can lead to improvements in metabolic performance (e.g., reduced basal oxygen demand) and maintenance of fitness related traits. This suggests that low AS may not be a central constraint on performance, and that other traits must be considered when making predictions about effects of elevated temperature on fishes.

Climate change in tropical ectotherms

Our understanding of the impacts of climate change on ectothermic species is derived primarily from research on temperate zones (Seebacher et al., 2015; Pecl et al., 2017; Myers et al., 2017), and for fishes, the majority of studies have come from marine systems (Dudgeon et al., 2006; Myers et al., 2017). However, climate change may not have the same physical effect at lower latitudes as in more-studied zones. Predictions of climate change impacts in tropical regions indicate smaller temperature increases compared to arctic or temperate zones, but more variability in both temperature and precipitation resulting in desertification of some regions and excessive rainfall in others (IPCC, 2014). In addition, a number of meta-analyses have shown that responses of ectotherms to change may not be the same across latitudes (Sunday et al., 2011, 2014; Seebacher et al., 2015; Gunderson and Stillman, 2015; Comte and Olden, 2017). From a conservation perspective, assessments of species vulnerability to climate change are lacking in tropical zones. A recent review quantified the number of vulnerability assessments conducted globally, and found much lower numbers in Africa, South America, and Asia compared with Europe, North America, and the South Pacific (Pacifi et al., 2015), with no studies predicting vulnerabilities of fishes in any continents containing tropical zones. The relative lack of information on how climate change may affect tropical inland systems is a major hindrance to management of freshwater environments and their resources in regions where the impacts of climate change are likely to be most potent (Niang et al., 2014).

Climate change and African fisheries

Problems associated with climate change are predicted to be especially severe in developing nations where the effects of climate change and the potential for adaptation are not well understood. For example, changes to fisheries production are predicted to disproportionately impact societies that are highly dependent on these resources for food security and livelihood stability (Allison et al., 2009; Badjeck et al., 2010). Africa has been designated by the Intergovernmental Panel on Climate Change (IPCC) as one of the most vulnerable continents to global warming (IPCC, 2014), and climate-related risks are likely to

intensify existing problems of resource-overexploitation and widespread poverty (Allison et al., 2009; Badjeck et al., 2010; Bele et al., 2013). Understanding the vulnerability of African fisheries to climate change depends not only on the adaptive abilities of fish species, but also on the responsiveness of management institutions and stakeholder communities to changes in the fishery (Allison and Ellis, 2001; Smit and Wandel, 2006; Fussel, 2007). In this dissertation, I focus specifically on the Nile perch (*Lates niloticus*) fishery of the Lake Victoria basin in East Africa to explore the adaptive capacity of the Nile perch and of the fisher communities. Lake Victoria is the largest tropical lake in the world, and Africa's most important source of inland fisheries production. The fisheries of the Lake Victoria basin supply more than 2 million people with their primary source of income, and approximately 22 million with > 50% of their annual protein intake (LVFO, 2016). The Nile perch is a large, piscivorous fish, introduced to the LVB in the mid-1900s, and becoming one of the most important commercial species through the 1990s (Goudswaard et al., 2008). Intense fishing and other changes in the lake basin have led to an apparent reduction in Nile perch biomass in some regions (Balirwa et al., 2003; Hecky et al., 2010), however the fishery continues to be highly exploited due to rapid human population growth (Taabu-Munyaho et al., 2016), and there is great interest in maintaining a sustainable fishery at maximum harvest. In terms of climate change effects, it is generally accepted that there will be an increase in mean annual temperature between 1.3°C and 4.3°C by ~2080 (IPCC, 2014), and that climate change will manifest in increasingly erratic rainfall, less predictable seasonality, and an increase in extreme weather events (Niang et al., 2014). Furthermore, the effects of climate change are likely to be exacerbated by other human-induced stresses such as over-exploitation and habitat degradation (Badjeck et al., 2010). Nevertheless, there have been only a handful of studies that test the effects of climate change on fisheries in this region (Timmers et al., 2012; Goulden et al., 2013; Musinguzi et al., 2015; Ogutu-Ohwayo et al., 2016).

Thesis structure

In the first chapter of my dissertation, I use a meta-analytical approach to perform a continent-wide climate-change vulnerability assessment of freshwater fish species in Africa.

This chapter integrates physiological, ecological, and evolutionary species traits and species' geographical distributions with projected climatic changes and current environmental stressors to provide refined predictions on species' risks to global warming. I identify critical areas for future research on freshwater fish conservation across Africa, and identify regions and species that are highly vulnerable to climate change to inform conservation planning and aid in the development of freshwater management policy. In the remainder of this thesis I focus on the Lake Victoria basin of East Africa to explore the effects of climate change on this system. In Chapters 2 and 3 I use the Nile perch, a commercially harvested species in the Lake Victoria basin of East Africa, as a model species to test predictions arising from current eco-physiology theory that link physiological plasticity to climate change adaptation (e.g., oxygen and capacity limited thermal tolerance; OCLTT), and that regard the physiological plasticity of tropical, freshwater species to elevated water temperatures. In Chapter 2 I focus on effects of thermal exposure time on the capacity of Nile perch to physiologically adjust to warmer waters using a series of experiments [respirometry (metabolic rate through Mo_2), critical thermal maxima (temperature tolerance)] to test the capacity of the Nile perch to adjust their thermal tolerance limits and improve their metabolic performance with acclimation to increased water temperatures. In Chapter 3 I use a similar methodological approach to quantify acclimation capacity in Nile perch over longer (developmental) timeframes and test various hypotheses regarding physiological and developmental mechanisms underlying metabolic compensation. In the final chapter I investigate how fishing-dependent communities in the Lake Victoria basin adjust to climate-mediated changes in the environment with the aim to determine vulnerability and resilience of stakeholder communities to projected changes in the fishery. Ecological and environmental data were combined with household survey, focus group, and interview data to determine lakeshore people's perceptions of climate change, identify events that have had a large effect on the fishery, pinpoint successful adaptation strategies for these communities, and evaluate factors that improve resilience to environmental change. I conclude this thesis by summarizing key findings from each chapter, and suggesting potential research avenues that can build on these findings.

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Chapter 1

Assessing the vulnerability of Africa's freshwater fishes to climate change: a continent-wide trait-based analysis

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1.1 Abstract

Climate change is a key driver of species extinction and biodiversity loss across the globe, and freshwater fishes are predicted to be among the most vulnerable of all taxonomic groups. African freshwater ecosystems are home to one of the most diverse and unique ichthyo-faunas on the planet, and inland fishes are essential to the social and economic stability of millions of people depending aquatic ecosystems for their livelihoods. Although nearly one sixth of African freshwater fishes have been designated as endangered or vulnerable to extinction by the IUCN redlist assessment, the effects of climate change on these species have never been explored on a continent-wide scale. In this study we present the first trait-based climate change vulnerability assessment (CCVA) comprising the majority (85%) of Africa's currently described freshwater fishes. We assembled data relating to three dimensions of species vulnerability to climate change including sensitivity, adaptive capacity, and exposure, with the first two dimensions based on species' life history, ecological, physiological, and genetic traits, and exposure based on predicted climatic changes across species ranges. In addition, we developed an index of 'conservation value' based on traditional conservation metrics including extinction risk, uniqueness (endemism), and importance for human use. We found that almost 40% of African freshwater fishes are vulnerable to climate change, mostly owing to the many species with highly specialized habitat and life-history requirements, and because of the numerous anthropogenic stressors faced by these species in their habitats. Furthermore, we highlighted several cases where traditional conservation approaches overlook species and regions that are predicted to be highly threatened by climate change, and identified several important knowledge gaps pertaining primarily to species population sizes, genetic variability, and life history traits. This study therefore identifies priority research areas for understanding vulnerability of African freshwater fishes, highlights the importance of integrating climate change into conservation plans, and provides recommendations for uses of these data to improve conservation strategies.

1.2 Introduction

1.2.1 Climate change vulnerability assessments

Recent assessments of the earth's climatic patterns indicate that global surface temperatures have increased by 0.72 - 0.85°C over the last century, and that alterations to the world's water cycle have changed precipitation patterns with higher frequency of extreme events, such as droughts and floods (Stocker et al., 2013). Ecological stresses associated with these climatic changes are important global drivers of species extinctions and biodiversity loss (Thomas et al., 2004; Cahill et al., 2013; Urban et al., 2015). Climate change effects on species include shifts in distribution (Parmesan and Yohe, 2003; Pecl et al., 2017), changes in habitat availability (Leadley et al., 2010), modifications to community structure (Walther, 2010), shifts in life-cycle phenology (Yang and Rudolf, 2010), and alterations to population growth trajectories (Martay et al., 2017). Identifying species, populations, and regions that will be most vulnerable to climate change has become a major focus of ecology and conservation biology (Nadeau et al., 2017).

The degree to which species are able to respond to climatic stressors will depend on the severity of change in their habitat, their biological and ecological sensitivities to change, and their ability to track shifting climate by colonizing new territory or adapting to novel conditions through physiological or behavioural modifications (Nadeau et al., 2017). Until recently, most large-scale, multi-taxa assessments of species vulnerability have not accounted for intrinsic, species-specific effects (e.g., niche breadth) that may influence their ability to cope (Williams et al., 2008; Pacifici et al., 2015). Climate change-related stresses can be mediated by species' biological, ecological, and physiological traits through a diversity of behavioural, plastic, and adaptive responses (Lavergne et al., 2010; Pacifici et al., 2017). Therefore, incorporating ecological and evolutionary characteristics with exposure estimates can improve forecasts of a species' vulnerability to climate change (Bellard et al., 2012; Pacifici et al., 2015). Vulnerability assessments that incorporate species characteristics are known as trait-based approaches (Williams et al., 2008; Chessman, 2013; Pacifici et al., 2015) and are effective in generating

novel insights to climate change risk assessments (Böhm et al., 2016) and conservation prioritization schemes (Dickinson et al., 2014).

In general, trait-based climate change vulnerability assessments (CCVAs) assemble data within various dimensions relating to vulnerability including species' sensitivity, adaptability, and exposure to climate change (Williams et al., 2008; Pacifici et al., 2015), with the first two dimensions based on species' life history, ecological, physiological, and genetic traits. Trait based CCVAs are an increasingly common method used to develop priorities for conservation under climate change (Williams et al., 2008; Pacifici et al., 2015), and have been adopted in recent global assessments of corals, amphibians, birds (Foden et al., 2013), and reptiles (Böhm et al., 2016). In this study, we perform a trait-based CCVA for freshwater fish species across the continent of Africa. We incorporate effects of other stressors, and compare results to outcomes from traditional conservation metrics.

1.2.2 Vulnerability of inland waters to climate change

Inland aquatic environments are predicted to be among the most vulnerable to climate change (Dudgeon et al., 2006; Heino et al., 2009; Woodward et al., 2010). Increases in surface water temperature have been documented in numerous lakes, rivers, streams, and wetlands around the world (Livingstone, 2003; O'Reilly et al., 2003; Adrian et al., 2009). Increases in temperature can lead to higher levels of primary production in lakes (Moss et al., 2011) reducing water clarity, limiting growth of submerged vegetation, altering food-web structure, and disrupting nutrient dynamics (Jeppessen et al., 2009, 2012). Changes in precipitation patterns can modify hydrological cycles and increase discharge into lake and river systems, which can exacerbate eutrophication and water turbidity through inputs of solutes, pollutants, and fertilizers to surface waters (Jeppessen et al., 2009; Knouft and Ficklin, 2017).

These fundamental alterations to ecosystem structure and function can affect many different aspects of the biogeography, life-history, and physiology of freshwater fishes (Myers et al., 2017). A recent worldwide assessment estimates that approximately 25% of freshwater fishes

are threatened with extinction (Collen et al., 2014), confirming that freshwater fishes are among the most threatened taxa, globally (Olden et al., 2010). Even when effects of environmental change are not lethal, impacts on fish growth and reproduction may cause significant alterations to fish populations and communities (Ficke et al., 2007; Myers et al., 2017). Fish species without dispersal barriers may shift northward with changing thermal conditions (Perry et al., 2005; Sorte et al., 2010; Poloczanska et al., 2013). However, for land-locked, inland fishes, distributional shifts may not be an option, and increases in temperature can be detrimental to reproductive output and may lead to different nutrient requirements, changes in local habitat use, and changes in diet (Ficke et al. 2007; Myers et al., 2017). Thus, the vulnerability of inland fish populations to climate change will depend on their capacity for genetic adaptation, phenotypic plasticity (behavioral and physiological), as well as dispersal capacity, all of which must be considered across multiple life-history stages (Heino et al., 2009; Brander, 2010; Chessman, 2013).

1.2.3 African freshwater fishes – Integration of climate change into conservation needs

According to the IPCC's 5th assessment report, temperatures across Africa have increased by approximately 0.5°C over the last 50 – 100 years, and climate change projections estimate mean temperature increases of between 2 - 4°C across most of Africa by the end of the 21st century, on par with global rates (Niang et al., 2014). Africa's freshwaters are home to an estimated ~3300 fish species (Lévêque and Paugy, 2010), comprising one of the most species-rich ichthyo-faunas on the planet (Thieme et al., 2005). Africa's freshwater fishes are especially unique because of the impressive array of diverse species flocks endemic to multiple lake and river systems across the continent, and because of the high proportions of extant basal and archaic species (Thieme et al., 2005; Lévêque and Paugy, 2010). Notable species radiations have occurred in the Upper and Lower Guinean regions and the Congo River basin (Fig. 1.1A); however the most famous example is the incredibly diverse radiation of an estimated 2000 species of haplochromine cichlid fishes in the Rift Valley lakes in East Africa (Roberts, 1975).

Africa's freshwaters are often divided into ichthyo-faunal provinces based on endemism, paleogeography, and physiological or ecological barriers (Roberts, 1975), which are used in our analysis for interpretive purposes (Fig. 1.1A).

African freshwater fishes have important socio-economic roles and are critical to livelihoods of millions of people across the continent. Many are used in commercial or artisanal fisheries (Carr et al., 2013), and fishing pressure has increased by approximately 37,000 tons per year since 1984 (FAO, 2014). Fishes are also commonly used in the aquarium trade, and are increasingly used for aquaculture to improve food security and reduce pressure on wild fisheries (FAO, 2014). Many of Africa's most important freshwater systems are threatened by habitat degradation, poor water management, introduction of invasive species, and pollution from agriculture and urbanization (Thieme et al., 2005), and of the currently described ~3300 freshwater fish species, more than one sixth (~580 species) are estimated to be endangered or vulnerable to extinction based on the IUCN redlist assessment. To date, no comprehensive trait-based CCVA has been performed on freshwater fishes of Africa (Pacifici et al., 2015).

In this study we performed a trait-based CCVA of African freshwater fishes to highlight species and regions that require conservation attention as climate change occurs. The objectives are to (1) explore availability of trait data for African freshwater fishes, (2) develop species-specific predictions about vulnerability to climatic change by integrating biological traits and exposure estimates, (3) identify geographic regions of high conservation priority due to concentrations of vulnerable species, and (4) compare species and regions that are climate change vulnerable with those that are considered of high conservation value by traditional metrics.

1.3 Methods

1.3.1 Fish species selection

All African freshwater fish species were included in this study if they met the following three criteria: 1) they spend any part of their life-cycle in freshwater habitat (including

diadromous, anadromous, and estuarine species), 2) their distribution ranges are mapped by the IUCN, and 3) their taxonomic classification could be resolved between our two primary sources of data, FishBase and the IUCN redlist.

1.3.2 Assessing climate change vulnerability: overview

We closely followed methods developed by Foden et al. (2013) whereby climate change vulnerability is assessed based on three vulnerability dimensions: *sensitivity* (the ability of a species to persist *in situ*), *low adaptive capacity* (the ability for a species to adjust to environmental change through dispersal or micro-evolutionary change), and *exposure* (the degree to which a species physical environment is predicted to change over the next 30 – 70 years). Species' *biological susceptibility* to climate change was evaluated through analyses of life history, ecological, physiological, and genetic traits that were grouped into sets of related traits corresponding to *sensitivity* and *low adaptive capacity (LAC)*. Species were ranked as 'high', 'low', or 'unknown' for each trait according to predefined qualitative or quantitative scoring regimes (Table 1.1). Exposure estimates were based on fine-scale projected changes in temperature and precipitation across water catchments where the species occur, and assigned scores of 'high' or 'low' based on thresholds of exposure. A species was considered vulnerable overall if they scored 'high' for all three dimensions (Fig. 1.2).

1.3.3 Data collection

1.3.3.1 Trait data

Trait data were collected primarily from the IUCN Redlist species information service (IUCN, 2018) and from FishBase (Froese and Pauly, 2018). We used the R packages *rfishbase* (Boettiger et al., 2017) and *rredlist* (Chamberlain, 2018) to extract trait data for 2793 species that met our three criteria. All extractions were performed in R studio v. 3.4.1 (R Core Team, 2017). We also integrated data from two IUCN reports that investigated climate change vulnerability of freshwater fishes in the Albertine Rift of East Africa (Carr et al., 2013) and in

West Africa (Carr et al., 2014). These studies contain expert-informed data for 551 species from the Albertine Rift and 517 species from West Africa (approximately 38% of all species in our dataset), which were used to add missing information to our data set, and to error check scores. Where scores from this study did not match those in the IUCN publications, additional literature searches were performed to confirm accuracy. Where no alternative information existed, the expert-informed (IUCN) scores were used.

1.3.3.2 Distribution data

Species distribution data were downloaded from the IUCN redlist spatial data service. IUCN species ranges are generalized polygons representing a species entire extent of occurrence. These ranges represent the best available estimates of species distribution limits (Foden et al., 2013); however, they often include areas that are not actually occupied by the species (e.g., land between two inhabited lakes). Species ranges were therefore refined by creating a detailed map of freshwater ecosystems across Africa. We combined data from the HydroSHEDS and Hydro LAKES databases (Lehner et al., 2008) and the Global Lakes and Wetlands Database (GLWD; Lehner and Doll, 2004), and clipped species ranges to only include zones of suitable habitat (Supplementary Methods 1.4). For this process, we assumed any freshwater habitat within a species range was habitable. Species ranges and water data were projected in Africa Albers Equal Area Conic (AAEAC) to account for the curvature of the earth. All mapping was performed in ArcGIS v. 10.5.1 (ESRI, 2017).

1.3.4 Defining vulnerability dimensions

1.3.4.1 Sensitivity and low adaptive capacity dimensions

Sensitivity is defined as the inability of a species to persist *in situ* (Foden et al., 2013). *Sensitivity* was split into six trait sets pertaining to: 1) specialized habitat or microhabitat requirements (based on depth ranges occupied, and the diversity, rarity, and vulnerability of habitats used, and microhabitat requirements of each species), 2) narrow environmental

tolerances (based on historical exposure to precipitation and temperature variability across its range [Supplementary Methods 1.4], reliance on seasonal patterns, and sensitivity to sedimentation), 3) dependence on interspecific interactions (based on prey specificity and other dependencies), 4) complexity of life history (based on requiring particular environmental conditions or social cues to complete life cycle), 5) rarity (based on abundances, distribution ranges, and population fragmentation), and 6) exposure to other disturbances (based on the number anthropogenic threats experienced in its range). In this dimension, some ‘traits’ are derived from climatic or environmental data rather than from empirical data relating directly to species ecology or physiology. For example tolerance to variance in temperature is based on historical environmental variability, and threat status is based on external anthropogenic stressors (Supplementary Methods 1.8).

Low adaptive capacity (LAC) is defined as the inability for a species to adapt to changes in the environment through dispersal or micro-evolutionary change. *LAC* was comprised of two trait sets pertaining to: 1) low potential to disperse (based on intrinsic qualities that affect dispersal ability in both adult and juvenile life stages, and on the existence of extrinsic geographical barriers), and 2) low potential to evolve (based on reproductive output [i.e., relative fecundity] and population growth rate). See Tables 1.1 and A1 for details on how variables within *sensitivity* and *LAC* were scored, and Supplementary Methods 1.3 and 1.8 for justification of each variable.

1.3.4.2 Exposure dimension

Exposure is defined as the degree to which a species’ physical environment is predicted to be altered by effects of climate change. In this study, exposure to climate change is encompassed by one trait set: *Predicted exposure to the effects of climate change*, which is based on four variables including changes in mean temperature, temperature variability, mean precipitation and precipitation variability across species’ geographic ranges.

Estimates of climate change variables were derived from projections of general circulation models (GCMs) developed by the Intergovernmental Panel for Climate Change (IPCC). To account for uncertainty in GCMs we used the mean projections of four models (UKMO HadCM3, MPIM ECHAM5, CSIRO MK3.5 and GFDL CM2.1) in all calculations (Foden et al., 2013; Supplementary Methods 1.4). In addition, we considered three emissions scenarios, moderate (A1B), high (A2), and low (B1) in all calculations. Global temperature and precipitation projections were downscaled to 10-min ($\sim 20 \text{ km}^2$) grid cells by WorldClim (Fick and Hijmans, 2017), and projected in AAEAC. Average absolute changes in temperature and precipitation were calculated as the difference between average values in 1975 (mean of 1961 – 1990) to 2050 (mean of 2041-2060), and 1975 to 2090 (mean of 2081 – 2100). Change in variability was estimated through calculations of average absolute deviation (AAD) across species ranges for the same years (Supplementary Methods 1.4). AAD is a variable that represents the tolerance to temperature and precipitation variability across time (months) and space (species ranges) for each species. Estimates of climatic changes were first calculated for the entire African continent. To find the averages within each species ranges, zonal statistics were applied using clipped species ranges as zonal boundaries (Supplementary Methods 1.4). All calculations were performed in ArcGIS v. 10.5.1 (ESRI, 2017). The main results of this paper present the mid-range emissions scenario (A1B) for projected changes from 1975 to 2050, but results are compared with the B1 and A2 scenarios and for 1975 – 2090 in the Supplementary Materials (Table A10, Fig. A3).

1.3.5 Assigning climate change vulnerability scores

Data extracted from the IUCN Redlist, FishBase, and WorldClim databases were summarized according to the above trait sets and variables (Supplementary Methods 1.1). Each species was given a score of ‘high’, ‘low’, or ‘unknown’ for each variable within the three vulnerability dimensions based on pre-defined scoring regimes in each trait (Tables 1.1 and A1, Supplementary Methods 1.3). If a species scored high for even one variable within one trait set under a given dimension it was given a high score in that dimension. A species was given a high

score for *vulnerability* if they scored high in all three dimensions. Species that scored high for both *sensitivity* and *LAC*, but were not considered highly exposed were categorized as ‘high latent risk’ (Fig. 1.2). Although species in this category are not predicted to experience as much change in their physical environment, if projections worsen they could become vulnerable in the future. Species that scored high for both *exposure* and *sensitivity*, but have good adaptive capacity are ‘potential adapters’ and may be able to cope through dispersal or micro-evolutionary change (Fig. 1.2). Species that scored high for *exposure* and *sensitivity*, but were characterized by *low adaptive capacity* may be naturally resilient to changes in their environment and are ‘potential persisters’ *in situ* (Fig. 1.2).

For qualitative traits (e.g., taxon requires rains to cue spawning migrations), ‘high’ or ‘low’ scores depended only on whether a species possessed that trait or not. However, for continuous traits (e.g., number of threats) there was no *a priori* basis for selecting scoring thresholds. For such traits we selected thresholds based on the distribution of trait values in our dataset. For example, fishes with estimates of climate change exposure that fell within the highest 25% of all fishes were given a ‘high’ score, while those in the lowest 75% were given a ‘low’ score. We tested the sensitivity of our analysis to these threshold selections by shifting thresholds to different cut-off points with lenient scenarios resulting in fewer species being given high scores (e.g., the top 15% scored as high) and strict thresholds resulting in more species being given high scores (e.g., the top 35% scored as high). Differences in results among *exposure* thresholds are compared in Tables A1 and A10, and Fig. A4. Another source of uncertainty in our data included traits within the *sensitivity* and *LAC* dimensions where there were unknown values. To address this uncertainty we calculated scores for these dimensions under both optimistic and pessimistic scenarios following Foden et al. (2013). In the optimistic scenario all unknowns were coded as low, and in the pessimistic scenario all unknowns were coded as high. The main results of this paper are presented under the lenient / optimistic scenario for all traits; however, we compared numbers of species with high scores under the strict / pessimistic scenario in Fig. 1.2 and Table A1, and explore differences in distribution of climate change vulnerable species under the two scenarios in Figs. A2 and A3. Details on

various threshold values and numbers of species with unknowns for each trait can be found in Table A1. Discussion on how various thresholds were selected and how unknowns were handled for each trait can be found in Supplementary Methods 1.8.

1.3.6 Assigning conservation value scores

Conservation value of species is defined in this study as the relative importance of species based on traditional conservation prioritization metrics including level of extinction risk defined by the IUCN redlist, uniqueness (endemism), and potential to provide ecosystem services through fisheries and other human uses. Species that scored high in any one of these traits were given a high score for *conservation value*. We used the same techniques described above for dealing various thresholds and unknown values. The main results of this paper are presented under the lenient / optimistic scenario for all traits; however, we compared numbers of species with high scores under the strict / pessimistic scenario in Fig. 1.2 and Table A1.

1.3.7 Mapping areas of greatest concentration of vulnerable species

Distributions of species that are highly vulnerable to climate change were mapped using R studio v. 3.4.1 (R Core Team, 2017) to identify regions with high concentrations of climate change-vulnerable and high conservation value species. We used univariate maps to show the spatial distributions of species with high scores in the different vulnerability dimensions (*sensitivity, LAC, and exposure*), overall *vulnerability*, and *conservation value*. We used bivariate maps to explore the spatial relationship among dimensions (i.e. *biological sensitivity* vs. *exposure*), and between climate change *vulnerability* and *conservation value*.

To create maps, we created a separate raster layer for every species in our dataset denoting presence or absence in every 10-min grid cell based on whether any part of their range intersected with a grid cell. We then created a file containing species' binary scores for *sensitivity, LAC, exposure, vulnerability*, and *conservation value* under all different scenario combinations (optimistic vs. pessimistic, emissions scenarios, years, and thresholds). Species

ranges were then stacked, and each grid cell was assigned a value indicating the number of species with high scores occupying that grid cell. In the univariate maps, each grid cell was assigned a colour that graduated from blues (to signify low species richness) to reds (to signify high species richness). We created univariate maps to show overall species richness (Fig. 1.1B) and to show distributions of fish that score high in each dimension, overall vulnerability, and conservation value (Fig. A1).

To create bivariate maps, values of species richness in the univariate layers of interest were split into 10 quantiles based on Jenks natural breaks. These layers were then overlaid, and bivariate plots were produced by assigning each grid cell a score based on the overlap in quantile scores. Each grid cell was assigned a colour on a bivariate colour scheme where cells with low frequencies were given duller colours and cells with higher frequencies were given more saturated colours, with tones approaching blue on the y-axis, yellow on the x-axis, and maroon where the two traits overlap. We created bivariate maps that overlay *biological susceptibility* (i.e., species with high scores for both *sensitivity* and *LAC*; y-axis) with *exposure* (x-axis; Fig. 1.3AB) and that overlay *conservation value* (y-axis) with *vulnerability* to climate change (x-axis; Fig. 1.4CD).

1.3.8 Trait and family analysis

To determine traits that contributed most to each *vulnerability* dimension (*sensitivity*, *LAC*, and *exposure*) and to *conservation value* we analyzed trait data in two ways. First, we calculated traits that had the highest proportion of high scores in each category after excluding unknowns, and ranked these traits in order of importance (Fig. A6). Second, we carried out a sensitivity analysis to determine how many species were given a high score within each dimension based exclusively on one trait (Table A1, Fig. 1.5). Traits that gave the highest number of species a high score in a given category were considered more influential in determining climate change vulnerability. We calculated families of African freshwater fish that had the highest proportion of vulnerable species, and assessed the dimensions of *vulnerability* that they were most likely to get high scores in (Fig. A5). We also assessed families most likely

to be classified as high *conservation value*. These analyses were done for families of ≥ 9 species (Tables 1.2 and A11). We compared the top 10 ranked families for both *vulnerability* and *conservation value* to assess how families would be differently prioritized for conservation (Table 1.2).

1.4 Results

1.4.1 Data availability and quality

We were able to obtain species ranges for 2984 species; however taxonomic anomalies, misclassifications, or missing data restricted the number of species that could be included in our dataset to 2793. This represents approximately 85% of the estimated 3300 freshwater fish species extant in Africa, and is likely to produce a broadly representative picture of spatial patterns of climate change risk. Species distributions are mapped in Fig. 1.1B. Data availability of traits varied from 100% (e.g., climate change projections) to only 4% of species having data (e.g., relative fecundity). For 76% (19 of 25) of the biological traits quantified, ‘unknowns’ comprised less than 10% of the data (Table 1.1). There were four traits within the *sensitivity* dimension that had large data gaps including length of spawning cycle, depth, prey specialization, and population fragmentation (Table 1.1). There were two traits within *LAC* that had large data gaps including dispersal of early life stages and reproductive capacity (Table 1.1).

1.4.2 Summary of vulnerability dimensions

Unless otherwise stated, the following summaries present data from the lenient/optimistic scenario, and under A1B emissions projection at a 25% exposure threshold for the year 2050, and percentages are calculated as the proportion of all species (2793) in the study. We identified 2375 freshwater fishes (84.8%) that scored as highly sensitive to climate change under the optimistic scenario (Fig. 1.2, Table 1.1, Fig. A1AB [distribution], Fig. A5, Table A11 [by family]), and 2698 (96.3%) under the pessimistic scenario (Fig. 1.2, Table A1). We found that 753 species (27%) qualified as highly sensitive because of a single trait, the most common

of which were low tolerance to temperature and precipitation change (24.7 and 24.4%, respectively), intense fishing pressure (24.5%), and/or high microhabitat specialization (23.3%; Fig. 1.5). The majority of species possessed multiple traits that categorized them as highly sensitive. We found 54.5% (1523) of all species to possess between two to five traits and a small proportion (3.5%, 99 species) with more than six. Other traits that contributed highly to sensitivity included low population abundance (16%, 455 species), narrow spatial range (14.2%, 397 species), and exposure to climate-change exacerbated threats (13.3%, 371 species). Apart from fishing, common threats included sedimentation (35% of species affected), dams and water diversion (29%), deforestation (14%), and mining effluents (13%; Table A5).

In our analysis, 71.6 % (2000) of freshwater fishes were deemed to have low adaptive capacity under the optimistic scenario (Fig. 1.2, Table 1.1, Fig. A1CD [distribution], Fig. A5, Table A11 [by family]). This increased to 97.5% (2724) under the pessimistic scenario (Fig. 1.2, Table A1). There were 1258 species (45%) that were given a high score for LAC because of a single trait, the most common of which was having low potential for population growth (Fig. 1.5). The traits that had the largest influence on low adaptive capacity in our study include dispersal of early life history stage (27.7%), physical barriers to dispersal (19.2%), and low estimated population growth rates (42.5%). There were 1620 fish (58%) that possessed between two and three traits that indicated LAC with a small proportion (1%, 32 species) possessing four traits.

Finally, we found that 54.1 % (1510) of freshwater fish species are predicted to be highly exposed to climate change (Fig. 1.2, Table 1.1, Fig. A1EF [distribution], Fig. A5, Table A11 [by family]). Under this scenario, there were 611 fish species (21.8 %) that were given a high score for exposure because of just one trait, the most common of which was exposure to high levels of temperature change (Fig. 1.5). We compare numbers of exposed species under different thresholds (15%, 25%, and 35%) in Table A1.

1.4.3 Summary of climate change vulnerability

We identified 1059 freshwater fishes (37.9%) as highly vulnerable to climate change under the optimistic scenario (Fig. 1.2, Table 1.1, Fig. A1GH [distribution], Fig. A5, Table A11 [by family]), and 1440 (51.6%) under the pessimistic scenario (Fig. 1.2). An additional 696 (24.9%) were identified as biologically susceptible to climate change (i.e., had high scores for *sensitivity* and *LAC*, but not for *exposure*) under the optimistic scenario, which increased to 1193 fish (42.7%) under the pessimistic scenario (Fig. 1.2). We compare numbers of vulnerable species under different scenarios (optimistic, pessimistic), years (2090, 2050), and emissions scenarios (B1, A1B, A2) in Table A10. We compare differences in concentrations of vulnerable species under optimistic vs. pessimistic scenarios in Fig. A2, among years and emissions scenarios in Fig. A3, and among various exposure thresholds (15%, 25%, and 35%) in Fig. A4.

1.4.3.1 Vulnerable regions

Bivariate maps of biological susceptibility (i.e., high scores for both *sensitivity* and *LAC*) vs. *exposure* highlight regions of overall climate change vulnerability across Africa (Fig. 1.3AB). In these maps, regions highlighted in blue represent high concentrations of species that have high *sensitivity* and *LAC*, but that are not highly exposed to climate change (i.e., high latent risk; Fig. 1.2). Regions with high concentrations and percentages of species of high latent risk include the Nile and Senegal rivers, the Congo River basin and its tributaries, and sections of south-eastern Africa (Fig. 1.3AB). Regions where species have a low *sensitivity* and a high *adaptive capacity* (i.e., potential persisters or potential adapters) but are expected to be highly *exposed* are highlighted in yellow. These regions include the Niger River, some of the non-coastal West African rivers, and tributaries of the Zambezi and Limpopo river drainages (Fig. 1.3AB). When analyzed by proportions of species, Lake Victoria also stands out along with much of the Orange River drainage in southern Africa (Fig. 1.3B). Areas containing the greatest numbers and proportions of fishes that are vulnerable overall are indicated in red (Fig. 1.3AB), and include the coastal Upper and Lower Guinea rivers and lakes, the Niger River delta, the Volta River drainage, the rift valley lakes (Victoria and Malawi), and much of the upper Zambezi River

drainage and Okavango delta. When analyzed in terms of proportions, regions within the Sahara desert also stand out.

1.4.3.2 Vulnerable families

Families that contained the highest percentage of climate change vulnerable species based on the optimistic scenario included the Cichlidae (63% of all cichlids), the Nothobranchiidae (60%), and families within the order Siluriformes (the catfishes) including Bagridae (44%), Malapteruridae (38%), Clariidae (33%), and Mochokidae (28%; Table 1.2). For cichlids, the most common traits that gave them high scores for *LAC* included poor dispersal of early life-history stages (249 species, 27% of all cichlids) and low population growth rate (429 species, 47%), and for *sensitivity* it was disruption of mate-finding due to turbidity (249 species, 27%), highly specified diets (188 species, 20%), and low abundances (219 species, 24%). For the Nothobranchiidae, the most common for *LAC* included barriers to dispersal (161 species, 76% of nothobranchids), and limited dispersal of early life history stages (74 species, 35%) and for *sensitivity* it was requiring specific microhabitats (188 species, 88%) and strong dependence on environmental triggers (43 species, 20%). The four most vulnerable catfish families all had *LAC* because of their low population growth rates (287 species, 63% of vulnerable catfish species), and were *sensitive* because of low tolerance to temperature changes (90 species, 31%), dependence on microhabitats (71 species, 25%), and fishing pressure (80 species, 28%).

1.4.4 Summary of conservation value

We identified 1714 freshwater fish species of high conservation value under the optimistic scenario based on the traditional metrics of endemism, threat status, and ecosystem services provided (Figure 1.4AB, Table 1.1, Fig. A1IJ [distribution], Fig. A5, Table A11 [by family]), and 2232 species that qualified under the pessimistic scenario (Fig. 1.2, Table A1). There were 973 species that scored high for *conservation value* because of one trait, the most common of which was endemism (Fig. 1.5). Twenty percent (571 species) scored high for conservation value based exclusively on this trait, followed by fishing pressure (207 species,

7%), IUCN threat status (171 species, 6%), and other uses (24 species, 0.8%; Fig. 1.5). The majority of species in our dataset (2167 fish) possessed between two to three traits that scored high for *conservation value*.

1.4.4.1 Regions and families of high conservation value

Regions with highest concentrations of species of high conservation value included the rift valley lakes in eastern Africa (Victoria, Tanganyika, and Malawi), the Congo River and its tributaries, and the Niger River delta (Fig. 1.4A). When analyzed by proportions of fish species, the Orange River drainage, regions of the northern Sahara desert, and some of the inland rivers and lakes in eastern and western Africa stand out (Fig. 1.4B). Families that contained many species of high conservation value included the Cichlidae (88% of all cichlids), the Nothobranchiidae (75%), the Mastacembelidae (69%), and families within the order Siluriformes (the catfishes) including Bagridae (67%), Claroteidae (55%) and Mochokidae (53%; Table 1.2). For cichlids, the most common traits that gave high scores for conservation value included endemism (738 species, 27%) and other uses (473 species, 51%), primarily the aquarium trade. These species are also important targets of artisanal fisheries (381 species; 41%). For nothobranchids, the most common traits included high human use (147 species, 69%), again mostly for the aquarium trade, endemism (98 species, 46%), and IUCN threat status (81 species; 38%). For the Mastacembelidae, 19 species (54%) scored high for endemism and 14 species (40%) for human use.

1.4.5 Comparison of vulnerability and conservation value

Of the 1059 species that were found to be vulnerable to climate change under the optimistic – A1B – 2050 scenario, 851 were also found to be of high conservation value representing 80% of climate change vulnerable species. Bivariate maps highlight regions where there is overlap in high concentrations of species of high conservation value and high climate change vulnerability (Fig. 1.4CD), and where these measures are at odds. Areas with low species vulnerability but high conservation value (highlighted in blue) include the Congo River

basin, much of the Nile River, Lake Tanganyika, and many of the smaller lakes and rivers in eastern Africa (Fig. 1.4CD). Regions where species are highly vulnerable to climate change, but not of high conservation value (highlighted in yellow) include many of the coastal rivers in the Upper Guinea ecoregion, Lake Tana, some tributaries of the Nile river in north-eastern Africa, and tributaries of the Zambezi and Limpopo rivers in southern Africa (Fig. 1.4CD). Areas containing the greatest numbers and proportions of fishes that are both climate change vulnerable and of high conservation value (indicated in maroon) include the coastal Upper- and Lower- Guinea rivers, particularly the Niger River delta, the Volta River drainage, some of the rift valley lakes (especially Victoria and Malawi), and much of the upper Zambezi River drainage the Okavango delta (Fig. 1.4CD). Family-level analysis revealed a different order of conservation prioritization based on climate change vulnerability vs. conservation value (Table 1.2).

1.5 Discussion

This study presents the first comprehensive trait-based CCVA of Africa's freshwater fish species. Results indicate that a high proportion of African freshwater fishes are likely to be negatively affected by climate change, with 38% of species qualifying as highly vulnerable under an optimistic, mid-range emissions scenario for 2050. This is similar to values found in regional assessments of freshwater fishes in the Albertine rift (31%; Carr et al., 2013) and West Africa (39%; Carr et al., 2014), but higher than proportions documented in global assessments of amphibians (22%), corals (15%), birds (24%; Foden et al., 2013), and reptiles (22%; Böhm et al., 2016). Although direct comparisons are limited by variation among studies' scoring systems, it is interesting that African freshwater fishes have one of the highest vulnerability percentages detected, supporting predictions that this group is highly susceptible to environmental change (Dudgeon et al., 2006).

This study offers several important contributions to nascent conservation strategies for this fauna. First, it identifies species and regions that are highly vulnerable to climate change, and pinpoints biological and ecological characteristics that most contribute to this vulnerability. Second, it highlights knowledge gaps that hinder our understanding of species vulnerability.

Third, it identifies species and regions where typical conservation metrics may under- or over-emphasize conservation priority, and provides information necessary to incorporate vulnerability into conservation planning.

1.5.1 Vulnerable species and families

Targeted conservation interventions require species- and region- specific information on threats to ecological systems (Abrahms et al., 2017). We identified regions with high concentrations of vulnerable species and family groups that are vulnerable, of high latent risk, potential persisters, or potential adapters (Tables A11 and A12). Species of high latent risk are considered to be biologically susceptible, but are not predicted to be highly exposed to climate change. However if climate change proceeds at a more extreme pace than predicted, they could become vulnerable in the future. These species should be closely monitored in their habitat and re-assessed as new projections emerge. Species that are potential adapters or potential persisters represent fishes whose environments are likely to change, but who have the capacity to avoid, adapt, or cope with these changes. These fishes may avoid extinction if they are able to use their survival capacities as predicted; data regarding these species adaptive capacity and sensitivity should be updated with new information when possible. Vulnerable species are very likely to be negatively affected by climate change, and are therefore of highest priority for climate change mitigation and conservation action. Here we cannot provide lengthy descriptions of families or species falling into these categories; however, details are provided in summary tables in the Supplementary Materials (Tables A11 and A12).

1.5.2 Species traits that contributed to vulnerability

The contributions of biological traits to vulnerability were highly variable among families, reflecting the diversity of life history strategies and ecological niches occupied by fish species across Africa. Microhabitat specialization was a very important sensitivity trait. Temporary pools (e.g., in flooded forests) emerged as an important microhabitat for many species, along with cool, clear rainforest streams, and shallow, fast flowing creeks, mirroring

findings of Carr et al. (2013, 2014). High dependence on microhabitats indicates that species have narrow environmental tolerances and are likely to have locally-adapted phenotypes (Hannah et al., 2014; Nadeau et al., 2017), and adverse effects on microhabitats are likely to expose such species to effects of climatic change. In addition, many species were classified as sensitive based on small population sizes, narrow distributions, or declining abundances. In general, species that have small population sizes are expected to be vulnerable to stressors as they are less likely to contain resilient individuals or to produce offspring with advantageous genetic combinations for coping with novel climatic scenarios (Willi and Hoffmann, 2008; Sgrò et al., 2011). Carefully monitoring rare species and identifying key causes of population decline can reduce their sensitivity to climate change.

Barriers to dispersal were important factors leading to low adaptive capacity in many fish species in this study. Freshwater fishes are embedded within terrestrial landscapes that limit dispersal within and among drainage basins. On both regional and global scales, it is often assumed that most freshwater fish occupy only a small percentage of possible localities, simply because they cannot access new locations (Olden et al., 2010; Bush and Hoskins, 2017). Climate change has been shown to shift environmental conditions across landscapes, and these shifts are expected to progress with time (Parmesan and Yohe, 2003). Species that have restricted capacities for dispersal will be unable to undergo range shifts at rates that match these changing conditions, and are likely of high extinction risk (Bush and Hoskins, 2017). For example, lakes Malawi and Tanganyika have shorelines comprised of rocky, swampy, and sandy microhabitats that act as ecological islands, many of which host their own species of small, specialized fishes (Lowe-McConnell, 1969). These species may not have the ability traverse inhospitable terrain to escape their current habitat if conditions should change, and are therefore likely to be vulnerable to climate change.

Low population growth rate also stood out as a barrier to adaptive capacity. Population growth rate was inferred from life history traits assuming that r-selected species with fast life-cycles will have higher population growth (and therefore better adaptive capacity). While there is

mixed evidence for this pattern in fishes (Pinsky and Byler, 2015), generally, species with faster generation times and higher fecundity have faster adaptive responses to environmental change (Lande, 1993; Williams et al., 2008; Pacifici et al., 2017). This being said, traits that are favourable to one aspect of adaptation may be harmful for another. For example, higher relative fecundity may be advantageous for faster rates of evolutionary adaptation, but these same species are often total spawners (i.e., laying all eggs in one spawning session), making them more susceptible unpredictable seasonal conditions (Jeppesen et al., 2010). Furthermore, species with fast generation times tend to be smaller-bodied and shorter-lived, which are traits that reduce capacity for distributional shifts in response to local environmental change (Comte and Olden, 2018). The degree to which various life-history traits or combinations of traits contribute to climate change vulnerability in fishes is a key area for future study.

1.5.3 Other environmental stressors

Freshwater fishes are exposed to a wide array of anthropogenic stressors in their natural habitats, including overexploitation, habitat degradation, and water pollution, among others (Dudgeon et al., 2006). Of the threats examined in this study, fishing was the most dominant with over 1000 species targeted for consumption across the continent, and expansions of urban and industrial areas, land conversion for agriculture, natural resource extraction (e.g., mining, deforestation), and introductions of invasive species were found to be widespread in African aquatic environments. Many CCVAs do not incorporate exposure to other stressors primarily because they are not based on species' intrinsic traits. We chose to account for them because, from a conservation perspective, they are an essential consideration in predicting climate change vulnerability, particularly because many of these stressors are likely to be intensified by climate change. For example, Xenopolous et al. (2005) projected that 25% of rivers could lose 22% of fish species by 2070 due to additive effects of water withdrawal and climate change, and increased water temperature has been shown to exacerbate effects of pollutants on fishes (Ficke et al., 2007). In addition, species already affected by other stressors are likely to be using physiological, genetic, and behavioural resources to cope, and are

therefore predicted to have acute responses to the additional impacts of climate change (Staudt et al., 2013).

1.5.4 Identifying research needs

One of the limitations of trait-based CCVAs is the paucity of data for some traits (Pacifi et al., 2015). In our analysis, large data gaps existed for several traits, especially those pertaining to species' potential to adapt to climate change through dispersal or micro-evolutionary change. For example, only 4% of species had data on relative fecundity, and estimates of natural mortality (1%) and individual growth rate (2%) were so rare that these traits could not be included in our analyses. In addition, there were very few direct measures of species' genetic diversity, population size, and population growth rate. Ecological traits were better represented, but still with significant gaps in species depth ranges, spawning cycle, and estimates of population fragmentation. Of these, basic life-history, population size, and spawning traits stood out as important for understanding climate change effects, and could help enormously in assessing species' vulnerability to climate change. Clearly, missing data can introduce uncertainty into interpretations for conservation goals and may bias our understanding of which traits confer vulnerability, or which species are the most vulnerable. Nevertheless, this method is effective in using available data to understand vulnerability patterns across broad geographic areas and large numbers of species (Pacifi et al., 2015) and can identify knowledge gaps to guide future research.

1.5.5 Conservation planning

Resources for the conservation of natural systems are limited, so efforts to protect biological diversity require prioritization (Arponen, 2012). Traditional indices of species' conservation value commonly incorporate estimates of economic or socio-cultural value, phylogenetic distinctiveness, endemism, extinction risk (e.g., IUCN status), and rarity, among others (Reece and Noss, 2014; Capmouteres and Anand, 2016). However, assessments that ignore climate change may overlook regions or species that are at risk from long-term

environmental shifts. Because our understanding of how climate change affects species is relatively recent, it is not often incorporated into conservation plans (Stewart et al., 2018), and the most recent conservation assessment of African freshwater ecosystems only peripherally integrates climate change in its prioritization scheme (Thieme et al., 2005). The main accomplishment of this study is to provide the first cohesive and thorough climate change vulnerability assessment of African freshwater fish summarizing current knowledge on the majority (85%) of freshwater fish species in Africa and regional level statuses that can be used to guide future ecosystem monitoring, conservation modelling, and experimental or field-based research.

1.5.5.1 Comparison of climate vulnerability to traditional conservation value metrics

Areas of high conservation value (based on extinction risk, endemism, and human use) did not always align with areas predicted to be highly affected by climate change (e.g., Upper Guinea rivers, Zambezi and Limpopo drainages). These regions might be ignored by traditional conservation assessments that do not incorporate climate change vulnerability. Species we identified as highly vulnerable to climate change but not of high conservation value represent new priorities for conservation. These include 208 freshwater fish species and represent 20% of all climate change vulnerable fish, including members of the commercially-harvested Polypteridae and amphiliid catfish families. In contrast, regions that are of high conservation value, but do not stand out as being highly climate change vulnerable (e.g. Congo River drainage, Lake Tanganyika) tend to have high numbers of unique, endemic species, but are not projected to have high exposure to climatic changes. We do not suggest that these regions should not be prioritized for conservation, but that they may not be as threatened in the near future.

Species that are both highly climate change vulnerable and of high conservation value, and the regions in which they are concentrated, deserve particular conservation attention to both mitigate current threats and to plan for future climate change adaptation interventions. Species in this category include members of the families Cichlidae, Nothobranchiidae, Bagriidae,

Claridae, Poeciliidae, and Mochokidae, and are concentrated in lakes Victoria and Malawi, the Lower guinea region and the upper Zambezi catchment. In addition, around 19% (203) of climate change vulnerable species are classified as data deficient according to the IUCN. Families where high proportions were vulnerable and of high conservation value but considered data deficient include the families Bagriidae, Nothobranchiidae, Clariidae, and Cichlidae. Species in this category need protection given their endemic and threatened status and their importance to human use (Thieme et al., 2005), but also require special monitoring in terms of response to climate change stressors.

1.5.5.2 Contribution to conservation management

This study has identified priority research areas for incorporating climate change into conservation plans for African freshwater fishes. Conservation plans require knowledge on the major biological and ecological constraints of species, (e.g., distribution, critical habitat), information on their conservation status, and key threats they face (Stewart et al., 2018). Having this information accessible in a cohesive dataset, such as the one produced for the present study, can facilitate creation of adaptive strategies, and can be used to include climate vulnerability in species-level and ecosystem models. The 6th IPCC global climate change assessment is currently underway (available in 2022), and can be used to track, monitor, and update spatial distributions of vulnerability projections developed in this study. This exemplifies how this dataset can be used as a tool to inform adaptive management strategies (Foden et al., 2013; Böhm et al., 2016).

Conserving species that are vulnerable to climate change requires a different approach than conservation based on distributions of other stressors; those that are vulnerable to climate change will need to adapt, while those affected by other stressors may be able to persist in their natural range if their remaining natural habitat is protected (Hannah et al., 2007). For species and families that are vulnerable to climate change, conservation actions should include preserving and restoring habitats, targeting research to fill data gaps to improve predictions of climate change vulnerability, and carrying out regular monitoring of vulnerable populations. For

species not highly climate change vulnerable, conservation should focus on preserving current habitats as they are, because these species are unlikely to need to move if their environments are kept intact (Stewart et al., 2018).

Effects of climate change are a moving target. Traditional approaches of static reserve designs need to be adjusted to incorporate the shifting nature of climatic space under future conditions (Williams et al., 2008; Bellard et al., 2012). Protected areas may not contain species after conditions within reserve boundaries change (Abrahms et al., 2017). Incorporating climate change projections into conservation planning is therefore an important challenge facing scientists and managers (Abrahms et al., 2017; Stewart et al., 2018), and recent approaches to conservation suggest developing networks of landscapes that contain a diversity of species and environmental conditions that promote connectivity and increase the likelihood of adaptive species responses (Webster et al., 2017).

1.6 Conclusion

The study represents the first comprehensive climate change vulnerability assessment of African freshwater fishes to climate change. We showed that high proportions of African freshwater fish are biologically susceptible to climate change, mainly owing to highly specific microhabitat requirements, barriers to dispersal, and the many small, isolated, and highly threatened populations of these species. While our capacity to make detailed predictions is limited by lack of data on key biological and ecological traits, this information is useful for understating general patterns of climate change vulnerability (Dickinson et al., 2014). Comparison of these data with classic conservation assessments showed that incorporating climate can highlight new priority regions for conservation, and provide impetus for incorporation of climate change in to future conservation management plans.

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1.8 Tables

Table 1.1 Description of trait sets, variables, and thresholds qualifying species as high or low for *Vulnerability* and *Conservation Value*, and the number of species classified as high, low, and unknown for each trait and threshold. Numbers and proportions of species qualifying for *Sensitivity*, *Low Adaptive Capacity*, *Exposure*, *Vulnerability* and *Conservation value* in each individual Trait Set are presented in column. All data are based on the optimistic scenario for the A1B climate change emissions scenario for 2050.

SENSITIVITY (n = 2375; 84.8% of all species in dataset)				
Trait set	Variable	Description	Threshold / Definition	n
I. Specialized habitat or microhabitat requirements (n = 727; 26.0% of all spp.)	1. Depth range	taxon is restricted to shallower habitats or shallow depths	high = restricted to shallow depths (< 3 m)	78
			low = not restricted to shallow depths	480
			unknown = no information	2235
	2. Habitat specialization	taxon is a habitat generalist or specialist	high = restricted to 1-2 rare or vulnerable habitats	79
			low = inhabits diverse or common habitats	2531
			unknown = no information	183
II. Narrow environmental tolerances (n = 1449; 51.2% of all spp.)	4. Tolerance of changes to precipitation	historical variability in precipitation across the taxon's range	high = lowest 25% precipitation variability (≤ 56.1 mm)	691
			low = highest 75% precipitation variability (> 56.1 mm)	2102
	5. Tolerance to changes in temperature	historical variability in temperature across the taxon's range	high = lowest 25% temperature variability (≤ 0.66 °C)	682
			low = highest 75% temperature variability (> 0.66 °C)	2111
	6. Sensitivity to increases in turbidity: mating	taxon's mate recognition system affected by changes in turbidity	high = requires clear water for mate recognition	267
			low = all other taxa	2526
	7. Sensitivity to increases in turbidity: food	taxon's food gathering or prey selection affected by changes in turbidity	high = requires clear water to find food	137
			low = all other taxa	2656
	8. Dependence on precipitation activated trigger	taxon requires rains at specific times to complete a portion of life cycle	high = breeding migration triggered by rains	154
			high = hatch during rains, require rains for resubmergence	47
			high = juvenile migrations triggered by water level	24
			low = all other taxa	2586
III. Dependence on interspecific interactions (cont)	9. Prey specificity	taxon is a prey generalist or specialist	high = relies exclusively on 1 prey type	266
			low = consumes a wide variety of prey	1287
			unknown = no information	1240

(cont) n = 316; 11.3% of all spp.)	10. Dependence on other taxa	taxon relies on another taxon for some aspect of survival	high = dependent on another species food, protection, or habitat	77
			low = all other taxa	2716
IV. Complexity of life history strategy (n = 307; 11.0% of all spp.)	11. Complexity in reproductive strategy	taxon relies on precise environmental / social cues, rare habitats for reproduction	high = taxon relies on seasonal, environmental or social cues for reproduction	242
			low = all other taxa	2551
	12. Complexity in early life history requirements	taxon's larvae or eggs rely on precise environmental cues, conditions, habitats for survival	high = taxon relies on seasonal or environmental cues or specific habitats for survival of eggs and larvae	49
			low = all other taxa	2744
	13. Spawning cycle	number and duration of a taxon's spawning events	high = spawns only once or over a short timeframe (<2 months)	70
			low = spawns several times, over longer timeframes (>2 months)	312
			unknown = no information	2411
V. Rarity (n = 774; 27.7% of all spp.)	14. Taxon abundance	taxon is rare or common	high = at least 2 of: rare, narrow distribution, declining	455
			low = at least 1 of: common, widespread, increasing	2035
			unknown = no information	303
	15. Range size: extent of occurrence (EOO)	total area the species extends across	high = small EOO (< 5000 km2)	350
			low = large EOO (> 5000 km2)	2443
	16. Range size: area of occupancy (AOO)	actual area occupied by the species	high = small AOO (< 500 km2)	397
			low = large AOO (> 500 km2)	2396
	17. Population fragmentation	taxon's populations are fragmented or very small	high = populations fragmented or very small	47
			low = populations large and contiguous	1028
			unknown = no information	1718
VI. Exposure to other disturbances (n = 1012; 36.2% of all spp.)	18. Fishing pressure	taxon is harvested for human consumption	high = fishery classified as either commercial or highly commercial	684
			low = not harvested or fishery classified as artisanal	2109
	19. Other threats	number of threats currently affecting the taxon	high = threatened by ≥ 7 additional anthropogenic stresses (top 25% threatened)	135
			low = threatened by < 7 additional anthropogenic stresses (lowest 75% threatened)	2658
	20. Threats intensified by climate change	number of threats will be directly intensified by climate change (see table A5)	high = threatened by ≥ 2 stresses	371
			low = threatened by < 2 stresses	2422

LOW ADAPTIVE CAPACITY (n = 2000; 71.6% of all species in dataset)				
Trait set	Variable	Description	Threshold / Definition	#species
VII. Low potential for dispersal (n = 1263; 45.2% of all spp.)	1. Intrinsic low probability of dispersal	taxon has traits that lead to low dispersal syndromes (see table A6)	high = combination of life history traits that indicate low intrinsic dispersal ability	386
			low = all other taxa	2407
	2. Barriers to dispersal	taxon's dispersal is limited by ecological barriers or strong habitat affinities as adults	high = adults dispersal restricted by biogeographic and ecological barriers	539
			low = all other taxa	2254
	3. Dispersal of early life stages	ability for taxon's eggs and larvae to disperse	high = eggs or larvae are entirely benthic	774
			low = egg or larvae have a pelagic stage	211
			unknown = no information	1808
VIII. Low potential to evolve (n = 1211 43.4% of all spp.)	4. Reproductive capacity	taxon's mean annual relative fecundity	high = low relative fecundity (< 200 eggs / gram / year)	23
			low = high relative fecundity (>200 eggs / gram / year)	77
			unknown = no information	2693
	5. Population growth	taxon's potential for population growth based on life history characteristics (low population growth = high LAC; Table A7)	high = combination of life history traits that indicate low population growth	1188
			low = combination of life history traits that indicate high population growth	1550
			unknown = no information	55

EXPOSURE (n = 1510; 54.1% of all species in dataset)				
Trait set	Variable	Description	Threshold / Definition	#species
IX. Predicted exposure to the effects of climate change (n = 1510; 54.1% of all spp.)	1. Changes in mean temperature	average change in mean temperature from 1975 to 2050 across taxon's range	high = highest 25% (≥ 3.14 °C)	538
			low = lowest 75% (< 3.14 °C)	2255
	2. Changes in temperature variability	average change in temperature AAD (variability) from 1975 to 2050 across taxon's range	high = highest 25% (≥ 3.64 °C)	834
			low = lowest 75% (< 3.64 °C)	1959
	3. Changes in mean precipitation	average change in mean precipitation from 1975 to 2050 across taxon's range	high = highest 25% (≥ 26.2 mm)	929
			low = lowest 75% (< 26.2 mm)	1864
	4. Changes in precipitation variability	average change in precipitation AAD (variability) from 1975 to 2050 across taxon's range	high = highest 25% (≥ 21.0 mm)	527
			low = lowest 75% (< 21.0 mm)	2266
VULNERABILITY (n = 1059; 37.9% of all species in dataset)				

CONSERVATION VALUE (n = 1714, 61.4% of all species in dataset)				
Trait set	Variable	Description	Threshold / Definition	#species
I. Endemism (n = 1267, 45.4% of all spp.)	1. Endemism	taxon is endemic to a region	high = endemic	1267
			low = not endemic	1526
II. IUCN redlist status (n = 585; 20.9% of all spp.)	2. Level of endangerment	taxon's listing under the IUCN vulnerability assessment	high = critically endangered (CR), endangered (EN), vulnerable (VU)	585
			low = least concern (LC), not threatened (NT)	1680
			unknown = data deficient (DD)	528
III. Importance for human use (n = 712, 25.5% of all spp.)	3. Fishing pressure	taxon is harvested for human consumption	high = fishery classified as either commercial or highly commercial	684
			low = not harvested or fishery classified as artisanal	2109
	4. Other uses	taxon is used by humans in other ways (apart from consumption; see table A9 for use categories)	high = used for 2+ other purposes	69
			low = used for < 2 other purposes	2724

Table 1.2 Numbers and proportions of species within families containing ≥ 9 species that are highly *vulnerable* and of high *conservation value*. Highlighted cells show the top 10 families for conservation priority based on vulnerability to climate change, conservation value (CV), and a combination of the two. These values are based on the optimistic scenario of the A1B emissions scenario for 2050.

FAMILY (Order)	CP1: Vul	CP2: CV	CP3: combined	Total spp.	# Vul.	% Vul.	# CV	% CV
CICHLIDAE (Perciformes)	1	1	1	920	579	63	807	88
NOTHOBRANCHIIDAE (Cyprinodontiformes)	2	2	2	213	127	60	160	75
BAGRIDAE (Siluriformes)	3	4	3	9	4	44	6	67
MALAPTERURIDAE (Siluriformes)	4			16	6	38	2	13
CLARIIDAE (Siluriformes)	5	8	5	73	24	33	38	52
MOCHOKIDAE (Siluriformes)	6	6	6	189	52	28	100	53
POLYPTERIDAE (Polypteridae)	7			11	3	27	3	27
AMPHILIIDAE (Siluriformes)	8		10	70	18	26	26	37
POECILIIDAE (Cyprinodontiformes)	9	7	8	59	14	24	31	53
CYPRINIDAE (Cypriniformes)	10	9	9	502	117	23	243	48
MASTACEMBELIDAE (Synbranchiformes)		3	4	35	8	23	24	69
MORMYRIDAE (Osteoglossiformes)				172	39	23	49	28
CLAROTEIDAE (Siluriformes)		5	7	73	16	22	40	55
GOBIIDAE (Perciformes)				19	4	21	4	21
ELEOTRIDAE (Perciformes)				12	2	17	2	17
SCHILBEIDAE (Siluriformes)				31	5	16	12	39
KNERIIDAE (Gonorynchiformes)				30	3	10	12	40
ALESTIDAE (Characiformes)				108	8	7	49	45
DISTICHODONTIDAE (Characiformes)				90	5	6	30	33
CLUPEIDAE (Clupeiformes)				24	1	4	9	38
ANABANTIDAE (Perciformes)		10		26	1	4	12	46

1.9 Figures

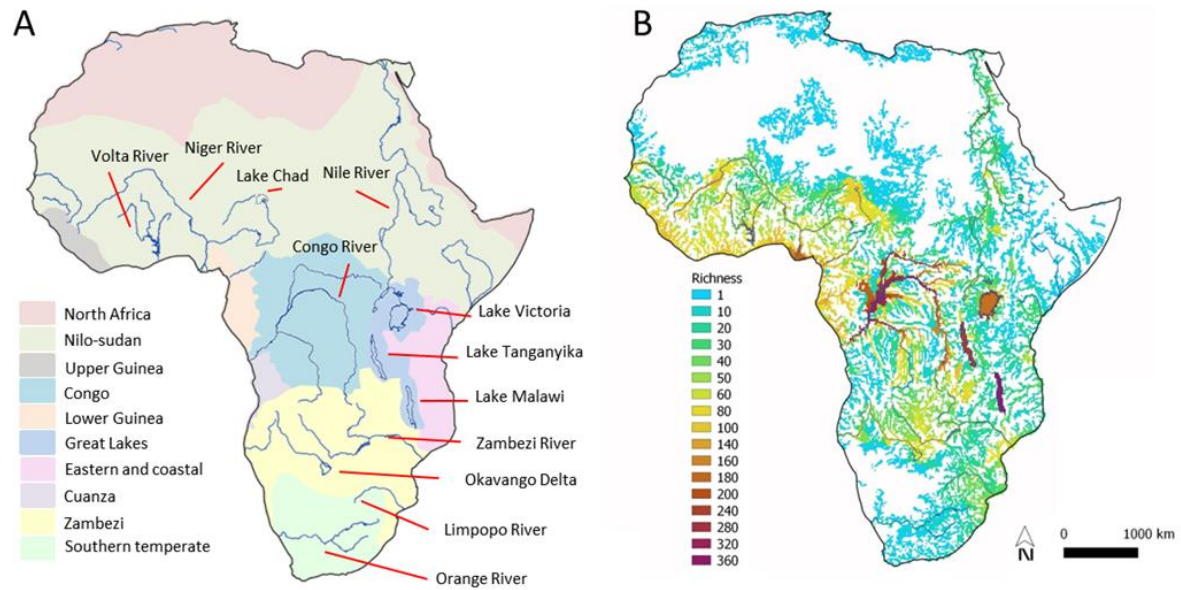
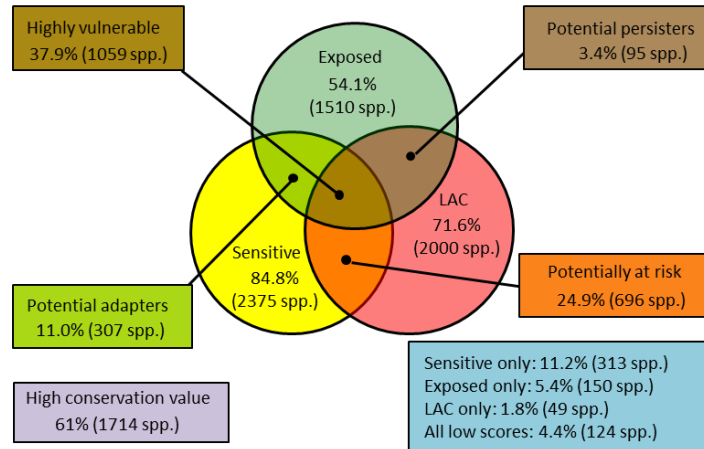


Figure 1.1 Map showing (A) the ichthyological provinces adapted from Roberts 1975 and Thieme et al., 2005, as well as the major lake and river systems in Africa, and (B) the distribution of species richness of freshwater fish in Africa.

A: Optimistic scenario



B: Pessimistic scenario

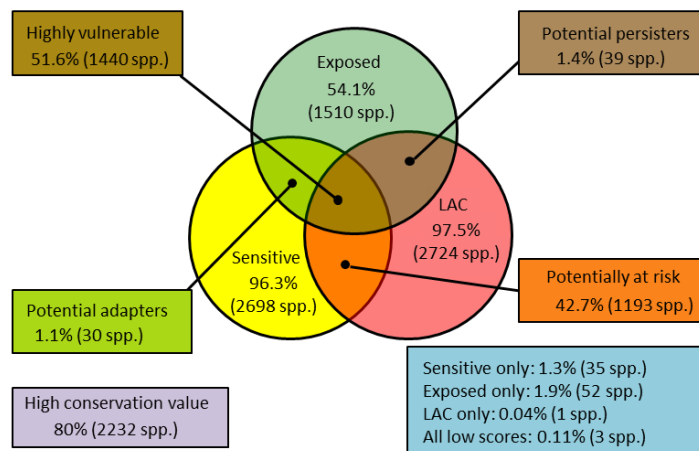


Figure 1.2 Numbers of species in each climate change vulnerability category and conservation value under the A) optimistic scenario (unknowns = low, lenient thresholds) and B) pessimistic scenario (unknowns = high, strict thresholds). For both scenarios, we have provided counts and percentages of all species that qualify for each category (sensitive, LAC, exposed, vulnerable, potential persisters, potential adapters, potentially at risk, and conservation value) as well as numbers of species classified as ONLY sensitive, LAC, or exposed, and those that scored low in all categories. All values contained within boxes (not including conservation value) add to 100%. All values are based on the A1B emissions scenario for 2050 at the 25% exposure threshold.

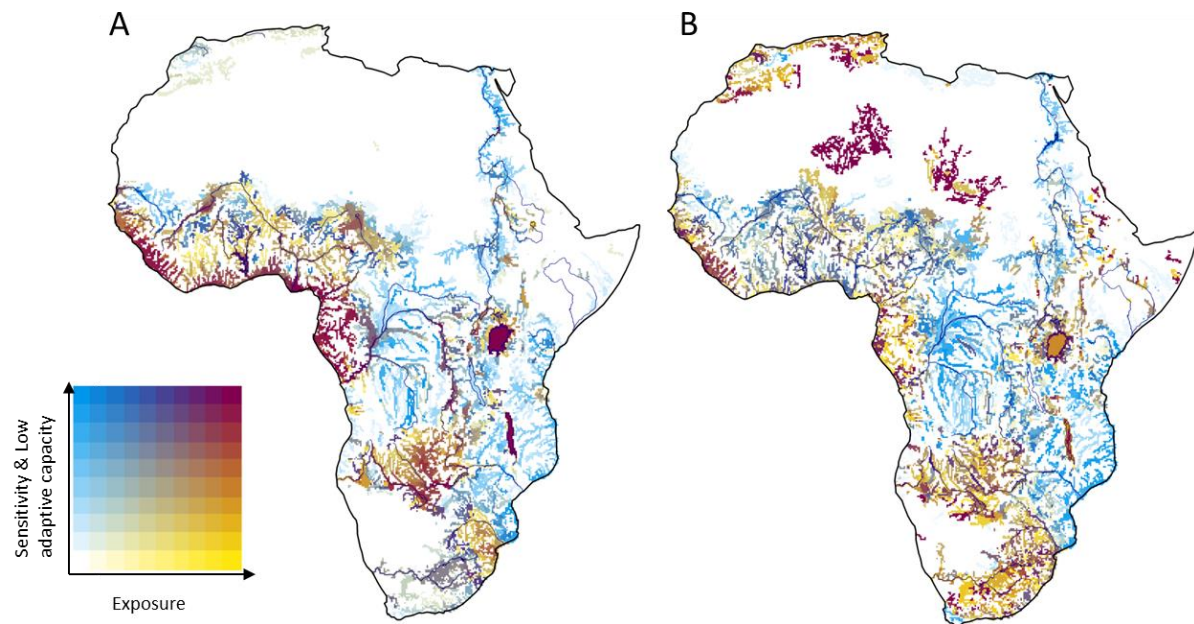


Figure 1.3 Bivariate maps showing regions where there is high overlap in the (A) total count and (B) percent of species that are highly biologically susceptible (scored high for *sensitivity* and *LAC*) and highly exposed to climate change. Distributions are based on the optimistic scenario for the A1B emissions projection and the 25% exposure threshold for the year 2050.

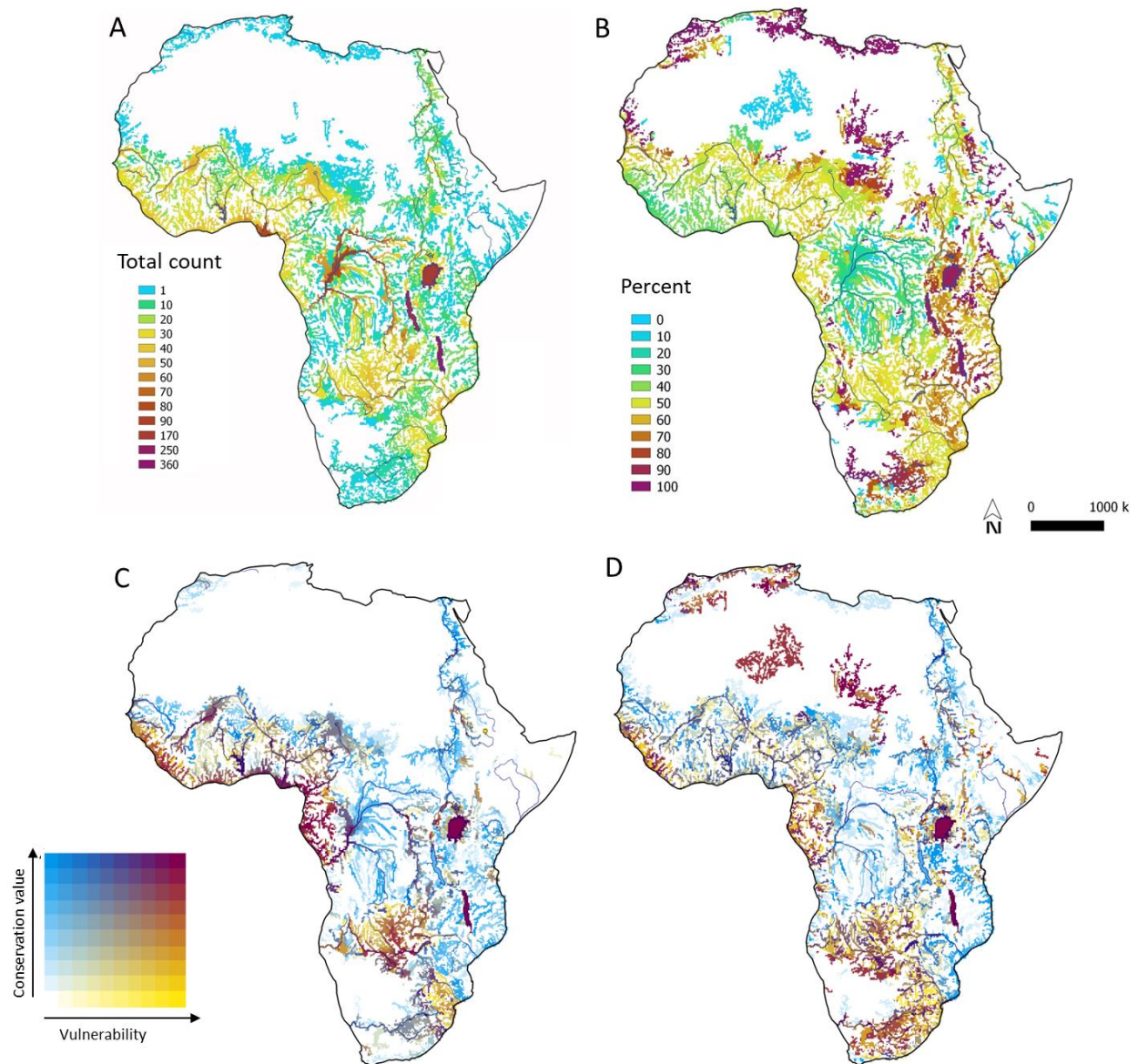


Figure 1.4 Univariate maps showing the total count (A) and proportion (B) of species that are of high conservation value, and bivariate maps showing total count (C) and percent (D) of regions where there is high overlap of species that are highly climate change vulnerable and of high conservation value. Distributions are based on the optimistic scenario for the A1B emissions projection and the 25% exposure threshold for the year 2050.

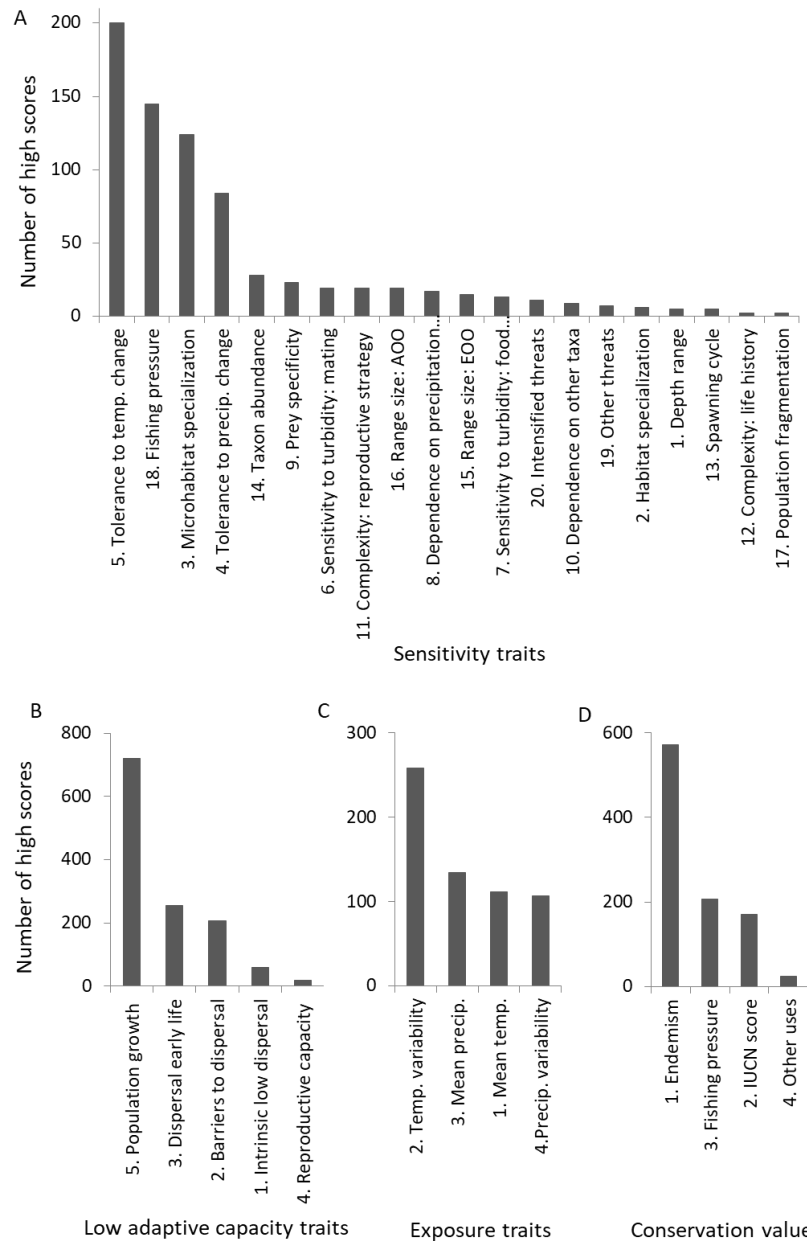


Figure 1.5 Summary of the number of species qualifying for high vulnerability exclusively due to single trait within the vulnerability dimensions of A) *sensitivity*, B) *low adaptive capacity*, and C) *exposure*, and for D) *conservation value*. For example, ~200 species were ranked high for Sensitivity exclusively because they got a high score for SV5. Tolerance to temperature change, but did not score high for any other *Sensitivity* variable. Traits are ranked by importance (from largest impact to smallest). Data are based on an optimistic scenario for unknown trait values under A1B climate change emission scenario at a 25% exposure threshold for 2050.

Preface to Chapter 2

In Chapter 1, I produced the first comprehensive climate change vulnerability assessment of Africa's freshwater fishes. This study highlighted regions and species where there are emerging environmental risks due to climate change, and demonstrated that including climate change in conservation assessments can help to identify areas of greatest overall concern. This work also identified species' traits, such as habitat specialization, narrow physiological tolerances, and low dispersal capacity, which contribute strongly to climate-change vulnerability in African freshwater fishes. In the remaining three chapters of this thesis I provide an in-depth examination of one region of Africa that was consistently highlighted as being vulnerable to climate change, the Lake Victoria basin of East Africa. Chapters 2 and 3 focus on understanding how climate change might affect the Nile perch (*Lates niloticus*), a species of high economic and food security importance in this region, and Chapter 4 assesses the vulnerability of fishery stakeholder communities to changes in the environment.

In the previous chapter, I used average trait values to represent entire species; however, it is equally important to think about how traits vary intra-specifically, and how they can be modified through phenotypic plasticity or genetic adaptation when populations are faced with novel conditions. In Chapters 2 and 3 I use a series of thermal acclimation experiments to investigate the physiological (metabolic) responses of Nile perch to elevated water temperature over various timescales. Chapter 2 examines effects of short-term thermal acclimation (3-day and 3-week exposures) to establish how predicted warming will affect the thermal tolerance and aerobic metabolic performance in Nile perch, and compares responses across acclimation exposure times.

Chapter 2

Elevated temperature and acclimation time affect metabolic performance in the heavily exploited Nile perch of Lake Victoria

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2.1 Abstract

Increasing water temperatures owing to anthropogenic climate change are predicted to negatively impact the aerobic metabolic performance of aquatic ectotherms. Specifically, it has been hypothesized that thermal increases result in reductions in aerobic scope (AS), which lead to decreases in energy available for essential fitness and performance functions. Consequences of warming are anticipated to be especially severe for warm-adapted tropical species as they are thought to have narrow thermal windows and limited plasticity for coping with elevated temperatures. In this study we test how predicted warming may affect the aerobic performance of Nile perch (*Lates niloticus*), a commercially-harvested fish species in the Lake Victoria basin of East Africa. We measured critical thermal maxima (CT_{max}) and key metabolic variables such as AS and excess post-exercise oxygen consumption (EPOC) across a range of temperatures, and compared responses between acute (3-day) exposures and 3-week acclimations. CT_{max} increased with acclimation temperature, however 3-week acclimated fish had higher overall CT_{max} than acutely-exposed individuals. Nile perch also showed the capacity to increase or maintain high AS even at temperatures well beyond their current range, however acclimated Nile perch had lower AS compared with acutely-exposed fish. These changes were accompanied by lower EPOC, suggesting that drops in AS may reflect improved energy utilization after acclimation, a finding that is supported by improvements in growth at high temperatures over the acclimation period. Overall, the results challenge predictions that tropical species have limited thermal plasticity, and that high temperatures will be detrimental because of limitations in AS.

2.2 List of abbreviations

AS – Aerobic Scope

CT_{\max} – critical thermal maximum

CT_{\min} – critical thermal minimum

EPOC – excess post-exercise oxygen consumption

K_{ratio} – condition ratio

LVB – Lake Victoria Basin

MMR – maximum metabolic rate

Mo_2 – oxygen consumption rate

OCLTT – oxygen- and capacity-limited thermal tolerance

RT – recovery time

SGR – standard growth rate

SL – standard length

SMR – standard metabolic rate

$T_{\text{crit,max}}$ – critical temperature, upper limit

$T_{\text{crit,min}}$ – critical temperature, lower limit

TL – total length

T_{opt} – optimal temperature

T_{optAS} – optimal temperature for AS

T_{optFIT} – optimal temperature for fitness-related traits

2.3 Introduction

Increasing water temperatures owing to anthropogenic climate change have been associated with shifts in the phenology, distribution, and abundance of aquatic ectotherms in both marine and freshwater systems (Perry et al., 2005; Ficke et al., 2007; Comte et al., 2013), and are known to have profound effects on the physiology of fish species that can lead to reduced fitness in wild populations (Ficke et al., 2007; Crozier and Hutchings, 2014). To cope with rapidly changing thermal regimes, fish must either relocate to more suitable habitats or adjust to novel conditions through phenotypic plasticity and/or genetic change (Rosset and Oertli, 2011). For fishes inhabiting inland systems where relocation to higher latitudes is not always possible, *in situ* responses to rising temperatures are essential. Predicting effects of climate change on inland fishes therefore requires an understanding of how thermal increases affect metabolic performance, fitness traits, and the capacity for physiological adjustments to rising water temperatures (Clark et al., 2011; Clark et al., 2013; Gräns et al., 2014; Norin et al., 2014).

In fishes and other ectothermic animals, temperature tolerance limits (thermal windows) can help to predict responses to changes in temperature. On a simplistic level, a thermal window can be understood as a uni-modal performance curve with functional efficiency of a given performance measure maximized under a range of optimal temperatures (T_{opt}) and falling to zero upon approaching critical temperatures at the upper ($T_{crit,max}$) and lower ($T_{crit,min}$) thermal limits (Fry, 1947; Brett, 1971; Huey and Stevenson, 1979; Pörtner, 2010; Schulte, 2015). The exact shape of this curve varies among species, and is determined in part by the temperature range in their natural habitat (adaptive background) and their ability to cope with thermal variability (phenotypic plasticity) (Huey and Stevenson, 1979; Pörtner, 2010; Schulte, 2015). For example, warm-adapted tropical species, having evolved in relatively thermo-stable environments, are predicted to have narrow thermal windows compared with their temperate counterparts, and are thought to be living near the upper edge of their thermal tolerance limit (Tewksbury et al., 2008) making them especially sensitive to temperature increases (Stillman, 2003; Tewksbury et al., 2008). Given the high levels of interspecific variation in this trait, a great

deal of species-specific testing is required to reveal whether such overarching patterns exist; however, tropical inland fishes are understudied compared with temperate and marine species (Comte et al., 2013). In this study, we test the thermal plasticity of a tropical freshwater fish (the Nile perch, *Lates niloticus*, Linnaeus, 1758) by examining their metabolic performance in a range of water temperatures and comparing responses across acclimation times.

Aerobic scope (AS), defined as the increase in an animal's oxygen consumption from its standard to its maximal metabolic rate (SMR and MMR, respectively), is a key measure of metabolic performance in fishes. For ectotherms, it has been hypothesized that decreases in AS set temperature limits at the upper and lower end of a species' thermal window through a process known as oxygen and capacity-limited thermal tolerance (OCLTT) (Pörtner, 2010). At the upper edge of a species' thermal tolerance limit (approaching $T_{crit,max}$), OCLTT predicts that SMR will increase at a faster rate than MMR because of limitations in the capacity of the cardiorespiratory system to deliver adequate oxygen to respiring tissues, which ultimately manifests as declines in AS (Pörtner and Farrell, 2008; Pörtner, 2010). OCLTT further predicts that AS is closely linked to fitness-related performance traits such as growth and reproductive success, implying that declines in AS may have negative fitness consequences for aquatic ectotherms (Pörtner and Farrell, 2008; Pörtner and Knust, 2007; Pörtner, 2010).

OCLTT has provided a useful conceptual framework for predicting how ectotherms may respond to thermal stress (Wang and Overgaard, 2007; Pörtner and Farrell, 2008; Farrell et al., 2008, 2009; Pörtner, 2010), however, studies that have tested links between AS and fitness-related traits suggest that the optimal temperatures for AS (T_{optAS}) may not match optimal temperatures for fitness-related traits (T_{optFIT}) (Healy and Schulte, 2012; Gräns et al., 2014), and for some species, maximum oxygen uptake curves lack meaningful temperature optima with MMR and AS increasing with temperature to near-lethal limits (Ern et al., 2014; Gräns et al., 2014; Norin et al., 2014). This suggests that low AS may not be a central constraint on performance, and that other traits must be considered when making predictions about effects of elevated water temperature on inland fishes.

In addition, relationships between metabolic rate and temperature in ectotherms are affected by exposure time (acclimation) to higher or lower water temperatures. Thermal acclimation occurs through the alteration of behavioural, physiological, and morphological characteristics to better suit an environment (Angilletta, 2009; Sandblom et al., 2014), and is thought to increase $T_{crit,max}$ and adjust T_{opt} by reducing basal energy expenditure allowing for maintenance of high AS at temperatures that would normally cause reductions in available energy (Sandblom et al., 2014). Short-term plastic responses such as these can help fishes to survive temperature shifts, and may allow persistence of populations in the face of long-term environmental change (Ghalambor et al., 2007). As such, there is increasing interest in developing predictions of climate change impacts in tropical species through assessments of metabolic acclimation capacity over different time scales (Sandblom et al., 2014).

The aim of the present study is to establish an understanding of how predicted warming will affect the aerobic metabolic performance of the Nile perch, a fish of high food security importance in the Lake Victoria basin (LVB) of East Africa. The Nile perch is a large, piscivorous fish, which was introduced to the LVB in the mid-1900s from Lake Albert in western Uganda (Pringle, 2005), and became one of the most important commercial species in the region through the 1990s. Although Lake Victoria's Nile perch population is showing signs of decline, the fishery continues to be heavily exploited by a rapidly growing human population that is both economically and nutritionally dependent on this species (Taabu-Munyaho et al., 2016). Although the impacts of climate change in East Africa are uncertain, water temperature increases of 0.2 - 1.5°C have been detected in Lake Victoria since 1900 (Sitoki et al., 2010; Marshall et al., 2013), and air temperature increases of 1.3 - 4.5°C are expected by the end of the 21st century (Ogutu-Ohwayo et al., 2016). The Nile perch provides an excellent model to test thermal tolerance hypotheses for two reasons. First, Nile perch are predicted to be sensitive to climate change as they inhabit relatively thermostable environments in both their historical range in Lake Albert (yearly range: 26 – 31°C, avg. max. temp. 28°C, Balirwa et al., 2010) and their introduced range in Lake Victoria (yearly range: 24 – 30°C, avg. max. temp. 27°C; Fig. B1). Second, Nile perch in Lake Nabugabo (near Lake Victoria) have displayed the ability to respond phenotypically to environmental variation in dissolved oxygen concentration

and habitat type (Paterson et al., 2010; Nyboer and Chapman, 2013), indicating that this species has high potential for phenotypic adjustments when faced with environmental challenges.

The specific objectives of this study are to (1) determine the response of Nile perch metabolic traits (SMR, MMR, AS, excess post-exercise oxygen consumption [EPOC] and recovery time [RT]) and upper thermal tolerance limits (estimated by critical thermal maximum [CT_{max}] experiments) upon acute (3-day) exposure to a range of temperatures, (2) test for thermal plasticity of these traits in response to 3 weeks of acclimation and (3) compare CT_{max} and metabolic trait responses across exposure times. Based on predictions derived from the OCLTT framework, we expect to find an increase in SMR across temperature treatments, which may lead to a decrease in AS at higher temperatures. If Nile perch are able to make physiological adjustments with acclimation, we would expect to see a lower SMR in acclimated fish than in acutely-exposed fish, and increases in magnitude of AS. However, it is possible that thermal acclimation will be physiologically costly (Nilsson et al., 2009), and we may find trade-offs in other physiological traits (i.e. EPOC) or reductions in growth or body condition over the acclimation period.

2.4 Materials and methods

2.4.1 Fish collection and holding

Juvenile Nile perch (*Lates niloticus*; Linnaeus, 1758) were collected at night using small-mesh boat seines from Entebbe Bay, Uganda, and transported by road to the Aquaculture Research Development Center (ARDC) in Kajjansi, Uganda, where they were stocked into 2 large (6 x 10 x 1 m) outdoor concrete tanks and maintained at 25°C until the start of acclimation trials. This research was conducted under McGill University Animal Care Protocol 5029.

2.4.1.1 3-week acclimation trials

A subset of Nile perch (n = 108) was transported to the laboratory and randomly distributed among three holding systems containing fresh well water. Each holding system comprised three 200-L replicate tanks, and one 300-L head tank (Fig. B2). Water from the head

tank was filtered, oxygenated, and circulated through the replicate tanks at an average rate of 120 L h^{-1} . Water temperature was regulated from the head tanks with Ecotherm® mt512 temperature controllers (Montréal, Québec, Canada) connected to submersible heating coils (Fig. B2). After 48 h of acclimation to laboratory conditions, temperatures were raised at a rate of 1°C day^{-1} to generate 3 experimental temperature treatments of 27°C , 29°C , and 31°C . These levels were selected based on data collected from inshore waters around Entebbe Bay (Fig. B1). The lowest experimental temperature was chosen to represent the average maximum temperature experienced by Nile perch in Lake Victoria (27°C , Fig. B1). While 27°C is at the upper edge of the Nile perch's current thermal environment, this water temperature is commonly recorded in Entebbe Bay, where Nile perch for this study were caught. The upper two temperatures encompass those that are predicted to occur under various emissions scenarios (IPCC, 2013).

Twelve Nile perch were stocked into each replicate tank (36 per temperature treatment) for use in both respirometry and CT_{max} trials. During acclimation, live tilapia fry were supplied for food at a rate of two fry per Nile perch per day. Water quality measures (temperature, oxygen, ammonia, and nitrite) were taken every morning and evening. There were no significant differences among replicates in any water quality variable, and no differences among treatments in ammonia and nitrite concentration. In all replicates, water temperatures were maintained within $\pm 0.5^\circ\text{C}$ of the target temperature. For respirometry trials, four fish from each replicate tank (12 per temperature treatment) were used to measure oxygen consumption and four fish (12 per treatment) were used in CT_{max} trials (see below). Sample sizes were selected to ensure adequate power based on known levels of variability in respirometry data.

2.4.1.2 Acute exposure trials

After completing the acclimation trials, a new subset of Nile perch ($n = 108$) was randomly selected from the outdoor holding ponds and distributed in the laboratory among the three holding systems for the acute (3-day) trials. Water temperature was gradually increased to 27°C , 29°C , and 31°C over 24 h, and then held at this temperature for 3 days (48 h in the

replicate tank and 24 h in the respirometer). Following this, a third group of fish was brought in, and the same protocol was followed for 33°C and 35°C to test metabolic parameters at extreme high temperatures.

2.4.2 Critical thermal maximum (CT_{max}) protocol

Upper thermal tolerance limits were estimated using established CT_{max} protocols (Fangue et al., 2006, Chen et al. 2013) for Nile perch from both exposure groups (3-week and acute) and all temperature treatments (27 – 35°C, see Table 2.1 for sample sizes and body size ranges). For each trial, 4-5 fish from a given temperature treatment were transferred in the evening into a water-filled cooler, and kept at the temperature of acclimation overnight (~8 h) to recover. In the morning, water temperatures in the coolers were raised at a rate of 0.3°C min⁻¹. This heating rate has been established as being low enough to allow the fish's body temperature to adjust, but rapid enough to prevent acclimation during the trial (Beitinger et al., 2000). Temperatures were steadily increased until the fish lost equilibrium for at least 10 seconds. At this time the temperature (CT_{max}) was recorded, and fish were removed from the cooler, weighed and measured, and placed in a bucket of aerated water for recovery.

2.4.3 Respirometry set-up

Oxygen consumption (Mo_2) was measured using automated intermittent closed-system respirometry. The experimental set-up comprised four polypropylene respirometers (volume = 1.57 – 2.80 L) submerged in a 300-L water bath (Fig. B2). Each respirometer was fitted with two sets of airtight tubing. The first formed a closed circulation loop fitted with a continuously operating water pump and a Firesting® fibre-optic cable focused on a contactless oxygen sensor spot (PyroScience Sensor Technology, Bremen, Germany). The second set of tubing was connected to a flush pump used to refresh water and oxygen levels inside the respirometers. Flush pumps were automated to flush for 5 min of every 10-min loop. Dissolved oxygen levels were maintained above 80% saturation at all times. Fibre optic cables and external temperature probes recorded oxygen and temperature every 2 sec for the duration of each trial.

Temperatures in the water bath were maintained within $\pm 0.2^{\circ}\text{C}$ of the target temperature. Respirometers were cleaned with bleach and rinsed thoroughly every 3 days.

2.4.4 Respirometry protocol

2.4.4.1 Time validation for Nile perch

Before beginning experimental trials, two tests were conducted to estimate the time required to obtain SMR for Nile perch, to detect diel cycles in activity and Mo_2 , and to investigate recovery times after handling stress and chasing (Clark et al., 2013; Chabot et al., 2016). These tests were conducted in part because Nile perch had never previously been tested in a respirometer, and also because logistical constraints with power supply in the Kajjansi laboratory prevented running overnight trials, so we needed to determine whether SMR could be reached within an 8 – 12 h working day. In the first test, 3 Nile perch were transferred into the respirometers (without chasing). Mo_2 was measured for 48 h and plotted against time of day. In the second test, recovery times of 3 fish were compared after transfer to the respirometer (without chasing) and after a standard chase protocol (described below). Each fish was subjected to each treatment sequentially, and metabolic rates were measured for 16 h after entry into the respirometer. Mo_2 was plotted against time and inspected visually to identify the point at which Mo_2 levelled off at its lowest point (SMR). To verify that this visual inspection was accurate, the Mo_2 x time plot was imported into R studio v.0.99.482, where the ‘breakpoints’ function in the ‘strucchange’ package was used to compute optimal breakpoints in the Mo_2 x time regression relationship (Zeileis et al., 2015). Chow tests were then used to determine whether the coefficients of slopes before and after the breakpoints differed from one another (Zeileis et al., 2015). The time of the last optimal breakpoint was used for comparison with visual estimates. Recovery times were compared between the two stressors (chase vs. transfer) within each fish.

We found that once metabolic rates had stabilized, they did not decrease further during the 48 h test period (Fig. B3A), nor did we detect diel variation over a 24-h cycle (Fig. B3B). Mo_2 measurements decreased rapidly post-transfer and post-chase, and levelled off after 2.4 and 3

h, respectively (Fig. B4). Recovery times (RT) of Nile perch were on average 45 min longer after chasing (avg. RT: 177 min) as compared with transfer without chasing (avg. RT: 143 min) (Fig. B4, Table B1). The breakpoint validation confirmed that our visual inspections were reasonably accurate, if conservative, with an average difference among estimates of +30 minutes (Table B1). From these findings we determined that a 9 h respirometry trial would be sufficient to obtain sequential measurements of MMR and SMR.

2.4.4.2 Respirometry trials

Metabolic traits (SMR, MMR, AS, EPOC, and RT) were measured on every individual from both acclimated and acute trials (see Table 2.1 for sample sizes and body size ranges). In preparation for each trial, 4 Nile perch from a given temperature treatment were fasted for 48 h to ensure a post-absorptive state. Before starting a trial, the respirometry system was calibrated, and background oxygen consumption was measured for 20 min. We used a 3-min exhaustive chase protocol to induce MMR in Nile perch following methods described in Roche et al. (2013). In this protocol, fish were transferred from their holding tank into a tub containing 25 litres of aerated water at the trial temperature. Fish were chased by hand within the tub for exactly 3 min; all fish were physically exhausted following the protocol. Each Nile perch was then weighed and measured [total length (TL) and standard length (SL)] and transferred into the respirometer within 20 seconds of the chase. This brief period of air exposure following the chase protocol can improve accuracy of MMR estimates when swimming respirometry is not possible (Roche et al., 2013). The respirometer was sealed rapidly following the transfer, and Mo_2 measurements were started immediately. Fish were then left to recover in the respirometers for a minimum of 9 h, until they reached their lowest metabolic rate. Fish were then removed and post-trial background respiration was quantified for 20 min.

2.4.4.3 Calculations of metabolic traits

Raw Firesting Mo_2 data files were processed with LabChart7 software (ADInstruments Inc., Colorado Springs, Colorado, USA) software to calculate linear regressions between oxygen concentration and time for each 5-min closed-loop sample. Metabolic rates ($mgO_2 \text{ min}^{-1}$) were

calculated from these regression slopes after accounting for respirometer volume and fish mass. We did not perform mass-corrections ($\text{mgO}_2 \text{ min}^{-1} \text{ kg}^{-1}$) on metabolic data because of allometric effects of body mass on metabolic rate, but accounted for effects of body size in our statistical analysis by including body mass (M_b) as a covariate in the ANCOVA models (described below) (Packard and Boardman, 1988; García-Berthou, 2001). Background respiration (on average 4.1% of SMR and 1.4% of MMR) was subtracted from the metabolic rates by assuming a linear change between measures taken at the start and end of each trial.

MMR was estimated as the highest Mo_2 measurement recorded over any 3-min period within any 5-min loop. SMR was calculated as the average of the lowest 10% of all Mo_2 measurements after complete recovery from exhaustive anaerobic exercise. This point was determined for each fish by plotting Mo_2 measurements against time, and visually assessing where the recovery curve leveled off, as described above. Outliers ± 2 SD from the mean of the lowest 10% were excluded from the calculation (Clark et al., 2013). This method of calculating SMR meant that for a small proportion (10%) of fish, only 1 Mo_2 slope was used to estimate SMR. To ensure that this did not bias our results by underestimating SMR, we recalculated all SMR values with the lowest 30% of slopes. This caused only minimal changes to SMR estimates (avg. $0.003 \text{ mgO}_2 \text{ L}^{-1}$) and resulted in the same overall patterns. AS was calculated as the difference between MMR and SMR. EPOC, or the amount of oxygen required to recover from MMR, was calculated as the area under the Mo_2 curve estimated by the LOESS (locally weighted smoothing) recovery function until the values of the curve were equal to SMR. LOESS is a non-parametric method often used to fit a smoothed curve to data points in time-series (Cleveland & Devlin, 1988), and is suitable for calculations of EPOC because estimates are comparable to summing individual Mo_2 values. Individual RT was calculated as the time (min) required for a fish's Mo_2 to return to SMR.

2.4.5 Growth and condition

To obtain basic estimates of how the process of acclimation impacted growth and body condition each fish was measured for TL, SL, and M_b prior to the start of the 3-week

acclimation period and again just before respirometry. Fish were tagged using visible implant elastomer (Northwest Marine Technology, Shaw Island, Washington, USA) during stocking for individual recognition. Daily specific growth rate (SGR) during the 3-week acclimation was calculated for each individual using the following equation:

$$\text{SGR} = 100 \times \frac{[\log(Mb_f) - \log(Mb_i)]}{t} \quad \text{Eqn. 1}$$

where Mb_f is the observed final mass at the time of respirometry, and Mb_i is the observed initial mass at the start of the 3-week acclimation and t is the number of growth days. While the standardized food ration used during acclimation may bias growth data because of inter-individual differences in energetic requirements, Mb_i did not vary significantly among temperature treatments or replicates, and growth rate and condition ratio were not related to Mb_i in any of the treatments. We therefore do not expect this to have had a large effect when comparing growth rates among treatments. In addition, when fish are fed a specific ration (as they were in this study), growth rates are usually lower at higher temperatures (Allen and Wootton, 1982; Russell et al., 1996). We interpret our findings in light of this observation.

Condition (K) was calculated at the beginning and end of the 3-week acclimation period using LeCren's equation:

$$K = Mb/aL^b \quad \text{Eqn. 2}$$

where Mb is the observed body mass, L is the observed total length, and a and b are species-specific constants obtained from the length-mass relationship: $Mb = aL^b$ (Froese, 2006). This relationship was derived by pooling data for all individuals in the 3-week acclimation experiment, and fitting a linear relationship between $\log TL$ and $\log Mb$. Change in K was calculated by dividing final by initial K , making a condition ratio (K_{ratio}) where values > 1 represent improved K over the course of the acclimation period.

2.4.6 Statistical analyses

Body mass and metabolic traits were log10-transformed prior to analyses to meet assumptions of statistical tests. Effects of experimental temperature on CT_{max} and all metabolic parameters (SMR, MMR, AS, EPOC, and RT) were tested within and between acute and 3-week exposure times. Differences within an exposure time were detected using univariate ANCOVA with experimental temperature as a fixed factor and $\log Mb_f$ as a covariate. The ANCOVA model accounts for variance in metabolic parameters owing to Mb by adjusting all rates to a common Mb based on pooled regression coefficients of the linear $Mo_2 \times Mb$ relationship (García-Berthou, 2001). This method has often been used as an alternative to mass-corrections when there are allometric effects of body size on the variable of interest (Packard and Boardman, 1988; Albrecht et al. 1993; García-Berthou, 2001). Differences between exposure times were tested by univariate ANCOVA with exposure time and experimental temperature as fixed factors, and $\log Mb_f$ as a covariate. Differences in SGR and K_{ratio} among temperatures for acclimated fish were assessed using univariate ANCOVA with $\log Mb_i$ as a covariate, to account for the influence of initial body size on growth and change in condition (Auer et al., 2015). In all analyses, interaction terms between the covariate and fixed effects were checked and removed from the model if not significant. All analyses were blocked for replicate, and followed by a Sidak multiple comparison procedure. Levene's test was used to confirm equality of error variances, and outliers ± 2 SD were removed from analyses.

2.5 Results

2.5.1 Critical thermal maxima

Acutely-exposed fish showed a significant overall increase in CT_{max} of 2.8°C over an 8°C temperature range (27 – 35°C) (Table 2.2, Fig. 2.1A), with Nile perch exposed to 35°C having CT_{max} values approaching 42°C, and a slope relating CT_{max} to acclimation temperature of 0.33 ± 0.024 . Post hoc tests revealed differences among all levels except 31°C and 33°C (Fig. 2.1A). CT_{max} in 3-week-acclimated fish also increased significantly with acclimation temperature (Table 2.2, Fig. 2.1B) showing an overall increase of 1.5°C over a 4°C acclimation range (27 – 31°C) with

a slope relating CT_{max} to acclimation temperature of 0.40 ± 0.058 . Post hoc tests revealed differences between 27 and 29°C and marginal differences between 29 and 31°C ($P = 0.068$; Fig. 2.1B). Comparisons of acutely-exposed and 3-week acclimated fish revealed that longer acclimation led to higher CT_{max} at all temperatures (Table 2.3, Fig. 2.1C), with an average 0.5°C increase in CT_{max} in acclimated fish at a given temperature.

2.5.2 Metabolic traits: SMR, MMR, AS, EPOC, RT

SMR, MMR, and AS all showed strong positive relationships with body mass for both acutely-exposed and 3-week acclimated fish (Fig. 2.2), a relationship that was consistent within each treatment x acclimation time combination (Table 2.4). MO_2 stabilized quickly after all trials, with an average RT of 308 min (5 h). This is longer than the 3 h determined in our time validation trials; however, all fish reached SMR within 7.5 hours providing a minimum of 1.5 hours (9 slopes) of MO_2 measures for SMR calculation.

The metabolic performance of Nile perch was influenced both by experimental temperature and exposure time. For acutely-exposed fish, there was a general increase in SMR and MMR with temperature (Table 2.2, Fig. 2.3A). The overall effect of temperature on AS in the full model was marginally significant; however, post-hoc tests revealed a sharp increase between 29°C and 31°C (Table 2.2, Fig. 2.3B). For acutely-exposed fish, there were no differences among temperatures for EPOC but RT was lowest in fish exposed to 35°C (Table 2.2, Fig. 2.3CD). The effects of replicate were significant for SMR, MMR, AS, and RT; however, partial η^2 values indicate a much lower influence than the treatment effect (Table 2.2). At the 2 highest temperatures in the acute exposure trial (33°C and 35°C) Nile perch experienced high mortality rates, with 29% and 42% loss of all fish stocked into these treatments, respectively.

Three-week-acclimated fish showed a significant increase in SMR and MMR with temperature, but there was no effect of temperature treatment on AS (Table 2.2, Fig. 2.3EF). Post hoc tests revealed that for SMR the main difference existed between the lower two levels (27 – 29°C) and 31°C, and for MMR between 27°C and the upper two levels (Fig. 2.3E). There were no differences among temperatures for EPOC or RT (Table 2.2, Fig. 2.3GH) in 3-week acclimated

fish. The effects of replicate were non-significant for all models except RT, where again partial η^2 values indicate that they had only minor influence (Table 2.2).

SMR, MMR, and AS were significantly lower in 3-week-acclimated fish compared with acutely-exposed fish, especially at 31°C, where they showed 25%, 26%, and 28% reductions, respectively (Fig. 2.4AB, Table 2.3). Consistent with previous analyses, there were significant temperature effects on SMR, MMR, and AS (Table 2.3); post hoc tests revealed significant differences between the lower two levels and 31°C for all three measures. Acutely-exposed fish had a higher EPOC and longer RT than 3-week acclimated fish (Fig. 2.4CD, Table 2.3). The difference was especially pronounced at 27°C where 3-week acclimated fish showed a 46% lower EPOC, and a 23% faster RT. There were no differences among experimental temperatures in EPOC or RT (Fig. 2.4CD, Table 2.3). Apart from SMR, there were no significant interactions between the exposure time and experimental temperature, and no effects of replicate in any analyses (Table 2.3).

2.5.3 Growth and condition

While many experimental fish showed mass loss and a $K_{ratio} < 1$, temperature had a marginally positive effect on both variables. We proceeded with post-hoc analyses given the marginal overall effect of temperature ($P = 0.067$ for K_{ratio} and $P = 0.1$ for SGR). Individuals at higher temperatures showed a greater improvement in body condition than those at cooler temperatures (Table 2.2, Fig. 2.5A), with K_{ratio} increasing by 12.0% and 10.8 % from 27°C to 29°C and from 27°C to 31°C, respectively. Temperature also had a marginally positive effect on SGR; fish at higher temperatures had better growth rates (Table 2.2, Fig. 2.5B), with a 18% and 24% improvement in growth between 27°C to 29°C and from 27°C to 31°C, respectively.

2.6 Discussion

Results from this study were remarkably consistent showing that juvenile Nile perch were able to make physiological adjustments that allow them to better tolerate higher temperature conditions. As a first line of evidence, both acutely-exposed and 3-week-

acclimated Nile perch exhibited plasticity in thermal tolerance as CT_{max} increased with acclimation temperature. Secondly, acutely-exposed Nile perch are able to achieve high AS at temperatures above those commonly experienced in their natural habitat, with the optimal temperature for AS in acutely-exposed fish registering at $\sim 31^{\circ}\text{C}$. Acclimated fish were able to maintain AS across $27 - 31^{\circ}\text{C}$; however, they exhibited reductions in SMR, MMR and AS relative to acutely-exposed fish, showing that longer exposure times induced different physiological responses to experimental temperatures. Decreases in Mo_2 in acclimated fish were accompanied by decreases in EPOC and RT across exposure time, indicating that drops in metabolic rate may reflect increased efficiency of cardio-respiratory function after acclimation. This finding is supported by improvements in growth and condition at higher temperatures over the acclimation period despite similar food rationing across temperature treatments.

2.6.1 Critical thermal maximum is affected by temperature and exposure time

Critical thermal tolerance limits have been measured in a wide variety of tropical and temperate fishes (Pörtner and Peck, 2010; Beitinger et al. 2000) and provide essential baseline information for evaluating the relative ability of species to persist in the face of climate warming (Madeira et al., 2012; Stillman, 2003). Numerous fish species have demonstrated high acclimation capacity for CT_{max} (Beitinger et al., 2000), and results from the present study indicate that Nile perch follow this trend. Nile perch acutely exposed to 35°C were able to achieve CT_{max} values of nearly 42°C , which are among the highest measured in any fish (reviewed in Beitinger et al., 2000), and both acutely-exposed and 3-week acclimated Nile perch showed a linear increase in CT_{max} with acclimation temperature at a rate comparable to that of eurythermal, temperate species (Beitinger et al., 2000). In addition, longer acclimation allowed Nile perch to push their upper thermal tolerance limit 0.5°C higher than acutely-exposed individuals at a given temperature, indicating that existing flexibility in thermal maxima may be further modulated to cope with persistent temperature increases. This finding challenges the assumption that warm-adapted tropical species have limited capacity for coping with thermal stress as they are able to increase thermal limits at the same rate as species that

are predicted to be more plastic. Having a flexible upper thermal tolerance may enhance Nile perch survival in elevated temperatures, particularly when variability in the system is high.

2.6.2 Metabolic variables are affected by temperature

Nile perch showed an increase in SMR, MMR, and AS when acutely exposed to increased temperature, with all three variables plateauing after 31°C. In fish, the T_{opt} for metabolism is predicted to correspond to the most frequently encountered environmental temperature in the species' natural range (Asbury and Angilletta, 2010), or closely match historical temperatures encountered by previous generations (Farrell et al., 2008; Eliason et al., 2011). For acutely-exposed Nile perch, AS appears to peak at ~31°C, higher than mean temperatures in their historical and introduced ranges. In addition, acutely-exposed fish were able to achieve very high AS even at temperatures that elicited clear signs of physiological stress (high mortality rates) during the experiment. While the high AS values documented at 33°C and 35°C could be due to selection imposed during the experiment, it is still ecologically meaningful that these individuals were able to achieve such responses as selection would have similar effects in natural settings. This finding is comparable to results from a growing number of studies showing that fish are capable of very high AS at temperatures well above their natural range (Clark et al., 2011; Norin et al., 2014), and are comparable to patterns found in Nile perch in a nearby lake (Lake Nabugabo) in the LVB (Chrétien and Chapman, 2016).

Similar to acutely-exposed individuals, 3-week acclimated Nile perch showed overall increases in SMR and MMR with elevated water temperature, but no change in AS. Given their thermo-stable background, it is remarkable that Nile perch are able to achieve the same AS at 29 - 31°C as at 27°C, especially because exposure to the higher two temperatures would have been extremely rare in their current environment (Lake Victoria) and in their historical range (Lake Albert). The fact that Lake Victoria Nile perch are near the upper edge of their geographic thermal range and are still able to make relatively rapid adjustments to high temperatures provides compelling evidence against the hypothesis that tropical ectotherms will be disproportionately negatively affected by small temperature increases. Much of the evidence

for this assertion is derived from studies on terrestrial species (Tewksbury et al., 2008; Deutsch et al., 2008), while data on aquatic species are mixed with variation in acclimation capacity depending on micro-habitat, heating rate, and population (Nguyen et al., 2011; Donelson and Munday, 2012). Further research is required to determine the generality of these patterns among tropical aquatic ectotherms.

2.6.3 Metabolic variables are affected by exposure time

Maintenance of AS in acclimated fish can be interpreted as evidence for metabolic compensation (Donelson and Munday, 2012), however comparing patterns among acclimated and acutely-exposed fish is key in evaluating plasticity in AS because metabolic responses can change dramatically with exposure time (Schulte et al., 2011). For example, acclimating Nile perch to 27°C, 29°C and 31°C for 3 weeks resulted in 38%, 7% and 25% respective reductions in SMR compared with acutely-exposed fish. Reductions in basal metabolic demands in acclimated fish are expected, and could be beneficial if they lead to lower nutritional requirements to sustain basal metabolism, more efficient metabolic performance, and improved physiological functioning (Stillman, 2003; Pörtner, 2010; Donelson et al., 2011). Mechanisms leading to decreases in SMR span multiple levels of biological organization from whole-animal to cellular and biochemical adjustments that collectively reduce metabolic expenditures. These include limitations in daily activity, reductions in gonadal development and growth, changes in cardio-respiratory operation, down-regulation of mitochondrial function (e.g., change in density), and structural changes to biological membranes allowing for efficient uptake and retention processes in mitochondria and cells (Sinensky, 1974; Pörtner, 2001; Pörtner, 2002; Hazel, 1995; Seebacher et al., 2010). However, adjustments at any of these stages may result in physiological, functional, and/or fitness-related trade-offs. For example, sea bass (*Dicentrarchus labrax*) that had higher temperature tolerance had better cardiac function and lower SMR, but also had reduced critical swimming speed compared with those with lower temperature tolerance (Ozolina et al., 2016).

Three-week acclimated fish also had significantly reduced MMR and AS compared with acutely-exposed fish, with the most extreme differences at 31°C where acclimation resulted in a 26% reduction in MMR and a 28% reduction in AS. Metabolic theory predicts that acclimation should facilitate maintenance or increase of AS through a reduction in basal metabolic demands, while maximum metabolic rates remain high (Pörtner, 2010). However, in 3-week acclimated Nile perch, drops in AS were instead due to large reductions in MMR relative to acutely-exposed fish. Even though the cardiorespiratory system of Nile perch is capable of higher oxygen uptake as evidenced by the high MMR and AS of acutely-exposed fish, maintenance of this cardiorespiratory performance may be costly, particularly if cellular oxygen demand is lower in acclimated fish (Schulte, 2015). Although mechanisms underlying reductions in oxygen demand are not well known, these processes are certainly temperature dependent, and may be as or more thermally sensitive than processes involved in energy supply (Schulte, 2015). Fish must balance trade-offs between maintaining AS and conserving energy for other physiologically expensive activities. If high MMR is not needed for daily functioning, adequate growth, or sufficient reproductive investment, then it may be unnecessary. Nile perch may therefore have the ability to modulate AS to conserve energy if high metabolic performance is not needed for daily activities (Norin et al., 2014).

2.6.4 Other performance measures provide insight

Given these patterns, it is important to integrate multiple interacting physiological and fitness-related traits with various exposure times to achieve a fuller picture of factors setting temperature tolerance limits in ectotherms. For Nile perch, AS in 3-week acclimated fish never reached its maximum; however, there was evidence for improved growth rate and condition at 29°C and 31°C relative to 27°C, suggesting that the lower MMR and AS did not represent loss of physiological capability. This important finding supports the hypothesis that the low SMR, MMR, and AS in acclimated fish (relative to acutely-exposed individuals) reflect improved energy utilization efficiency (Zeng et al., 2010) and indicates that allocation of energy to maintenance of high MMR may not be beneficial for individual fitness. Although these changes in growth could be due to natural variations in energy requirements across temperatures, most

studies show that higher temperatures elicit lower growth rates when fish are fed a standard ration (Allen and Wootton, 1982; Russell et al., 1996), so higher growth rates at the upper temperatures further support this conclusion.

In addition to higher in growth at elevated temperatures, acclimated Nile perch had lower EPOC and faster RT than acutely exposed fish. A lower EPOC indicates that less oxygen is required to recover from exercise (e.g. rebuilding high-energy phosphates, restoring biochemical balances in metabolites, and replenishing stores of myoglobin and haemoglobin in the blood [Wood, 1991; Wang et al., 1994; Zeng et al., 2010]), and a faster RT indicates that less time is needed to deliver sufficient oxygen to depleted tissues. EPOC and RT can have fitness consequences for ectotherms relying on anaerobic activities for survival (e.g., prey capture and predator avoidance), as prolonged recovery times may limit their capacity to perform repeated locomotive functions (Zeng et al., 2010). The ability to improve EPOC and RT with acclimation may therefore be important to juvenile Nile perch, who are both predators and prey in their natural environment.

Our results suggest that acutely-exposed Nile perch have a higher reliance on anaerobic metabolic pathways to support exhaustive chase and lower energy utilization efficiency (i.e., use more energy stores when exercised) than fish that have had time to adjust to high temperatures (Zeng et al., 2010). While this could explain the larger EPOC and a longer RT of acutely-exposed fish, we did not establish the level of anaerobic effort by measuring lactate or pH in either muscle or blood, so this remains speculative. Another possible explanation is that 3-week-acclimated fish have developed improved aerobic metabolism, including more efficient oxygen uptake and/or delivery strategies. While improved cardio-respiratory efficiency may not intuitively fit with a reduced MMR, this pattern is not unprecedented (Zeng et al., 2010; Killen et al., 2015), and plastic changes in heart function have been shown occur on very short time scales (Gamperl and Farrell, 2004; Franklin et al., 2007; Keen et al., 2017). Future studies that assess gill size and RVM in warm-acclimated Nile perch would help to elucidate whether such mechanisms underlie changes in metabolic efficiency.

2.6.5 Implications for climate change

Measurements of AS are often used to predict impacts of climate warming on aquatic ectotherms assuming that the thermal optimum for AS (T_{optAS}) coincides with the optimal temperature for physical condition and other fitness measures (T_{optFIT}). While some studies have confirmed this (Brett, 1971; Del Toro-Silva et al., 2008; Grenchik et al., 2013), there is mounting evidence that temperatures that maximize AS do not always match those that elicit the highest growth rate or reproductive output (Healy and Schulte, 2012; Ern et al., 2014; Gräns et al., 2014; Norin et al., 2014). Likewise, the relative drops in AS in acclimated Nile perch do not necessarily indicate physiological weakening as these individuals also show lower EPOC, faster TR, and higher growth and condition ratio at high temperatures. Results such as these challenge the assumption that AS is an important determinant of evolutionary fitness in Nile perch, and indicate that limitations in AS may not be the primary physiological restraint acting on fishes' thermal optima, nor are they likely to be the direct cause of fitness declines in these species (Schulte, 2015). In addition, fishes that show the ability to maintain AS well above their most frequently encountered temperatures may provide an argument against the relevance of T_{optAS} for predicting responses of fish species to climate change (Clark et al., 2014; Schulte, 2015). The increasing trend in SMR and MMR, and the lack of change in AS up to 31°C in acclimated Nile perch could indicate that our experimental temperatures did not push juvenile Nile perch past their T_{optAS} ; however, considering that 31°C is at the upper edge of ecological relevance for this species, this further calls into question the power of T_{optAS} to predict T_{optFIT} in Nile perch (Clark et al., 2014).

Finally, our study highlights the importance of acclimation when experimentally predicting performance of ectotherms at high temperatures. In the context of climate change it is important to distinguish short-term from long-term responses to understand how persistent temperature increases may change, because phenotypic plasticity acting over different exposure times has the capacity to differently alter the position of the thermal optimum. Considering the T_{opt} of only acutely exposed or acclimated fish may cause erroneous conclusions when developing predictions of the effects of climate change (Schulte et al., 2011).

It is therefore possible that the advanced thermal compensation mechanisms achieved by Nile perch could lead to resilience of Nile perch populations to warming lake temperatures despite apparent declines in acclimated fish in AS relative to acutely exposed fish.

2.7 Conclusions

Results from this study challenge assumptions about tropical species' metabolic capabilities, and predictions from the OCLTT hypothesis that higher temperatures will be detrimental owing to limitations in AS. We found that Nile perch have a significant capacity to acclimate to elevated water temperatures, and physiological adjustments made over short time scales could pave the way for reducing the impacts of global warming and improve the chances that Nile perch populations will persist under predicted warming scenarios. This is a significant finding considering the economic and food-security importance of this species in East Africa, however longer exposure times spanning the lifetime of the organism, studies across life-history stages, and investigations into trans-generational plasticity and genetic adaptation would improve our predictions by elucidating long-term effects of chronic thermal stress, which may have consequences for population fitness and fishery sustainability.

2.8 References

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2.9 Tables

Table 2.1 Sample sizes and body size [mass, standard length (SL) and total length (TL)] of acutely-exposed and 3-week-acclimated Nile perch in each temperature treatment for oxygen consumption (Mo_2) and critical thermal maximum (CT_{max}) trials.

		Mo_2				CT_{max}			
3-week-acclimated									
Trait	Temperature (°C)	N	Mean \pm s.e.m.	Min.	Max.	N	Mean \pm s.e.m.	Min.	Max.
Mass (g)	27	12	24.53 \pm 1.77	15.8	36.2	8	17.2 \pm 2.24	6.6	25.9
	29	11	29.49 \pm 4.72	7.3	54.5	7	18.2 \pm 2.22	9.6	28.8
	31	10	33.39 \pm 2.59	23.5	52.3	11	19.4 \pm 2.42	7.8	35.0
SL (cm)	27	12	11.6 \pm 0.33	9.6	13.4	8	10.2 \pm 0.50	7.6	12.2
	29	11	11.6 \pm 0.69	8.1	15.4	7	10.2 \pm 0.45	8.2	12.2
	31	10	12.7 \pm 0.35	10.9	14.2	11	10.5 \pm 0.43	7.9	12.8
TL (cm)	27	12	13.7 \pm 0.40	11.5	16.1	8	12.2 \pm 0.55	9.3	14.3
	29	11	13.8 \pm 0.82	9.6	18.2	7	11.9 \pm 0.58	9.7	14.7
	31	10	15.2 \pm 0.42	13.3	17.2	11	12.6 \pm 0.53	9.5	15.7
Acutely exposed (3-day)									
Mass (g)	27	10	21.5 \pm 2.18	11.1	34.1	7	11.6 \pm 1.97	8.0	21.6
	29	12	28.5 \pm 2.26	16.5	41.3	13	13.6 \pm 1.40	6.7	24.3
	31	10	28.2 \pm 2.56	18.1	42.8	11	12.1 \pm 1.81	6.1	24.1
	33	12	17.9 \pm 2.82	4.6	34.1	5	5.7 \pm 0.36	4.5	6.6
	35	9	15.2 \pm 3.44	6.2	35.8	5	5.6 \pm 0.69	4.6	8.4
SL (cm)	27	10	10.8 \pm 0.44	8.7	12.7	7	8.4 \pm 0.48	7.0	10.8
	29	12	11.6 \pm 0.32	9.7	13.0	13	9.1 \pm 0.35	7.3	11.4
	31	10	11.5 \pm 0.36	9.7	13.2	11	8.6 \pm 0.38	7.1	10.8
	33	12	9.9 \pm 0.60	6.5	12.2	5	6.8 \pm 0.19	6.3	7.3
	35	9	9.3 \pm 0.0	7.1	13.0	5	7.0 \pm 0.31	6.5	8.2
TL (cm)	27	10	12.9 \pm 0.52	10.4	15.4	7	10.2 \pm 0.56	8.7	12.6
	29	12	13.9 \pm 0.37	11.6	15.4	13	10.9 \pm 0.42	8.7	13.5
	31	10	13.7 \pm 0.46	11.6	16.3	11	10.5 \pm 0.44	8.8	13.0
	33	12	12.0 \pm 0.72	7.7	15.3	5	8.1 \pm 0.08	7.8	8.3
	35	9	11.3 \pm 0.81	8.7	15.5	5	8.5 \pm 0.40	7.9	10.1

Table 2.2 Results of a univariate ANCOVA testing for differences in critical thermal maximum (CT_{max}), standard and maximum metabolic rate (SMR and MMR), aerobic scope (AS), excess post-exercise oxygen consumption (EPOC), and recovery time (RT), and fitness-related traits [condition ratio (K_{ratio}) and standard growth rate (SGR)] across experimental temperatures (27°C, 29°C, and 31°C) in acutely exposed (3-day acclimated) and 3-week-acclimated Nile perch. Bold P -values are significant at $\alpha < 0.05$.

		Acutely exposed			3-week-acclimated			
Variable		Temperature	Replicate	Mass (Mb_f)		Temperature	Replicate	Mass (Mb_i)
CT _{max}	$F_{4, 37}$	37.74	0.99	0.01	$F_{2, 25}$	9.122	2.805	1.317
	P	<0.001	0.474	<0.001	P	0.022	0.057	0.267
	η^2	0.922	0.255	0.942	η^2	0.788	0.452	0.072
SMR	$F_{4, 37}$	5.45	2.35	334.58	$F_{2, 24}$	9.12	1.27	55.71
	P	0.011	0.029	<0.001	P	0.015	0.31	<0.001
	η^2	0.665	0.388	0.9	η^2	0.75	0.24	0.699
MMR	$F_{4, 37}$	5.75	2.25	266.37	$F_{2, 24}$	6.03	0.86	69.6
	P	0.009	0.036	<0.001	P	0.036	0.536	<0.001
	η^2	0.676	0.378	0.878	η^2	0.663	0.177	0.744
AS	$F_{4, 37}$	2.9	3.18	135.65	$F_{2, 24}$	2.401	0.698	26.02
	P	0.074	0.005	<0.001	P	0.169	0.698	<0.001
	η^2	0.519	0.462	0.786	η^2	0.437	0.138	0.52
EPOC	$F_{4, 37}$	0.92	1.86	1.84	$F_{2, 24}$	0.595	2.189	7.075
	P	0.485	0.083	0.183	P	0.581	0.08	0.014
	η^2	0.247	0.335	0.047	η^2	0.164	0.354	0.228
RT	$F_{4, 37}$	3.57	2.39	<0.001	$F_{2, 23}$	0.13	2.962	0.221
	P	0.042	0.027	0.99	P	0.88	0.027	0.643
	η^2	0.566	0.392	<0.001	η^2	0.041	0.436	0.01
CR								Mass (Mb_i)
					$F_{2, 20}$	4.737	0.648	3.810
					P	0.067	0.666	0.065
				η^2	0.646	0.139	0.160	
SGR					$F_{2, 20}$	3.404	1.1250	7.882
					P	0.100	0.320	0.011
					η^2	0.562	0.239	0.068

Table 2.3 Results of univariate ANCOVA examining the effects of experimental temperature (27°C, 29°C, and 31°C), exposure time (acutely exposed, 3-week-acclimated), and their interaction on critical thermal maximum (CT_{max}), standard and maximum metabolic rate (SMR and MMR), aerobic scope (AS), excess post-exercise oxygen consumption (EPOC), and recovery time (RT) of Nile perch. Bold *P*-values are significant at $\alpha < 0.05$.

Variables		Temperature (T)	Replicate	Exposure time (E)	Mass	T x E
CT _{max}	F _{1, 44}	36.67	1.85	8.31	0.64	0.1
	<i>P</i>	<0.001	0.111	0.006	0.427	0.903
SMR	F _{2, 53}	25.557	0.772	31.402	168.454	4.267
	<i>P</i>	0.001	0.596	<0.001	<0.001	0.019
MMR	F _{2, 53}	12.443	1.288	23.351	194.43	1.61
	<i>P</i>	0.006	0.279	<0.001	<0.001	0.21
AS	F _{2, 53}	5.726	1.095	8.132	83.046	1.158
	<i>P</i>	0.037	0.378	0.006	<0.001	0.322
EPOC	F _{2, 53}	1.252	1.374	8.41	3.932	0.821
	<i>P</i>	0.348	0.242	0.005	0.053	0.446
RT	F _{2, 52}	1.201	2.063	27.671	1.968	0.593
	<i>P</i>	0.362	0.074	<0.001	0.167	0.556

Table 2.4 Pearson's correlations of body mass with metabolic traits [standard and maximum metabolic rate (SMR and MMR) and aerobic scope (AS)] for 3-week-acclimated and acutely-exposed (3-days) Nile perch. Bold *P*-values are significant at $\alpha < 0.05$.

3-week-acclimated			
Relationship	Temperature (°C)	R	<i>P</i>
SMR x body mass	27	0.697	0.012
	29	0.905	<0.001
	31	0.621	0.041
MMR x body mass	27	0.855	<0.001
	29	0.934	<0.001
	31	0.531	0.051
AS x body mass	27	0.818	0.001
	29	0.824	0.002
	31	0.305	0.363
Acutely Exposed			
SMR x body mass	27	0.839	0.002
	29	0.766	0.004
	31	0.932	<0.001
	33	0.988	<0.001
	35	0.987	<0.001
MMR x body mass	27	0.855	0.002
	29	0.71	0.010
	31	0.931	<0.001
	33	0.985	<0.001
	35	0.936	<0.001
AS x body mass	27	0.771	0.009
	29	0.542	0.069
	31	0.909	<0.001
	33	0.979	<0.001
	35	0.785	0.012

2.10 Figures

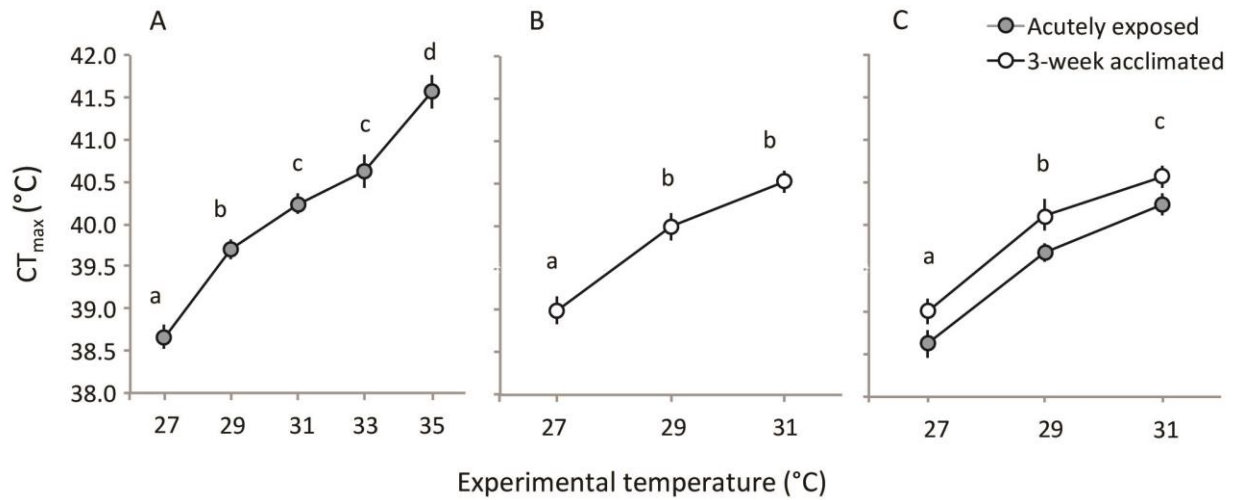


Figure 2.1 Critical thermal maxima (CT_{max} ; mean \pm 1 SEM) for Nile perch across acclimation time and experimental temperature. Panels A and B show results of ANCOVA for acutely exposed and acclimated Nile perch, respectively. Panel C shows results of two-way ANCOVAs comparing CT_{max} across exposure time and experimental temperature. CT_{max} differed significantly among temperatures for both acclimation groups, and also differed among acclimation times (see Tables 2.2 and 2.3). Different lowercase letters in all panels indicate differences in CT_{max} among acclimation temperatures. In C, these letters indicate overall differences pooled within acclimation time.

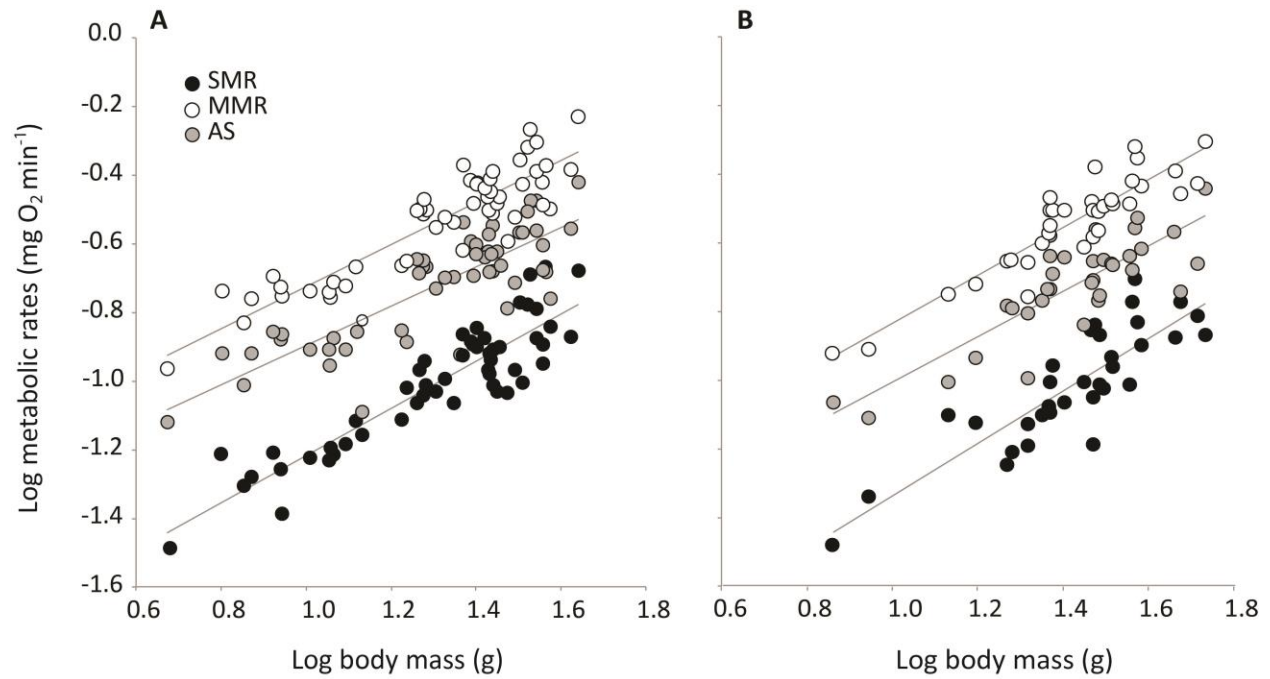


Figure 2.2 Linear relationships between log body mass and log standard metabolic rate (SMR), maximum metabolic rate (MMR) and aerobic scope (AS). Panels A and B show results for acutely exposed (SMR: $R=0.914$, $P<0.001$; MMR: $R=0.896$, $P<0.001$; AS: $R=0.829$, $P<0.001$) and 3-week-acclimated (SMR: $R=0.856$, $P<0.001$; MMR: $R=0.908$, $P<0.001$; AS: $R=0.829$, $P<0.001$) Nile perch, respectively. Data from all temperatures were pooled for these figures, but trends were similar when separated by temperature treatment (see Table 2.4).

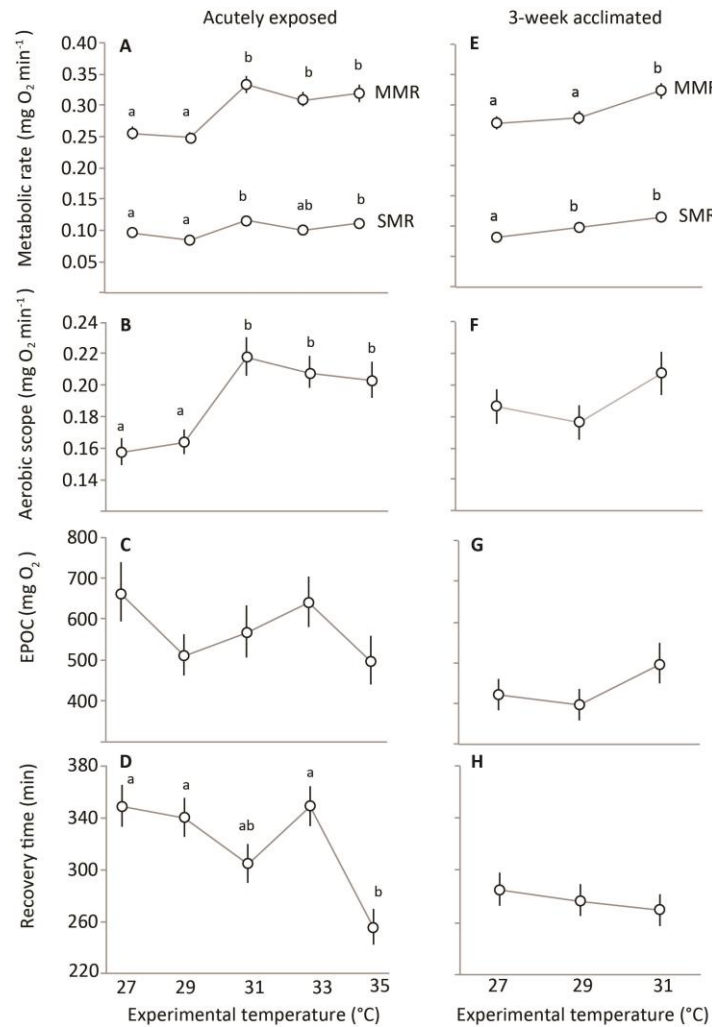


Figure 2.3 Results of ANCOVA testing aerobic metabolic performance (means ± 1 SEM) of juvenile Nile perch over a range of experimental temperatures. (A – D) Acutely exposed fish; (E – H) thermally acclimated fish. From top to bottom: Standard metabolic rate (SMR) and maximum metabolic rate (MMR; A & E); aerobic scope (B & F); excess post-exercise oxygen consumption (EPOC; C & G); and recovery time (D & H), (see Table 2.2). Different lowercase letters indicate significant differences between measurements. Values are estimated marginal means adjusted to a common body mass of 26.7 g with mass exponents for each variable based on pooled regression coefficients within groups. For panels A and E, error bars are present but fall within the markers.

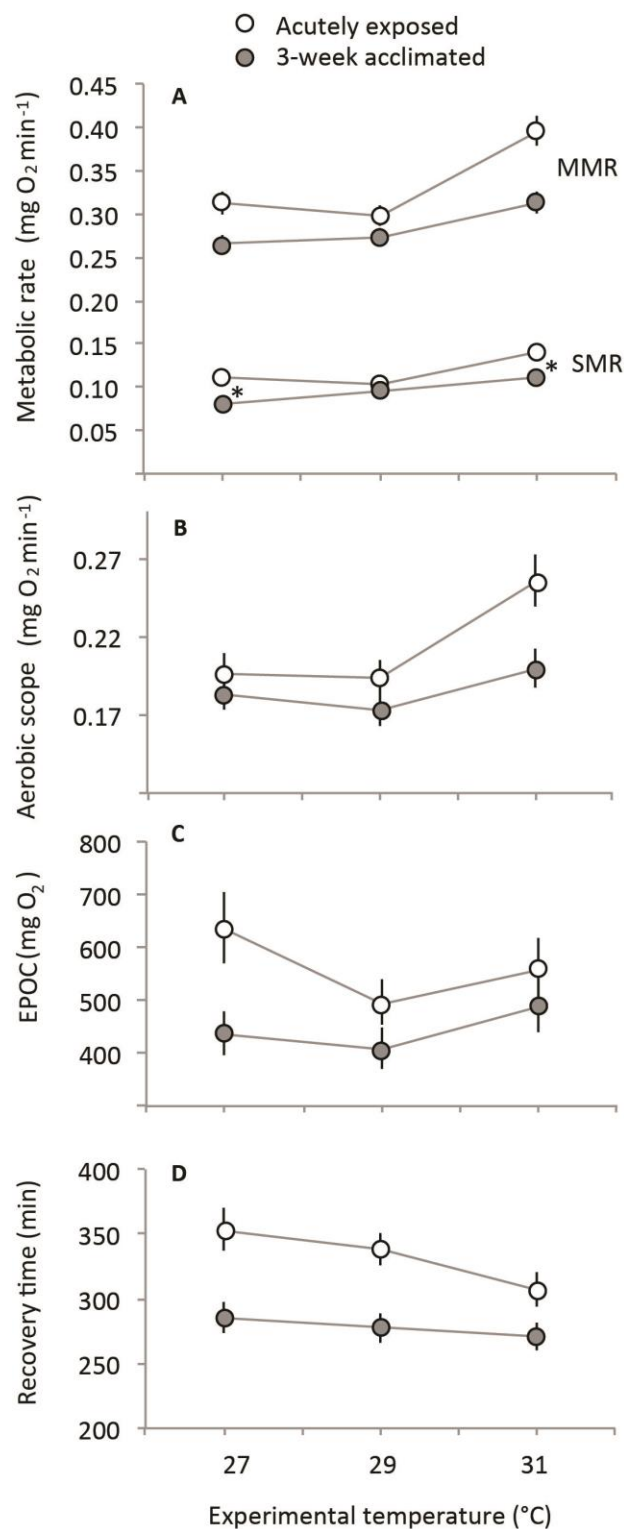


Figure 2.4 Results of ANCOVA comparing aerobic metabolic performance (means ± 1 SEM) among acutely exposed (open circles) and thermally acclimated (shaded circles) juvenile Nile perch over a range of temperatures. From top to bottom: Standard metabolic rate (SMR) and maximum metabolic rate (MMR; A); aerobic scope (B); excess post-exercise oxygen consumption (EPOC; C); and recovery time (D), (see Table 2.3). Values in these figures are estimated marginal means adjusted to a common body mass of 25.8 g with mass exponents for each variable based on pooled regression coefficients within groups. For panel A, error bars are present but fall within the markers. Asterisks in (A) indicate significant differences among acclimation times within temperature categories for tests where there was a significant interaction among fixed factors.

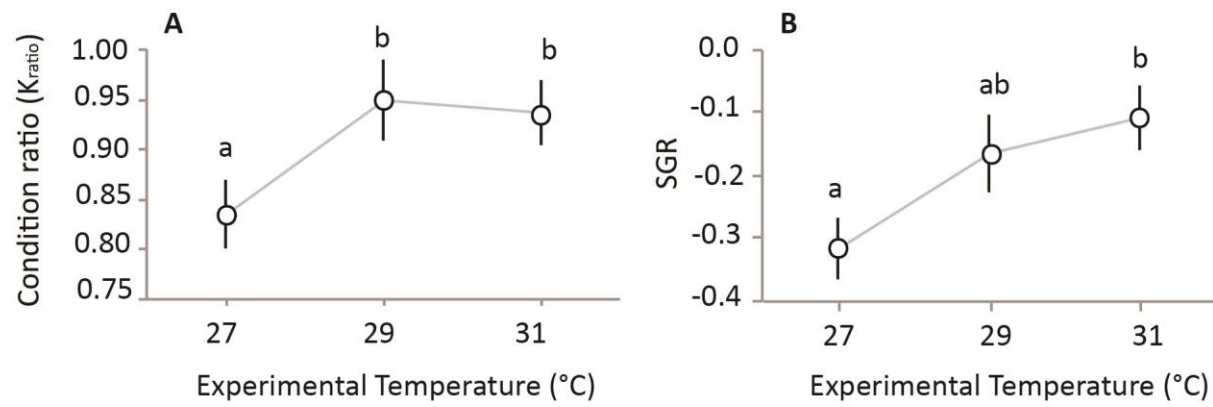


Figure 2.5 Changes in condition and growth across experimental temperatures. Results of ANCOVA exploring differences in (A) condition ratio (K_{ratio} ; mean \pm 1 SEM) and (B) specific growth rate (SGR; mean \pm 1 SEM) for Nile perch during 3 weeks of acclimation to 27, 29 and 31 $^{\circ}\text{C}$.

Preface to Chapter 3

In Chapter 2, I established short-term metabolic and thermal tolerance responses of Nile perch to elevated water temperature, and I compared responses across acclimation times. The key findings from this work were that Nile perch have significant capacity to acclimate to elevated water temperatures, and that the thermal flexibility exhibited by this species rivals fishes that experience much wider temperature ranges in their natural habitat. This finding is consistent with results of a recent meta-analysis showing that ectotherms from more stable environments have greater capacity for thermal plasticity than eurythermal, temperate species (Seebacher et al., 2015¹), and challenges the prediction that tropical species can be pushed over thermal limits by small increases in temperature. Secondly, comparing responses between exposure times (3 days versus 3 weeks) revealed that exposure time has an important effect on metabolic rates under elevated temperature, and that thermal limitation on aerobic scope may not be the direct cause of fitness reductions in this species.

While it is possible that physiological adjustments made over short timescales can lead to resilience over long-term warming under climate change, a more thorough understanding of responses to thermal increases can be obtained by examining acclimation over longer timeframes, because persistence of fish will depend on their successful development in new thermal regimes. In Chapter 3, I quantify acclimation capacity in juvenile Nile perch over a longer (3-month) timeframe and test various hypotheses regarding physiological and developmental mechanisms underlying metabolic compensation. For example, adjustments in cardiorespiratory function are often invoked as key mechanisms underlying thermal plasticity because limitations in oxygen supply are predicted to define thermal optima in fishes, however few studies have explicitly linked cardiorespiratory plasticity to metabolic compensation and, these questions have never been tested in a tropical species.

¹ Seebacher, F., White, C.R. and Franklin, C.E. (2015). Physiological plasticity increases resilience of ectothermic animals to climate change. *Nature Climate Change*. 5, 61-66.

Chapter 3

Cardiac plasticity influences aerobic performance and thermal tolerance in a tropical, freshwater fish at elevated temperatures

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3.1 Abstract

Fishes faced with novel thermal conditions often modify physiological functioning to compensate for elevated temperatures. This physiological plasticity (thermal acclimation) has been shown to improve metabolic performance and extend thermal limits in many species. Adjustments in cardiorespiratory function are often invoked as mechanisms underlying thermal plasticity because limitations in oxygen supply have been predicted to define thermal optima in fishes; however few studies have explicitly linked cardiorespiratory plasticity to metabolic compensation. Here we quantified thermal acclimation capacity in the commercially harvested Nile perch (*Lates niloticus*) of East Africa, and investigated mechanisms underlying observed changes. We reared juvenile Nile perch for three months under two temperature regimes, and then measured a series of metabolic traits (e.g., aerobic scope, AS) and critical thermal maximum (CT_{max}) upon acute exposure to a range of experimental temperatures. We also measured morphological traits of heart ventricles, gills, and brains to identify potential mechanisms for compensation. We found that long-term (3-months) exposure to elevated temperature induced compensation in upper thermal tolerance (CT_{max}) and metabolic performance (standard and maximum metabolic rate and aerobic scope), and induced cardiac remodeling in Nile perch. Furthermore, variation in heart morphology influenced variations in metabolic function and thermal tolerance. These results indicate that plastic changes enacted over longer exposures lead to differences in metabolic flexibility when organisms are acutely exposed to temperature variation. Furthermore, we established functional links between cardiac plasticity, metabolic performance, and thermal tolerance, providing evidence that plasticity in cardiac capacity may be one mechanism for coping with climate change.

3.2 List of abbreviations

AGFL – average gill filament length

AS – aerobic scope

AS_{Q10} – Q10-corrected aerobic scope

CT_{max} – critical thermal maximum

CT_{max,adj} – adjusted critical thermal maximum

DO – dissolved oxygen

FBL – filament base length

FD – filament density

HSI – hepatosomatic index

K – LeCren's condition factor

M_b – body mass

MMR – maximum metabolic rate

MMR_{Q10} – Q10-corrected maximum metabolic rate

$\dot{M}O_2$ – oxygen consumption rate

OCLTT – oxygen- and capacity-limited thermal tolerance

RVM – relative ventricular mass

SL – standard length

SMR – standard metabolic rate

SMR_{Q10} – Q10-corrected standard metabolic rate

*T*_{avg} – average rearing temperature (~25°C)

TFN – total filament number

TGFL – total gill filament length

THA – total hemibranch area

TL – total length

*T*_{warm} – warm rearing temperature (~29°C)

V_b – total cardiac output (volume of blood pumped per minute)

%CM – percent of compact myocardium

3.3 Introduction

Climate change models forecast persistent, global temperature increases of 1 – 4°C, and increases in the frequency of extreme climatic events over the next century (IPCC, 2014; Seneviratne et al., 2014). Such drastic changes will directly affect aquatic ecosystems, and threaten the ecological and physiological stability of fish species in freshwater habitats (Ficke et al., 2007). As ectotherms, fish depend on their thermal environment to regulate metabolic functions, and when water temperatures exceed specific optima they face performance limitations at all levels of biological organization. To cope, fish must either relocate to more suitable habitats or adapt to novel conditions through genetic change and/or environmentally induced phenotypic plasticity (Schulte et al., 2011; Seebacher et al., 2015). Fish species often modify physiological functioning through thermal acclimation (Angilletta, 2009; Seebacher et al., 2015), a type of phenotypic plasticity that can alter thermal tolerance limits and optimize performance under novel temperature regimes (Schulte et al., 2011). Capacity for thermal acclimation varies dramatically among species and is hypothesized to be lower in tropical fish that experience little seasonal variation in their thermal environment (Tewksbury et al., 2008). Given the significance of many inland tropical fishes to local and regional food security (FAO, 2014; Lynch et al., 2016), it is of increasing importance to understand the capacity for and mechanisms underlying modifications of thermal tolerance in these species.

For ectotherms, metabolic rate sets the pace for many physiological functions, and can have important fitness implications (Brown et al., 2004). Measurements of metabolic performance can therefore serve as comprehensive indicators of physiological condition (Sibly et al., 2012), and can be used to assess ability to cope with various environmental stressors (Brown et al., 2004). Key metabolic parameters often measured in this context include standard and maximum metabolic rate (SMR and MMR, respectively), which represent the lower and upper limits of oxygen uptake for fishes. SMR corresponds to basal oxygen demand, or the lowest possible metabolic rate in a resting, post-absorptive fish (Fry, 1971; Brett and Groves, 1979), and MMR corresponds to the maximum rate of oxygen consumption, usually measured after

exhaustive exercise (Fry, 1971; Clark et al., 2011; Roche et al., 2013; Norin and Clark, 2016). Aerobic scope (AS), which is calculated as the difference between SMR and MMR, determines the range of oxygen-demanding processes that can be performed simultaneously by a fish, and is thought to be a key mechanism determining energy allocation, fitness, and biogeography in ectotherms (Pörtner and Farrell, 2008; Pörtner, 2010; Clark et al., 2013).

As first observed by Fry (1947), and quantified in several recent studies (Healy and Schulte, 2012; Gräns et al., 2014; Norin et al., 2014) SMR increases exponentially with temperature, whereas MMR is predicted to increase initially, and then decline at the highest temperatures, ultimately bringing about a decline in AS at high temperatures. According to the oxygen- and capacity-limited thermal tolerance (OCLTT) concept, declines in performance (i.e., AS) at high temperatures are predicted because the cardiorespiratory system cannot keep pace with oxygen demands in respiring tissues as increasing temperatures elevate metabolic demands (Pörtner and Knust, 2007; Pörtner et al., 2017). Mismatches between oxygen supply and demand are therefore thought to define thermal limits in teleost fishes, and may have negative fitness consequences (e.g., reductions in body mass or condition) if, as predicted, drops in AS are causally linked to key processes such as growth (Pörtner and Knust, 2007). A corollary of this hypothesis is that alterations to the cardiorespiratory system that increase efficiency of oxygen uptake and delivery can improve thermal tolerance and aerobic performance in fishes exposed to elevated water temperatures. Although the OCLTT hypothesis proposes a clear mechanistic explanation for thermal limitation, numerous recent empirical studies have shown that declines in performance at high temperatures may be driven by mechanisms other than a mismatch between oxygen supply and demand, and have provided convincing evidence that optimal temperatures for AS do not necessarily elicit maximal performance in all fitness-related measures (Clark et al., 2013; Gräns et al., 2014; Norin et al., 2014; Wang et al., 2014; Brijs et al., 2015; Ern et al., 2016), raising questions about the broad applicability of this framework (Jutfelt et al., 2018). In addition, there are many pathways for fish to respond to oxygen limitation, scaling from whole-body to cellular levels (Pörtner, 2002; Angilletta, 2009; Biro and Stamps, 2010), and alterations to any of these pathways can lead to improvements in metabolic performance (e.g., reduced basal oxygen demand) and maintenance of fitness related traits.

Nevertheless, cardiorespiratory function may still play an important role in metabolic compensation, and investigating relationships between cardiorespiratory traits and thermal tolerance and/or metabolic performance can allow a straightforward test of at least one prediction generated by OCLTT. If cardiorespiratory function can sustain performance at high temperatures, plastic changes in heart and gill morphology that improve oxygen uptake and delivery may be key to acclimation capacity (Sollid et al., 2005; Farrell et al., 2009; Dalziel et al., 2012; Anttila et al., 2013; Jayasundara and Somero, 2013). Both heart and gill morphology have been shown to change with exposure to increased temperatures (Sollid et al., 2005; Klaiman et al., 2011; McBryan et al., 2016; Keen et al., 2017). The heart is the primary power generator for the circulatory system, and is often a central focus in investigations of physiological plasticity in fishes (Farrell et al., 2009; Jayasundara and Somero, 2013). Changes in temperature have a significant effect on heart rate in teleosts, which influences total cardiac output (V_b , volume of blood pumped per minute). However morphological changes induced by long-term exposure to different water temperatures can facilitate maintenance of V_b across a wide thermal range (Gamperl and Farrell, 2004; Klaiman et al., 2011; Keen et al., 2017). For example, fishes exposed to warmer temperatures generally have decreased relative ventricular mass (RVM), leading to reduced stroke volume (Keen et al., 2017); however, V_b can be maintained through improved force of contraction (Gamperl and Farrell, 2004), which is often enabled by adjustments to the proportions of the myocardial layers (i.e., spongy vs. compact) in the ventricle. Gills, in contrast, function primarily in oxygen uptake. Changes in the environment that lead to new respiratory or osmoregulatory demands can result in alterations to gill structure over varying time-scales (Sollid et al., 2003, 2005; Langerhans et al., 2007; Chapman et al., 2008). For example, fish that are exposed to low dissolved oxygen concentrations (DO) can increase gill size, which presumably improves efficiency of oxygen uptake (Chapman et al., 2008). In addition, elevated temperature may affect other physiologically demanding organs if the bulk of energetic resources are allocated to basal functions. For example, brain size has been observed to decrease under stressful conditions (Crispo and Chapman, 2010; Toli et al., 2016). Given the high metabolic cost associated with the development of large brains, the

ability to reduce brain size through plasticity when a large brain is not critical for fitness is likely to be favoured (Crispo and Chapman, 2010).

Alterations in cardiorespiratory function and morphology have been shown to improve thermal tolerance and performance in a number of fish species (Eliason et al., 2011, 2017; Anttila et al., 2013; Keen et al., 2017). For example, increases in cardiac scope correlate positively with aerobic scope within populations of sockeye salmon (Eliason et al., 2011), and larger RVM correlates positively with upper thermal tolerance limits (i.e., critical thermal maximum, CT_{max}) in some populations of Atlantic salmon (Anttila et al., 2013). Likewise, gills can undergo surface area increases that improve oxygen uptake upon exposure to warmer temperatures (McBryan et al., 2016), however few studies have explicitly linked plasticity in heart or gill morphology to metabolic compensation, and these patterns have, to our knowledge, never been tested in tropical fishes. In addition, little is known about how developmental plastic responses will benefit fishes faced with rapidly changing thermal environments (i.e. acute exposure to novel temperatures), which is relevant when predicting climate change effects where both long-term increases and rapid changes in temperature are expected.

In this study we investigated these patterns in a tropical, freshwater teleost, the Nile perch (*Lates niloticus*, Linnaeus 1758), a large, primarily piscivorous fish that was introduced to the Lake Victoria basin in East Africa in the mid-20th century, and currently forms the basis of a lucrative 250-310 million USD yr⁻¹ export fishery (Indian Ocean Commission, 2015). Nile perch regularly experience temperatures in the range of 23 - 27°C in Lake Victoria, and similarly stable temperatures in their ancestral habitat in Lake Albert (range: 26 – 31°C; Nyboer and Chapman, 2017). Despite these narrow thermal ranges, recent studies have demonstrated high levels of acclimation capacity in metabolic rate and upper thermal tolerance of Nile perch under both short (3-day) and longer-term (3 week) exposures (Chrétien and Chapman, 2016; Nyboer and Chapman, 2017), making it an interesting subject for testing responses over longer acclimation times (i.e., time enough for developmental differences to take place) and for evaluating mechanisms underlying thermal flexibility. The objectives of this study were to (1) determine the acclimation capacity of upper thermal tolerance limits (CT_{max}) and metabolic rates of

juvenile Nile perch reared for 3-months under elevated temperature, (2) examine links between variation in metabolic function, body mass and condition, and plastic responses in oxygen uptake and delivery capacities of cardiorespiratory organs, and (3) assess whether plastic changes associated with rearing are beneficial for coping with rapid temperature changes (i.e., acute exposures to a range of temperatures).

We predicted that we would detect plasticity in metabolic traits and CT_{max} leading to metabolic compensation in fish reared under warmer conditions. We also anticipated finding differences in heart and/or gill morphology among rearing temperatures; specifically we expected smaller RVM, thicker compact myocardium, and larger gill sizes in warm-reared fish as these are possible mechanisms for coping with the increased oxygen demand likely to be experienced under elevated temperatures. If these morphological changes improve thermal tolerance and metabolic performance, we would expect to find relationships among these traits within rearing groups.

3.4 Materials and methods

3.4.1 Overview

Wild-caught juvenile Nile perch were captured in July and reared for three months under two temperature regimes, one resembling annual average temperatures in Lake Victoria (~25°C maximum; control) and one resembling temperatures predicted under climate change (~29°C maximum). Fish from these rearing temperatures were then acutely-exposed in the laboratory (three days) to a range of experimental temperatures encompassing both rearing temperatures and a higher temperature (33°C) not previously experienced in either rearing temperature, thereby testing their ability to cope with rapid changes in temperature. SMR, MMR, AS, and CT_{max} were measured, and organs (livers, hearts, gills, brains) were examined to identify potential mechanisms for metabolic compensation. This research was conducted under McGill University Animal Care Protocol 5029.

3.4.2 Fish collection and rearing

Young (<2 months old) juvenile Nile perch [$12.4 \text{ cm} \pm 0.67 \text{ cm}$ total length (TL), mean \pm s.e.m., $n = 600$] were collected by fishers in July, 2015 with small-mesh beach seines at Entebbe Bay, Uganda. Specimens were transported to the Aquaculture Research and Development Center in Kajjansi, Uganda, where they were stocked into six large ($6 \times 10 \times 1 \text{ m}$) outdoor concrete aquaculture ponds and reared for 3-months (02-July to 05-October 2015). This rearing period was chosen as we anticipated this time frame would allow for some morphological and developmental responses to occur based on Nile perch growth rates (Nkalubo, 2012), and because it spanned a portion of one dry and one rainy season capturing some natural seasonal variation. The ponds were organized into three blocks, each with one replicate of the two thermal regimes described above (Fig. C1A). These rearing temperatures shall be referred to as the average rearing temperature, or T_{avg} ($\sim 25^\circ\text{C}$), and the warm rearing temperature, or T_{warm} ($\sim 29^\circ\text{C}$). To create these divergent thermal regimes, wooden frames were constructed over each pond and covered with either greenhouse plastic (TeraMax®, Teris, Montréal, QC, Canada), or agricultural shade-cloth (GreenTek Shade-Rite®, Teris, Montréal, QC, Canada; Fig. C1B). Prior to stocking, pond water quality parameters including temperature ($^\circ\text{C}$), luminosity (i.e. lux, expressed in lm m^{-2}), DO, turbidity (Secchi depth, expressed in cm), and pH, were carefully monitored for 4 months to ensure that water temperatures and physicochemical conditions were stable. Each pond was equipped with flow-through inlet and outlet mechanisms so that water inside the ponds could be flushed directly with $\sim 25^\circ\text{C}$ local river water (see Fig. C1B for a schematic diagram of the pond set-up).

During stocking, all ponds were filled with river water and maintained at the natural $\sim 25^\circ\text{C}$. Experimental fish ($n = 100$ per rearing pond) were weighed to the nearest 0.01 g, and measured for TL and standard length (SL) to the nearest 0.1 cm to ensure uniformity of initial stocking size (Table C1). After 3 days, T_{warm} ponds were heated to $\sim 29^\circ\text{C}$ over 48 h. This was accomplished by temporarily cutting inflow of cool river water to the T_{warm} ponds, which allowed the water in the ponds to warm under the greenhouse covers. During this time DO concentrations were monitored to ensure maintenance of adequate oxygen levels. After T_{warm} ponds had warmed to

the desired temperature ($\sim 29^{\circ}\text{C}$), all ponds (T_{avg} and T_{warm}) were flushed each day for the same amount of time with fresh river water. The large volume (60 m^3) of the ponds ensured that the T_{warm} ponds stayed within 3°C of the desired temperature, even during periods of flushing. Throughout the experiment, water quality parameters (temperature, luminosity, DO, turbidity, and pH) were recorded twice daily, once in early morning and once in mid-afternoon to capture daily fluctuations. Twenty-four-hour HOBO™ light and temperature loggers (Onset®, Bourne, MA, U.S.A.) took hourly temperature and luminosity readings for the duration of the rearing period (see Table C2, Fig. C2 for a summary of all water quality parameters). To determine how water quality parameters varied between rearing temperatures (T_{avg} and T_{warm}), and among rearing pond replicates (blocks 1, 2, and 3), data from the HOBO loggers (temperature and lux) and from daily water-sampling (DO, turbidity, and pH) were plotted over time for visual assessment (Fig. C2A-E) and analyzed with two-way ANOVA, with rearing temperature and block as fixed effects. Water temperatures in the T_{warm} rearing ponds had higher maximum (28.6°C) and minimum (27.1°C) daily temperature than those in the T_{avg} regime (maximum = 24.5°C ; minimum = 23°C ; Table 3.1, Table C2, Fig. C2A). There were significant effects of block and block x rearing temperature; however the effect size (η^2) of these factors was small compared to rearing temperature alone (Table 3.1). Post-hoc tests revealed that differences among blocks were only apparent in the T_{warm} rearing tanks, with replicate 1 of T_{warm} significantly warmer than replicates 2 ($p = 0.002$) and 3 ($p < 0.001$). Average lux (lm m^{-2}) also differed among rearing temperatures with T_{warm} having higher luminosity than T_{avg} , however the effect size was small, and differences were apparent only in blocks 1 and 3 (Table 3.1). There were no differences in any other water quality variables (DO, turbidity, pH) between rearing temperatures or among blocks (Table 3.1, Table C2, Fig. C2B-E).

During rearing, Nile perch were fed daily on live, aquaculture-reared Nile tilapia fry, which were graded to ensure appropriate prey sizes. Daily feeding rations were calculated to equal $\sim 15\%$ of the biomass of Nile perch stocked in each pond to ensure adequate food supply at rates similar to natural conditions as estimated by Nile perch bioenergetic analyses (Kitchell et al., 1997) and from previous trials of Nile perch rearing. The levels were adjusted based on estimates of mortalities and estimated growth rates of Nile perch in the ponds.

3.4.3 Laboratory experiments

After completing three months in the rearing ponds, Nile perch were transported from ponds to the laboratory where they were placed in temperature-controlled tanks ($n = 4$ per tank) containing filtered, oxygenated, well water (see Nyboer and Chapman, 2017 for a description of the laboratory system). All fish were individually marked using Visible Implant Elastomer (Northwest Marine Technology Inc., Shaw Island, WA, U.S.A.). We employed a fully-crossed experimental design for laboratory tests so that individuals from each rearing temperature (T_{avg} and T_{warm}) and block (3 replicates) were subjected to each experimental laboratory temperature for metabolic rate experiments (Fig. C1A, Table 3.2). Laboratory tanks were initially held at the average maximum rearing temperature (29°C or 25°C) and then slowly raised or lowered to the desired experimental temperature (25°C, 29°C or 33°C) over a 12-h period, and then held for 3 days. Fish were brought into the laboratory in a staggered fashion so that each batch was held for the same 12-h + 3-day period before experimental trials. On the first day of acclimation, Nile perch were fed two tilapia fry each, and thereafter (48 h) food was withheld to ensure a post-absorptive state during trials. In total, the respirometry experiments were completed over a 3-week period (5 – 26 October 2015), so fish brought into the laboratory last had an extra 17 days in the rearing ponds.

3.4.3.1 Metabolic traits

Metabolic traits (SMR, MMR, AS) were estimated for Nile perch from each rearing temperature x block x experimental temperature combination (Table 3.2) by measuring oxygen consumption (Mo_2) using intermittent-flow respirometry. The experimental set-up is described in detail in Nyboer and Chapman (2017), but briefly, four polypropylene respirometers (volume = 1.57 – 2.80 liters), each fitted with a Firesting® temperature probe and fiber-optic cable focused on a contactless oxygen sensor spot (PyroScience Sensor Technology, Bremen, Germany), were submerged in a temperature-controlled water bath held at the desired experimental temperature. Oxygen and temperature were recorded every 2 sec, and outputs were monitored and recorded by Firesting® Profix software (PyroScience, Bremen, Germany)

for the duration of each trial. Respirometers were set on automated 10-min loops comprising a 5-min closed portion during which DO levels were measured, and a 5-min open portion during which fresh water was flushed through the respirometry chambers.

For each trial, MMR was measured first using an established 3-min exhaustive chase protocol (Roche et al., 2013). In short, this protocol involved hand-chasing individual Nile perch to exhaustion and then transferring them to the respirometer, where they were held for an average of 10 h after the chase, allowing ample time for recovery and to derive estimates of SMR (Nyboer and Chapman, 2017), with oxygen consumption measured throughout the 10-h period. Twenty-minute 'empty' runs were conducted before and after each trial to quantify background respiration. Prior to this study, a number of exploratory trials were conducted on recovery times of Nile perch to validate this protocol. Results from these experiments showed that reliable SMR measures could be obtained <10-h after employing exhaustive-chase (Nyboer and Chapman, 2017). Fish were weighed for body mass (M_b) and measured for SL and TL after the trials.

3.4.3.2 Critical thermal maximum

After respirometry trials, fish were returned to their rearing ponds for ~10 days to recover, after which a subset were returned to the laboratory and re-acclimated to the same experimental temperature for 3 days to measure CT_{max} as an estimate of thermal tolerance. Owing to stresses incurred during this transfer process, a smaller sample size was used for CT_{max} trials (Table C3); however, both this current work and previous studies showed low variance in CT_{max} values, thus even with low sample sizes these findings are likely to be accurate. CT_{max} was measured following Chen et al. (2013). In these trials, groups of 2 - 4 Nile perch from each rearing temperature x experimental temperature combination were transferred into a water-filled cooler, held overnight (~8-h), and then subjected to a constant temperature increase of $0.3^{\circ}\text{C min}^{-1}$. This heating rate does not allow for acclimation during the trial, but also does not lethally shock the animal (Beitinger et al., 2000). CT_{max} was determined as the temperature at which each fish lost equilibrium for 10 seconds.

3.4.4 Calculations of metabolic traits

Metabolic rates (SMR and MMR) were estimated by calculating linear regressions between oxygen concentration and time for the closed period of each loop, omitting the first and last 30 sec of each closed portion to ensure the water in the chamber had fully mixed. Oxygen concentrations were converted to metabolic rate ($\text{mgO}_2 \text{ min}^{-1}$) after accounting for respirometer volume and fish mass. Background respiration (on average 9.9 % of SMR and 3.6% of MMR) was subtracted from the metabolic rates by assuming a linear change between the two 20-min 'empty' runs. MMR is the highest Mo_2 measurement recorded over any 3-min period throughout the trial. To calculate SMR, Mo_2 measurements were plotted against time to detect the point where the recovery curve leveled off (on average 4.4 ± 1.6 h, mean \pm s.d.). SMR was then calculated as the mean of the lowest 10% of all Mo_2 measurements after this point. Outliers ± 2 SD from the mean were excluded from this calculation (Clark et al., 2013). We followed methods outlined in Nyboer and Chapman (2017) to ensure that calculations of SMR did not over- or under-estimate this trait. We detected allometric effects of body mass on metabolic rate, and therefore used mass-adjustments (following Ultsch, 1995) instead of classic mass-corrections ($\text{mg min}^{-1} \text{ kg}^{-1}$) to account for the effects of body size on metabolic rate. Mass-adjusted AS was calculated as the difference between mass-adjusted MMR and SMR (note that from here on mass-adjusted metabolic traits will be referred to as MMR, SMR, and AS).

3.4.5 Body size, condition, and organ measurements

To estimate fish condition (K), fish were weighed for body mass (M_b) to the nearest 0.01 g and measured for TL and SL to the nearest 0.1 cm before respirometry trials. K was calculated using LeCren's equation as detailed in Froese (2006). Because there was homogeneity of slopes in the bi-logarithmic $M_b \times \text{SL}$ relationship among rearing temperatures and blocks, coefficients were derived by pooling data for all individuals.

At the end of all experimental trials, fish were euthanized with a sharp blow to the head, and livers, hearts, gills, and brains were removed. Livers were weighed fresh to the nearest 0.001 g,

and hepatosomatic index (HSI) was calculated as a percentage of *Mb*. All other tissues were preserved in 10% formalin until processing.

Preserved heart ventricles for a subset of fish (Table C3) were isolated from the rest of the heart tissues (Fig. 3.1A), blotted to remove excess liquid, and weighed five times to the nearest 0.01 g. The mean was used to calculate RVM as a percentage of *Mb*. Ventricles were then embedded horizontally in paraffin, sectioned (4 μm thickness) along the dorso-ventral axis (Fig. 3.1AB), stained with hematoxylin and eosin, and photographed at 4.5x magnification with a Leica 6SD zoom microscope with a Lumenera Scientific Infinity camera (Ottawa, ON, Canada). ImageJ v. 1.50i (<https://imagej.nih.gov>) was used to quantify the areas of the spongy and compact myocardial layers (Fig. 3.1B). The area of compact myocardium was divided by the total area (compact + spongy) of the heart section to calculate the percent of compact myocardium (%CM).

To quantify gill size, four gill arches from the left side of the branchial basket of 9-10 fish (Table C3) from each rearing temperature were extracted, laid flat, and photographed at 6.3x magnification on both hemibranchs using the same microscope setup described above. A series of six gill traits were selected to represent the overall size and area of the hemibranchs. These measures were taken to the nearest 0.1 mm or 1 mm² and included: total filament number (TFN), total hemibranch area (THA), total gill filament length (TGFL), average gill filament length (AGFL), filament base length (FBL), and filament density (FD) (Chapman et al., 2008; Crispo and Chapman, 2010). TFN was calculated as the number of filaments along the filament base on both hemibranchs. THA was the sum of the area of all filaments on both hemibranchs. TGFL was quantified by measuring the length of every 10th filament, and using the average of the two outer measures to estimate the lengths of the nine filaments in between (Fig. 3.1C). AGFL was calculated as the TGFL / TFN ratio on each hemibranch. FBL was calculated as the length of the filament base of each hemibranch (Fig. 3.1C). Filament density was calculated as the FBL/TFN ratio on each hemibranch. To obtain estimates for the whole gill, values for TFN, THA, TGFL, and FBL were summed across the four arches, and then multiplied by two to account for both sides of the branchial basket. Values for FD and AGFL were averaged across the four arches

(Chapman et al., 2008; Crispo and Chapman, 2010). We did not measure total gill surface area; however, previous inter-population and rearing studies have found that populations or treatments of fish with a larger TGFL are characterized by a larger TGSA (Chapman and Hulen, 2001; Chapman, 2007; Chapman et al., 2008). We therefore assume that a larger TGFL per gram of Nile perch reflects greater oxygen uptake capacity.

Preserved brains for a subset of fish (Table C3) were processed by trimming excess tissue and ensuring all brains were severed from the spinal cord 1 mm past the cerebellum (Fig. 3.1D). Blotted brains were weighed five times to the nearest 0.001 g, and the mean was used to calculate relative brain mass (RBM) as a percentage of *Mb*.

3.4.6 Statistical analysis

Effects of rearing temperature and experimental temperature on SMR, MMR, and AS were tested with three-way ANOVA with rearing temperature, block, and experimental temperature as fixed factors. Mass-adjusted metabolic traits were \log_{10} -transformed to meet assumptions of statistical tests. Interactions among fixed effects were removed from the model if not significant. Effects of rearing temperature and experimental temperature on CT_{max} were tested with a two-way ANOVA with rearing temperature and experimental temperature as fixed factors. For CT_{max} , not all blocks were represented in all rearing temperature x experimental temperature combinations; block was therefore not included as a fixed effect. For tests where the rearing temperature x experimental temperature interaction term was significant, and overall trends across experimental temperature were visually similar, post hoc tests for the effect of experimental temperature within rearing temperature and rearing temperature within experimental temperature were conducted to detect differences among levels. Equality of variances and normality of residuals were assessed with diagnostic residual plots and normal Q-Q plots.

Effects of rearing temperature on *K*, *Mb*, SL, TL, RVM, %CM, RBM, and HSI were analyzed with two-way ANOVA with rearing temperature and block as fixed effects. Non-significant interaction terms were removed from models. Potential interactive effects of *Mb* and rearing

temperature on organ masses were tested using ANCOVA with raw organ masses as response variables, rearing temperature and block as fixed effects, and *Mb* as a covariate. Raw liver mass was \log_{10} -transformed to meet assumptions of statistical tests. Results of ANCOVAs revealed similar outcomes as the two-way ANOVAs (except for a significant *Mb* x rearing temperature interaction for ventricle mass) so only ANOVA results are reported (but see Table C4 for comparison with Table 3.3). Gill traits were first analyzed with each metric separately using ANCOVA with rearing temperature and block as fixed effects, and *Mb* as a covariate. Second, principal components analyses (PCA) was used to reduce gill metrics to major axes, and PCA scores were used as response variables in ANOVA models with rearing temperature and block as fixed effects. To perform PCA, we first standardized gill traits to a common body mass following Crispo and Chapman (2010).

ANCOVA was used to test the hypothesis that variation in RVM, %CM, and gill size had an effect on metabolic performance (SMR, MMR and AS) and thermal tolerance (CT_{max}). Before these tests, Q_{10} corrections were applied to SMR, MMR, and AS to adjust for the effects of experimental temperature on metabolic traits. Q_{10} temperature coefficients were calculated using the van 't Hoff equation (McNab, 2002); these values were subsequently used to adjust metabolic rates at a given experimental temperature to the rearing temperature of the individual (e.g., adjusted to 29°C for T_{warm} fish). Q_{10} -corrected metabolic traits are denoted as SMR_{Q10} , MMR_{Q10} , and AS_{Q10} . CT_{max} was adjusted using the slope for the linear equation of CT_{max} x experimental temperature within each rearing temperature. Adjusted CT_{max} is denoted as $CT_{max,adj}$. ANCOVAs with $CT_{max,adj}$ or MR_{Q10} as response variables, rearing temperature and block as fixed effects, and organ traits (e.g., RVM, %CM, gill PCs) as covariates were applied to detect whether these organ traits had an overall effect on metabolic traits or CT_{max} . Significant effects were confirmed with Pearson's correlation of $CT_{max,adj}$ or MR_{Q10} with organ traits. Alpha values were set to 0.05 to confirm significance for all statistical tests. All analyses were performed in IBM SPSS Statistics, version 22.0 (IBM Corp., Armonk, NY, USA).

3.5 Results

3.5.1 Body size and condition

Nile perch from both rearing conditions achieved the same Mb , SL, TL, and K over the three-month rearing period (Fig. 3.2AB). Because the stocking size and feeding regime were the same among rearing temperatures, fish were assumed to have similar growth rates between rearing conditions, although we could not quantify precise feeding rates or activity levels. There were, however, strong effects of block for all body size traits (Table 3.3). *Post hoc* pairwise comparisons revealed that fish from block 2 were significantly larger for all measures than those from block 1 (Mb : $P = 0.002$, TL: $P = 0.001$, and SL: $P = 0.001$) and significantly or marginally larger than those from block 3 (Mb : $P = 0.064$, TL: $P = 0.043$, and SL: $P = 0.0064$). K was stable across rearing temperature and block (Table 3.3). Mortality rates of Nile perch in the rearing ponds averaged 65%, and were similar across rearing temperatures (64.3% in T_{avg} , 66% in T_{warm}), with most (73%) of the mortality occurring in the first 3 weeks of the rearing treatments. Although the source of mortalities could not be determined, we believe that the initial stress of capture and transfer was key, in addition to competition for food because of the emaciated appearance of non-surviving fish and the excellent condition of survivors. Although selection imposed by these mortality rates may bias results, similar rates across rearing temperatures validate comparisons.

3.5.2 Metabolic traits and critical thermal maximum

Nile perch reared under warm conditions had low SMRs compared with T_{avg} fish (Fig. 3.3A, Table 3.4), a difference that was especially pronounced at 29°C and 33°C, where T_{warm} fish showed a 37% and 27% reduction in Mo_2 , respectively. At 25°C, SMR values did not differ between fish from the two rearing temperatures (Fig. 3.3A). There was a significant rearing temperature x experimental temperature interaction, and *post hoc* tests revealed that T_{warm} fish performed equally well at 29°C as at 25°C, but that SMR increased at 33°C, whereas T_{avg} fish showed significant increases in SMR at each experimental temperature (Fig. 3.3A). Overall, SMR of T_{avg} fish increased 37% across experimental temperatures compared with a lower 22%

increase in T_{warm} fish. Rearing temperature and experimental temperature both had significant effects on MMR (Table 3.4). T_{warm} Nile perch had a 10 – 19% lower MMR than T_{avg} fish at all experimental temperatures (Table 3.4, Fig. 3.3B). Patterns of increase across experimental temperatures were remarkably similar between rearing temperatures, with MMR remaining constant from 25 to 29°C, and showing an exponential 31% increase at 33°C (Table 3.4, Fig. 3.3B). T_{warm} Nile perch showed reduced AS overall, with lower values at both the coolest and warmest experimental temperatures (Table 3.4, Fig. 3.3C). At 29°C, however, AS of T_{warm} fish equaled that of the T_{avg} fish. AS showed a general increase with experimental temperature in fish from both rearing temperatures (Table 3.4, Fig. 3.3C).

Nile perch from both rearing temperatures showed a significant increase of 1.89°C (T_{warm}) and 1.95°C (T_{avg}) in CT_{max} over an experimental temperature range of 7°C (Table 3.4, Fig. 3.3D), with a slope relating CT_{max} to temperature of 0.218 ± 0.060 for the T_{warm} fish and 0.244 ± 0.067 for the T_{avg} fish. T_{warm} fish had higher overall CT_{max} (Table 3.4, Fig. 3.3D) with values 2.4 – 2.8°C higher at all experimental temperatures. These individuals were able to achieve CT_{max} of nearly 40°C after only 3 days of acclimation to 33°C, whereas T_{avg} fish reached only 37.5°C.

3.5.3 Organ development and plasticity

Cardiac remodeling was apparent in Nile perch, with T_{warm} fish having reductions in RVM and increases in %CM (Fig. 3.2CD, Table 3.3), as predicted. The average RVM of T_{warm} fish (0.046 ± 0.002 g, mean \pm SEM) was approximately 20% smaller than that of T_{avg} fish (0.057 ± 0.002 g). Linear regressions of Mb with ventricle mass showed that ventricle size diverged at larger body sizes, indicating possible growth-related changes in the onset of cardiac remodeling (Fig. C3A). We tested this interaction with ANCOVAs with ventricle mass as a response variable and Mb as a covariate, and these tests revealed a significant Mb x rearing temperature interaction for raw ventricle mass. However differences between Rearing temperature were similar to the ANOVA results (Table C4, Table 3.4). For simplicity, only ANOVA results were retained in the main text (but see Table C4 for comparison). For %CM, ANOVA revealed that T_{warm} fish had a higher %CM compared with T_{avg} fish (Fig. 3.2D, Table 3.3). For tests of how variability in

ventricle morphology affects Q_{10} -corrected metabolic rates and $CT_{max,adj}$, ANCOVAs with RVM or %CM as covariates reveal that variation in %CM had a negative effect on SMR_{Q10} and a positive effect on AS_{Q10} , but did not influence MMR_{Q10} or $CT_{max,adj}$ (Fig. 3.4, Table 3.5), and that variation in RVM had a positive effect on $CT_{max,adj}$ (Table 3.5). Pearson's correlations confirmed these patterns, and revealed a positive relationship between RVM and AS in T_{avg} fish (Fig. 3.4).

Gill traits did not differ between rearing temperatures (Table 3.6). PCA on mass-standardized gill traits extracted 2 components with eigenvalues >1, with PC1 explaining 66.5%, and PC2 explaining 26.9% of the variance. Gill metrics related to filament and hemibranch size (AGFL, TGFL, and THA) loaded on PC1, and those related to gill width (AFN and FBL) loaded on PC2 (Table C5). FD was not included in the PCA as it did not correlate with the other traits. Results of ANOVA using PC scores as response variables confirmed the lack of divergence in gill size among rearing temperatures (Fig. 3.2EF, Table 3.3). Rearing temperature had a significant effect on HSI (Fig. 3.2G, Table 3.3), with T_{warm} fish having 41% smaller HSI values (0.47 ± 0.03 , mean \pm SEM) than T_{avg} fish (0.81 ± 0.05). Rearing temperature had no effect on RBM (Fig. 3.2H, Table 3.3), with fish from both T_{avg} and T_{warm} temperatures having remarkably similar values (0.54 ± 0.034 and 0.531 ± 0.045 , respectively). None of the gill traits, HSI, or RBM had an effect on any Q_{10} -adjusted metabolic traits or $CT_{max,adj}$.

3.6 Discussion

The three most important findings of this study were that 1) Nile perch reared under elevated temperatures showed evidence for compensation in upper thermal tolerance and metabolic rate, and attained similar body size and condition between rearing treatments; 2) Nile perch are capable of cardiac remodeling, and variation in heart morphology correlated with metabolic function in fish from both rearing treatments; and 3) plastic changes enacted over longer exposures effected differences in metabolic flexibility when acutely exposed to temperature change. This work has important implications for climate change resilience in this species, which is of major economic importance to inland fisheries in East Africa.

3.6.1 Developmental plasticity in upper thermal tolerance and metabolic traits

Rearing Nile perch under different temperature regimes for three months led to adjustments in upper thermal tolerance (CT_{max}). Given the stenothermal evolutionary history of the Nile perch used in this study, one might expect low thermal plasticity in this population (Tewksbury et al., 2008). However, Nile perch experiencing chronically elevated temperatures were able to increase thermal tolerance without having restrictions on their ability to further modulate thermal limits upon acute temperature increases. This is evidenced by the similar linear increases in CT_{max} with experimental temperature, which indicates comparable levels of plasticity in thermal tolerance between rearing temperatures. These results confirm previously documented trends in Nile perch thermal plasticity over shorter exposures (Nyboer and Chapman, 2017), and are in line with findings in recent meta-analyses that do not find evidence for predicted latitudinal trends in ectotherm thermal plasticity (Seebacher et al., 2015; Gunderson and Stillman, 2015).

Rearing temperature affected metabolic performance with warm-reared fish showing overall reductions in SMR, MMR and AS relative to T_{avg} fish at most experimental temperatures, indicating that compensatory mechanisms underlying basal metabolic reductions are effective during rapid transfer to temperatures both above and below their rearing temperature (as opposed to incurring costs of thermal specialization). Decreases in SMR are very likely indicative of thermal compensation because lower self-maintenance costs presumably allow more energy allocation to growth and reproduction (Priede, 1985; Sandblom et al., 2014). Reductions in SMR in warm-reared fish were accompanied by even greater reductions in MMR, which ultimately resulted in reduced AS relative to the T_{avg} -reared fish. Although decreases in MMR and AS are not necessarily predicted outcomes of thermal compensation, such patterns have been reported in a previous study on acclimated Nile perch (Nyboer and Chapman, 2017), possibly indicating that long-term exposure invokes mechanisms that reduce SMR but also lead to reductions peak performance (MMR). Similar trends have been found in a congener of Nile perch, the tropical barramundi (Norin et al., 2014), and in northern populations of shorthorn sculpin (Sandblom et al., 2014), and suggest that there may be energetic costs associated with

maintenance of high MMR. Reducing basal oxygen demand at the expense of a very high MMR may be the most efficient strategy for coping with elevated temperature conditions over longer time periods (Norin et al., 2014; Sandblom et al., 2014; Nyboer and Chapman, 2017), particularly if total aerobic capacity is rarely (if ever) used in the wild (Norin and Clark, 2016). Interestingly, Nile perch from both rearing temperatures showed similar patterns of increase in MMR across experimental temperatures, with a sharp increase at 33°C, indicating similar metabolic flexibility between rearing temperatures. Rapid increases in MMR upon acute exposure to extreme high temperatures have been documented in previous studies on Nile perch (Nyboer and Chapman, 2017), and other in fish species (Claireaux et al., 2006; Gräns et al., 2014; Norin et al., 2014). Such patterns may reflect stress responses and mobilization of functional reserves (hormone-activated performance capacity) that stimulate cardiovascular activity (Pörtner et al., 2017), and may not be stable over the long term as shown by the diminished MMR sometimes evident after acclimation (Norin et al., 2014; Sandblom et al., 2014; Nyboer and Chapman, 2017).

Reductions in AS in warm-acclimated fish (at 25°C and 33°C) relative to T_{avg} fish may indicate that mechanisms of oxygen uptake and delivery are not able to adjust fast enough to keep pace with increased cellular oxygen demand during aerobic exercise (Pörtner and Knust, 2007; Pörtner et al., 2017). However, these findings are at odds with the increases in AS across experimental temperatures. Fish achieved high AS upon acute exposure to extreme high temperatures suggesting that, at least for acute exposures, oxygen transport capacity does not immediately decline at high temperatures (and therefore does not limit AS), as previously reported for Atlantic halibut (Gräns et al., 2014), barramundi (Norin et al., 2014), and turbot (Claireaux et al., 2006), among others. These findings challenge one of the fundamental assumptions of the OCLTT concept that reduction in AS owing to oxygen limitation is a key physiological restraint acting on fishes' thermal optima. Although it is possible that our experimental temperatures were not high enough to observe the predicted reductions in AS, this calls into question the relevance of AS in predicting effects of climate change on aerobic performance given that 33°C (our highest experimental temperature) is at the upper end of what would be experienced in nature, even in the most extreme climate change predictions.

In addition, the relative drops in AS in the warm-reared Nile perch do not necessarily indicate reductions in fitness as the lower overall AS in warm-reared Nile perch did not correspond to decreases in body size or condition in this treatment (Clark et al., 2013; Gräns et al., 2014; Norin et al., 2014; Nyboer and Chapman, 2017). However, one must keep in mind that measurements of oxygen consumption are not perfect proxies for energy use (Nelson, 2016). It is possible that there were differences in activity level, food consumption rates, and/or costs of food assimilation (specific dynamic action) among rearing ponds, all of which are important for understanding growth and energy allocation (Chabot et al., 2016a,b). Although we did not measure these aspects of bioenergetics in this study, we did find reductions in HSI in warm-reared fish, indicating possible energetic costs to chronic exposure to elevated temperatures. The liver is a major energy store in fishes, and HSI is an indicator of energetic reserves in fish. HSI is often used as an alternative predictor of condition (Chellappa et al., 1995), and has been shown to relate to reproductive potential (Donelson et al., 2011). HSI can be affected by many factors including food availability, season, and reproductive cycle (Chellappa et al., 1995); however, given the similar age structure, condition, and food supply between the two rearing temperatures, these are unlikely to be sources of differentiation in the present study. The reduced HSI in warm-reared fish could indicate that physiological adjustments made upon chronic exposure to warm temperatures are energetically costly given this reduction in energetic reserves. Given that fish in both rearing temperatures were able to achieve the same body size and condition, the lower HSI in T_{warm} fish may indicate that they had to allocate more energy to growth at in the higher rearing temperature.

3.6.2 Responses of organ traits

There were no differences in RBM among Nile perch from divergent rearing temperatures. Large brains can enhance individual fitness through improved cognitive ability (Kotrschal et al., 2013), but are highly metabolically demanding, and reductions may be advantageous under physiologically stressful conditions to reduce basal maintenance costs (Poulson, 2001; Crispo and Chapman, 2010; Toli et al., 2016). Although some studies have shown high levels of plasticity in brain traits (Gonda et al., 2011; Kotrschal et al., 2012), the

absence of a response in Nile perch brain size may suggest genetic limitations (lack of ability to change brain size via plasticity), but may also indicate that mechanisms employed to compensate for increased temperature are adequate to maintain brain size at both rearing temperatures.

Nile perch also displayed a striking lack of plasticity in gill size and shape among rearing temperatures. This was somewhat surprising given previous work that showed variation in gill size in wild Nile perch occupying divergent oxygen habitats (Paterson et al., 2010), and evidence from other species that exposure to increased temperature can induce alterations in gill morphology to compensate for higher basal metabolic rate and lower oxygen availability (Sollid et al., 2005; McBryan et al., 2016; Phuong et al., 2017). We had predicted a larger gill size in warm-reared fish to enhance oxygen uptake in an environment where oxygen demand would be greater, at least initially. It is of course possible that gill traits not measured in this study (e.g., lamellar area, interlamellar cell mass) or other mechanisms such as changes in blood hemoglobin levels compensate for increased oxygen demand (Weber et al., 1976; Farrell et al., 2009; McBryan et al., 2016). However, because warm-reared Nile perch actually show *reductions* in oxygen demand (lower SMR) after three months of acclimation, it is possible that improvements in oxygen uptake were not necessary. Maintaining small gills may decrease energy required to maintain osmotic balance in the blood, and may be beneficial when larger gills are not needed (Crispo and Chapman, 2010). This finding may indicate that capacity for oxygen uptake is not the limiting factor in the maintenance of aerobic performance, and that Nile perch cope with elevated temperatures through some other, more efficient means (e.g., improvements in efficiency of oxygen delivery). The finding that gill traits do not correlate with any metabolic traits supports this conclusion.

Despite finding no evidence for plastic changes in gill metrics or brain size, results from this study showed clear evidence for cardiac remodeling. To our knowledge, this is the first study to measure heart plasticity in a tropical species exposed to elevated temperatures, and it is interesting that trends documented here are very similar to those found in temperate and arctic fishes; warm acclimation induced smaller RVM and higher %CM, with the opposite effect

in fish reared under average temperatures (Klaiman et al., 2011; Gräns et al., 2014; Anttila et al., 2015; Keen et al., 2017). Fish exposed to higher water temperature must increase cardiac output (V_b) to meet increased oxygen demand of tissues. This can be accomplished by quickening heart rate (common during acute thermal stress), developing larger ventricles (increased volume), and developing stronger contractile muscles (increased pressure), among others (Farrell et al., 2009; Farrell, 2009; Klaiman et al., 2011; Keen et al., 2017; Pörtner et al., 2017). In most cases, RVM correlates tightly with V_b (Dalziel et al., 2012), however this relationship may be altered based on changes in proportions of the myocardial layers (Klaiman et al., 2011; Keen et al., 2017). For example, increases in spongy myocardium (often corresponding to increased RVM) enhance stroke volume at cooler temperatures, allowing the heart to maintain high V_b at a lower heart rate, thereby reducing heart oxygen demand (Keen et al., 2017). In the present study, T_{avg} Nile perch had a larger RVM, so this may be the most efficient strategy to maximize cardiac output at cooler temperatures. Generally, when fishes are acutely-exposed to higher temperatures, V_b is decreased because of loss of pressure generating ability (Klaiman et al., 2011). Given time, however, fish often develop stronger compact myocardial layers (at the expense of RVM) so that the greater force generated by this layer can offset the otherwise negative effects of warmer temperatures (Klaiman et al., 2011). For Nile perch, increasing %CM may be a way of increasing V_b without requiring high heart rates and extra energy reserves. If the changes to the heart result in more efficient oxygen delivery strategies, this could lower basal oxygen demand and contribute to maintenance of a lower SMR (possibly partly explaining the lack of change in gill size). Evidence that warm-reared fish have improved cardiorespiratory function is corroborated by the CT_{max} results insofar as warm-reared fish had higher CT_{max} at all experimental temperatures.

3.6.3 Cardiac plasticity affects thermal tolerance and metabolic function

Changes in cardiorespiratory capacity are often invoked as explanations for alterations in thermal tolerance and metabolic performance in ectotherms (Gamperl and Farrell, 2004; Pörtner and Farrell, 2008; Farrell et al., 2009; Donelson et al., 2011; Jayasundara and Somero, 2013). For fish, much of the evidence for this is derived from studies on salmonid species that

link cardiorespiratory function to swim performance and thermal tolerance (Farrell et al., 2009; Anttila et al., 2013, 2014; Eliason et al., 2011, 2017). However, studies that demonstrate functional links between heart morphology and metabolic traits are rare, and the generality of these trends has not been extended to tropical fishes.

Morphological changes in Nile perch ventricles were related to variability in SMR, AS, and CT_{max} . For example, larger RVM corresponded to higher CT_{max} and higher AS, especially in T_{avg} fish. Because T_{avg} Nile perch have larger RVM, this may indicate that T_{avg} fish rely on stroke volume (over long-term exposures) to maintain high cardiac output and support better oxygen supply to tissues. This suggests that heart traits are important in determining thermal tolerance and metabolic performance at the level of the whole organism, and supports findings of studies on salmonid species that demonstrated positive relationships among different aspects of cardiorespiratory function and aerobic metabolic performance. For example, Anttila et al. (2013) showed positive correlations of RVM with CT_{max} among families of Atlantic salmon, and Eliason et al. (2011) showed positive relationships between AS and cardiac scope within several families of Pacific sockeye salmon. For T_{avg} Nile perch, the direction of plasticity for both RVM and AS was the same as the direction of covariation among these traits, leading to the conclusion that Nile perch in this group rely on a larger RVM to maintain aerobic performance.

Per cent CM correlated negatively with SMR, especially among T_{warm} individuals; so again, plastic variation among individuals supported the between-treatment effects. In the warm-acclimated fish, it is likely that adjustments in heart rate, stroke volume, and pressure generation that accompany increases in %CM all play a role in ensuring adequate oxygen delivery to respiring tissues (which have likely made their own adjustments to reduce basal oxygen demand; Schulte, 2015), while using fewer energy reserves when exposed to higher temperatures. This may allow T_{warm} fish to maintain a lower SMR. Our results also showed a positive relationship of AS with %CM (especially in T_{avg} fish). Because AS is calculated as the difference between MMR and SMR, the fact that SMR changes with cardiac morphology, and MMR does not, may be why AS is correlated with heart traits, and indicates that mechanisms controlling MMR may not necessarily be directly related to cardiac morphology. Whatever the

case, the finding that temperature-related developmental cardiac plasticity can influence aerobic function provides insight into one of the possible mechanisms (of many) that may underlie resilience to climate warming.

Cardiorespiratory function is likely to be a key mechanism underlying physiological plasticity in metabolic performance, aerobic capacity, and thermal tolerance in Nile perch). These data are consistent with one of the predictions generated by the OCLTT framework, namely that cardiorespiratory function is a key mechanism underlying thermal plasticity in fishes and can be useful to compensate of increased oxygen demand (Anttila et al., 2013). These relationships are complex, however, and are not always in the direction predicted by the OCLTT framework (i.e., lower MMR and AS in warm-reared fish, high AS and MMR in individuals acutely exposed to extreme temperatures), highlighting how physiological benefits of heart plasticity are context dependent and likely to change based on interacting stressors, strategies, and physiological challenges. The fact that Nile perch from Lake Victoria are near the upper edge of their thermal range and are still able to make plastic adjustments to high temperatures on multiple timescales provides compelling evidence against the prediction that tropical ectotherms will be disproportionately negatively affected by climate warming. This knowledge is especially important because the ability of tropical species to cope with unstable thermal environments is largely unknown, and because tropical fish species, including the Nile perch, provide vital sources of protein in developing nations and regions, such as the Lake Victoria basin in East Africa.

3.7 References

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3.8 Tables

Table 3.1 Results of 2-way ANOVA on water quality variables. Variables include maximum and minimum water temperature, lux (luminosity), dissolved oxygen (DO), pH, and turbidity (Secchi depth), across rearing temperatures (T_{avg} , T_{warm}) and among blocks. Bold P -values indicate significance at $\alpha < 0.05$.

Variables	2-way ANOVA			
		Rearing temperature	Block	Rearing temperature x Block
Maximum temperature (°C)	$F_{(1,511)}$	1832.797	5.866	9.337
	P	<0.001	0.003	<0.001
	η^2	0.782	0.022	0.035
Minimum temperature (°C)	$F_{(1,511)}$	1766.408	18.962	10.882
	P	<0.001	<0.001	<0.001
	η^2	0.776	0.069	0.041
Lux (lm m ⁻²)	$F_{(1,511)}$	29.049	0.848	9.249
	P	<0.001	0.429	<0.001
	η^2	0.048	0.003	0.031
Average DO (mg l ⁻¹)	$F_{(1,377)}$	0.428	0.694	
	P	0.513	0.500	
	η^2	0.001	0.004	
pH	$F_{(1,232)}$	1.819	0.59	
	P	0.179	0.555	
	η^2	0.008	0.005	
Secchi	$F_{(1,372)}$	1.081	1.279	
	P	0.299	0.28	
	η^2	0.003	0.007	

Table 3.2 Sample sizes (*N*) and means \pm s.e.m. of body mass (*Mb*), standard length (*SL*), total length (*TL*), and LeCren's condition factor (*K*) of juvenile Nile perch used in respirometry experiments. Each rearing temperature x experimental temperature x block combination is represented. Sample sizes were selected to ensure adequate power based on known levels of variability in respirometry data, and accounting for availability of specimens in ponds.

Rearing temperature	Experimental temperature and block	N	<i>Mb</i> (g)	<i>TL</i> (cm)	<i>SL</i> (cm)	<i>K</i>
T_{avg}	25	7	49.11 \pm 4.45	16.98 \pm 0.17	14.2 \pm 0.24	1.01 \pm 0.015
	1	2	34.12 \pm 2.01	15.55 \pm 0.04	13 \pm 0	0.97 \pm 0.023
	2	2	51.4 \pm 2.18	17.3 \pm 0.02	14.35 \pm 0.09	1.03 \pm 0.007
	3	3	57.57 \pm 4.83	17.73 \pm 0.14	14.9 \pm 0.21	1.01 \pm 0.017
	29	9	30.95 \pm 3.26	14.66 \pm 0.24	12.26 \pm 0.3	1.04 \pm 0.026
	1	2	25.56 \pm 3.34	13.95 \pm 0.1	11.65 \pm 0.06	1.06 \pm 0.04
	2	3	34.19 \pm 1.87	15.1 \pm 0.11	12.6 \pm 0.15	1.11 \pm 0.027
	3	4	30.68 \pm 7.16	14.7 \pm 0.35	12.32 \pm 0.44	0.99 \pm 0.011
	33	9	23.44 \pm 2.27	13.94 \pm 0.24	11.67 \pm 0.26	0.95 \pm 0.013
	1	2	18.77 \pm 1.43	12.75 \pm 0.24	10.75 \pm 0.22	1.04 \pm 0.046
	2	3	27.45 \pm 3.6	14.7 \pm 0.13	12.4 \pm 0.18	0.91 \pm 0.037
	3	4	22.77 \pm 4.04	13.97 \pm 0.24	11.6 \pm 0.26	0.93 \pm 0.019
T_{warm}	25	9	42.9 \pm 5.26	15.91 \pm 0.27	13.31 \pm 0.36	1.09 \pm 0.023
	1	3	36.52 \pm 3.26	15.46 \pm 0.15	12.96 \pm 0.15	1.04 \pm 0.018
	2	3	56.24 \pm 12.77	17.26 \pm 0.33	14.33 \pm 0.5	1.11 \pm 0.035
	3	3	35.95 \pm 5.02	15 \pm 0.17	12.63 \pm 0.25	1.11 \pm 0.01
	29	10	33.33 \pm 4.8	15.31 \pm 0.32	12.69 \pm 0.41	0.98 \pm 0.038
	1	3	20.69 \pm 0.28	13.6 \pm 0.19	11.13 \pm 0.16	1.02 \pm 0.054
	2	4	48.16 \pm 6.38	17.1 \pm 0.21	14.17 \pm 0.3	1 \pm 0.04
	3	3	26.22 \pm 3.45	14.63 \pm 0.14	12.26 \pm 0.17	0.9 \pm 0.012
	33	7	30.9 \pm 4.9	15.17 \pm 0.27	12.65 \pm 0.36	0.91 \pm 0.023
	1	2	19.94 \pm 0.67	14.1 \pm 0.03	11.55 \pm 0.06	0.86 \pm 0.028
	2	3	42.67 \pm 5.19	16.6 \pm 0.16	13.93 \pm 0.24	0.94 \pm 0.011
	3	2	24.2 \pm 7.02	14.1 \pm 0.2	11.85 \pm 0.24	0.92 \pm 0.04

Table 3.3 Results of two-way ANVOA testing for differences in body size and organ traits across rearing temperatures and blocks. Traits include body mass (*Mb*), total and standard length (TL and SL), LeCren’s condition factor (*K*), relative brain mass (RBM), relative ventricular mass (RVM), per cent compact myocardium (%CM), hepatosomatic index (HSI), and two principal components for gill traits (PC1 and PC2). Rearing temperatures include T_{avg} and T_{warm} , and each regime was represented by three blocks. Bold *P*-values indicate significance at $\alpha < 0.05$.

Trait	Factor	F	d.f.	<i>P</i>	η^2
<i>Mb</i> (g)	Rearing temperature	0.442	1, 47	0.509	0.009
	Block	6.953		0.002	0.228
TL (cm)	Rearing temperature	0.842	1, 47	0.363	0.018
	Block	7.589		0.001	0.244
SL (cm)	Rearing temperature	0.606	1, 47	0.44	0.013
	Block	7.473		0.002	0.241
<i>K</i>	Rearing temperature	0.031	1, 47	0.861	0.001
	Block	0.536		0.589	0.022
RBM (%<i>Mb</i>)	Rearing temperature	0.013	1, 20	0.911	0.001
	Block	4.459		0.025	0.308
RVM (%<i>Mb</i>)	Rearing temperature	9.219	1, 33	0.005	0.218
	Block	2.227		0.124	0.119
%CM	Rearing temperature	11.966	1, 32	0.002	0.272
	Block	0.404		0.671	0.025
HSI (%<i>Mb</i>)	Rearing temperature	17.825	1, 28	<0.001	0.389
	Block	0.076		0.927	0.005
PC1 Gills	Rearing temperature	0.116	1, 15	0.738	0.008
	Block	0.984		0.398	0.116
PC2 Gills	Rearing temperature	0.002	1, 15	0.969	0.000
	Block	0.043		0.958	0.006

Table 3.4 Results of two- and three- way ANOVAS examining the effects of rearing temperature and experimental temperature on critical thermal maximum (CT_{max}) and metabolic traits. The two-way ANOVA tested the effects of rearing temperature (T_{avg} , T_{warm}), experimental temperature (25, 29, and 33°C), and their interaction on CT_{max} . The three-way ANOVA tested the effects of rearing temperature, experimental temperature, block, and the interaction between rearing temperature and experimental temperature on standard and maximum metabolic rate (SMR and MMR) and aerobic scope (AS). Bold P -values indicate significance at $\alpha < 0.05$.

Variables		Rearing temperature	Experimental temperature	Block	Rearing temperature x experimental temperature
CT_{max} (°C)	F _(2, 13)	87.974	14.02		0.199
	P	<0.001	0.001		0.822
	η^2	0.871	0.683		0.03
SMR (mgO ₂ kg ⁻¹ min ⁻¹)	F _(2, 43)	23.623	33.148	0.171	4.929
	P	<0.001	<0.001	0.843	0.012
	η^2	0.355	0.607	0.008	0.187
MMR (mgO ₂ kg ⁻¹ min ⁻¹)	F _(2, 43)	12.914	32.288	0.174	0.366
	P	0.001	<0.001	0.841	0.696
	η^2	0.231	0.6	0.008	0.017
AS (mgO ₂ kg ⁻¹ min ⁻¹)	F _(2, 43)	4.749	16.545	0.13	1.949
	P	0.035	<0.001	0.878	0.155
	η^2	0.099	0.435	0.006	0.083

Table 3.5 Results of two-way ANCOVA testing for the influence of cardiac traits on thermal tolerance and metabolic performance of Nile perch from different rearing temperatures (T_{avg} , T_{warm}). Outcome variables included adjusted critical thermal maximum ($CT_{max,adj}$), and Q_{10} -corrected standard and maximum metabolic rates and aerobic scope (SMR_{Q10} , MMR_{Q10} and AS_{Q10}). Cardiac trait covariates included relative ventricular mass (RVM), and per cent compact myocardium (%CM). Block and the covariate x rearing temperature interaction were included as factors in the model. Bold P -values indicate significance at $\alpha < 0.05$.

Variables			Rearing temperature	Block	Covariate	Covariate x rearing temperature
Outcome	Covariate					
CT_{max}	SMR_{Q10}	$F_{(1, 11)}$	139.898		9.737	
		P	<0.001		0.01	
		η^2	0.927		0.47	
	RVM	$F_{(1, 11)}$	22.644		10.728	7.233
		P	0.001		0.008	0.023
		η^2	0.694		0.518	0.42
SMR_{Q10}	%CM	$F_{(1, 31)}$	8.031	0.456	6.184	
		P	0.008	0.638	0.018	
		η^2	0.206	0.029	0.166	
	RVM	$F_{(1, 31)}$	13.89	0.17	0.724	
		P	0.001	0.844	0.401	
		η^2	0.303	0.011	0.022	
MMR_{Q10}	%CM	$F_{(1, 31)}$	8.597	0.412	2.464	
		P	0.006	0.666	0.127	
		η^2	0.217	0.026	0.074	
	RVM	$F_{(1, 31)}$	3.484	0.336	0.236	
		P	0.071	0.717	0.63	
		η^2	0.098	0.021	0.007	
AS_{Q10}	%CM	$F_{(1, 31)}$	0.168	1.009	9.471	
		P	0.684	0.376	0.004	
		η^2	0.005	0.061	0.234	
	RVM	$F_{(1, 31)}$	14.244	2.584	1.935	11.958
		p	0.001	0.092	0.174	0.002
		η^2	0.315	0.143	0.059	0.278

Table 3.6 Results of two-way ANOVA testing the effects of rearing temperature (T_{avg} , T_{warm}) on a series of gill traits. Gill traits include total filament number (TFN), total hemibranch area (THA), total gill filament length (TGFL), filament base length (FBL), average gill filament length (AGFL) and filament density (FD). Body mass (Mb) was included as a covariate, and block as a fixed factor in the model. Bold P -values indicate significance at $\alpha < 0.05$.

Gill trait		Rearing temperature	Block	Mb
TFN	$F_{(1,14)}$	0.199	0.154	10.385
	P	0.662	0.858	0.006
	η^2	0.014	0.022	0.426
THA (mm ²)	$F_{(1,14)}$	0.094	0.234	30.933
	P	0.764	0.794	< 0.001
	η^2	0.007	0.032	0.688
TGFL (mm)	$F_{(1,14)}$	0.57	0.719	30.065
	P	0.463	0.504	< 0.001
	η^2	0.039	0.093	0.682
FBL (mm)	$F_{(1,14)}$	0.000	0.307	23.030
	P	0.986	0.741	< 0.001
	η^2	0.000	0.042	0.622
AGFL (mm)	$F_{(1,14)}$	0.202	0.483	17.26
	P	0.66	0.627	0.001
	η^2	0.014	0.065	0.552
FD (TFN/FBL)	$F_{(1,14)}$	0.402	1.762	6.634
	P	0.536	0.208	0.022
	η^2	0.028	0.201	0.322

3.9 Figures

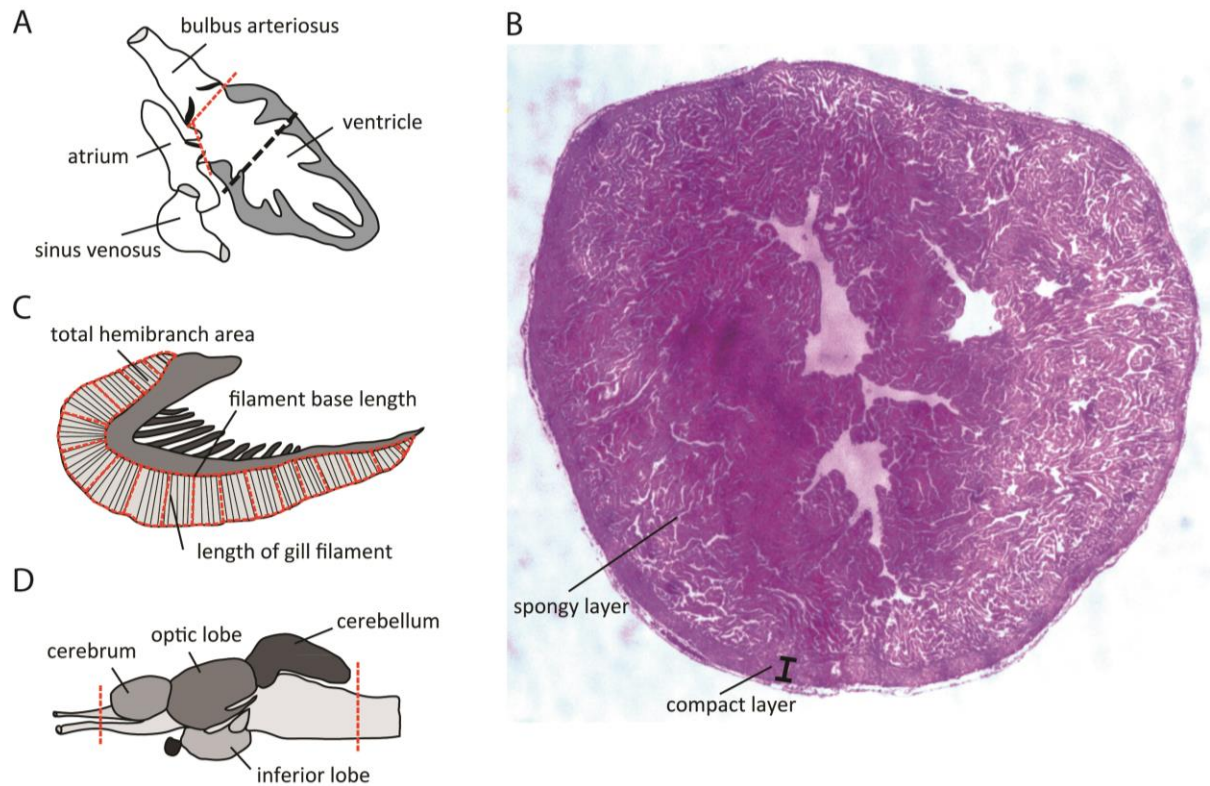


Figure 3.1 Illustrations depicting morphology and dissection points for Nile perch organs. (A) Dissection points (dashed red lines) and the location of the cross-section (dashed black line) for the heart ventricles. (B) A low magnification image of an H&E-stained cross-section of a heart ventricle with the spongy and compact myocardium layers indicated. (C) One side of a gill arch with measurements used for analysis of gill size (dashed red lines). (D) Dissection points for brains (dashed red lines).

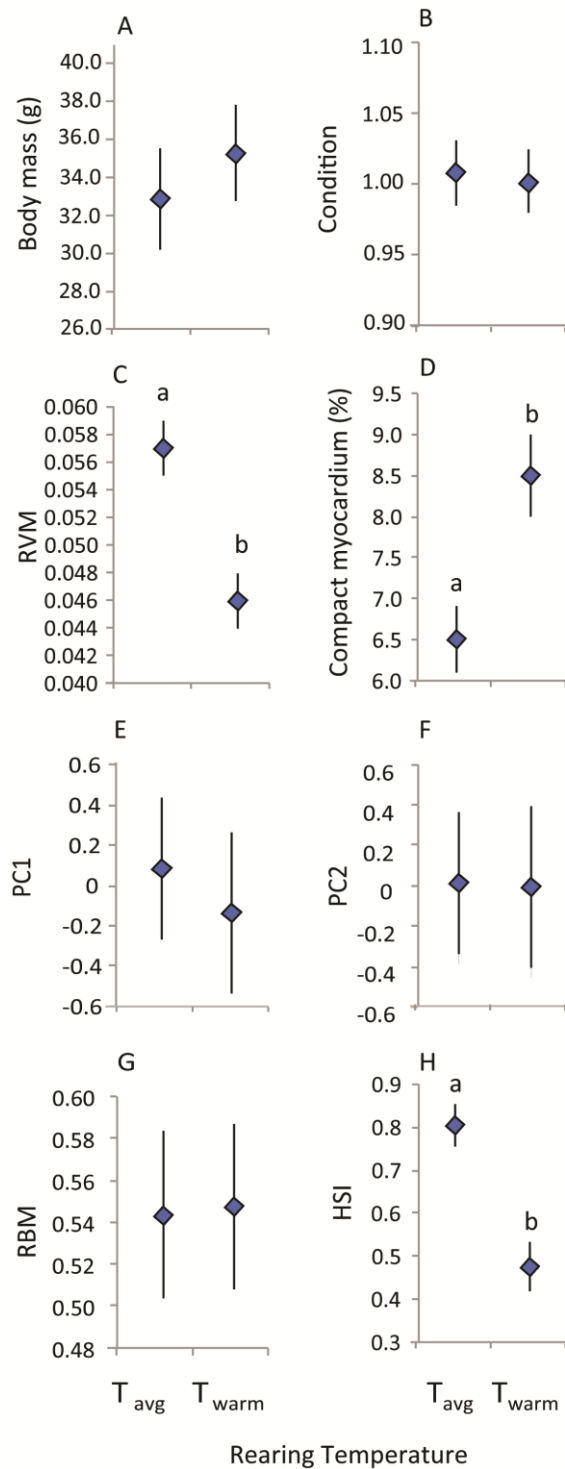


Figure 3.2 Results of ANOVA examining the effects of rearing regime on fitness-related traits and organ traits. Fitness-related traits include (A) body mass and (B) LeCren's condition factor (B). Organ traits include (C) relative ventricular mass (RVM), (D) percent compact myocardium, (E) PC1 of gills representing gill area, (F) PC2 of gills representing gill width, (G) relative brain mass (RBM), and (H) hepatosomatic index (HSI). Values are presented as means \pm s.e.m. Different letters indicate significant differences ($\alpha = 0.05$) among rearing temperatures [average rearing temperature (T_{avg}), ~25°C; warm rearing temperature (T_{warm}), ~29°C]. Block was included as a fixed factor in ANOVA models.

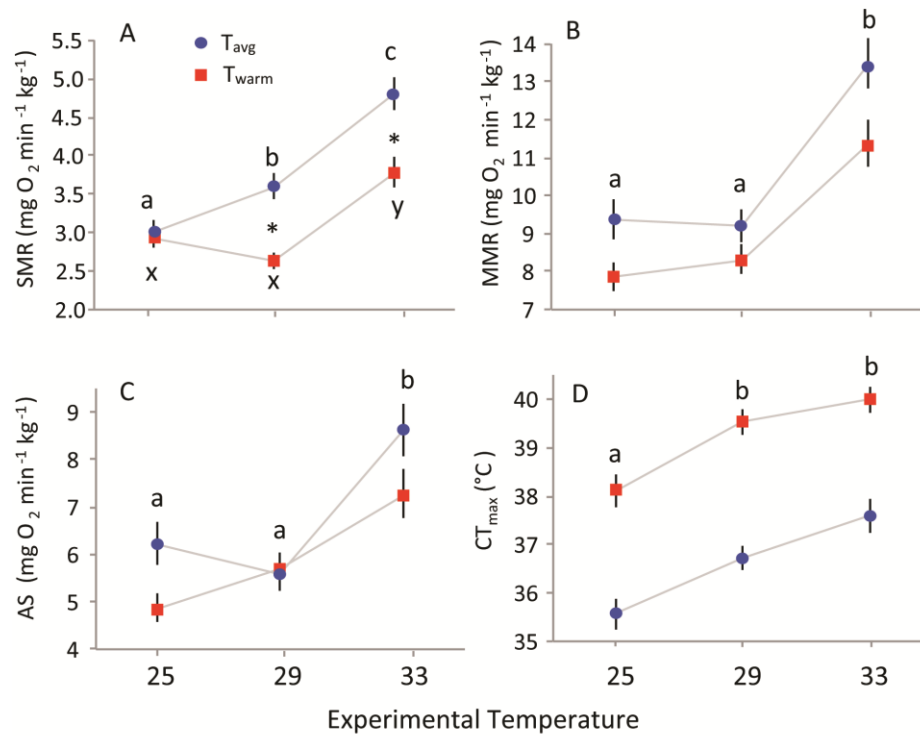


Figure 3.3 Results of ANOVAS comparing metabolic traits and thermal tolerance limits in Nile perch among experimental temperatures and between rearing temperatures. (A – C) Results of three-way ANOVA comparing means \pm SEM for (A) standard metabolic rate (SMR), (B) maximum metabolic rate (MMR), and (C) aerobic scope (AS) between rearing temperatures across a range of experimental temperatures. (D) Results of 2-way ANOVA comparing means \pm SEM of critical thermal maximum (CT_{max}) between rearing temperatures and across experimental temperatures. Different letters in A indicate significant differences among experimental temperatures within a rearing temperature, and asterisks indicate significant differences between rearing temperatures within an experimental temperature. Different letters in B – D indicate overall differences in metabolic traits among experimental temperatures. Significance of results is presented in Table 3.4. Sample sizes are presented in Table 3.1.

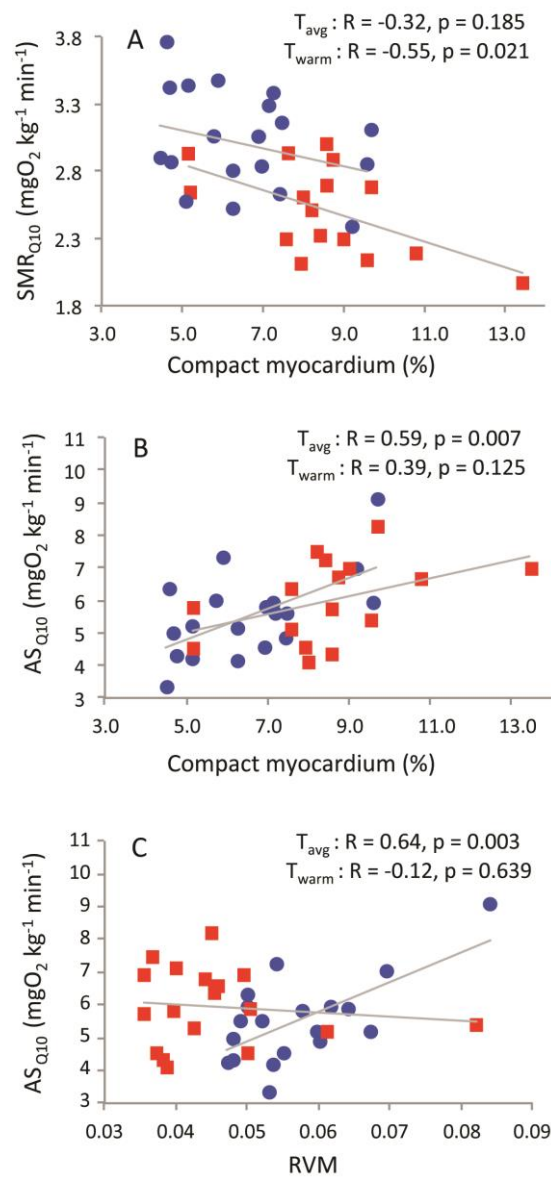


Figure 3.4 Linear relationships between metabolic traits and heart traits. (A-C) Q₁₀-corrected metabolic traits (SMR_{Q10} and AS_{Q10}) and heart traits including relative ventricular mass (RVM), and per cent compact myocardium (%CM). Colours indicate different rearing temperatures (T_{avg} , blue; T_{warm} , red). Correlations for CT_{max} with RVM (not shown in fig) had similar patterns as AS_{Q10} (Panel C), with a marginally significant positive correlation in the T_{avg} group ($R = 0.756$, $p = 0.082$).

Preface to Chapter 4

The previous two chapters explored the acclimation capacity of the Nile perch, a commercially harvested species in the Lake Victoria basin with high importance for livelihood stability and food security. In Chapter 3, I reared Nile perch under two temperature conditions for three months to examine the capacity for metabolic acclimation over ‘developmental’ timeframes, and to determine possible mechanisms underlying this capacity. I found that Nile perch show evidence for compensation in upper thermal tolerance and metabolic rate, and showed for the first time clear evidence of cardiac remodelling in a tropical species in the same direction as is seen in temperate fishes. The finding that temperature-related developmental cardiac plasticity can influence aerobic function provides critical insight into the mechanisms that may underlie resilience to climate warming in this species. These results support the findings of Chapter 2 in that limitations in aerobic scope do not appear to be the direct cause of fitness reductions in this species, and in that Nile perch perform on par with eurythermal species in terms of thermal flexibility.

This work has important implications for climate change resilience in the Nile perch, and it is perhaps encouraging that this one economically valuable species appears to have mechanisms for coping with thermal shifts over multiple timescales. Despite these physiological capabilities, however, it is unlikely that acclimation will fully compensate for climate change effects, which are likely to occur on many dimensions within and across populations and species. Climate change-related shifts in distribution, abundance, and movement patterns in wild populations may occur and affect availability of stocks to fishing communities. In the Lake Victoria basin, freshwater fisheries provide an important source of livelihoods to lakeshore residents, and changes in fish assemblages may require adjustments in harvest activities. Understanding the various decision making pathways or adaptive strategies used by communities faced with environmental change can identify actions that can be taken to improve communities’ resilience to climate change. In Chapter 4, I aim to understand what motivates the actions of fisher people by exploring their perceptions of the impacts of climate change on fishery productivity, and understanding how communities respond to these changes.

Chapter 4

Assessing the vulnerability and adaptive capacity of fishing communities to climate change in the Lake Victoria basin of East Africa

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4.1 Abstract

Inland fisheries of the Lake Victoria basin of East Africa support the livelihoods of millions of people in riparian communities. However, climate change represents an ever-growing threat to freshwater resources, and fishery-based social-ecological systems will require adaptive strategies to cope with these emerging stressors. In this study, we examine pathways through which climate change affects fishing-dependent communities in the Lake Victoria basin in Uganda, and assess livelihood responses of households to these changes. We conducted surveys, focus group discussions, and key informant interviews in five villages ranging from low to high-dependence of fishing to determine fishers' perceptions of climate change and the consequences to their livelihoods, and to assess the extent of household vulnerability in terms of their adaptive capacity in the face of climatic shocks (i.e., droughts and floods). We found that climate change disrupts fishery-based livelihoods by increasing the unpredictability of seasonal patterns and by increasing the frequency of droughts and floods. These changes are perceived to drive reductions in fish abundances and limit diversification options (e.g., crop agriculture) with negative consequences for food security and income. This situation has pushed communities to rely even more heavily on fishing entrenching them in social-ecological traps that exacerbate reductions in fishery resources. Households were limited in their diversification potential by widespread poverty, lack of access to financial and natural capital (i.e., land), and weak governance structures. However, fishers' growing awareness of these social-ecological feedbacks and effects of climate change can lead to adaptive actions that can improve community resilience. Useful pathways forward include creating interventions to enable household diversification, advancing communication and cohesion among stakeholder groups, incorporating traditional knowledge into management plans, and developing responsive and adaptive management practices.

4.2 Introduction

In many parts of Africa, freshwater fisheries provide an important source of livelihoods and food security. In East Africa alone, the fishery sector supplies more than three million people with their primary source of income (LVFO, 2016), and approximately 22 million with > 50% of their annual protein intake (FAO, 2014). However, there is growing concern that global warming may have negative consequences for inland waters and the fishing communities that rely on them (Badjeck et al., 2010). Increases in air and water temperature, alterations in precipitation patterns, and increases in storm frequency can bring about significant biophysical changes to aquatic ecosystems and their resident fish populations (Ficke et al., 2007; Myers et al., 2017) with far reaching impacts on the livelihoods and economies of fishery-based communities, making it crucial to develop adaptive strategies designed to deal with emerging stressors (Allison et al., 2009; Badjeck et al., 2010; Cinner et al., 2018). In this study, we examined pathways through which climate change affects fishing-dependent communities in the Lake Victoria basin in Uganda, East Africa, and assessed livelihood responses of households to these changes.

4.2.1 Theoretical framework

The social-ecological system (SES) framework defines an SES as a natural resource base (e.g., a fishery) embedded in social structures and governance systems whereby interactions among stakeholders and the environment drive system dynamics (Ostrom, 2009; Carpenter et al., 2009; McGinnis and Ostrom, 2014). The adaptive capacity of a SES to climate change is often defined as a set of plausible actions (adaptations) that can be undertaken to mitigate adverse effects, take advantage of opportunities, and/or cope with consequences of environmental shocks or disturbances (Bele et al., 2013; Cinner et al., 2018), and is therefore influenced by factors that are both internal (financial and social capital, livelihood diversity) and external (institutions, management policy) to the community (Smit and Wandel, 2006; Goulden et al., 2013; Cinner et al., 2018). It is often suggested that experiences of past climate variability can influence the ability of households or communities to cope with current environmental change (Berkes and Jolly,

2001), and that climate change adaptation policy is most effective when informed by existing adaptive strategies and coping mechanisms (Badjeck et al., 2010). Developing adaptive strategies thus requires integration of human and natural sciences, as well as traditional and local ecological knowledge (Berkes and Jolly, 2001; McClanahan et al., 2006; Cinner et al., 2018).

The sustainable livelihoods approach (SLA; Chambers and Conway, 1992) has been widely adopted in development research as a means to understand social relations and institutions that influence livelihood activities and natural resource management (Allison and Ellis, 2001; Ellis and Bahiigwa, 2003). In this context, a 'livelihood' is defined as the activities and capital assets (natural, physical, social, financial and human) that together determine the living gained by an individual or household (Ellis, 2000). In the climate change literature, the concept of livelihoods is used to understand vulnerability of communities to climate change, and to determine adaptive measures that can be implemented to cope with or adapt to ecosystem shocks and changes (Badjeck et al., 2010; Goulden et al., 2013; Berman et al., 2014). We follow the Intergovernmental Panel for Climate Change (IPCC) definition of *vulnerability* as the degree to which a social-ecological system is susceptible to and unable to cope with adverse effects of climate change (Adger et al., 2007), where vulnerability is conceptualized as a function of *exposure* (to climate variation), *sensitivity* (dependence of households on natural resources), and *adaptive capacity* (ability to adjust to climate change; Timmers, 2012; Bele et al., 2013).

Past studies that have used the SLA have found that livelihood diversification is a key mechanism for adapting to climate variability and change, thereby reducing household vulnerability (Cinner et al., 2018). Livelihood diversification is the process by which households grow assets and increase the variety of activities practiced to improve their standard of living (Ellis, 2000). Although fisher people in East Africa often try to pursue diversified livelihoods, options are often limited and not always viable (Allison and Ellis, 2001). In many parts of Africa, for example, key diversification options are crop agriculture or livestock rearing, both of which are likely to be impacted by climate change (Allison and Ellis, 2001; Hepworth, 2007; Badjeck et al., 2010). In addition, access to such

options in many African fishing societies is constrained by widespread poverty, poor health, weak governance structures, and low education levels (Allison et al., 2007; Hepworth, 2007; Goulden et al., 2009; Cinner et al., 2018).

Constraints on livelihood diversification can lead societies into social-ecological traps due to over-dependence on a single resource base (Cinner, 2011). Social-ecological traps arise when sudden changes to the environment cause phase shifts in ecosystem function or social organization that result in undesirable outcomes for the sustainability of a natural resource, but are difficult or impossible to reverse (Carpenter and Brock, 2008; Cinner, 2011; Boonstra and Hanh, 2015; Boonstra et al., 2016). Overexploitation of common-property resources resulting from feedbacks among rapid population growth, widespread poverty, and declining resource availability is a common manifestation of the social-ecological trap paradigm (Cinner, 2011; Enfors, 2013; Long and Lake, 2018). In these cases there is often awareness within stakeholder communities that certain actions reduce system resilience, but ‘social inertia’, or a lack of ability to adjust practices due to real or perceived limitation to other options, results in further deepening of resource degradation (Scheffer and Westley, 2007; Cole et al., 2018). Although social-ecological traps are common in small-scale African fisheries (Cinner, 2011; Laborde et al., 2016; Hänke et al., 2017; Cole et al., 2018), this concept has not been applied to fisheries of the Lake Victoria basin in the context of climate change adaptation. Recent studies have shown that the concept of social-ecological traps can be a fruitful avenue for understanding how climate change can affect the ecological and social dynamics of small scale tropical fisheries (Boonstra and Hanh, 2015; Cole et al., 2018). Here we unite the sustainable livelihoods approach with the concept of social-ecological traps to understand climate change vulnerability, assess existing livelihood responses, and elucidate possible adaptive actions that can be taken by households or governments to reduce vulnerability to climate change.

4.2.2 Research context: History and social-ecological changes in the Lake Victoria basin

The Lake Victoria basin (LVB) is a large region in equatorial East Africa composed of a complex network of lake and river systems, many of which are host to economically

important inland fisheries. Lake Victoria is the largest tropical lake in the world, and supports millions of fisher people among the three riparian countries that share its waters; Uganda, Kenya, and Tanzania (LVFO, 2016). For many decades, Lake Victoria supported a productive multi-species fishery, but the 20th century brought massive social and ecological changes to the region as human population density increased and demand for aquatic resources intensified. During this period, species introductions and increased eutrophication altered the trophic structure of the lake changing the species composition and biomass of catches (Chapman et al., 2008).

The most dramatic ecological change occurred in the mid-20th century with the introduction of the Nile perch (*Lates niloticus*) to a number of lakes in the LVB, primarily to boost overexploited and declining native fisheries (Pringle 2005). The Nile perch experienced rapid increases in abundance in the 1980s, which coincided with increased eutrophication and continued exploitation of native species to effect further declines or disappearances of many native fish species (Witte et al. 1992; Chapman et al. 2008; Taabu-Munyaho, 2014; Marshall, 2017). This ultimately shifted the Lake Victoria fishery from a complex, multi-species system to one dominated by three species; the introduced Nile perch and introduced Nile tilapia (*Oreochromis niloticus*), and a native cyprinid, *Rastrineobola argentea*, locally known as mukene in Uganda (Taabu-Munyaho, 2014; Marshall, 2017). In the meantime, the highly productive Nile perch fishery fueled the development of a lucrative fish-freezing export industry through the 1990s (Balirwa et al., 2003; Balirwa, 2007) bringing about an economic boom among fishing communities. These ecological and social shifts spurred changes in fishing practices and fisheries management policies (Ogutu-Ohwayo, 1993; Barratt et al., 2015), and the extremely valuable open-access fishery drew great numbers of fishers, contributing to high population growth in the region.

Over the last decade, continuous intense fishing and other changes in the lake basin have led to an apparent reduction in Nile perch biomass in some regions (Balirwa et al., 2003; Matsuishi et al., 2006; Hecky et al., 2010), and the fishery continues to be exploited at ever-increasing rates (Taabu-Munyaho et al., 2016). It is becoming clear that social-ecological trap dynamics are at play in this system as reductions in fish stocks combined

with high population growth has resulted in a growing demand for fish. Dwindling stocks have motivated the use of illegal fishing practices contributing to further reduction of fishery resources (Timmers, 2012; Mbabazi et al., 2016), and leading to widespread poverty among fishing communities. In addition, weak regulatory institutions have made effective law enforcement and fishery management difficult or impossible to achieve. Over the last 20 years, efforts have been made to shift responsibilities away from a central government towards fishing communities through locally regulated beach management units (BMUs); however, the effectiveness of these structures has been highly variable (Barratt et al., 2015; Nunan et al., 2015).

Ecologically, the LVB is extremely sensitive to climatic variation (Nicholson, 1996; Goulden et al., 2009; Goulden et al., 2013). Over the past 60 years numerous drought and flood events have led to fluctuations in lake levels (Goulden et al., 2009), which have affected ecosystem function through changes in species distribution and habitat degradation (Chapman et al., 2008). Water temperature increases of 0.2 - 1.5°C have been detected in Lake Victoria since 1900 (Sitoki et al., 2010; Marshall et al., 2013), and further air temperature increases of 1.3 - 4.5°C are expected by the end of the 21st century (Niang et al. 2014). Predictions also indicate that climate change in this region will manifest in less predictable seasonality and increased occurrence of extreme weather events (Niang et al. 2014; Ogutu-Ohwayo et al., 2016). A major challenge facing the LVB is the need to develop appropriate strategies for improving the adaptive capacity of this complex and dynamic SESs (Enow and Muhongo, 2007; Liu et al., 2008).

In Uganda specifically, freshwater fisheries provide a substantial contribution to the national economy through local markets, employment, and foreign export earnings. Fisheries provide approximately 30–50% of dietary protein and constitute the primary source of livelihoods for 1.2 million people living in Uganda's riparian areas (Timmers, 2012). A number of recent international assessments rank Uganda as one of the world's most vulnerable countries to climate change based on its dependence on primary production and natural resources (Liu et al., 2008; Allison et al., 2009; Kansiime, 2012; Ogutu-Ohwayo et al., 2016). Despite this, little directed local-scale analysis has examined the consequences of changing fishery ecosystems on human communities in Uganda,

creating barriers to coping with risks posed by global warming. In this study we determined the pathways through which climate change impacts fishing-dependent households in lakeshore communities in Uganda, and what measures can be taken to improve the adaptive capacity of these communities. The specific objectives of this study were to: 1) determine the perceptions of fisher people on the effects of climate variability and change on fishery productivity and livelihood stability, and 2) assess the current extent of household vulnerability to climate change. We focus especially on adaptive capacity by highlighting activities and assets that most contribute to successful livelihood diversification. Results are discussed in the context of social-ecological feedbacks and traps.

4.3 Methods

4.3.4 Site selection

Data for this study were collected during two field seasons from February – April, 2016, and from September – December, 2016 from two lakes in the Lake Victoria basin in Uganda: Lake Victoria and a satellite water body, Lake Nabugabo (Fig. 4.1). Lake Victoria is the largest tropical lake in the world with a surface area of 68,000 km² and a mean depth of 40 m. Much of Lake Victoria's shoreline is edged by dense papyrus swamp, however widespread development has led to large-scale conversion of forested and wetland habitats and increased agricultural and industrial inputs to the lake. Lake Nabugabo was formerly a bay of Lake Victoria, but became isolated from the main lake approximately 5000 years ago (Stager et al., 2005). It is smaller and shallower than Lake Victoria, with a surface area of 33 km² and a mean depth of 3.1 m (Nyboer and Chapman, 2013). Dense wetlands surround most of the lake, except for its west side, bordered by forest and fishing villages. The two lakes experience similar climatic conditions with two rainy and two dry seasons per year (Fig. 4.2), with average annual rainfall of 1200 mm, and average temperature of 24°C (UBOS, 2009), and both lakes experienced introduction of the Nile perch.

We selected five villages for this study; three on Lake Victoria (Lambu, Ggolo, and Nakiga) and two on Lake Nabugabo (Bbaale and Kaziru; Fig. 4.1). All villages were based in or near

the Masaka district of Uganda where the dominant local language is Luganda, and the dominant tribe is Baganda. Landing sites were chosen to represent a broad range of population size, wealth status, and fishing capacity. Bbaale and Kaziru landing sites (Lake Nabugabo) have approximately 20 -30 actively-operating fishers, and are separated by only a few kilometers, although fishers from these sites tend to operate in different areas of the lake (Vaccaro et al., 2013). Relative to Ggolo and Lambu, Bbaale and Kaziru have smaller populations (Table 4.1) and are less developed, with limited access to electricity and fewer public services. Fishers on Lake Nabugabo use small (~2.5 m) wooden paddle-powered canoes. Nile perch (*Lates niloticus*) and Nile tilapia (*Oreochromis niloticus*) are the most important commercial catches, and size selective gill nets and long lines are the predominant (legal) gears on the lake. There is frequent use of illegal gears including non-selective beach and boat seines, and tycoonning (the practice of hitting the water to scare fish into nets). Fishing pressure on the lake has been intense, with both size and abundance of Nile perch in the catch declining (Paterson and Chapman, 2009), and in recent years fishers have responded to this through the development of a mukene (*Rastrineobola argentea*) fishery, which are fished with hand-operated scoop seines at night. Small-sized fish are generally kept for personal consumption, while larger specimens are sold to traders who bring the fish to Lake Victoria and sell to fish processing factories (Vaccaro et al., 2013). Apart from fishing, livestock and agriculture are the principal activities of most households.

For Lake Victoria, data were collected from three sites ranging from mid-sized Nakiga to large, industrial-scale Ggolo and Lambu (Fig. 4.1). All three sites are located on the western shore of Lake Victoria, west of the Ssese Island archipelago. Nakiga is a smaller landing site situated in a seasonal wetland. There are few amenities, no electricity, and no paved roads leading to this site, which is often cut off by flooding during the rainy season. Fishers in this site use paddle-powered boats and fish in crews of 3-6 fishers. They target mainly Nile tilapia, but fishers also revert to lungfish (*Protopterus aethiopicus*), various catfishes, and other species that tend to inhabit wetland zones. Nile perch and mukene are also targeted in Nakiga. Fish are transported by bicycle or motorbike to Bukakata trading center for transport to local and international markets. Like the Nabugabo sites, fishers at Nakiga tend to be long-term residents. Fishers in Ggolo

and Lambu use large (7-10 m) wooden motor-powered boats that accommodate crews of 3-10 fishers, and can access the offshore waters of the lake. Mukene are a very important part of the catch at these sites, and are fished in large teams operating boat seines. Long lines and gill nets are also used to target large Nile perch and Nile tilapia. The prevalence of illegal fishing (targeting juveniles of these species) is very high at these sites. Catch is consumed locally, exported internationally within Africa (e.g., to the Democratic Republic of the Congo), and sold on-site to fish freezing factories for overseas export. Fishers at these sites have benefitted from government investment in infrastructure to fuel the Nile perch export market including access to electricity and well-maintained roads. Apart from fishing, trade and service are the most common livelihood activities of most households (UBOS, 2009).

4.3.2 Research approach

Primary data were collected at the household level using a mixed-methods approach employing a series of quantitative surveys (n = 203), focus group discussions with members of fishing communities (n = 16), and key informant interviews with community leaders and government employees (n = 13). All methods aimed to determine lakeshore people's perceptions of climate change, identify its effects on fishery-based livelihoods, pinpoint successful adaptation strategies and barriers to adaptation, and evaluate factors that improve resilience to environmental change.

4.3.2.1 Survey methods

Household surveys were based on the livelihoods framework (Ellis, 2001) and were designed to capture information on household demographics, access to capital assets (financial, social, human, physical and natural), diversity of livelihood activities, perceptions of environmental change, adaptation and coping strategies during droughts and floods, and barriers to these adaptations. We estimated the effectiveness of adaptation strategies by asking fishers how various activities affected their income and food security (increase, decrease, or no change) when faced with these climatic shocks (Document D.1.1). We selected participants using purposive and stratified random sampling techniques. Purposive sampling was used to select the two focal lakes and five

landing sites that were broadly representative of the fishery. Participants were recruited by approaching potential respondents at landing sites, assessing their status, and arranging meeting times with the aid of community leaders. Sampling was stratified by age, wealth status, and involvement type in the fishery including boat owners, male fish traders, boat crew, and female trader-processors. Boat owners are the proprietors of fishing gears (boats, nets, engines, etc.) and are thus the members with the highest financial investment in the fishery (Odongkara, 2006). Boat owners hire crew members to operate the gears (usually at night), splitting earnings 50/50, after expenses (Odongkara, 2006). Fish traders (male and female) meet crews in the morning to buy fish. Male traders tend to deal in lucrative (larger-sized) Nile perch and Nile tilapia catches selling to higher-up traders or exporters, while female traders deal in mukene and smaller (illegal) Nile perch or Nile tilapia, and process the fish through sun-drying or smoking before selling or bringing to markets (Timmers, 2012). Sample sizes of participants at each landing site were roughly proportional to the number of fishers working at those sites, with the exception of Ggolo and Lambu where surveys were administered until saturation (Baxter and Eyles, 1997). Surveys were piloted with fishing community members on Lake Nabugabo (non-participants in the actual survey), and refined with fisheries scientists and social scientists at the National Fisheries Resources Research Institute (NaFIRRI) of Uganda before being administered at all landing sites. Household surveys were administered in Luganda, and translated on-the-spot to English.

4.3.2.2 Survey analysis

Survey questions with categorical responses (e.g., stated impacts of droughts and floods on livelihoods) were analyzed by examining frequencies and percentages of responses. We compared fishers' perceptions of seasonal changes (rainy vs. dry months) to climate data (temperature and precipitation) from the World Bank Climate Knowledge Portal (World Bank Group, 2016), and compared fishers' estimates of monthly catch rates of Nile perch, Nile tilapia, and mukene with catch data collected in landing site surveys conducted by NaFIRRI (Mbabazi et al., 2016). Survey questions with continuous numerical responses are presented as means with standard deviation (SD), and were analyzed using Pearson's correlation to detect relationships among variables, with a Bonferroni

correction for multiple comparisons (Abdi, 2007). We used ANOVA to detect differences in continuous traits among landing sites, involvement type, and gender. The remaining survey responses were combined into nine continuous indices summarizing the five capital assets proposed by the sustainable livelihoods framework (financial, social, human, physical, and natural), concurrent diversity, and three dimensions of climate change vulnerability (sensitivity, exposure, and adaptive capacity). Definitions and descriptions of each index, as well as survey information used to calculate each index are available in Table 4.2. All indices were created by calculating standard scores (z-scores) for each element of each index. Z-scores reflect the number of standard deviations a household falls above or below the population mean. Z-scores of index elements were then summed to create various indices. Finally, indices of the five capital assets were combined into one variable called ‘livelihood stability’, and the three vulnerability dimensions were combined into one variable called ‘climate change vulnerability’ (Table 4.2). Each of these indices can be used to predict how households or communities will cope with stressors related to climate change. Pearson’s correlation was used to test for relationships between pairs of indices with a Bonferroni correction for multiple comparisons, and ANOVA was used to detect differences in indices among landing sites, involvement types, and between genders.

4.3.2.3 Focus groups and key informant interview methods

Focus group discussions (FGDs) were held at the same five landing sites and targeted the same four involvement types, with separate focus groups for each involvement type. In Bbaale and Kaziru, there were too few male traders and women for a separate focus group at each site, so we brought individuals from the two sites together for these groups. In addition, there is not as strong a distinction between boat owner and boat crew at the Lake Nabugabo sites, so these were conducted together (Table 4.3). When selecting participants for the FGDs we attempted to include representatives from the three major fisheries (Nile perch, Nile tilapia, and mukene), and tried to include a broad range of wealth statuses and ages within each group. FGDs were conducted in Luganda and recorded using voice recorders after obtaining permission from participants.

One individual on the research team led the discussion, while a second individual took detailed field notes.

Focus group questions were designed to follow up on key issues emerging from the survey data, and to probe more deeply into areas of interest especially regarding perceptions of environmental change, adaptation strategies for coping with this change, and barriers to adopting these strategies (Document D.1.2). A central question in the FGD required participants to rank five items (representing the five capital assets) in order of importance for diversification and sustainable livelihoods. The five items were: education and skill training, strong community cohesion, steady environmental conditions, financial or asset-based capital, and access to infrastructure and facilities (roads, hospitals, potable water, etc.). This question promoted discussion among participants, provided context for other discussion points, and gave insight into deficiencies or needs within each community. Key informant interviews (KIIs) were conducted with one to two community leaders at each landing site (village chair people, fishery managers) and government fishery officers. KIIs were used to get estimates daily harvest rates (kilograms of fish per day), understand trade routes, and clarify key points in terms of environmental changes and barriers to adaptation (Documents D.1.3 and D.1.4).

Data from FGDs and KIIs were translated from Luganda to English by a single translator, and transcribed in full. Transcripts were compared to field notes to cross-check translation consistency. FGD and KII transcripts were coded according to themes relating to specific research questions. These included perceptions of changes in the environment and in the fishery, diversification options, adaptation and coping strategies used during climatic shocks, barriers to adaptation (including governance issues), and possible ways to overcome those barriers.

4.4 Results

4.4.1 Differences among landing sites, involvement types, and between genders

Fishers ranged in age from 19 to 78 years [average = 38.2 ± 9.7 (SD) years] with the eldest fishers at Nakiga landing site and the youngest at Bbaale (Fig. 4.3, Table 4.1). In

general, boat crews included the youngest members of the fishing community, and the boat owners comprised the eldest (Fig. 4.3). Education levels were generally low, with an average of 5.2 ± 3.0 years of education, and only 4.4% of participants had completed secondary school. Education level did not vary among landing site, involvement type, or gender (Fig. 4.3). Wealth varied widely among participants; however, the disparity was greater at the larger landing sites (Lambu, Ggolo) with more homogeneous wealth at the smaller sites (Bbaale and Kaziru; Table 4.1). There was also variation in residence times in the village (Fig. 4.3). Respondents from the villages of Bbaale, Kaziru, and Nakiga tended to have longer residence times than Ggolo and Lambu, which tended to have more migratory fishers (Table 4.1). Crew members and female trader-processors were generally newer to the fishing industry than boat owners and traders, and tended to have migratory lifestyles, especially at the larger sites (Fig. 4.3).

There were differences among landing sites, involvement types, and genders for many of the indices calculated from the survey data (Figs. 4.4 and 4.5). For landing sites, one of the most striking patterns was that Lambu, the largest and most industrial of the landing sites with excellent access to physical capital (roads, electricity etc.; Fig. 4.4), was also the one where participants had the lowest financial capital (Fig. 4.4), lowest score for concurrent diversity (Fig. 4.5), and the lowest adaptive capacity (Fig. 4.5), whereas the small-scale landing sites such as Bbaale and Kaziru on Lake Nabugabo had the highest score for adaptive capacity and concurrent diversity (Fig. 4.5), and are among the highest for financial capital (Fig. 4.4), despite low scores for physical capital (Fig. 4.4). In addition, one of the sites on Lake Victoria (Nakiga) had the lowest score for social capital, indicating a lack of community cohesion and trust (Fig. 4.4). In terms of overall livelihoods, Nakiga was the lowest, and Ggolo the highest (Fig. 4.4). There were no differences in human or natural capital, or in sensitivity, exposure, or climate change vulnerability among landing sites. Boat owners generally scored the highest for capital assets (except for physical and natural capital), livelihood stability, concurrent diversity, and adaptive capacity, while female trader-processors and boat crew generally scored the lowest (Figs. 4.4 and 4.5). There were no differences in sensitivity, exposure, or vulnerability among the involvement types (Fig. 4.5). Women scored lower in financial

and human capital, in overall livelihood stability, and tended to be less diversified than men (Figs. 4.4 and 4.5).

4.4.2 Relationships among indices

In general, all indices describing capital assets were positively correlated with each other (Table 4.4), the only exception being natural capital, which correlated only weakly or not at all with the other capital assets. Concurrent diversity correlated positively with all capital assets (except physical and natural), and with overall livelihood stability (all capital assets summed; Table 4.4) indicating that having access to capital assets can lead to increased diversification opportunities. Of the three vulnerability dimensions, adaptive capacity and sensitivity were strongly negatively related to each other, but neither was related to exposure (Table 4.4). Adaptive capacity and sensitivity also had positive and negative relationships, respectively, with financial and human capital, livelihood sustainability, and concurrent diversity (Table 4.4).

4.4.3 Perceptions of climate change, and impacts on livelihoods

Fishers had accurate perceptions of typical annual seasonal changes (rainy vs. dry season) when compared to actual climatic patterns (Fig. 4.2). Fishers' observations that catch rates increase during rainy seasons and decrease during dry seasons were also corroborated by NaFIRRI catch survey data (Fig. 4.2). At all landing sites fishers perceived stochastic climatic events such as droughts and floods to be the most important environmental shocks to affect their households (Table 4.5). At all landing sites respondents indicated increased frequency of droughts (86%) and floods (81%; Table 4.5). Most fishers stated that rainy and dry seasons were becoming more intense (85%) and less predictable (51%). Other important environmental changes included structural, man-made changes such as deforestation (56%), degradation of wetlands (37%), and rapid human population growth (22%; Table 4.5). All of these environmental changes were perceived by participants to have noticeable effects on the availability of fish resources (Table 4.5). At all landing sites, fishers noticed drastic decreases in harvest rates of two of the three most important commercially harvested fish species, Nile perch and Nile tilapia, and many cited decreases in mukene catches as well.

Survey participants had mixed responses on effects of droughts and floods on livelihoods (Fig. 4.6A-D). Droughts were generally associated with decreased fish catches and sizes, crop failure, reduced incomes, and high food insecurity (Fig. 4.6A). However, some participants stated that income from fisheries could increase during droughts. This was primarily female mukene traders, who take advantage of the excellent conditions for sun-drying mukene by purchasing more of it during times of drought (Table 4.5, Fig. 4.6B). This can also lead to increases in food security as dried mukene can be stored for weeks, and excess fish can be consumed within households (as stated in FGDs). Others stated that times of drought can be used to prepare gardens in hopes that coming rains will provide income (Fig. 4.6B). According to survey respondents, effects of floods varied depending on the severity. Floods were perceived to enhance catch of all fish species, both in quality (fish size) and quantity (abundance; Fig. 4.6D). When not too severe, floods were associated with increased incomes for many households from both fishery and non-fishery activities reflecting better catches, high quality pasture for animals, and good germination and growth of crops (Fig. 4.6D; Table 4.5). However excessive flooding can have negative consequences for fishing such bad weather preventing fishing and therefore reducing income and decreasing catches (Fig. 4.6C). In addition fishers noticed increases in crop failure (rot), road blockages, damage to infrastructure (boats, houses, roads, landing sites, fishing gear), increases in human and animal disease, and greater post-harvest losses in the fishery under severe flooding (Fig. 4.6C; Table 4.5). While extreme weather events generally had negative impacts on livelihood stability, proportionately more households reported increases in fish consumption and income during floods, and more reported decreases in fish consumption and income during droughts (Fig. 4.6BD).

4.4.4 Diversification options, adaptive strategies, and coping with climate change

4.4.4.1 Diversification

The average score for concurrent diversity (different livelihood activities within a household) was 4.9 ± 3.1 (SD). The majority of survey respondents (81%) indicated were diversified into more than one livelihood activity, however 15% of these stated that their

main diversification option was another activity within the fishery, leaving only 66% diversified outside of fishing. The maximum number of simultaneous activities within any household was 16; however, only 17% of respondents were engaged in over eight activities, which has been used as a cut-off point to determine 'high diversification' in rural communities (Kristjanson et al., 2011; Musinguzi et al., 2015). Crop agriculture and livestock rearing were the most common areas of non-fishery diversification (Fig. 4.7); the most common crops included cassava, sweet potato, maize, and beans, and the most common animals were pigs, chickens, and goats (Fig. D1). A small proportion of respondents had diversified into non-fishery trading, service jobs (e.g., general labour, brickmaking, driving), or business (e.g., shop owner) (Fig. 4.7; Fig. D1).

The diversification options available to fishers were often different than the options they would prefer to do, according to the surveys (Fig. 4.7). Many respondents indicated that, in addition to crops and livestock, they wished to diversify into trade and service or business ventures (Fig. 4.7). The most common areas of trade and service identified included trading in coffee and local staple bananas (matooke), working in another industry (e.g., construction), or driving transportation motorcycles (boda boda; Fig. D1). The most commonly suggested businesses included shops for food or household items, small restaurants, or housing rentals (Fig. D1). For crops, many fishers indicated that they would like to diversify into high value crops such as coffee or tomatoes in addition to their current crops (Fig. D1). For livestock, many participants in surveys and FGDs indicated that they prefer to pigs and zero-grazing cattle (Fig. D1) as these animals require little space, are easy to feed, and have good market value. However, survey and FGD respondents also noted that crops and livestock are heavily influenced by climate change, and that they have adapted to this by planting early-maturing crops, or crops that are drought and flood-resistant.

4.4.4.2 Adaptive strategies and outcomes

To adapt to major climatic shocks (i.e., droughts or floods) that result in changes in fish distribution and abundance, decreases in fishing-related incomes, and decreases in food security, a large proportion of respondents stated that they have no strategy and simply continue business-as-usual (53% during droughts; 37% during floods) making no

changes to their daily patterns. The majority of households employing this strategy reported decreased incomes and reduced food security owing to this response. However, some respondents indicated that they increased fishing pressure by working more hours or using more nets (especially during droughts), but with little improvement to food security and incomes (Fig. 4.8A). In addition, during both droughts and floods some fishers shifted to new fishing grounds, used different fishing techniques, or targeted different species (Fig. 4.8AB), which was generally perceived to improve (or not change) income and food security of households during both types of shocks (Fig. 4.8AB). However, data from the focus groups revealed that focusing more energy on fishing during low seasons were understood to be maladaptive since fishers are more likely to revert to illegal practices and harvest juvenile fishes.

Despite high percentages of households with no adaptation strategy (i.e., staying within fishing or increasing fishing effort), several respondents indicated that they focused more energy on non-fishing activities to improve their livelihoods (Fig. 4.8AB), although the frequency and success of these activities varied between droughts and floods. For example, more people turned to crop agriculture during floods, with a higher proportion reporting increases in income and food security relative to droughts (Fig. 4.8AB). Survey respondents indicated that reverting to crops during floods was especially beneficial as crops germinate and grow well during periods of rain, especially when precautions were taken for draining excess water from gardens (e.g., building trenches and drainage troughs). FGD participants stated that people abandon crop agriculture during droughts because lack of access to irrigation facilities makes this option futile. Livestock agriculture, business (e.g., shops, restaurants), trade (e.g., agricultural products) and service (e.g., informal employment, rentals) were strategies used approximately equally during both droughts and floods (Fig. 4.8AB). Livestock rearing was generally perceived to bolster income and food security for households during times of drought and flood (Fig. 4.8AB), and FGDs revealed that livestock are understood to be more resilient to climatic effects (except in extreme circumstances when diseases are prevalent and feed is difficult to obtain). Those who were able to transition to non-fishery business, trade, or service generally reported increased income, however only 10 - 14% of all respondents indicated that they had done this.

In terms of preparing for future drought and flood events, the majority of respondents (53%) indicated that they had no strategy. A few respondents have planned ahead by planting crops (23%) however, only 8% planted drought or flood resistant varieties. Others maintained livestock herds (11%), saved money (7%), invested in various businesses such as house rentals and shops (7%), acquired land (3%), planted fruit trees (2%), and built storage facilities for food (2%). Some mentioned that they dug trenches in gardens to prepare for floods (1%), and some that they had dug wells near their gardens to aid in irrigation (0.5%).

4.4.4.3 Coping strategies

During times when food security and incomes are low in both fishing and non-fishing activities, respondents indicated that they coped by borrowing money or other forms of capital (e.g., seeds; 7%), selling off livestock and other assets (46%), relying on support from the community (35%), using up savings (6%), or exiting the fishery entirely to return to their home villages (2%).

4.4.5 Barriers to diversification

The main barriers to diversification and adaptation in these communities include lack of capital (81%), and lack of access to land (35%), limited access to credit facilities (26%), lack of government support (18%), lack of training (3%), and lack of planning and awareness (3%). Only 22% have skills to seek other employment opportunities, and fewer still (15%) are able to invest in other businesses (e.g. shops, rental homes, non-fishery trading). Several of these barriers are discussed in detail below. Participants suggested that interventions providing low-interest credit (53%), asset-based support (24%), training on financial planning and diversification options (19%), education on sustainable resource use (16%), and sensitization to the effects of climate change (3%) would be beneficial.

4.5 Discussion

The Lake Victoria basin is an example of a complex social-ecological system that has undergone several regime shifts in terms of fish species composition and population

growth, first with the overharvesting of native species in the early 20th century, second with the introduction of the Nile perch and the subsequent fishery boom, and third with the second fishing-down cycle and the apparent overexploitation of Nile perch and Nile tilapia fish resources. In addition, this system is increasingly under threat from the effects of climate change and other anthropogenic stressors. These factors have triggered a variety of societal changes, including high rates of immigration to the fishery, alterations in fishing techniques, higher harvest intensity, and changes to governance structures.

4.5.1 Perceptions of environmental change

In general, people in fishing households on Lake Victoria and Lake Nabugabo are highly aware of changes in the environment (i.e., less predictable seasonality, increased frequency of drought and flood events). These findings differ from perceptions of climatic shifts in other regions of Uganda (e.g., Lake Wamala, Lake Kyoga) where fishers noticed increased floods but not droughts (Goulden et al., 2013; Musinguzi et al., 2015), indicating that effects of climate change are likely to vary with location. Data for this study were collected during the 2015/2016 El Niño event, with both extreme rainfall (February - April) and intense drought (May - December) experienced in the focal villages during the study period. These events are likely to have influenced fishers' perceptions regarding the relative frequency of droughts and floods.

Fishers had accurate impressions of changes to fish abundances with seasons (wet vs. dry). There was general agreement among landing sites that fish sizes and abundances in the catch declined during dry seasons (and crashed during droughts), and increased during wet season and during flood events. These patterns were affirmed by formal catch surveys conducted across various months and seasons from 2005 – 2015 (Mbabazi et al., 2016); however, these fluctuations in catch abundance are more likely to reflect the increased movement patterns of fish during rains than actual variations stock recruitment. Similar precipitation-related variations in fish availability and consequences on income and food security have been reported in other inland fisheries in sub-Saharan Africa, including lakes in Uganda (Goulden et al., 2013; Musinguzi et al., 2015), Tanzania (Kihila, 2018), Malawi (Limuwa et al., 2018), and Zimbabwe (Ndhlovu et al., 2018),

possibly pointing to at least one generalizable effect of climate change on inland fishery livelihoods in this area.

There was also general agreement among households and communities that, regardless of seasonal variation in fish availability, there has been an overall decline in fish resources over the last decade, which FGD respondents attributed to rapid human population, poor fishery management, and environmental degradation (deforestation, wetland destruction, pollution), in addition to climatic changes. Although the cause is not determined, this observation was affirmed by catch assessment data which showed reduced catch rates in all key species from 2005 - 2015 (Mbabazi et al., 2016), despite increased fishing effort (Taabu-Munyaho et al., 2014). Consistency among fisher perceptions and environmental data provides some evidence for the oft-cited claim that rural communities that rely on natural resources have the capacity to accurately detect changes in the local climate and resource bases (Howe and Leiserowitz, 2013). Awareness of changes to the environment is an important precursor for communities to have the motivation and urgency to develop adaptation and mitigation strategies around climatic change (Wise et al., 2014).

4.5.2 Climate change narrows the walls of social-ecological traps

Overall we found household vulnerability to be high as households are highly exposed to the effects of climate change (i.e., droughts and floods are having noticeable and frequent impacts on fishery productivity), many of them are highly reliant on fisheries for their main source of income (highly sensitive), and they have limited ability or knowledge on adapting to climate change stressors (low adaptive capacity). Developing adaptive strategies is an important challenge for fishery based social-ecological systems faced with major climatic changes (Smit and Wandel, 2006; Wise et al. 2014). However, resource shortfalls often promote increasingly intense resource extraction eroding ecological capacity for recovery, and leading households into social-ecological traps (Cinner, 2011; Boonstra and Hanh, 2015). In the Lake Victoria basin, this is especially true of impoverished households that have no choice but to alleviate immediate pressures of food insecurity by relying more heavily on the fishery rather than

transforming the behaviors that led to the resource depletion to begin with. This point was articulated by a crew member as follows:

At Lambu we used to have a lot of fish. But now during times of fish scarcity, we use a lot of effort. We go during the day, during the night, all the time without rest because people have to look for what to eat. That is why people are ever on the lake because we need to survive and we can't go anywhere else to look for survival. And now we are using these illegal gears, but [the fish] keep decreasing and we are not seeing any change – Crew FGD, Lambu

Increases in fishing pressure therefore occur during months when the fishery is already less productive, even though it is understood that these actions are unsustainable. Households that follow this pattern often experience further decreases in income, and are forced to revert to maladaptive practices such as selling off assets or incurring debts that are often impossible to pay back. These findings are consistent with a growing number of studies that indicate that low-income households have lower capacity to mobilize resources necessary for coping with climatic stressors (Cinner, 2011); and have been replicated in numerous small-scale fisheries in developing nations (Cinner et al., 2011; Boonstra and Hanh, 2015; Laborde et al., 2016; Cole et al., 2018). For example, in Kenya, the poorest fishers with the fewest livelihood options were the least likely to exit the fishery when resources declined (Cinner et al., 2009), and in Malawi, fishers attempted to move to agriculture and small business, however those without capital were unable to do so, and continued fishing with increased effort (Limuwa et al., 2018).

The many interactions and feedbacks between social and ecological dynamics in the LVB fisheries illustrate how climate change can increase the threat of poverty lock-in for households or communities (Fig. 4.9). Lakeshore communities in the LVB have experienced some of the highest population growth rates in the world, both through high birth rates and immigration (Odada et al., 2006). Compared to agriculture or business, fisheries are a 'soft-landing' industry that is open access, require little to no capital to join, and can produce daily income without long waiting periods (Nunan, 2006, 2010; Barratt et al., 2015). Ever increasing unemployment rates, crop failure, loss of pasture, and food insecurity have resulted in increased immigration to the fishery (Odongkara and Ntambi, 2007), with the consequence that a fast-dwindling resource is being shared among a growing number of stakeholders. In addition, FGD data revealed that increasing

competition among fishers means that the fishery no longer experiences 'resting periods' as it did in the past when there were traditional daily and seasonal rhythms during which fishers were not on the lake. Respondents explained that until approximately 10 years ago, fishers were active only at night leaving the fishery during daytime hours to sleep. In addition, older fishers recalled a time when there was a general exodus from fishing during the long dry season (June – August) when fish catches were naturally low, and gardens required preparation for the coming rains (Fig. 4.9). Many experienced fishers stated that there was a noticeable decrease in fishery productivity as competition soared and traditional rules around 'no take' months slipped.

In addition to increased competition for fishery resources, local fisher/farmers are no longer able to predict weather patterns as accurately, so it has become risky (or financially impossible) for many fishers to leave fishing entirely for two months to focus on their gardens. Those who do this are liable to experience losses if the rains do not come when expected, or come in too great a quantity. An elderly fisher explains:

These days even the rains have changed so that even in June and July you can see rain when it was not supposed to rain. And now those that were known as rain months, like April, now they see sunshine. Even those that tried to cultivate have left cultivating and are persisting on going to the lake because these droughts caused all the crops to fail – Boat owner FGD, Lambu

In this way changes in climate and socio-ecological changes can synergistically impact fishery stability, allowing social-ecological traps to take root (Fig. 4.9).

This complex set of interactions and feedbacks among social and ecological aspects of fishery conservation highlights several barriers to diversification, but also identifies areas that could improve adaptive capacity and reduce household vulnerability. These include: livelihood diversification, access to social capital, use of traditional knowledge, and increased household agency through improved governance. In the next four sections I describe these key aspects to climate change adaptation in the Lake Victoria basin fisheries.

4.5.3 Developing capacity for livelihood diversification

Diversification to non-fishery activities has been identified as a key adaptation strategy for fishing households faced with climate-change stressors (Cinner et al., 2018), and is known to reduce trap dynamics in fishery-based social-ecological systems (Boonstra and Hanh, 2015). Our analysis of livelihood indices supports this finding, as having a diversified income portfolio was shown to reduce the sensitivity and increase the adaptive capacity of households. Key areas of diversification identified in the present study included crop agriculture and livestock rearing, and although such practices are also at risk from climate change, they have been shown to reduce vulnerability in small-scale fisheries as each livelihood source can be used to sustain the other, as long as climatic conditions are not too extreme (McGrath et al., 2007; Allison et al., 2007; Musinguzi et al., 2015; Cinner et al., 2018). According to FGD data, this is especially true for farmers who planted fast-maturing or drought- and flood-resistant crops, and for those that constructed irrigation wells or trenches around gardens to prepare for eventual drought and flood events. This highlights several positive adaptation measures that can be taken by fishing households already diversified into crops; however, it is ultimately households that practice activities that are not weather-dependent (e.g., small businesses) that will be the most stable (Musinguzi et al., 2015). For example, in very extreme conditions livelihoods can be destabilized despite diversification to agricultural activities as was experienced in communities during the data collection for the present study. As one participant explained:

It's not only in fishing but also in other activities like farming where we are suffering. These droughts affect you on both sides. If you fail in fishing you go to farming and vice versa, but these days neither one is profitable. That's why we prefer if we can be helped with a shop or a salon – Female trader-processor
FGD, Ggolo

Diversification is therefore especially effective if households expand to activities that are not sensitive to climate-related stressors. Despite the desire and the motivation to do so, livelihood diversity remains low in these communities primarily owing to several socio-economic roadblocks.

Poverty represents the most important barrier to diversification for households in rural social-ecological systems (Barrett and Carter, 2001; Cohen et al., 2016; Cinner et al., 2018), and this is certainly true for the Lake Victoria basin where many households (in this and other studies) have been found to be confined to hand-to-mouth existence so that the costs and risks of diversification are difficult or impossible to endure (Timmers et al., 2012; Goulden et al., 2013). Analyses of livelihood indices among communities and involvement types provided context-specific information to understand factors that can contribute to improved diversification opportunities. For example, we showed that opportunities for diversification depended on the access to capital assets, with financial, social, and human capital all contributing to variation in concurrent diversity of households.

A key factor contributing to a household's ability to access these assets was residence time in a community. For example, the fishing communities around Lake Nabugabo (Bbaale and Kaziru) are permanent; each fisher owns or has access to a plot of land in the village and is therefore diversified into various agricultural activities. On the other hand, many fishers from larger landing sites (e.g., Lambu on Lake Victoria) are migratory and do not have access to land proximal to the landing site, so their incomes tend to be solely based on fishing. This pattern is present among involvement types as well; boat owners tended to be individuals who are permanent residents at village or landing site, and tended to have high scores for capital assets and adaptive capacity, while boat crews tended to be migratory, with shorter residence times at the landing site and lower scores for capital assets and adaptive capacity. Lack of access to land is therefore an important barrier to diversification for many members of fishing communities. In addition to diversification into farming, long-term residency in a community can provide opportunities for diversification into non-climate-reliant activities. In general, trade and service activities were only conducted by wealthier households, however maintaining residence within a village can allow people to diversify as residents can mobilize savings, make investments, accumulate wealth (land, livestock, houses for rent), and gain access to credit services through social groups (Odongkara and Ntambi, 2007; Nunan et al., 2010).

4.5.4 Building social capital

Directly related to the above example is the concept that strong institutions and good trust relationships among actors (i.e., strong social capital) are essential for adaptive capacity and diversification (Adger, 2003; Pelling et al., 2008; Cinner et al., 2018). Households are rarely able to adapt to climate change in isolation, and social organization provides the necessary avenues for communities to engage in collective action, and to facilitate cooperation and knowledge sharing among stakeholders (Smith et al., 2001; Adger, 2003; Pelling et al., 2008; Cinner et al., 2018). Several studies have demonstrated that strong community cohesion promotes adaptation to environmental shocks and stressors in rural societies (Andersson and Gabrielson, 2012; Goulden et al., 2013; Barratt et al., 2015).

Although social capital does not emerge as a strong predictor of adaptive capacity in the survey results of this study, it does have a strong positive effect on concurrent diversity, and is associated with lower sensitivity to climate change. In addition, participants in FGDs suggested that involvement in community groups is one of the key entry points for livelihood diversification. Community groups are semi-formal, organized groups of around 5-10 members that facilitate access to credit and savings or government-aided livelihood expansion projects, and previous studies have found that group membership provided motivation and hopefulness for adaptation (O’Riordan and Jordan, 1999; Goulden et al., 2013; Andersson, 2014). Participants suggested that being involved in groups reduces costs and risks of engaging in new activities, provides opportunities to learn new skills, and opens access to government interventions.

A key demographic exemplifying this in the Lake Victoria fishery are women. FGDs revealed that women working in the fishing industry face a number of unique challenges in their livelihoods; they are often solely responsible for child care, tend to be relegated to lower value fish products or confined to informal, unpaid tasks, and generally have fewer diversification options and lower financial capital than men. Interestingly, however, women had good scores for social capital, and ranked social cohesion among the most

important factors for sustainable livelihoods. FGDs revealed that the formation of groups has allowed women to engage in unique diversification options. In one example, a women's group was given credit through a government intervention program to build solar dryers and storage facilities for mukene to prevent post-harvest losses. Post-harvest losses are a major cost to small-scale fisheries, and have recently been implicated as a possible driver of social-ecological traps in inland fisheries in Zambia (Cole et al. 2018). While this intervention does not diversify fishers away from harvest activities, preventing losses through storage is an important innovation that can improve livelihoods if it stabilizes harvest activities. For groups to be effective, however, there must be willingness to cooperate and solid trust relationships within the community (Rothstein, 2005). FGD respondents indicate that groups can fail because of to lack of trust in the community. Government fishery officers suggest that this is primarily because of the highly migratory nature of many individuals in fishing communities which can deteriorate social cohesion in fishing communities and undermine the success of group interventions. This suggestion has been affirmed by studies that have investigated the impacts of migrant fishers on fishery management (Odongkara and Ntambi, 2007; Nunan, 2010).

4.5.5 Using traditional knowledge to inform fishery sustainability

One of the key avenues for adaptation is to promote sustainable fishing practices within communities. Accounting for options that have community support can increase the likelihood of successful implementation (McClanahan et al., 2006), and there is a growing consensus that combining traditional forms of fishery control with contemporary science can improve management of fishery social-ecological systems (McClanahan et al., 2006; Aswani et al., 2007; Cinner and Aswani, 2007; Kihila, 2018). Indigenous societies often have traditional strategies for coping with natural spatial and temporal variation in fish abundance that can contribute to sustainability even if the initial motive was not necessarily conservation-oriented (McClanahan et al., 2006). In the case of Lake Victoria, as discussed above, traditional 'no-take' months during dry seasons allowed resting periods for the lake. In tropical lake ecosystems even short resting periods can result in noticeable increases in fishery productivity via recruitment and growth. For example, fishing communities in Tanzania implemented fishing seasons and no-take zones based

on traditional methods to improve fish catch, and fishers are noticing improvements in fishery yields (Kihila, 2018). Amongst participants in the present study, reinstating rest months is an idea that has been met with considerable support from experienced and invested fishers that have alternative livelihood strategies, (although resisted by younger fishers with fewer diversification options). Nevertheless, research focused on community elders' memories of traditional fishing methods and experiments demonstrating possible effectiveness of no-take months could provide insight to developing a sustainable fishery in the face of climate change.

4.5.6 Promoting community agency through improved governance

Adaptive capacity of households depends on access to resources, but also on a sense of agency and empowerment (Brown and Westaway, 2011; Cinner et al., 2018). Agency of a household or community depends on their ability to effect change in societal processes, to control and influence events that impact their lives, and to manage crisis situations while maintaining livelihoods (Bandura, 2000; Brown et al., 2011; Coulthard, 2012; Cinner et al., 2018). Agency of households and communities is mediated through government and collective-action institutions; therefore, weaknesses in these institutions can undermine capacity for adaptive action, often contributing to social-ecological trap dynamics (Cinner et al., 2018).

Negative interactions among governing bodies and fishing communities appear to have developed through various routes in the Lake Victoria fishery. Although surveys for this study were not designed to capture this information, this became a core topic for FGDs as poor governance is perceived to be at least as important a threat to livelihood stability as climate change, and was especially pertinent as the BMU co-management system was in the process of being disbanded during the course of this study. FGDs revealed an overwhelming sense within the fishing communities in this study of being left behind or forgotten by the government. Lack of enforcement of fishery rules and regulations has led to rampant illegalities, unchecked overharvesting, and massive degradation of the fishery (Timmers, 2012). Although fishers wish to maintain their fishery, the sense of not being supported and lack of capacity to do so on their own has led to a feeling of hopelessness. One individual explained:

We are tired of those who do illegal fishing but we have no power to do anything or take anybody to the police. Even if the community struggled to see that the lake was well managed, if the government is out of it nothing can be done. The government has left the lake, yet this was our resource and all of us were depending on this lake – Male trader FGD, Ggolo

In addition, there is a common perception within fishing communities that environmental degradation and reduced fishery productivity are the result of policies that allow widespread development of lakeshore areas, primarily by foreign investors. For example, FGD respondents suggested that the replacement of massive swaths of natural forest with industrial palm plantations on a nearby island archipelago (Ssesse Islands) has coincided with increased occurrence and severity of drought events in the Masaka region. In addition, respondents believe that destruction of wetlands limits suitable breeding grounds for many fish species and decreases water quality of inland zones of the lake, both of which contribute to declines in fishery productivity. However, these developments are not perceived by respondents to increase employment opportunities or improve conditions in fishing communities (e.g., through improved access to facilities at landing sites). Finally, while the fishing industry is earning millions of US dollars per year, community members perceive that the majority of these profits go to foreign exporters. Although this is not entirely true, investigations of value chains have shown that high level earnings from the most lucrative sectors of the fishery rarely trickle down to the poorest members of these communities (Ikwaput-Nyeko, 2004; van der Knaap and Ligtoet, 2010; Timmers, 2012; Ntara et al., 2015). For many fishers that are trapped in poverty, these perceptions promote a sense of disenfranchisement, reducing the motivation to follow rules and care for a resource of which they are no longer the main beneficiaries. For example, one participant stated:

If you say to yourself: 'Let me protect this place, especially this area which is near my home', you can never be sure when the government will come to take it away. So for us, before the government comes in, we would also destroy it because we know the government will just give it away to...people that are not from here. So we indigenous people have to try to also benefit – Boat owner FGD, Nakiga.

Problematic relationships between fishing communities and governing bodies can undermine the effectiveness of communities to adapt to stressors in the environment (Goulden et al., 2013), and evidence from interviews with community members and government fishery officers revealed a breakdowns in the perceptions and motivations of

both groups. Communication and clarity among stakeholders, and frequent meetings where fishers' voices are heard may help to overcome this.

4.6 Conclusions

Results from this study have shown that climate change is an important emerging stressor in the Lake Victoria basin that is disrupting fishery productivity and livelihood stability in this complex social-ecological system. A central problem is that effects of climate change are exacerbating the declining availability of fish resources, and simultaneously restricting access to other non-fishery livelihood options leading fishery-dependent households to social-ecological traps whereby they become increasingly dependent on fish resources even as stocks become less available. Understanding factors that contribute to entrapment of households or communities can provide insights on adaptive strategies to facilitate escape. A key mechanism for improving adaptive capacity is livelihood diversification. Fishers in the present study had clear ideas about the types of diversification options that would promote sustainability; however they also identified several barriers to adaptation. The main constraints included limited access to financial capital, land for agriculture, and diversification options (i.e., government interventions). For households in chronic poverty, it is important to develop strategies where risks associated with diversification options are buffered. This can be accomplished through skill training (Goulden et al., 2013; Cinner et al., 2018), education on financial planning (Timmers, 2012; Musinguzi et al., 2015; Cinner et al., 2018), and providing financial capital either through fair loans or access to credit facilities (Krishna et al. 2004; Cinner et al., 2018). In addition, steps should be taken to sensitize fishers to the impacts of illegal fishing and improving knowledge on diversification options. This may be particularly critical among migrant fishers who often view moving as their only option (Odongkara and Ntambi, 2007). In addition, promoting strong social capital within communities and facilitating the formation of cooperative groups can provide entry points for poor households to build resilience against effects of climate change (Adger et al., 2005). Finally, promoting communication among stakeholder groups and incorporating traditional knowledge into management practices is key for increasing a sense of agency in communities, which can increase motivation to protect natural resources.

4.7 References

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4.8 Tables

Table 4.1 Landing site characteristics and respondent demographics from household surveys.

Landing site characteristics		Lake Nabugabo		Lake Victoria			Total
		Bbaale	Kaziru	Nakiga	Ggolo	Lambu	
Population		180	150	200	1500	12000	14030
Men in fishing		35	20	50	550	750	1405
Women in fishing		4	5	12	200	300	521
Migrant fishers		0	3	15	100	500	618
Daily fish catches (kg)	Nile perch	15	15	15	60	1200	1305
	Tilapia	30	5	50	10	800	895
	Mukene	20	0	0	500	4000	4520
Survey respondent demographics							
Gender	Male	22	31	29	30	43	155
	Female	1	2	4	15	26	48
	Total	23	33	33	45	69	203
Involvement type	Boat owner	12	20	15	17	17	81
	Crew member	7	7	8	11	23	56
	Trader	3	4	6	2	3	18
	Women	1	2	4	15	26	48
Wealth ranking	Wealthy	0	1	0	1	2	4
	Well off	2	1	5	4	4	16
	Medium	11	19	9	12	14	65
	Poor	10	12	15	24	40	101
	Very poor	0	0	4	4	9	17
Age	Under 20	1	0	0	0	0	1
	20-29	7	7	1	13	8	36
	30-39	12	10	13	12	27	74
	40-49	4	12	9	16	29	70
	50-59	0	2	6	3	4	15
	60+	0	2	4	1	1	8

Table 4.2 Description and definitions of nine continuous indices calculated from household surveys.

Combined Index	Index	Description
Livelihood stability (sum of financial, social, human, physical, and natural capitals)	Financial capital	Definition <i>Financial resources that people use to achieve their livelihood objectives</i>
		Survey information <i>Asset values, income estimates (summed), amount of livestock and poultry</i>
	Social capital	Definition <i>Social resources (networks, membership to groups, trust relationships) that enable one to pursue livelihood objectives</i>
		Survey information <i>Group involvement, sense of social cohesion, whether they helped by or were of help to community members</i>
	Human capital	Definition <i>Skills, knowledge, ability, and good health that enable one to pursue different livelihood strategies</i>
		Survey information <i>Years of education, number of skills, household size, leadership roles</i>
	Physical capital	Definition <i>Basic infrastructure (transport, shelter, water supply, communications, etc.) needed to support livelihoods</i>
		Survey information <i>Housing type, access to facilities (water, school, health center, bank), access to transportation (roads), bicycles, motorbikes, and vehicles</i>
	Natural capital	Definition <i>Natural resources, stocks, and services from which livelihoods are derived</i>
		Survey information <i>Access to land, barriers to land access, changes to fish availability</i>
Concurrent diversity		Definition <i>The number of different livelihood activities undertaken by one household to support livelihoods</i>
		Survey information <i>Variety of fishing activities, crops and livestock, trade and service, business, and natural-resource based activities, summed.</i>
Vulnerability to climate variability and change (sum of negative adaptive capacity, exposure, and sensitivity)	Adaptive capacity	Definition <i>The actions undertaken by a household to improve well-being when exposed to disturbances</i>
		Survey information <i>Adaptation actions, protective measures, and survival tactics used during drought and flood events, and the outcomes of those actions (positive or negative) on livelihoods in terms of food security and income</i>
	Exposure	Definition <i>The frequency and severity of environmental shocks experienced by communities</i>
		Survey information <i>Effects of droughts and floods on fish abundances, income, and food security, and perceived frequency and severity of unpredictable weather events</i>
	Sensitivity	Definition <i>Degree of reliance on fish for income and food</i>
		Survey information <i>Amount of income earned from fishing / total income, plus the degree to which environmental shocks affect fish eaten in a household</i>

Table 4.3 Number of participants and groupings for focus group discussions (FGDs).

Involvement types	Lake Nabugabo		Lake Victoria		
	Bbaale	Kaziru	Nakiga	Ggolo	Lambu
Women	8		12	14	13
Traders	10		10	11	10
Boat crew	16	23	11	13	14
Boat owners			15	10	12

Table 4.4 Results of Pearson's correlations of all indices, and with age. Colours indicate positive (blue) or negative (red) relationships. Dark colours are significant at $P < 0.001$, and light colours are significant at $0.001 < P < 0.00455$. White boxes are not significant at the Bonferroni corrected P-value of 0.00455.

	Age											
Financial capital	0.120	Financial										
Social capital	0.090	0.350	Social									
Human capital	0.080	0.600	0.560	Human								
Physical capital	0.010	0.310	0.210	0.380	Physical							
Natural capital	0.140	0.200	-0.010	0.070	0.210	Natural						
Livelihood stability	0.120	0.720	0.700	0.780	0.680	0.390	Live. St.					
Concurrent diversity	0.090	0.690	0.400	0.560	0.160	0.020	0.540	Con. Div.				
Adaptive capacity	-0.040	0.380	0.060	0.320	0.150	0.120	0.290	0.370	Ad. Cap.			
Sensitivity	0.030	-0.500	-0.210	-0.410	-0.290	-0.180	-0.470	-0.600	-0.460	Sens.		
Exposure	<0.001	0.030	0.050	0.040	-0.110	0.020	<0.001	-0.040	-0.150	0.070	Exp.	
Vulnerability	0.030	-0.34	-0.06	-0.27	-0.23	-0.11	-0.29	-0.4	-0.75	0.59	0.7	

Table 4.5 Ranks and frequencies of common environmental impacts perceived by fishers, and descriptions of the type of change and effects of these changes on livelihoods as stated by survey and focus group respondents. Environmental changes are categorized as stochastic/climatic referring to climate change events, or structural/man-made referring to anthropogenic effects.

Rank	%	Type	Environmental change	Description and effects
1	86%	stochastic / climatic	Increased frequency of droughts events	<i>Dry seasons are longer, hotter and more intense, and are unpredictable in timing. Crops fail, fish catches drastically reduce, famine and food insecurity increase. Fish processing can be easier due to good conditions for sun-drying.</i>
2	81%	stochastic / climatic	Increased frequency of flood events	<i>Rainy seasons are shorter, but more intense than in the past, and unpredictable in timing. Sudden intense rains destroy crops, cause diseases among livestock, damage infrastructure at landing sites, cause post-harvest losses (fish rot) and block transportation routes. Floods can increase catch rates as fish tend to move with fresh water inputs.</i>
3	56%	structural / man-made	Deforestation	<i>Large swaths of land deforested on the Ssesse Islands for industrial agriculture. Removal of natural forests has exacerbated drought conditions resulting in fewer fish and crop failures.</i>
4	37%	structural / man-made	Wetland destruction	<i>Wetlands have been developed for agriculture, urban development, and tourism. Loss of breeding ground for fishes results in recruitment failures and reductions in fish catch. Loss of natural filtration system for the lake causes increases in pollution and eutrophication.</i>
5	22%	structural / man-made	Population growth	<i>Population has grown due to economic boom, both through higher birth rates, and through influx of migrants. Increased competition in the fishery leads to reduction in fisheries and higher demand for fish in lakeshore communities.</i>

4.9 Figures



Figure 4.1 Map indicating locations of the five participant landing sites in (or near) the Masaka District of Uganda. Insets show (A) the location of the study sites within the Lake Victoria basin, and (B) the location of the Masaka district within Uganda.

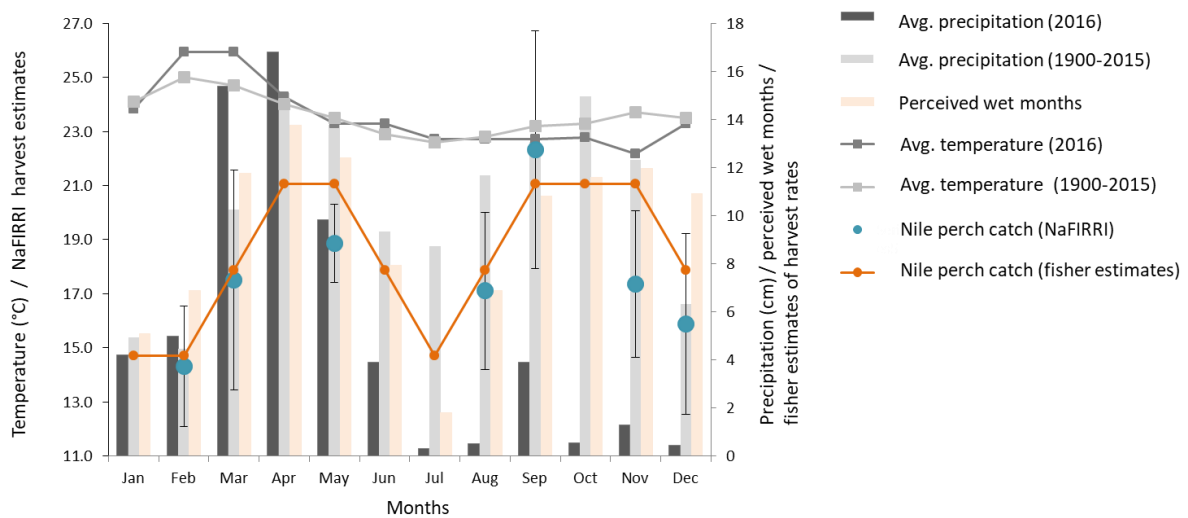


Figure 4.2 Yearly climatic variation (temperature and precipitation) and yearly fish catches with comparisons of fishers' perceptions and environmental data. Climatic temperature and precipitation values are displayed both as historical monthly averages from 1900 – 2015 (light grey) and for 2016 alone (dark grey). Fisher's perceptions of rainy and dry seasons (orange bars) are presented as numbers of fishers who selected each month as rainy. These were \log_{10} -transformed, and multiplied by 6 to match the secondary axis scale. Overlaid are the monthly harvest rates of fish (average of Nile perch, Nile tilapia, and mukene) per fisher in kilograms, as estimated by fishers (divided by 4 to match the secondary axis scale). Blue points indicate estimated average monthly fish catches \pm SD (in thousands of tonnes) in the Ugandan waters of Lake Victoria from 2005 – 2015 as collected by the National Fisheries Resources Research Institute (NaFIRRI) of Uganda.

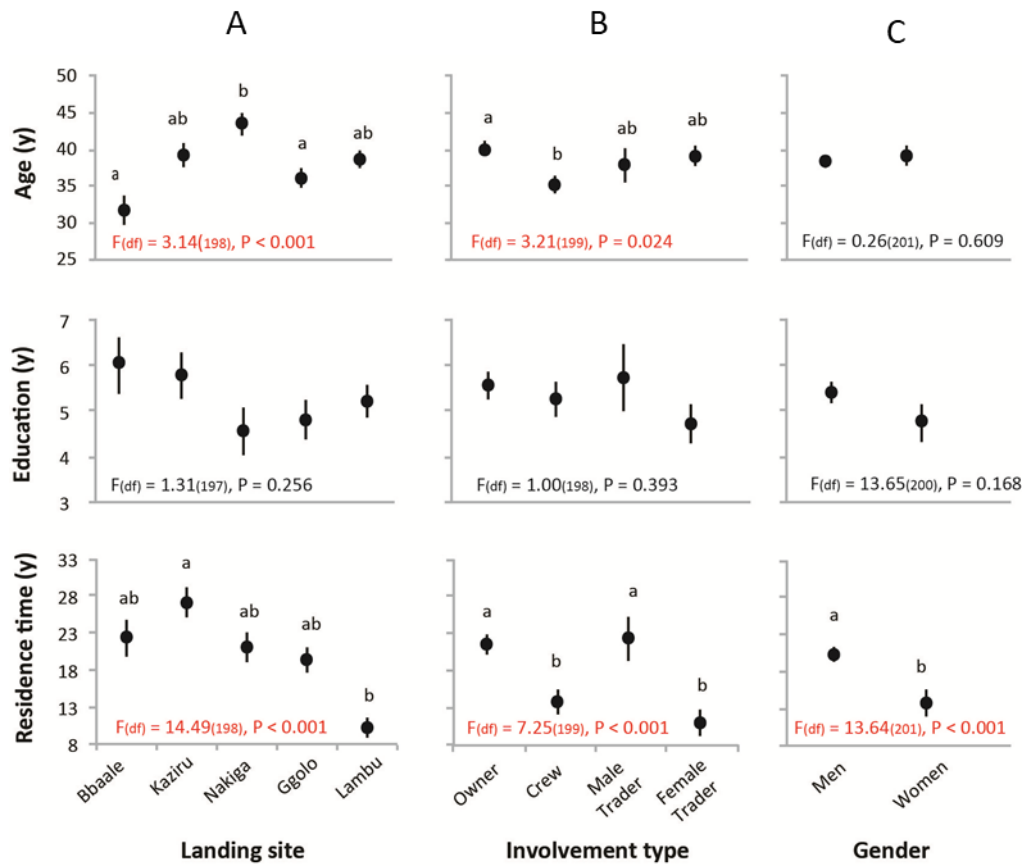


Figure 4.3 Results of ANOVAS to detect differences in age, education, and residence among (A) landing site, (B) involvement type, and (C) gender. P-values indicate the significance of the overall ANOVA model; red-highlighted values are significant at the $\alpha = 0.05$. Different letters indicate significant differences ($\alpha = 0.05$) between groups according to post-hoc tests.

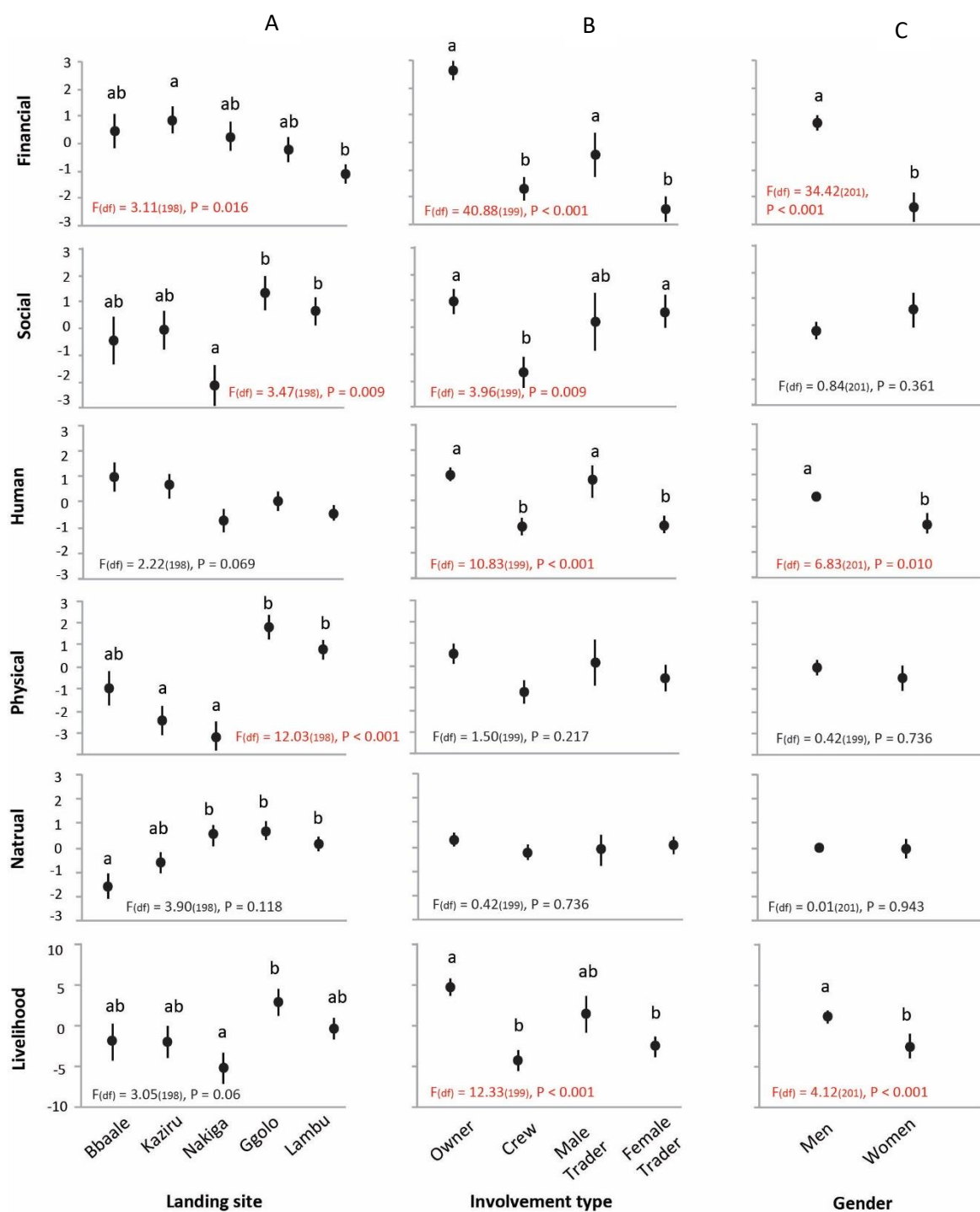


Figure 4.4 Results of ANOVAS to detect differences in financial, social, human, physical and natural capital, and in overall livelihood stability among (A) landing sites, (B) involvement types, and (C) genders. P-values indicate the significance of the overall ANOVA model; red-highlighted values are significant at the $\alpha = 0.05$. Different letters indicate significant differences ($\alpha = 0.05$) between groups according to post-hoc tests.

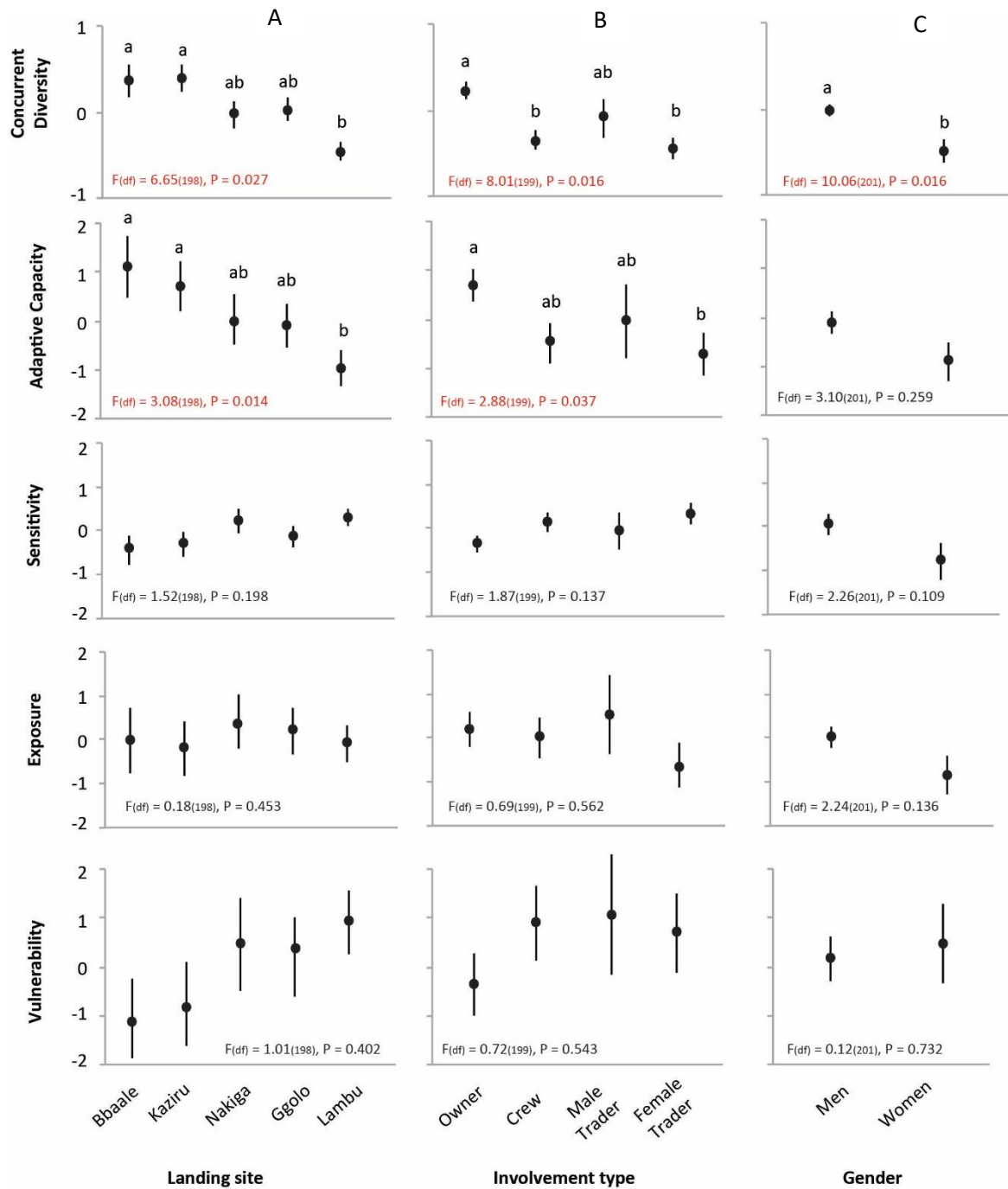


Figure 4.5 Results of ANOVAS to detect differences among concurrent diversity, adaptive capacity, sensitivity, exposure, and vulnerability to climate change compared among (A) landing sites, (B) involvement types, and (C) genders. P-values indicate the significance of the overall ANOVA model; red-highlighted values are significant at the $\alpha = 0.05$. Different letters indicate significant differences ($\alpha = 0.05$) between groups according to post-hoc tests.

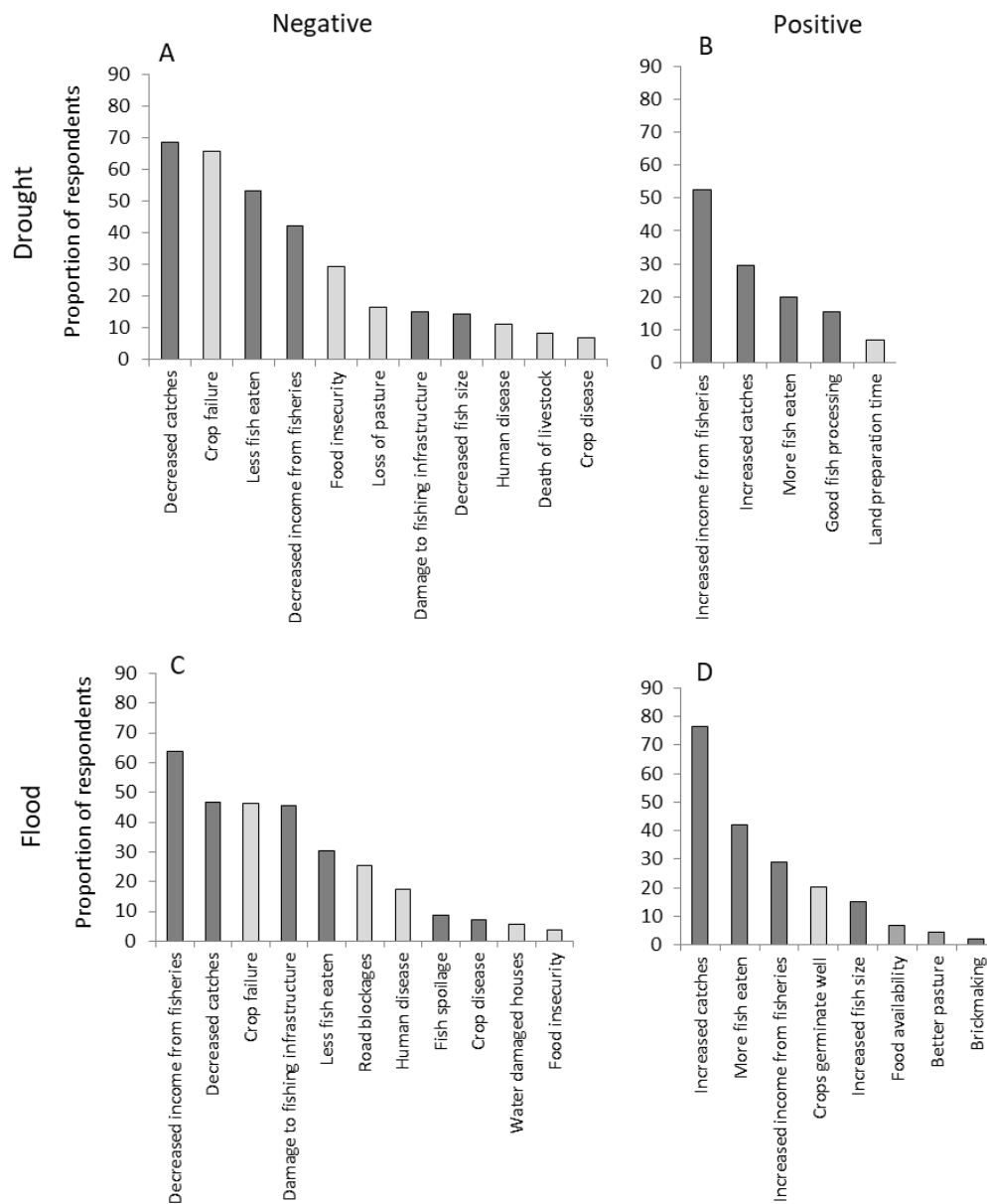


Figure 4.6 Negative (A & C) and positive (B & D) consequences of droughts (A & B) and floods (C & D) on fisher people's livelihoods based on survey responses. General livelihood effects are in light grey, and fishery-specific livelihood effects are in dark grey.

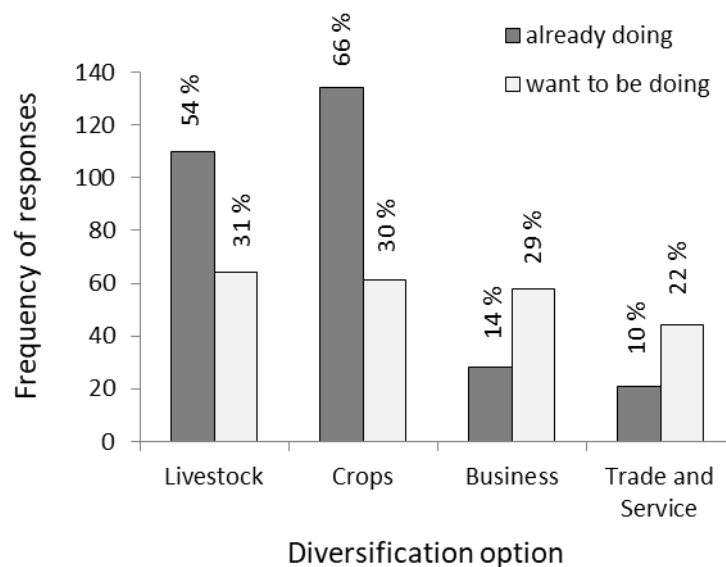


Figure 4.7 Frequencies of diversification options that fishers stated they have already exploited, and that they want to exploit. Proportions of survey respondents selecting each category are displayed above the bars. (Proportions add up to more than 100% because several respondents selected more than one diversification category). See Fig. D1 for a detailed breakdown of diversification options.

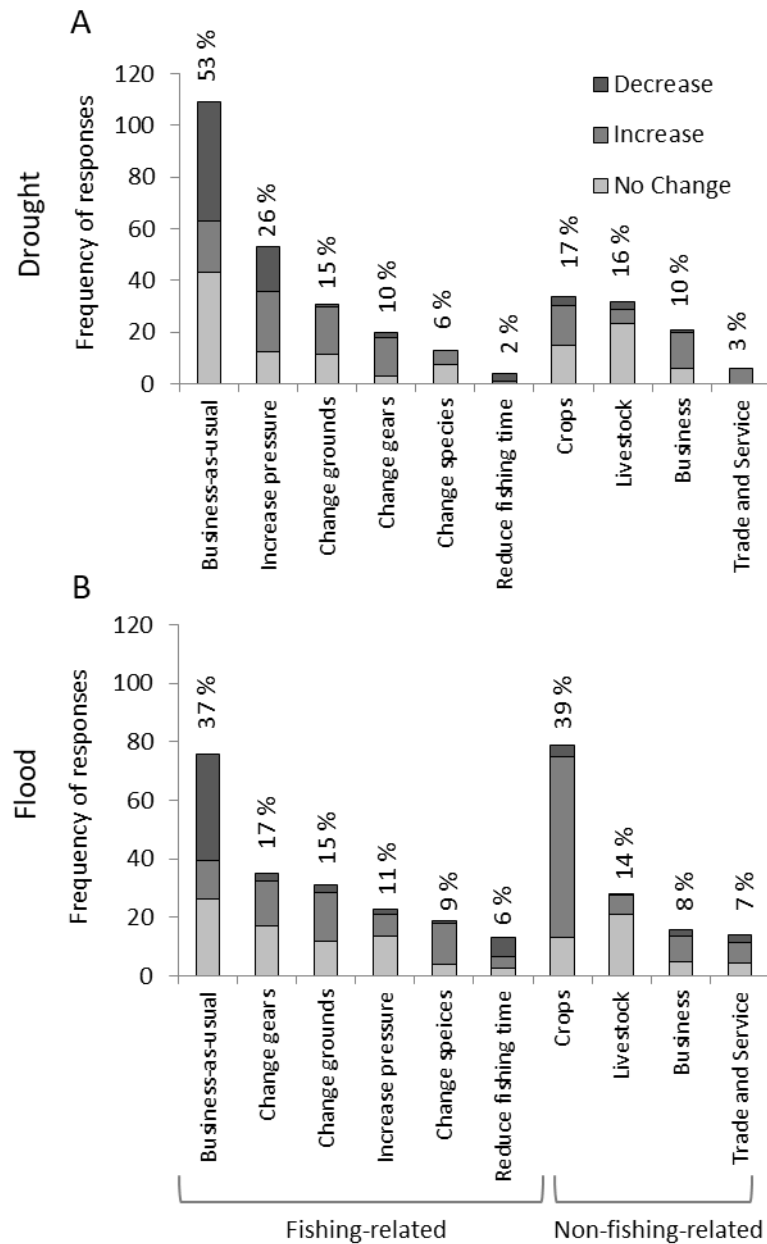


Figure 4.8 Frequencies of fishing-related and non-fishing related actions taken by fishers during (A) droughts and (B) floods to improve livelihoods, and the effect of these actions on food security and incomes (increase, decrease, no change). Proportions of survey respondents selecting each category are displayed above the bars. (Proportions add up to more than 100% because several respondents selected more than one action).

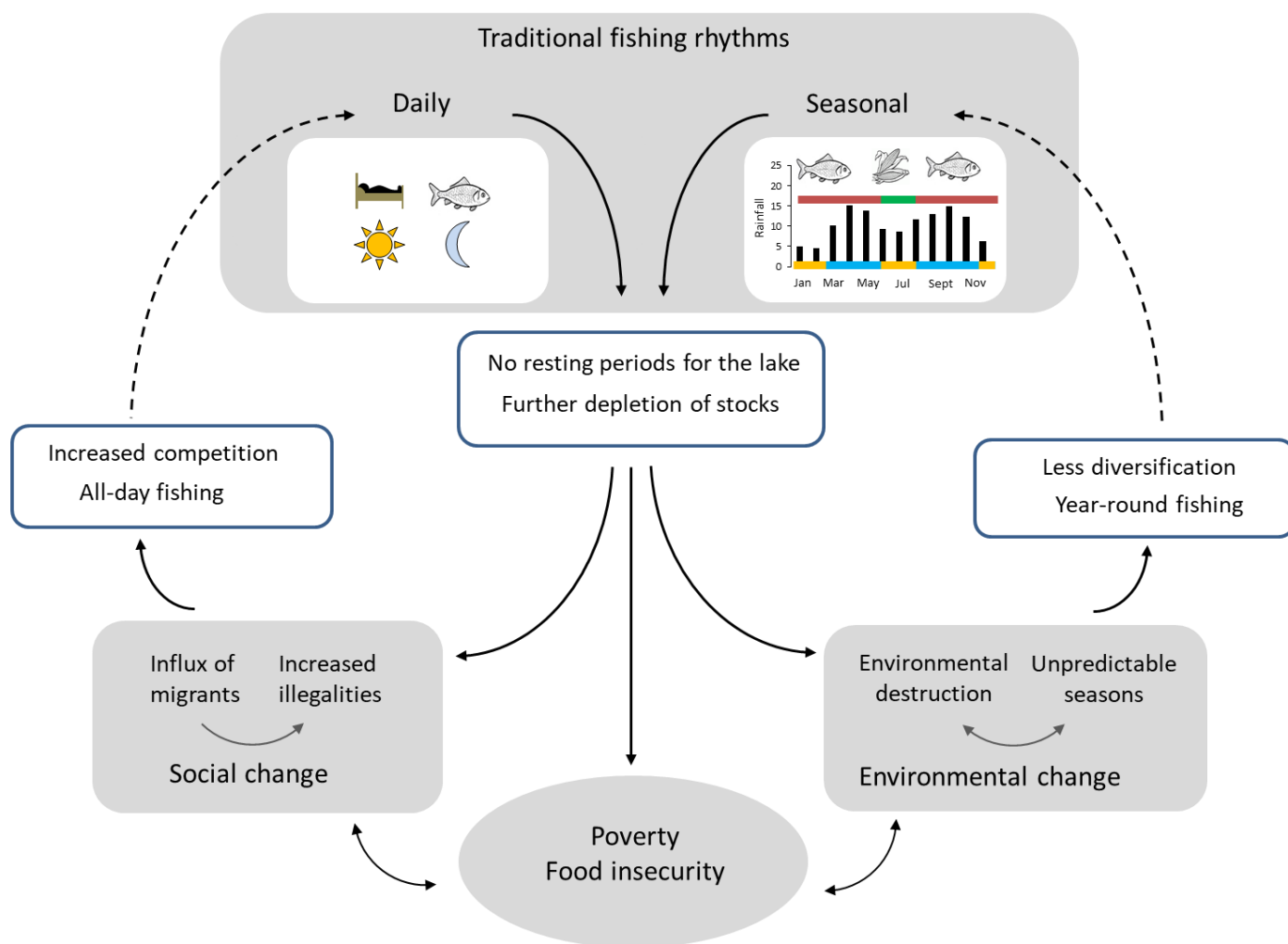


Figure 4.9 Schematic diagram illustrating how both social and ecological changes can combine to form social-ecological feedbacks further exacerbating depletions of stocks and environmental degradation, worsening poverty, and undermining food security. Dashed lines indicate breakdowns in relationships while solid arrows indicate strengthening of relationships. Double ended arrows indicate relationships that go both ways.

Summary and general conclusion

The goal of this thesis was to develop our understanding of the effects of climate change on African inland fisheries. Using a trait-based climate change vulnerability assessment (CCVA), I demonstrated that nearly 40% of Africa's freshwater fishes are likely to be negatively impacted by climate change, and I identified regions and species that should be considered of high conservation concern. I then employed a cross-disciplinary research approach to zero-in on one region highlighted as vulnerable: the Lake Victoria basin of East Africa. I combined eco-physiology experiments with social science methodologies to integrate ecological, environmental, and socio-economic data for a holistic understanding of the vulnerability and adaptive capacity of this system to climate change stressors. In this general conclusion, I summarize the key findings and contributions of each chapter, and I discuss areas for future study that emerge from this body of work.

Chapter 1 comprises a continent-wide climate change vulnerability assessment of Africa's freshwater fishes that integrates species' ecological, physiological, biogeographic, and genetic traits with future climatic exposure. I compiled data on 2793 species of African freshwater fish (~85% of extant species), and mapped vulnerability distributions across the continent to identify species and regions most at risk to climate change. In addition, I approximated 'conservation value' by assembling a second index based on traditional conservation metrics, and compared distributions of climate change vulnerable species and regions to distributions of high conservation value. I found substantial vulnerability among African freshwater fishes primarily because of their highly specialized habitat and life-history requirements, and because of the pervasive human threats faced by these species. In addition, I highlighted several vulnerable regions and species that are neglected by traditional conservation approaches, demonstrating that incorporating climate change effects in conservation planning could substantially improve decision making for ecosystem management.

In Chapters 2 and 3, I used a series of thermal acclimation experiments to investigate the physiological responses of the commercially-harvested Nile perch (*Lates niloticus*) to elevated water temperature over various exposure times. Chapter 2 established a baseline understanding of the flexibility in upper thermal tolerance and aerobic metabolic performance in this species by measuring critical thermal maxima (CT_{max}), standard and maximum metabolic rates (SMR and MMR), and aerobic scope (AS; calculated as the difference between SMR and MMR) across a range of temperatures encompassing current average temperatures and those predicted under climate change. I compared responses between 3-day and 3-week acclimation times to detect whether exposure time affects thermal acclimation capacity. I found that Nile perch have highly flexible upper thermal tolerance limits (CT_{max}), and have the capacity to maintain a very high AS at temperatures well beyond their current thermal range. Findings from this chapter suggest that Nile perch have significant capacity for plastic responses to elevated water temperatures, challenging predictions that tropical species have limited thermal flexibility. In addition, the capacity for rapid physiological adjustments may be indicative of longer-term resilience of Nile perch to warming lake temperature (Farrell et al., 2009). However, a more thorough understanding of responses to thermal increases can be obtained by examining acclimation over longer timeframes, and by exploring mechanisms underlying the observed metabolic changes. For example, adjustments in cardiorespiratory function are often invoked as key mechanisms underlying thermal plasticity because limitations in oxygen supply are predicted to define thermal optima in fishes (Farrell et al., 2009; Eliason et al., 2011; Anttila et al., 2013); however, few studies have explicitly linked cardiorespiratory plasticity to metabolic compensation. In Chapter 3, I reared Nile perch juveniles for three months under two thermal regimes encompassing current and predicted temperatures, quantified their aerobic metabolic performance across a range of acute temperatures, and paired these measures with body size and morphological measurements of cardio-respiratory organs (e.g., gills, hearts). We found that Nile perch were able to increase upper thermal tolerance and develop more efficient metabolic performance (e.g., lower SMR) over long-term exposure to elevated temperature, and that fish from both thermal regimes achieved the same body size. Rearing temperature did not affect gill size; however, fish reared under warmer conditions showed cardiac remodelling manifested in differences in heart size (i.e.,

relative ventricular mass), and in proportions of compact and spongy myocardium. Changes in heart structure were related to variation in SMR and AS, providing evidence that plasticity in cardiac capacity may be a mechanism underlying compensation in metabolic performance, and offering insight into pathways by which this species might achieve resilience to climate warming over longer timescales. Taken together Chapters 2 and 3 provide evidence that limitation in AS due to a mismatch in oxygen supply and demand is not the direct cause of fitness reductions in the Nile perch, and that this tropical species performs on par with temperate fishes in terms of thermal flexibility. These results, though perhaps surprising based on several studies predicting that tropical ectotherms will be disproportionately negatively affected by climate warming (Ghalambor et al., 2006; Tewskbury et al., 2008; Wright et al., 2009), corroborate findings of two recent meta-analyses (Seebacher et al., 2015; Comte and Olden, 2017).

The capacity of the Nile perch to cope with elevated water temperatures is encouraging given the importance of this species to the livelihoods of millions of people living in fishing communities in the Lake Victoria basin. However, eco-physiological effects of climate change are likely to interact with other stressors on the stocks, particularly intense fishing pressure. In Chapter 4, I investigate the pathways through which climate change affects livelihood stability of human communities in the lakeshore social-ecological systems of the Lake Victoria basin. I combined ecological and environmental data with socio-economic survey, focus group, and interview data to determine lakeshore people's perceptions of climate change effects on the fishery, assess the responses of households to these impacts, and identify adaptive actions to reduce climate change vulnerability of these communities. I found that climate change is disrupting fishery-based livelihoods by increasing the unpredictability of seasonal patterns and increasing the frequency of droughts and floods. These changes are perceived to drive reductions in fish abundances and limit diversification options (e.g., crop agriculture), with negative consequences for food security and income. This situation has pushed communities to rely even more heavily on fishing entrenching them in social-ecological traps that exacerbate reductions in fishery resources. However, fishers' growing awareness of these interactions can lead to adaptive actions that can improve community resilience, with useful pathways forward including advancing communication and cohesion among

stakeholder groups, and developing management practices that are adaptive, and that incorporate traditional knowledge on sustainable fishing practices.

The results of this thesis improve on several deficiencies in the climate change literature that were outlined in the introduction. Chapter 1 provides the first comprehensive CCVA of African freshwater fishes, offering essential, updated knowledge on conservation priorities for regions and species across the continent. This study confirmed that high proportions of African freshwater fishes are vulnerable to climate change, and demonstrated that incorporating climate change into conservation planning can emphasize regions and species that might otherwise be overlooked under classical management plans. In addition, I produced the first comprehensive dataset for online archiving summarizing current knowledge of African freshwater fishes' ecological traits, identifying research areas that are necessary for improving conservation of this faunal group.

One key area identified by the climate-change vulnerability assessment was the Lake Victoria basin of East Africa. This region is host to a tremendous diversity of endemic species as well as harbouring Africa's largest inland fishery and international fish export market driven by the introduced Nile perch (*Lates niloticus*). Chapter 2 provides the first thermal acclimation study on Nile perch across exposure times (3-day and 3-week) providing insights into this species' capacity to cope with increasing water temperature and improving our ability to predict how the Nile perch (and other tropical species, generally) may fare under future climate warming scenarios. Chapter 3 elaborates on these findings by evaluating effects of elevated temperature on metabolic rate and organ development over longer (3-month) exposure times. This study was the first to experimentally test the effects of elevated temperature on the heart structure of a tropical fish, and to show that cardiac plasticity plays a role in metabolic compensation, similar to findings in temperate and arctic species. The role of cardiac plasticity in metabolic compensation under high temperature is an active area of research, and this work opens doors for further research to examine the generality of these patterns in tropical fishes.

Chapters 2 and 3 also contribute valuable knowledge to broader theoretical frameworks in the rapidly growing field of eco-physiology and climate warming. There is currently strong debate regarding the generality of mechanisms proposed by oxygen- and capacity-limited thermal tolerance (OCLTT) in governing species ability to cope with elevated water temperature, particularly in the context of climate change. These studies have both demonstrated that a lower AS in acclimated fish does not necessarily represent constraints on performance, and that limitations at the upper end of the thermal performance curve may be driven by mechanisms other than a mismatch between oxygen supply and demand. The capacity for Nile perch to maintain a high AS even at temperatures at the upper end of ecological relevance bolsters the argument that this measure alone may not be relevant to predictions about species' abilities to respond to climate change. This work also provides a detailed example of a tropical species that exhibits effective physiological strategies for coping with elevated water temperatures across multiple exposure times (three days to three months) challenging the long-held assumption that thermal plasticity is limited in stenothermal tropical fishes (as compared to eurythermal, temperate fishes). Both of these topics are currently widely discussed in the ecophysiology and climate change literature (Comte and Olden, 2017; Jutfelt et al., 2018), making this work a timely and important contribution to these ongoing debates.

Chapter 4 comprises one of three academic studies examining the socio-ecological impacts of contemporary climate variability and change on fishing communities in the Lake Victoria basin in Uganda (see also Goulden et al., 2013; Musinguzi et al. 2015), and is the first to investigate patterns across a range of community sizes from large industrial landing sites to small communities. These local-scale data are urgently needed so that adaptation policies can be tailored to the specific conditions and challenges faced by communities with varying socio-economic statuses. This study elucidates some key social-ecological feedbacks in the Lake Victoria fishery, and identifies a number of barriers to adaptation and strategies to overcome them. This work adds to earlier studies by identifying generalities in vulnerability and adaptive capacity to climate change among lakes and fishing villages in Uganda, and expands on them by finding fine-scale differences among communities and involvement types to identify actions that can

improve resilience to a variety of stakeholders. Together, these findings can be used to inform and design effective climate change adaptation policy in Uganda's fisheries sector.

The contributions of this thesis have significantly advanced our understanding of climate change impacts on tropical, inland fisheries, and have also highlighted promising avenues for future research both within the Lake Victoria system, and more generally in the eco-physiology and social-ecological climate change adaptation fields. First, Chapter 1 identified several data gaps that may limit the accuracy of climate change vulnerability assessments in freshwater fishes (and likely in other taxonomic groups as well). These data gaps represent a key challenge in understanding general patterns of climate change vulnerability of species across broad geographic ranges, and need to be addressed to improve conservation planning. On a practical level, one way forward would be to implement ecological surveys designed to collect data on key traits identified as highly relevant for predicting species' climate change vulnerability. From the results of this and other CCVAs, these include basic life-history traits (e.g. individual growth rate, size and age at maturity, and relative fecundity; Foden et al., 2013; Bohm et al., 2016; Liu et al., 2017), information on reproductive behaviour (e.g., spawning cycles; Carr et al., 2013, 2014; Hare et al., 2016), and estimates of species population sizes (Hare et al., 2016), population connectivity (Fraser et al., 2014), and dispersal ability (Foden et al., 2013; Bohm et al., 2016; Hare et al., 2016). If possible, surveys should focus on species groups that are both data deficient and likely to be climate-change vulnerable, however owing to limitations on research funds interpolation techniques can be used to reliably estimate values among closely related species where traits have a strong phylogenetic signal (Revell, 2013; Comte et al., 2014). Filling in knowledge gaps on the basic ecology and biology of species can considerably improve our ability to predict their vulnerability to climate change.

On a theoretical level, CCVAs could be improved with better knowledge of actual relationships of various traits to climate change vulnerability. CCVAs tend to lean on several assumptions including that 1) species with large populations are more likely to be resilient to stress than those with small populations, 2) species with high reproductive rates and rapid generation turnover are more likely to adapt to environmental change

than those with slower life history strategies, and 3) species with high levels of historical climatic variability across their range are likely to have a wider realized temperature tolerance than those with low variability. These assumptions have been contested in various studies testing how traits influence species responses to environmental stress (Pinsky and Byler, 2015 [population growth rate]; Lanfear et al., 2014; Fraser, 2017; Schou et al., 2017 [population size]; Jiguet et al., 2017; Pacifici et al., 2017 [fast life-histories]; Seebacher et al., 2015 [thermal niche]), and require further validation. In terms of the first assumption, the effect of starting population size on extinction risk is a focus in the field of evolutionary rescue (Gonzales et al., 2013). Although the majority of studies indicate that smaller populations are likely to go extinct more quickly (Bell, 2013; Gonzales et al., 2013), some studies have found that smaller populations are not prone to lower genetic diversity (Schou et al., 2017), suggesting that these populations may not be as threatened as previously assumed (Fraser et al., 2017). Further study along these lines and those expanding to more ecologically relevant systems than the experimental populations that are normally the focus of evolutionary rescue experiments can help to solidify the validity of this assumption for CCVAs. In the cases of the latter two assumptions, sufficient data exist to test them using meta-analyses. In terms of life history traits, species that have been successful in overcoming environmental stressors can be compared to those that are considered to be highly threatened by such stressors. For example, Liu et al., (2017) showed that invasive fishes (i.e., those capable of adjusting to novel ecological settings) were often characterized by a combination of traits that are not necessarily as predicted; they tended to have larger body sizes, longer life spans, and longer maturation times, going against the fast life history hypothesis. A similar analysis investigating species' responses to environmental stressors related to climate change (e.g., elevated temperature, increased eutrophication), could validate (or invalidate) common assumptions about how life history traits relate to climate change vulnerability. In terms of range-level temperature variability (third assumption), species' actual thermal tolerances can be compared with the range of temperatures they are known to experience, both locally (i.e., in a given habitat) and across their entire latitudinal range, as performed by Comte and Olden (2017). This study suggests that measures of climatic niche generated through analyses of historical climatic variability across species' ranges can provide robust assessments of climate change sensitivity (Comte and Olden, 2017).

However, this contrasts with studies on other ectotherms that have found a lack of covariance among upper thermal limits and ambient temperatures (Araujo et al., 2013). In addition, the majority of studies testing these hypotheses in fishes operationalize thermal tolerance through measures of critical thermal maxima (CT_{max}) (Sunday et al., 2011; Gunderson and Stillman, 2015; Comte and Olden, 2017), which may not be as ecologically relevant as traits relating directly to species' physiological responses (e.g., metabolic rate). Meta-analyses investigating physiological tolerances from this angle could be useful in confirming these patterns.

Key questions emerging from Chapters 2 and 3 relate to the thermal specialization paradigm insofar as they call into question the assumption that tropical species will have limited thermal plasticity compared to species that experience wider fluctuations in their habitat. While this question has been the subject of several recent meta-analyses (Sunday et al., 2011; Seebacher et al., 2015; Gunderson and Stillman, 2015; Comte and Olden, 2017), we still do not understand whether the relative importance of fine-scale temporal variability within a population's range (i.e., ecological temperature range) is more important than the coarser species-range level variation (i.e., evolutionary temperature range). A growing body of evidence suggests that local adaptation of populations to prevailing climatic conditions at narrower spatial scales is often quite strong, and possibly more relevant when thinking about the effects of climate change (Eliason et al., 2011; Sorte et al., 2011; Kelly et al., 2012). This could be tested through a meta-analysis relating species thermal plasticity (preferably based on intrinsic physiological traits) to the ecological (local) temperature range of the tested population, as well as the broader evolutionary range of the entire species. On a species-specific experimental level, this could be tested by comparing the physiological plasticity of biogeographically isolated populations from habitats that vary in thermal regimes (e.g., Eliason et al., 2011).

Other important avenues for research emerging from these studies are mechanisms underlying correlations between heart morphology and metabolic performance. Additional long-term (developmental) thermal acclimation studies on tropical species with various life-styles and physiological capabilities (e.g., more or less 'athletic'; more or

less flexibility in metabolic rate) would advance our understanding of the generality of these patterns. Experiments testing effects of heart performance (e.g., cardiac output, heart rate, stroke volume, heart contractility, cardiac oxygenation) on metabolic rate have been successful in understanding mechanisms underlying temperature effects on performance in a variety of temperate fishes (Eliason et al., 2011; Jensen et al., 2017; Motyka et al., 2017; Perrishon et al., 2017; Ekström et al., 2018) and could represent a promising avenue to further understand such relationships in tropical fishes.

Another obvious extension of these chapters is to explore the effects of multiple stressors on physiological function (Ormerod et al., 2010; Kimberly and Salice, 2015). Climate change is in itself altering much more than water temperature, and is likely interacting with other stressors. Thus, quantifying effects of interacting stressors on the eco-physiological functioning of aquatic ectotherms is a crucial for conservation of biodiversity in inland waters. Protective behavioural, plastic, or genetic responses to a given stressor may not be beneficial for fish simultaneously faced with a second challenge (Christensen et al., 2006), and combinations of stressors often have unexpected antagonistic, additive, or synergistic effects that further influence survival capacity (Darling and Côté, 2008). Population-level differences in acclimation responses to multiple stressors can be tested on fish populations across landscapes with varying stress levels. Fish can be collected from habitats with distinct stress levels, and reared under laboratory conditions in which fish from the various populations are exposed to combinations of the two stressors in fully crossed experiments (Kimberly and Salice, 2015). This will allow for evaluation of independent and interactive effects of the stressors on various performance traits (e.g., aerobic metabolism, swim performance), allowing for a more ecologically accurate examination of the resilience of fish species in the future.

Chapter 4 explores the consequences of climate change in fishing communities in Lake Victoria opening the door for a multitude of in-depth studies on the social and ecological interactions of human communities and their natural resource bases. For example, directed research on the implementation of assisted diversification in impoverished communities could help to identify successful intervention strategies (Cole et al., 2018), and research directed towards minimizing migratory behaviour could help to improve

social cohesion and the effectiveness of governance structures (Nunan et al., 2010). Finally, measuring outcomes of various management practices (e.g., stronger enforcement, removal of illegal gears, closed seasons, protected areas, etc.) on the abundance of fish stocks and on the socio-economic well-being of stakeholder communities would be very useful in determining the efficacy of such actions, and in bolstering motivation of fishing communities to abide by regulations. Evaluations of management performance in coral reef systems provide an excellent model for how successes or failures of specific actions can be measured in a standardized and comparable way (Christie and White, 2007). A recent meta-analysis showed that reducing secondary threats to fisheries, ensuring community involvement, and having strong enforcement are all factors that achieve both ecological and socio-economic goals in reef fisheries (Hargreaves-Allen et al., 2017). Finding such trends in the freshwater fisheries of the Lake Victoria basin and other tropical inland fisheries can promote the social and ecological sustainability of these systems.

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Appendix A: Supplementary materials for Chapter 1

A.1 Supplementary Methods

A 1.1 Species selection and data collection

A.1.1.1 Species selection

Species selected for this study were restricted to those that spend any part of their life cycle in a freshwater ecosystem (including those that may spend the majority of their time in marine systems), had range-maps available for download from the IUCN spatial data service, and whose taxonomic classifications could be resolved between FishBase (Froese and Pauly, 2018) and IUCN redlist (IUCN, 2018) databases (see below). We were able to download range data for a total of 2984 species of African freshwater fishes. Of these, 2621 had exact matches on FishBase. We were then able to resolve mismatches in taxonomic classifications for an additional 172 species by using the *resolve* function from the *taxize* package in R studio v. 3.4.1 (R Core Team, 2017). This resulted in a total of 2793 species being retained in our data set, representing approximately 85% of the estimated 3300 freshwater fish species extant in Africa today. Species whose taxonomies could not be resolved were primarily subspecies in the super-diverse Cichlidae and Cyprinidae families. In previous large-scale CCVAs, samples of 1,500 species (~50% of all species in a given taxonomic group) were found to be sufficient for accurate representation of spatial patterns in climate change assessments (Böhm et al., 2016), so we are confident that the representation of species in this study is sufficiently comprehensive to draw rigorous conclusions about concentrations of climate-change vulnerable fish species across Africa.

A.1.1.2 Data collection

Trait data were collected primarily from the IUCN redlist species information service and from FishBase. We used the R packages *rfishbase* (Boettiger et al., 2017) and *rredlist* (Chamberlain, 2018) to access the website APIs and extract trait data for all 2793 species. We also integrated data from two IUCN publications that investigated climate

change vulnerability of freshwater fishes in the Albertine rift of East Africa (Carr et al., 2013) and in West Africa (Carr et al., 2014). Raw data for the West Africa study were provided generously by the authors, and processed data for the Albertine rift study are contained within that publication. All data extractions and analyses were performed in R studio v. 3.4.1 (R Core Team, 2017).

IUCN redlist data were extracted using the *threats*, *habitats*, *search*, and *narrative* queries in the *rredlist* package. The *threats* and *habitats* queries return categorical data on anthropogenic threats currently experienced (not including climate change), and habitats used by each species. The *search* query returns data on species taxonomic classifications and their IUCN threat status, and the *narrative* query returns a written description containing much of the above information, plus other details on dietary preferences, life history characteristics, and many other biological and ecological traits. These *narrative* paragraphs were read by the authors, and details contained within were categorized into the different trait sets required for this study (described below). IUCN data are based on information provided by expert assessors in each region.

FishBase data were extracted using the *diet*, *ecology*, *fecundity*, *larvae*, *length*, *maturity*, *spawning*, *reproduction*, and *species* queries in the *rfishbase* package. These queries returned information on dietary preferences, basic ecology and life history, relative and mean fecundity, aspects of larval requirements, average and maximum body length, average size and age at maturity, spawning style, and reproductive requirements, respectively. The *species* query returns a written paragraph describing many other aspects of life history characteristics, general biological and ecological information, human uses, threats, and other biological and ecological traits. Details on the information contained in each of these categories can be found at www.fishbase.org/manual/English/contents.htm. Outputs from the *ecology*, *fecundity*, *spawning*, *reproduction*, and *species* queries each contained a column labelled 'comments' that contained written descriptions of details pertaining to each of these categories. As above, these paragraphs were read by the authors, and details contained within were distributed among trait sets.

After all available data were extracted, the datasets resulting from IUCN redlist and FishBase queries were combined and summarized into pre-determined trait sets used to

estimate species vulnerability to climate change. Much of the information on habitat, diet, and spawning was identical between the two databases; however each contained some unique information. For example, FishBase had more detailed information on human uses, whereas IUCN had more detailed information on threats and habitat use. Where continuous numerical traits (e.g., total length, fecundity, depth range) did not match between the FishBase and IUCN redlist data, we used the average value. Where categorical traits (e.g., habitat or diet information) did not match, additional searches were performed, and the most likely choice was retained based on similarity to congeners. Data from the two IUCN studies (Carr et al., 2013, 2014) were then incorporated into our data set and used to add potential missed information, and to error check scores. Where information from the present study did not match that presented in Carr et al., 2013 and 2014, additional literature searches were performed to confirm accuracy.

A1.2 Brief description of climate change vulnerability assessments (CCVAs), vulnerability dimensions, trait sets, and variables

Trait based climate change vulnerability assessments (CCVAs) are an increasingly common method used to develop priorities for conservation under climate change, and have been adopted in recent global assessments of corals, amphibians, birds (Foden et al., 2013), and reptiles (Böhm et al., 2016). This technique has also been used in localized analyses of fish species in parts of Africa (Carr et al., 2013, 2014) and North America (Hare et al., 2016). These assessments provide estimates of relative vulnerabilities of species within taxonomic groups based on traits, and have gained traction recently because they are rapid and straightforward to perform, and can cover large numbers of species and large geographic areas in relatively short periods of time (Pacifiçi et al., 2015).

In general, CCVAs assign relative, binary (high or low) *vulnerability* scores to species by combining information from three key dimensions including: 1) *sensitivity*; a species' ability to persist *in situ*, 2) *low adaptive capacity*; a species' inability to cope with environmental change through dispersal or micro-evolutionary adaptation, and 3) *exposure*; how much a species' physical environment is expected to change based on predictions generated by general circulation models (GCMs) (Foden et al., 2013; Pacifiçi

et al., 2015). Species that get a high score in all three of these dimensions are considered to be highly vulnerable to climate change.

The first two dimensions (*sensitivity* and *low adaptive capacity; LAC*) are based on species' scores (high, low, or unknown) in trait sets that fall within these dimensions. In our study, *sensitivity* was comprised of six trait sets pertaining to: 1) specialized habitat or microhabitat requirements, 2) narrow environmental tolerances, 3) dependence on interspecific interactions, 4) complexity of life history, 5) rarity, and 6) exposure to other disturbances. *LAC* was comprised of 2 trait sets pertaining to: 1) low potential to disperse, and 2) low potential to evolve (Table A1). These trait sets are in turn comprised of a number of variables that are specific to the target taxonomic group under study (Foden et al., 2013, Carr et al., 2014; Böhm et al., 2016). In our analysis we used 20 variables to measure *sensitivity* across the six trait sets outlined above, and six variables to measure *LAC* across the two trait sets outline above (Table A1). Our data had high levels of unknown scores for some of the variables in these trait sets. For details on how we dealt with uncertainties around these data deficiencies please see Sections 1.6 (Dealing with uncertainties) and 1.8 (Caveats) in this document.

Exposure is similarly based on species' scores (high or low) in trait sets describing projected environmental changes. In our study, *exposure* was comprised of one trait set called *predicted exposure to the effects of climate change* comprised of four variables including: 1) change in average temperature, 2) change in temperature variability, 3) change in average precipitation, and 4) change in precipitation variability. All of these scores were based on predictions from various GCMs (Table A1). If a species scored high in any one variable within any trait set of *sensitivity*, *LAC*, or *exposure*, it was given a high score for that vulnerability dimension.

One aspect lacking from many CCVAs is a comparison of the species and regions that are highlighted by the CCVA, and species and regions that are the focus of common species-level conservation prioritization schemes. For example, species are often considered to be of high conservation value based on endemism, uniqueness, extinction risk, and whether they provide important ecosystem services, but these are not necessarily always the same species or regions that are highly vulnerable to climate change. To make this

comparison, we assigned relative *conservation value* scores to each species by combining information from three trait sets that are commonly used to assign conservation priority. These include: 1) endemism; whether or not a species is endemic to one region, 2) threat status; a species' listing category on the IUCN redlist, and 3) importance for human use, split into 2 variables including a) importance to fisheries, and b) other uses (Table A1; Benschoter et al., 2013). Again, if a species was given a high score in any variable, they were given a high conservation value score.

Below, we describe in detail the nine trait sets and 30 variables used across the *sensitivity*, *LAC*, and *exposure* dimensions of climate change *vulnerability*, and the three trait sets and four variables used across the *conservation value* category. We provide justifications for their inclusion in this assessment, discuss their relationship to climate change or conservation value, and describe the scoring system used to assess each species as high or low in each category.

A1.3 Justification and discussion of traits and variables

A1.3.1 VULNERABILITY TO CLIMATE CHANGE

A.1.3.1.1 DIMENSION 1: SENSITIVITY

In CCVA assessments, *sensitivity* is defined as the inability of a species to persist *in situ* (Foden et al., 2013). Any species that has characteristics in its life-history, biogeography, habitat use, physiological tolerances, and interactions with other species that may mean it will be adversely affected by climate change is given a high score in this trait. In our analysis, *sensitivity* is split into six trait categories (termed 'trait sets' after Böhm et al., 2016), which have been adapted from previous studies on fish species (Carr et al. 2013, Hare et al., 2016). Distributions of African freshwater fishes that are highly sensitive to climate change (total count and proportion) are mapped in Fig. A1AB.

Trait Set I. Specialised habitat or microhabitat requirements

Climate change is predicted to have far-reaching effects on freshwater habitats (Schindler, 2001; Dudgeon et al., 2006), making it highly likely that fish species will

experience drastic changes to or complete loss of habitats and microhabitats as climate change progresses (Ficke et al., 2007; Myers et al., 2017). Species with specialised habitat requirements are therefore likely to be more vulnerable to climate change than generalist species as they may lose access to habitats that are essential to their survival. Species that are less dependent on specific habitats may be more resilient since they can select from a wide variety of habitats and are likely to be more versatile when habitats are altered.

Sensitivity Variable (SV) 1 - Depth range

Relationship to climate change: Shallow waters are directly influenced by changes in air temperature and are therefore more likely to experience thermal spikes with heat waves (Knouft and Ficklin, 2017). Shallower waters are also heavily affected by storm surge and runoff that can occur during times of excessive precipitation (Jeppesen et al., 2009). Species that inhabit very shallow environments or those that are confined to littoral zones of lakes are therefore more likely to be more affected by climate change-related stressors. Fishes that span a wide range of water depths, on the other hand, have the option to use deeper waters as thermal refuges during periods of high temperature fluctuations. It is therefore likely that fish with wider depth ranges have better capacity to cope with fluctuating or changing temperatures, and other climate change-related stressors (Hare et al., 2016).

Scoring system: Estimates of minimum, maximum, and/or average depths were obtained from IUCN and FishBase. Fish known to be restricted to <3 m depth, or that occur in naturally shallow habitats (e.g., small streams) were given a high score for *sensitivity*, whereas those that span a wide depth range were given a low score.

SV 2 – Habitat specialization

Relationship to climate change: Climate change is likely to exacerbate loss of important freshwater habitats for fishes (Schindler, 2001). Fish species that are limited to one or very few rare habitat types are highly susceptible to habitat loss (Carr et al., 2013, Hare et al., 2016). These species are likely to be sensitive to climate change as they rely on their

habitat to stay intact in addition to their own ability to cope with stressors (Hare et al., 2016). Conversely, species that use many different habitat types and span multiple microclimates are more versatile, and more likely to show resilience to climatic change. In addition, species whose habitats are widespread and plentiful (e.g., pelagic zones of lakes) will likely fare better than those that rely on relatively rare habitats (e.g., high mountain rivulets). Similarly, species inhabiting complex biological habitats (e.g., mangrove forests) and seasonal habitats (e.g., ephemeral pools) are likely to be more affected by climate change than those from habitats that are more defined by their physical structure (e.g., lakes with rocky bottoms) (Hare et al., 2016), because biological and weather-dependent habitat features are more likely to be affected by climate change than physical features.

Scoring system: In this category, we considered the number of different habitats occupied, the relative abundance of each, and the vulnerability of the habitats to climate change. Habitat types were defined using the IUCN Habitat Classification Scheme, which can be found at: <http://www.iucnredlist.org/technical-documents/classification-schemes/>. IUCN habitat types occupied by fish species in this study, and the frequency of occurrence of each habitat type in our dataset are presented in Table A2. Each IUCN habitat type was classified as being rare or common based on frequencies in the Global Lake and Wetlands Database (GLWD) of the World Wildlife Fund (<https://www.worldwildlife.org/pages/global-lakes-and-wetlands-database/>). The GLWD splits habitats into 12 categories, nine of which are represented in Africa including: 1) freshwater marsh or floodplain, 2&3) lakes and rivers (combined for this analysis), 4) intermittent wetland, 5) swamp forest or flooded forest, 6) pans and brackish or saline wetland, 7) coastal wetlands, 8) reservoirs, and 9) bogs / fens, in that order of prevalence (Table A2). While most of the IUCN habitat types could be slotted into one of the GLWD categories, a few could not be accurately classified. In such cases, habitat types that were *a priori* known to be rare in Africa (e.g., freshwater springs and oases, alpine wetlands) were also classified as rare (Table A2). In addition, IUCN habitat types were given a second classification as either climate-change vulnerable or resilient. Habitats that are seasonal (i.e., water bodies that rely on rainfall for refilling), or those that are prone to

effects of temperature change (i.e., shallow, exposed, or standing water bodies) were classified as vulnerable (Table A2).

We calculated the total number of different IUCN habitat types occupied by each species. If the species inhabited only one to two habitat types that were classified as either rare or climate change vulnerable, they were given a high score for *sensitivity* for this trait. Any species that occupied three or more habitat types, or very common habitat types were given a low score, the only exception being if they were documented to spend high proportions of their life cycle in rare or vulnerable habitats even if they use other habitats occasionally.

SV 3 - Microhabitat specialisation / site affinities

Relationship to climate change: Species that depend on specific microhabitats or environmental conditions are likely to be more sensitive to climate change because these habitats may be lost or altered, and because microhabitats are often not contiguous throughout wider lake or river habitats. Species with high site affinities may not have the capacity to move from their microhabitat even if conditions are no longer optimal. For example, the numerous rheophytic species in the Congo River drainage rely on cool, fast-flowing waters within forested watersheds throughout their lifecycle. If water levels drop, these species can become isolated in slow-moving pools with high temperatures and low dissolved oxygen (DO) concentrations, and may not be able to transverse long sections of river to find suitable habitats (Chapman and Chapman, 2003).

Scoring system: Species were considered dependent on specialised microhabitats (and therefore given a high score for *sensitivity*) if they were documented to rely on one of the following microhabitats or conditions: specific temperatures; specific DO concentrations; specific soil types; temporary pools (seasonal water bodies); mountain rivulets or rapids; small streams; flooded areas; forest streams (riverine or gallery forests); submerged roots; mangroves; estuaries/lagoons; freshwater springs and oases; caves; and pools below waterfalls. This list was derived from previous studies on African freshwater fishes (Carr et al., 2013, 2014) and other fish species (Hare et al., 2016), and adapted from studies on other ectotherms (Foden et al., 2013; Böhm et al., 2016). If a species was not

documented to rely exclusively on one of the above microhabitats it was given a low score for *sensitivity* for this trait.

Trait Set II: Narrow environmental tolerances

Ectothermic species with physiological and ecological dependencies on specific temperature or precipitation regimes may be more sensitive to climate change than those that are exposed to a broad range of conditions. For example, many species rely on specific seasonal cues (e.g., rainfall) to trigger key events (e.g., spawning migrations) in their life cycle. Others rely on water clarity or specific chemical balances in their habitat, both of which can be affected by changes to precipitation patterns. Species that rely on such predictable seasonal patterns or specific water conditions are likely to be vulnerable to climate change. In addition, it is often assumed that species inhabiting highly thermo-stable environments (e.g., equatorial species) will have narrower thermal ranges, and reduced capacities to cope with temperature changes (Deutsch et al., 2008; Tewskbury et al., 2008). It is possible that populations from highly variable climates (spatial or temporal) will maintain higher genetic or phenotypic diversity allowing them to cope with climatic changes within or across generations (Nadeau et al., 2017).

SV 4 – Tolerance to changes in precipitation

Relationship to climate change: One of the most important manifestations of climate change will be disruptions to precipitation patterns (IPCC 2014). In Africa, decreases in rainfall over large portions of the Sahel, and increases in rainfall in East and Central Africa have been documented during the 20th century, and shifts in natural variability of precipitation are expected (Niang et al., 2014). Predictable periodicity in rainfall is very important for the life-cycles of many African fish species from the Okavango delta (Hocutt and Johnson, 2001; Mosepele et al., 2009), the Congo River drainage (Chapman and Chapman, 2003), and many other river basins across the continent (Lowe-McConnell, 1969, 1993). Fish in these habitats require rains to inundate nursery areas, maintain water levels, provide connectivity among habitats, allow access to specific food sources, and ensure balanced water chemistry (Lowe-McConnell, 1969, 1993; Chapman and Chapman, 2003). Excessive rain can cause flooding and increased runoff from terrestrial

ecosystems, which can degrade water quality through sedimentation and nutrient loading (Jeppesen et al., 2009), whereas too little rain can result in habitat fragmentation, increases in water temperature, changes to flow regimes, and eutrophication. Changes in the periodicity, predictability, and extremity of rainfall patterns are likely to have adverse effects on species that require stable or predictable environments. On the other hand, species that are accustomed to large fluctuations in water levels are likely to have adaptations to maintain high fitness levels under various precipitation conditions.

Scoring system: We used the absolute average deviation (AAD) in precipitation across a species ranges as an estimate of the historical (1960 – 1990) yearly variation in rainfall experienced by this species (see Section 1.4 for descriptions of AAD calculations). Species that experience the lowest amount of historical variability in precipitation across their range were assumed to be intolerant to changes in precipitation, and were given a high score for *sensitivity* in this category. To split species into low and high categories we followed methods outlined in Foden et al., 2013 where species that fell within the lowest 25th percentile of precipitation AAD were given a high score, and all other taxa were given a low score.

SV 5: Tolerance to changes in temperature

Relationship to climate change: Average temperature increases of ~0.7°C have been documented over most of the Africa during the 20th century, and further increases of approximately 0.2°C per decade are expected (Niang et al., 2014). Increases in the earth's surface temperature can have negative impacts on freshwater ecosystems (Schindler, 1997), including alterations to thermal regimes (Livingstone, 2003; O'Reilly et al., 2003; Adrian et al., 2009). Fish species are generally adapted to distinct thermal niches that are closely related to their habitat of origin (Eliaison et al., 2011). Species that experience a wider range of temperatures in their natural environment are likely to have intrinsic mechanisms for coping with fluctuating thermal regimes, whereas those from thermostable environments may be easily pushed beyond their optimum and experience declines in fitness (Huey and Stevenson, 1979; Tewskbury et al., 2008). A recent meta-analysis has provided fairly convincing evidence that species that have a wider range of temperatures across their ranger are more likely to have higher upper thermal tolerance,

and therefore are likely to fare better under climate change (Comte and Olden, 2017). Species that are adapted to a wide range of temperatures are therefore likely to be better equipped to cope with climate change than those from thermostable environments.

Scoring system: We used the absolute average deviation (AAD) in temperature across each species range as an estimate of historical (1960 – 1990) yearly variation in thermal fluctuations experienced by this species (see Section 1.4). Species that experience the lowest amount of historical variability in temperature were assumed to have narrower thermal limits, and were therefore given a high score for *sensitivity* in this category. As with precipitation, species were classified as having high *sensitivity* if they fell within the lowest 25th percentile of temperature AAD, and all other taxa were given a low score.

SV 6: Sensitivity to increases in turbidity: mating

Relationship to climate change: Turbidity and sedimentation are likely to increase with climate change as a result of changed precipitation regimes (Jeppesen et al., 2009; Knouft and Ficklin, 2017), and may be further exacerbated by human activities such as deforestation and agriculture. Species that rely on clear waters for recognition of conspecifics during mating are therefore likely to be more sensitive to climate change if they experience declines in reproductive output (Carr et al., 2013), or if poor mate recognition results in hybridization of species, as has been documented in the mouthbrooding haplochromine cichlids of Lake Victoria (Seehausen et al., 1997).

Scoring system: Any species known to use visual systems to attract mates (e.g., body colouration), and any species where hybridization was mentioned as a potential threat, was given a high score for *sensitivity* in this category. All other species were given a low score.

SV 7: Sensitivity to increases in turbidity: food collection

Relationship to climate change: Any species documented to rely on clear water to locate appropriate prey items are likely to be more sensitive to the effects of climate change as

they may experience declines in growth rate or fitness due to lack of food, decreasing food quality, or inability to locate prey (Carr et al., 2013).

Scoring system: Any species known to feed exclusively on zooplankton or phytoplankton from the water column (e.g., sardines), or species that are exclusively visual hunters were given a high score for *sensitivity* in this category. All other species were given a low score.

SV 8: Dependence on precipitation-activated triggers

Relationship to climate change: Many African freshwater fish are dependent on specific precipitation patterns or flooding regimes to complete their life cycle (Matthes, 1964; Lowe-McConnell, 1969, 1987). For example, fishes living in seasonal floodplains such as the Okavango delta in Southern Africa require regular rainfall patterns to cue spawning events (Mosepele et al., 2009). Similarly, fishes such as the African tigerfish (*Hydrocynus vittatus*) remain in wetlands as juveniles, and are signalled by retreating waters during the dry season to migrate upriver to seek better conditions (Froese and Pauly, 2018). Fishes requiring specific rainfall regimes and water level changes are likely to have limited tolerance to climate change as the frequency, intensity, and predictability of precipitation is anticipated to change. This trait differs from SV 4 as it highlights specific traits that make species sensitive to changes in precipitation (as opposed to historical fluctuations).

Scoring system: We inferred dependence on specific rainfall regimes based on three key trait categories common to African freshwater fish. These categories include: 1) a taxon's breeding migration is triggered by rains, 2) a taxon's eggs develop in dry mud following rains and require rains to allow hatching, and 3) juveniles migrate to the main river or lake as water retreats. If a species scored positively in any of these components they were given a high score for *sensitivity* in this category. All other species were given a low score.

Trait Set III. Dependence on interspecific interactions

Many fishes rely on interactions with other taxa for their survival. For example, fish species may rely on another taxon for provision of food or habitat (e.g., prey specialists, shell-dwelling cichlids), interact with specific pathogens that keep populations in check,

or exist in competitive, parasitic, mutualistic, or symbiotic relationships with others. Climate change can have an indirect effect on a species by altering the distribution, habitat use, or phenology of its 'partner' taxon (Macnab and Barber, 2011; Nagelkerken et al., 2016). This may manifest in reduced abundance of the species of interest, particularly if there are no other species to fill the role of the lost taxon.

SV 9: Prey specificity

Relationship to climate change: Fishes that rely on a single prey item or taxonomic group for food may be more sensitive to climate change because they rely on the resilience of their food source in addition to their own ability to cope with climate change stressors (Carr et al., 2014, Böhm et al., 2016; Hare et al., 2016). If a prey item is susceptible to climate change and undergoes changes in abundance, distribution, or phenology, this may disrupt important predator-prey interactions. For example, many cichlid species in Lakes Malawi and Tanganyika rely on biocover growing on rocky surfaces (Lowe-McConnell, 1969), which is likely to be affected by increasing temperatures through many pathways (e.g., eutrophication, shifting food web structure). In another example, many rainforest-dwelling fish species are highly dependent on terrestrial inputs for food, and there is a strong association between the phenology of terrestrial taxa and food availability in aquatic environments which can regulate ecological rhythms for forest fishes (Chapman and Chapman, 2003). Species that rely on such ecologically sensitive prey items are likely to experience reductions in available food items and may undergo their own reductions in abundance.

Scoring system: Dietary information from the IUCN redlist and FishBase were classified into 16 distinct categories (Table A3). They are: 1) fishes and their larvae, 2) insect larvae, 3) adult/terrestrial insects, 4) crustaceans, 5) molluscs, 6) other macroinvertebrates, 7) macrophytes, 8) mud/detritus, 9) fish eggs, 10) fish scales/fins, 11) zooplankton, 12) seeds, 13) phytoplankton, 14) algae, 15) rocks with biocover, and (16) other (for anything that did not fall into one of the categories). If a species was documented to feed exclusively on one to two prey types within categories 1 – 8, or to feed exclusively on categories 9-15, it was determined to have highly specialized diet and was given a high score for *sensitivity* in this category. All other taxa were deemed prey generalists and

were given a low score for this trait. Species lacking in dietary information were classified as unknown.

SV 10: Dependence on interspecific interactions

Relationship to climate change: Species that rely on interspecific interactions for any necessary step in their life cycle are likely to be vulnerable to climate change as alterations to the environment can disrupt these interactions through the pathways outlined above. For example, Lamprologine cichlids of Lake Tanganyika use the shells of specific snail species (*Neothauma* spp.) to live in as adults, and to provide shelter for eggs and larvae (Sefc, 2011). Displacement or disappearance of *Neothauma* species would likely have a negative effect on these fishes by removing important habitat structure.

Scoring system: Any species documented to rely on another taxon for provision of resources (habitat, protection, access to food), as a host for parasitic behaviour, or for any other activity necessary to their life cycle was given a high score for *sensitivity* in this category. Species with no interspecific dependencies were documented were given a low score. Table A4 provides a list of interspecific dependencies of African freshwater fish species, and their frequency of occurrence in our dataset

Trait Set IV. Complexity of life history strategy

Fish species with complex life history strategies that depend on social, environmental, or ecological cues to complete reproductive or early-life stages are likely to be vulnerable to climate change as these conditions may be destabilized. Alterations in temperature, precipitation, and seasonal patterns can upset spawning aggregations, interrupt periodicity of flood regimes, expose spawning grounds, and displace important food items for larval stages (Ficke et al., 2007; Rijnsdorp et al., 2009; Petitgas et al., 2012), which can jeopardize the survival of species that depend on these cues. This category captures some of the more idiosyncratic environmental or social dependencies of fish species that have not already been covered in Trait Set I: *Specialised habitat or microhabitat* requirements and Trait Set II: *Narrow environmental tolerances*.

SV 11: Complexity in reproductive strategy

Relationship to climate change: Species with complex reproductive strategies that require precise environmental conditions, specific social cues, or a complex sequence of events may be sensitive to climate change as these patterns are likely to be disrupted in the future (Hare et al., 2016). For example, the Nothobranchiidae are a family of African rivuliines that have an annual life cycle spent entirely within temporary pools. These fishes lay their eggs in the mud near the end of the rainy season. As the pools dry up, the adults die and the eggs go into diapause requiring rains in the following season to hatch (Froese and Pauly, 2018). Species such as this that require specific environmental conditions for successful reproduction are more likely to be negatively affected by climate change.

Scoring system: Any species documented to rely on precise temperatures, seasonal patterns (e.g., flooding regimes), aggregations of conspecifics (e.g., lek breeders, group spawners), rare or vulnerable habitats (e.g., dependent on gravel/coarse sand/temporary streams/vegetation), or other environmental cues (e.g., peaks in food availability) to reproduce or to cue reproductive behaviour were given a high score for *sensitivity* in this category. Those that were not documented to have these characteristics were given a low score.

SV 12: Complexity in early life-history requirements

Relationship to climate change: Early life stages (i.e., eggs and larvae) are often when fish experience the highest mortality rates. There are multiple interacting causes for juvenile mortality, including predation, lack of food, unfavourable conditions, and drastic changes in the environment (Houde, 2008). Eggs or larvae that depend on particular settlement habitats, specific physical conditions (e.g., calm or fast-flowing waters), and high food availability to reach maturity can be strongly affected by small changes in the environment. For example, many fish species in the forested Congo River basin move into inundated forests to release their young during the rainy season. Conditions in the forest act as a nursery for juvenile fishes providing protection and access to suitable food sources. For these fishes, it is essential that the waters stay high enough for the juveniles

to grow to an appropriate size in the forest before they make their way back to the main river or lake (Chapman and Chapman, 2003). If such conditions are not accessible to these species, chances of survival to adulthood are diminished.

Scoring system: Any species with egg or larval stages that depend on specific environmental conditions (e.g., temperature and oxygen conditions, current velocity, clear water, specific settlement habitat, etc.), or that rely on precise environmental cues or vulnerable habitats for early survival were given a high score for *sensitivity* in this category. Those that were not documented to have these characteristics were given a low score.

SV 13: Spawning cycle

Relationship to climate change: Fish species have very diverse spawning behaviour with many differences in the timing, frequency, and duration of spawning events. Some species spawn multiple times per year completing their spawning over longer periods and across multiple seasons, while others spawn all at once (total spawners) over short periods of time, and only when conditions are perfect. While having long spawning seasons may be physiologically taxing, it can be an important bet-hedging strategy to ensure that at least some eggs will be spawned when environmental conditions are favourable. As climatic patterns change, species that follow this strategy are more likely to have successful spawning events as they are less limited by single spawning event that may coincide with poor environmental conditions (Poff et al., 2001; Hare et al., 2016).

Scoring system: Fish species that are documented have only one spawning event per year (total spawners), those that have short windows (≤ 2 months) during which spawning can occur, or those that spawn a few times a year but only during specific seasons were given a high score for *sensitivity* in this category. Species that spawn continuously throughout the year, or several times across more than one season were given a low score. Species with no spawning information were classified as unknown.

Trait Set V. Rarity

Fish species that have low abundances, narrow distributions, or whose populations are small or highly fragmented are likely to be sensitive to climate change. These scenarios are likely to correspond to low genetic diversity, which can compromise a species' ability to adapt to environmental change (Hoffmann and Sgrò, 2011). In addition, species that have narrow or restricted ranges are likely to be vulnerable as the entire region they inhabit could be negatively affected by climate change (Schwartz et al., 2006).

SV 14: Taxon abundance

Relationship to climate change: Fish species that have high abundances are likely to be more resilient to changes in climate. Large populations can buffer a species against environmental change because they are more likely to have individuals capable of coping with a diversity of conditions, and sufficient genetic diversity for adaptation to change (Fraser et al., 2014). Species with low abundances are less likely to contain resilient individuals, or to produce offspring with advantageous genetic combinations for coping with novel climatic scenarios.

Scoring system: Estimates of taxon abundance were based on descriptions of fish species' population sizes and trajectories provided by experts to the IUCN redlist or FishBase databases. We gave species scores in 3 abundance categories: 1) population size (abundant/common or rare), 2) distribution (widespread, narrow, or very narrow), and 3) population trajectory (increasing, stable, or decreasing). Fish that had at least two of the characteristics that indicate low abundance (i.e., rare, very narrow distribution, declining population) were given a high score for *sensitivity* in this category. Species that had at least 1 trait that indicated high abundance (common, widespread, or increasing) were given a low score. Species with no information were scored as unknown.

SV 15: Range size - extent of occurrence (EOO)

Relationship to climate change: Extent of occurrence (EOO) is a measure that describes a species distribution across a landscape, and is defined by the IUCN as the area contained within the shortest continuous boundary that encompasses all the known sites of

occurrence of a taxon (Rodríguez et al., 2015). Larger EOOs generally correspond to a higher degree of 'risk spreading', and therefore a lower extinction risk for a taxon (Rodríguez et al., 2015). For example, a species with occurrences spread across a large area has a higher chance of surviving under climate change than a species with a narrow distribution since it is less likely that their entire range will be compromised by the negative impacts of climate change.

Scoring system: EOO was calculated by drawing a minimum convex polygon around all water bodies inhabited by a given species, and calculating the area within that polygon. We followed the recommended IUCN redlist guidelines (IUCN, 2012) to assign high and low scores for this trait, with species with the smallest EOOs ($< 5000 \text{ km}^2$) classified as highly *sensitive* to climate change. Species with EOOs $> 5000 \text{ km}^2$ were given low score in this category.

SV 16: Range size - area of occupancy (AOO)

Relationship to climate change: Area of occupancy (AOO) is a measure that describes the actual areas occupied by a species within their EOO (Rodríguez et al., 2015) and is calculated in this study as the summed surface area of water bodies inhabited by each species. Species with restricted spatial distribution (small AOO) usually have restricted habitat availability, tend to be habitat specialists, and are considered to have an increased risk of extinction (Rodríguez et al., 2015). In addition, species that cover larger areas tend to have larger population sizes (depending on population density) and experience a greater range of conditions, giving them a higher chance of finding suitable habitats even if parts of occupied territory are subject to change (Carr et al., 2014). Species that have a large AOO are therefore less likely to be susceptible to climate change than those with smaller AOO.

Scoring system: AOO was calculated by summing the area of all water bodies occupied by the species (see Section 1.4 for a description of how species ranges were mapped). We followed the recommended IUCN redlist guidelines (IUCN, 2012) to assign high and low scores for this trait, with species with the smallest EOOs ($< 500 \text{ km}^2$) classified as highly

sensitive to climate change. Species with EOOs >500 km² were given low score in this category.

SV 17: Population fragmentation

Relationship to climate change: Habitat fragmentation is a critical factor affecting the survival and distribution of species. A high degree of habitat fragmentation can prevent species from shifting ranges (Opdam and Wascher, 2004), and can restrict gene flow from neighbouring populations, reducing the capacity for genetic adaptation (Fraser et al., 2014). Species with highly fragmented populations are therefore less likely to be able to adapt to the effects of climate change.

Scoring system: Species that were documented to have highly fragmented populations were given a high score for *sensitivity* in this category. Species inhabiting large, contiguous water bodies (e.g., large river basins, pelagic zones of large lakes lakes) were given a low score. All other taxa were classified as unknown.

Trait Set VI. Exposure to other disturbances

Freshwater fish species are exposed to a wide array of stressors and disturbances in their natural habitats. Some of the most pervasive stressors for freshwater fishes include overexploitation, water pollution, habitat degradation, exotic species invasions, and poor water management (Dudgeon et al., 2006). Climate change is a slow-acting stressor that, apart from effecting its own changes, is predicted to exacerbate effects of other anthropogenic stresses on fish species (Mooney et al., 2009; Staudt et al., 2013). In addition, species that are already affected by other stresses are likely to already be using physiological, genetic, and behavioural resources to adapt, and are therefore predicted to have especially acute responses to the additional impacts of climate change (Hare et al., 2016). By looking at exposure to other disturbances we aim to account for stresses that might compromise species' ability to cope with the additional stress of climate change.

SV 18: Fishing pressure

Relationship to climate change: Fishing pressure depletes population sizes, increases mortality rates, and often selects the largest individuals in a population for harvest leaving smaller and possibly less fit individuals behind (Brander, 2007). Fishes that are intensely harvested are therefore likely to be more sensitive to climate change since heavily fished populations have depleted population sizes, and may experience unstable population dynamics (e.g., reduced intrinsic growth rates) and reduced fitness of individuals remaining in the population (Hsieh et al., 2006; Anderson et al., 2008).

Scoring system: Species were categorized into four groups describing harvest rates including: 1) not fished, 2) subsistence / artisanal, 3) commercial, and 4) highly commercial (industrial). Any species that is part of a commercial or highly commercial fishery (categories 3 and 4) were given a high score for *sensitivity* in this category. Those that are not fished or fished for subsistence only were given a low score.

SV 19: Other threats

Relationship to climate change: Fish species that experience many stresses are likely to be more vulnerable to climate change than those that live in otherwise unaltered environments as the effects of climate change are likely to exacerbate existing problems (Staudt et al., 2013). For example, high temperatures can worsen hypoxic conditions because warmer waters hold less dissolved oxygen than cooler waters, and because increased temperatures can accelerate bacterial decay of organic matter further reducing oxygen levels (Rabalais et al. 2009). In addition, more frequent or extreme rainfall events can exacerbate problems with eutrophication and turbidity by increasing inputs of solutes into waterways from agricultural and industrial runoff (Jeppesen et al., 2009). Fishes that are already compromised in their environments are likely to show acute responses to additional stresses, and physiological or behavioural adjustments that are beneficial for coping with one stressor may be detrimental for coping with another. For example, increased temperature can intensify the toxicity of common pollutants to fish, and elevated metabolic rates of fish species that compensate for higher temperatures can amplify rates of toxin uptake (Murty, 1986; Ficke et al., 2007).

Scoring system: Threat types were defined using the IUCN Threat Classification Scheme, which can be found at <http://www.iucnredlist.org/technical-documents/classification-schemes/>. Key threats to African freshwater fish include agricultural effluents, deforestation and logging, effluents from mining, and changes in water levels due to dams and water abstraction. All threat types affecting fish species in this study, and their frequency of occurrence in our dataset are presented in Table A5. First, any threats that were predicted to be directly intensified by climate change (Table A5) were removed and included in SV19 (see below). The remaining threats were tallied for each species. Any species currently affected by ≥ 7 threats (top 25%) was given a high score for *sensitivity* in this category. Any species affected by ≤ 6 threats was given a low score.

SV 20: Threats intensified by climate change

Relationship to climate change: Similar to the above arguments, species that are currently threatened by stressors that will be directly intensified under climate change are likely to become more vulnerable with time. Threats that are directly intensified under climate change include those related to water temperature (e.g., eutrophication; hypoxia) or water level (e.g., water abstraction). These threats can have synergistic effects with climate warming. For example, Xenopoulos et al. (2005) projected that increases in water withdrawals combined with climate change could cause the loss of more than 22% of fish species by 2070, and that in most US rivers the combined effects of these two stressors together were greater than the effect of climate change or water withdrawal alone.

Scoring system: Any threats that were predicted to be intensified by climate change (Table A5) were tallied up for each species. Any species that is currently threatened by ≥ 2 threats that are likely to be intensified under climate change was given a high score for *sensitivity* in this category. Any species that is threatened by ≤ 1 of these threats was given a low score.

A.1.3.1.2 DIMENSION 2: LOW ADAPTIVE CAPACITY (LAC)

In CCVA assessments, *Low Adaptive Capacity (LAC)* is defined as the inability for a species to adapt to changes in the environment through dispersal or micro-evolutionary

change. A species may have LAC due to traits that prevent it from undergoing range shifts to favourable environments, or because their life cycles are too slow or reproductive rates too low to allow for genetic adaptation. Species that are able to circumvent the effects of climate change through dispersal or adaptive change may be able to persist. In this study, LAC is split into two trait sets that have been adapted from previous studies on fish species (Carr et al., 2013, 2014, Hare et al., 2016) and other ectotherms (Böhm et al., 2016). Distributions of African freshwater fish that have a low adaptive capacity (total count and proportion) are mapped in Fig. A1CD.

Trait Set VII. Low potential for dispersal

Climate change has been shown to shift environmental conditions across landscapes such that current species ranges no longer contain conditions optimal for survival (Parmesan and Yohe, 2003). Species that have restricted capacities for dispersal may be unable to change location or undergo range shifts at a rate that matches these changing conditions, and are likely to face higher extinction risk than species that are able to disperse to more suitable environments (Massot et al., 2008). Dispersal can be restricted in adult fishes by intrinsic features in a species' ecology (e.g., low dispersal capacity) or by extrinsic physical or geographical barriers (e.g., large expanses of unsuitable habitat), and in juvenile fishes, if the egg and larval stages are non-pelagic.

LAC Variable (LACV) 1: Intrinsic low probability of dispersal

Relationship to climate change: Intrinsic dispersal ability refers to the built-in capacity for a species to move across landscapes to find suitable habitat and colonize new areas. This is a key trait for coping with climate change as conditions in the location currently inhabited by a species may no longer support growth, survival and reproduction (Massot et al., 2008). Species that have intrinsic qualities that improve their capacity to disperse are likely to be less vulnerable to climate change than those that cannot relocate (Bush and Hoskins, 2017). Intrinsic dispersal ability can be estimated for freshwater fish species based on known dispersal syndromes, which are linked to life history, ecological, and behavioural traits (Comte and Olden, 2018).

Scoring system: We developed scores to describe dispersal capacity based on dispersal syndromes in freshwater fishes outlined in a recent meta-analysis by Comte and Olden (2018), where evidence was found for strong associations among various life history, ecological, and behavioural traits, and dispersal ability. These included positive associations with body length, length at maturity, age at maturity, longevity, and fecundity, and negative associations with degree of parental care and degree of habitat specialization (Comte and Olden, 2018). We used data on habitat and prey specificity, climatic specialization, parental care, and available life history traits to create a continuous measure describing *intrinsic low probability of dispersal* (Table A6). Species were awarded either one or two points for each trait that meant they were likely to have low dispersal capacity (Table A6), and the scores were summed for each species. Any species with >5 low dispersal points were assigned a high score in LAC. All other taxa were given a low score.

LACV 2: Barriers to dispersal

Relationship to climate change: Many fish species inhabiting inland waters face geographic, climatic, and physical barriers to dispersal which confine them to their current habitats (Woodward et al., 2010). For example, Lake Malawi and Lake Tanganyika both have shorelines comprised of rocky, swampy, and sandy microhabitats that act as ecological islands. These microhabitats can be highly isolated from each other to the point that several of them are known to host their own species of small, specialized fishes that are able to live their entire life cycle on one rock island (Lowe-McConnell, 1969). Lake Malawi has a diverse flock of cichlids known as the mbuna with this life style (Lowe McConnell, 1969) that are so site-specific they are only known from a few locations throughout the entire lake, and are not known to traverse large areas of sand or swamp to inhabit new areas. These species will not have the opportunity to escape their current habitat if conditions should change. Species that encounter such barriers will have a low adaptive capacity in terms of their dispersal ability.

Scoring system: Data on biogeographic or other physical barriers to dispersal were quite sparse in our dataset. This category is therefore mostly based on fishes that occupy specific habitats that are difficult or impossible to disperse from, either because of

physical barriers or because of ecological requirements. These include fishes who are cave or rock dwellers, live in small crater lakes with no outlet, require high altitudes, or those who rely on rapids, temporary pools, rainforest brooks, mountain rivulets, swamps, estuaries, lagoons, or oases. Any site-dependent species that is unable to relocate was given a high score for *LAC* in this category. If a species was not pointed out to have biogeographic barriers to dispersal it was given a low score. The list of sites that prevent dispersal was adapted from Carr et al., 2013, 2014, and Hare et al., 2016.

LACV 3: Dispersal of early life stages

Relationship to climate change: While adult mobility is crucial in determining a species' ability to relocate, the capacity for dispersal of early life stages may also influence their ability to colonize new habitats. The capacity for larval dispersal is primarily determined by the location of the larval and/or egg stage in the water column (i.e., benthic or pelagic) and the length of time it takes to settle. Species with egg and larval stages that have long, planktonic periods, or those that move with currents and do not require specific settlement habitats are more likely to colonize new territories through drifting. Conversely, species that deposit eggs in sediments, under rocks, or attach eggs to the surface of plants or other benthic structures, or where the larvae require very specific nursery habitats will not be good dispersers.

Scoring system: Species that were documented to have long, pelagic or planktonic early life stages were given a low score for *LAC* in this category since they are likely to have a high ability to disperse, while species whose eggs and larvae were documented to be restricted to a small region, nests, or nursery grounds were given a high score for *LAC* since they are likely to have a low ability to disperse. Any species with no information was given a score of unknown.

Trait Set VIII. Low potential to evolve

Species that are capable of rapid micro-evolutionary change may have potential to adapt genetically to climate change-related stressors. Generally, adaptive change is expected to proceed more quickly in species with high levels of genetic diversity. However, estimates

of genetic diversity in natural populations are extremely rare, so indirect measures of evolvability are used. These measures relate to the speed (i.e., generation time) and output (i.e., relative fecundity) of reproduction, as this is assumed to reflect the rate at which advantageous novel genotypes can arise (Chevin et al., 2010). Other factors that can contribute to evolvability include large population sizes or fast-growing populations. Species with that have long generation times, low reproductive rates, and low population growth rates may not be capable of producing sufficient novel characteristics to facilitate adaptation to environmental change.

LACV 4: Reproductive capacity

Relationship to climate change: Freshwater fishes show great variability in reproductive strategy. Some species produce few, large eggs, and invest energy in various forms of parental care, while others broadcast spawn millions of eggs and provide no protection to their eggs after spawning. In addition, fish vary in the frequency of spawning events throughout the year. All approaches represent adaptations intended to increase reproductive success, and may be beneficial in different contexts. In general, however, species that have higher relative fecundity (i.e., higher numbers of eggs per gram of fish per year) have a better chance of coping with environmental change than those who lay fewer eggs, less often (Purvis et al., 2000; Williams et al., 2008).

Scoring system: Relative fecundity was used as an estimate of reproductive output, and was calculated the number of eggs spawned per year, per gram of fish. Where there was more than one estimate, different estimates among databases, or where only maximum and minimum values were reported, we used the mean. Species that had a relative fecundity of $< 200 \text{ eggs gram}^{-1} \text{ year}^{-1}$ (lowest 75% of relative fecundity) were given a high score for LAC as lower reproductive output likely means that they will take longer to evolve novel characteristics. Species that had relative fecundity $> 200 \text{ eggs gram}^{-1} \text{ year}^{-1}$ were given a low score.

LACV 5: Capacity for population growth

Relationship to climate change: Populations of species that have faster growth rates are generally more likely to recover from stresses caused by changes in the environment (Lande, 1993). It is therefore often assumed that fish species with faster population growth will have a higher capacity to adapt to stresses related to climate change (Hare et al., 2016).

Scoring system: For the fish species in this study, direct estimates of population growth rate were very rare. However, there are several biological parameters that can be used to estimate population growth potential (Musick, 1999; Denney et al., 2002). These include: 1) longevity (maximum age reached in the wild), 2) age at maturity (the age at which 50% of the population reaches reproductive maturity), 3) length at maturity (the length at which 50% of the population reaches reproductive maturity), and 4) fecundity (total number of eggs produced per year). Generally, fishes that are R-selected (fast growing, small body size) exhibit high population growth and are assumed to have a high capacity to adapt to climate change, whereas fishes that are K-selected (slow growing, large body size) exhibit low population growth and are likely to have a low adaptive capacity (Table A7). We collected data on all the above-listed traits and used them to calculate an overall score describing population growth (Table A7). Because there were very limited data for all traits contributing to population growth scores, we also included body length since this trait was well represented in our dataset and was closely correlated to all the other traits (Table A8). To calculate population growth scores we created bins for each trait based on percentile thresholds. If species scored above a given threshold for a given trait it was given a point for high growth rate (Table A7). Since these traits are closely correlated (Table A8), if a species received a point for high growth in any traits they were given a high score for population growth potential (and therefore a low score for *LAC*). If a species did not have any traits that indicate potential for high growth it was given a low score for population growth rate (and therefore a high score for *LAC*). Species with no data in any category were classed as unknown.

A.1.3.1.3 DIMENSION 3: EXPOSURE

In CCVA assessments, *exposure* is defined as the degree to which a species' physical environment is predicted to be altered by the effects of climate change across their geographic range. Climatic parameters that are likely to affect fish species include changes in the mean and variability of temperature and precipitation regimes. If a species is predicted to experience large shifts in these parameters over the next 30-70 years, they will be highly exposed to climate change and will require strategies to adjust. Exposure to climate change is encompassed by one trait set split into four variables, all of which are derived from calculations of projected changes based on general circulation models (GCMs). Methods for performing these calculations have been adapted from Foden et al. (2013). Please see Section 1.4 below for detailed descriptions of these calculations. Distributions of African freshwater fishes that are highly exposed (total count and proportion) are mapped in Fig. A1EF.

Trait Set IX. Predicted exposure to the effects of climate change

Climate change projections from GCMs estimate changes to terrestrial environments, but it has long been established that these effects cause changes to freshwater systems as well (Schindler, 1997; Vincent, 2009; Woodward et al., 2010). Increases in surface water temperature concomitant with increased air temperature have been documented in numerous lakes, rivers, streams, and wetlands around the world (Livingstone, 2003; O'Reilly et al., 2003; Adrian et al., 2009), and alterations in hypolimnetic temperatures of large, deep lakes have also been documented (Hondzo and Stefan, 1993; DeStasio et al., 1996). Increases in temperature can have secondary effects in freshwater systems, with higher levels of primary production leading to increases in eutrophication in many lakes (Moss et al., 2011). This can alter water clarity limiting plant growth, altering food-web structure, and disrupting nutrient dynamics and hypolimnetic oxygen levels (Jeppesen et al., 2015). In addition, changes in precipitation can cause increases in discharge into lake and river systems (Jeppesen et al., 2009), contributing to temperature changes, and increased inputs of solutes, pollutants, and fertilizers to surface waters further exacerbating eutrophication and turbidity (Jeppesen et al., 2009; 2014). Changes in the pattern and intensity of precipitation can also affect water levels in lakes and wetlands. In

extreme cases, dry conditions can cause loss of connectivity in river systems leading to increased fragmentation (Woodward et al., 2010). Because direct measurements of changes in freshwaters are rare, we measure projected changes to global surface temperature and precipitation assuming that where these effects are more extreme, so will be the effects on freshwater ecosystems.

Exposure Variable (EV) 1. Changes in mean temperature

Relationship to climate change: Fish species are ectotherms relying on temperature to regulate biological processes. Many fish species, especially those in the tropics, tend to have narrow thermal tolerances since they have evolved under thermostable conditions (Tewksbury et al., 2008). Small changes in temperature are therefore predicted to have a large impact on physiological functioning of many fishes. Species whose geographical ranges are predicted to be exposed to the most severe temperature changes are likely to be the most exposed to the effects of climate change as environmental temperatures are likely to reach or exceed species' optima.

Scoring system: Methods used to calculate climate change predictions across species ranges are described in detail in Section 1.4. Briefly, we estimated change in temperature by comparing historical average temperatures to temperature predictions for 2050 and 2090 across individual species ranges for three emissions scenarios: moderate (A1B), high (A2) and low (B1). We calculated mean temperatures across species ranges for all three time periods and then found the absolute difference between historical (1975) and future projected (2050 and 2090) average temperatures. Species that fell within the highest 25% of average temperature change were classified as having high *exposure* to climate change in this category, while those with the lowest 75% of change were given a low score.

EV 2: Changes in temperature variability

Relationship to climate change: Similar to above, fish species whose ranges will be exposed to the most severe changes in temperature variability according to future climate projections are likely to be the most exposed to the effects of climate change. Fish species that are adapted to small fluctuations in temperature may not have the

thermal flexibility necessary to cope with unpredictable or drastic fluctuations in temperature. Large fluctuations could drive a species over its thermal limits, which can cause mortality over short time frames.

Scoring system: We used the same climate change models and scenarios as above to calculate the absolute average deviation (AAD) in temperature across each species' range for the same years (1975, 2050, and 2090) and for all three emission scenarios (A1B, A2, and B1). We found the absolute difference in AAD between 1975 and each of the future projected temperature AAD. Again, a 25% threshold was used to find species that will experience the greatest change in temperature variability, and these species were given a high score for *exposure*.

EV 3: Changes in mean precipitation

Relationship to climate change: Changes in precipitation can have drastic effects on freshwater systems, and many fish species rely on predictable precipitation patterns for their life histories. Fish species that are adapted to highly variable precipitation are require such fluctuations, while those that are adapted to stable rainfall conditions may not have the ability to cope with changes in precipitation due to climate change.

Scoring system: Using the same climate change prediction models, scenarios, and years as described above, we estimated change in precipitation by comparing historical average precipitation to future projected precipitation across individual species ranges. We then found the absolute difference between historical and future precipitation. Species that fell within the highest 25% of average precipitation change were classified as having high *exposure* to climate change in this category, while those with the lowest 75% of change were given a low score.

EV 4: Changes in precipitation variability

Relationship to climate change: Similar to above, fish species whose ranges are projected to be exposed to the highest changes in variability in precipitation are likely to be the most exposed to the effects of climate change. Fish that are adapted to small fluctuations

in precipitation may not have the necessary adaptations to cope with extreme drought or flood scenarios as species adapted to high levels of variability in precipitation.

Scoring system: We used the same climate change models, scenarios, and years as described above to calculate AAD in precipitation across species' ranges. We found the absolute difference in AAD between 1975 and each of the future projected precipitation AADs. Again, a 25% threshold was used to find species that will experience the greatest change in precipitation variability, and these species were classified as having high *exposure* to climate change.

A.1.3.1.4 VULNERABILITY

A species was given a high score for *vulnerability* if they scored high in all three of *sensitivity*, *LAC*, and *exposure*. Summaries of these scores are presented in Fig. 1.2. Distributions of African freshwater fishes that are highly *vulnerable* (total count and proportion) are mapped in Fig. A1GH.

A.1.3.2 CONSERVATION VALUE

Resources for the conservation of natural systems are limited, so efforts to protect biological diversity require prioritization (Arponen, 2012; Capmourteres and Anand, 2016). Conservation value assessments are often used to inform decisions about regions and species that are the most beneficial to preserve, usually taking into account biodiversity, provision of ecosystem services, and rarity or threat status of landscapes or species (Brooks et al., 2009; Capmourteres and Anand, 2016). While the majority of conservation plans focus on the ecological integrity of landscapes (Capmourteres and Anand, 2016), conservation value can also be a species-level prioritization (Arponen, 2012; Reece and Noss, 2014). Indices of species conservation value commonly incorporate estimates economic and/or socio-cultural value, phylogenetic distinctiveness, endemism, status on national or international vulnerability lists (e.g., IUCN redlist), keystone species, rarity, and threat status (Reece and Noss, 2014; Capmourteres and Anand, 2016). Here we assign each species a score of conservation value based on their level of endangerment, their uniqueness (endemism), and their potential to provide

ecosystem services through fisheries and other human uses. Distributions of African freshwater fishes that are of high *conservation value* (total count and proportion) are mapped in Fig. A1IJ.

Trait Set I. Endemism

Relationship to conservation value: In general, a taxon that is endemic to one region, lake, or hydrological system should be considered of higher conservation value than a species that is widespread (Benscoter et al., 2017), especially if the endemic species is also rare. Endemic species are of high conservation value because they are irreplaceable if lost, and constitute extinctions (rather than local extirpations) resulting in high-consequence biodiversity loss (Hartley and Kunin, 2003; Brooks et al., 2009).

Scoring system: Any species that was documented as being endemic to one region, lake, or river system in Africa was given a high score for *conservation value* in this category. Species that were not listed as endemic were given a low score.

Trait Set II. IUCN Redlist status

Relationship to conservation value: A species that is listed as being globally endangered or vulnerable to extinction is of higher conservation value than one that is least concern (Carr et al., 2014; Capmourteres and Anand, 2016; Benscoter et al., 2017). The IUCN redlist provides the world's most comprehensive listing of global species endangerment. Where there is a documented extinction risk, it is highly likely that these species could be lost unless immediate conservation action is taken (Brooks et al., 2009). Species' vulnerability to extinction therefore continues to be one of the most common priorities when considering conservation action (Rapoport et al., 1986; Lee and Jetz, 2008; Shokri and Gladstone, 2013)

Scoring system: Species statuses were taken from IUCN redlist species information service. Following protocols adopted by Foden et al., 2013, any species that is categorized as least concern (LC) or not threatened (NT) were given a low score for *conservation value* in this category, and species categorized as critically endangered (CE), endangered (EN) or vulnerable (VU) were given a high score. Species that were categorized as data

deficient (DD) were given a score of unknown. Detailed information on how species are assigned these scores are provided online at: <http://www.iucnredlist.org/technical-documents/categories-and-criteria>.

Trait Set III. Importance for human use

Habitat destruction and other anthropogenic stressors have precipitated the loss of biodiversity worldwide. These losses compromise the benefits (ecosystem services) derived from these systems, including provisioning of intact species populations that can be accessed for sustainable harvest. For example, inland fisheries directly support the livelihoods of millions of people living in poverty worldwide (FAO, 2014), and the growing aquaculture industry holds promise to improve food security in sub-Saharan Africa (Hishamunda and Ridler, 2006). Protecting ecosystems and species that provide such services are critical for economic development, poverty alleviation, and human well-being (Millennium Ecosystem Assessment, 2005). Species that are important for human use are therefore often ranked high in assessments of conservation value.

Human use variable 1: Fishing

Relationship to conservation value: Freshwater fisheries provide an important source of livelihoods in many regions of Africa, and there is increasing concern over the consequences of global warming for fishing communities that rely on fish for food security and economic stability (Badjeck et al., 2010). Climate-induced instability in fish stocks can therefore have far reaching implications for in fish-dependent communities (Miller et al., 2010, Lynch et al., 2016). Species that are important to fisheries are therefore of high conservation value, and if a taxon is heavily fished it should be the focus of conservation for socio-economic purposes.

Scoring system: Fish were categorized according the level of current exploitation, as described in SV18. These included non-fished species (NF), and fishes that are harvested at the subsistence/artisanal (low), commercial (mid-range), and highly commercial (industrial) levels. Fishes that were part of any fishery got a high score for *conservation value* in this category. Fishes that were not fished were given a low score.

Human use variable 2: Other uses

Relationship to conservation value: African freshwater fishes are used for a great variety of purposes other than consumption. Common uses of freshwater fish species in Africa include rearing aquaculture, use as bait fish, capture for the aquarium trade, quarry for sport fishers, use as biocontrol agents, and use for medicinal purposes. Similar to harvested species, those that are important for human use may have economic, social, or cultural value, and should be prioritized for conservation for the preservation of livelihoods.

Scoring system: The number of uses was summed for each species, and those that had two or more uses were given a high score for *Conservation Value* in this category. Species that had one or fewer uses were given a low score. Frequencies of uses are summarized in Table A9.

A.1.4. Calculating climatic variables

In this study, we followed techniques developed by Foden et al., 2013 to derive estimates of species' exposure to climate change. This required first mapping species distributions, and then calculating future and historical temperature and precipitation conditions across these ranges. To map species ranges, we first gathered species' distribution data from the IUCN spatial data download, and ensured the accuracy of these distributions by refining ranges to areas of known occurrence. In the following sections we outline key steps in this process.

A.1.4.1 Mapping species distribution ranges

Freshwater fish species distribution maps produced by the IUCN were downloaded in the form of range polygons from the IUCN website at: <http://www.iucnredlist.org/technical-documents/spatial-data>. These ranges are based on recorded localities of each species and extrapolation to areas of known habitat suitability, and represent the best available estimates of species distribution limits (Foden et al., 2013). Ranges were available for 2984 species of African freshwater fish (~90% of all freshwater fish species in Africa); however, we retained only 2793 for which sufficient

trait data were available. The IUCN ranges consisted of multiple range polygons per species, which were dissolved into a single polygon for each.

IUCN ranges represent a species' entire extent of occurrence (EOO). These ranges often include within them areas that are not actually occupied by the species. For example, the IUCN range of a fish species that inhabits three different lakes will incorporate all of the uninhabitable land masses between the lakes as well. Therefore, species ranges need to be refined to exclude unsuitable habitat to reflect the species' actual area of occupancy (AOO).

To refine the species ranges, we created a detailed map of the distribution of freshwater ecosystems across Africa by combining river, lake and wetland data from the Global Lake and Wetland Database (GLWD; Lehner and Doll, 2004) of the World Wildlife Fund (<https://www.worldwildlife.org/pages/global-lakes-and-wetlands-database>) with HydroSHEDS and HydroLAKES data (Lehner et al., 2008; <http://www.hydrosheds.org/>). The GLWD contains information on major rivers, lakes, wetlands, and other inland water bodies (GLWD Levels 2 and 3), but lacks information on smaller rivers and lakes. To add smaller rivers and lakes we used HydroSHEDS river flow accumulation data with a cut-off of 2500 cells, and to add smaller lakes we used HydroLAKES data. All water layers were merged into a single polygon shapefile, and projected into the Africa Albers Equal Area Conic projection to retain accuracy of areal proportions. The extent of the freshwater dataset encompassed -19.1333°W to 55.0667°E and -35.035596°S to 38.164404°N, covering the entire African continent.

After preparing the complete freshwater dataset, the water polygon was used to clip the dissolved IUCN species ranges, so that fish distributions only included areas where there were freshwater habitats. For this process, we assumed that any freshwater habitat within a species range was inhabitable by the species. Area of occupancy (AOO) was derived from the resulting species ranges. Extent of occurrence was obtained from the minimum convex polygon surrounding all water bodies occupied by the species. Species ranges were then converted into raster layers set to the same extent as the freshwater layer with a resolution of 20 x 20 km, which was deemed to be a suitable level of precision for the scale of the analysis. When converting to raster we used the 'vector to

raster' function on ArcGIS v. 10.5.1 (ESRI, 2017), and selected the 'maximum combined area' option to ensure we retained ranges smaller than 20 x 20 km (i.e., fish that live in one very small lake). This technique also ensured that a species is regarded as present in a certain cell if any part of its range polygon overlaps with it. Finally, all species ranges were reclassified with a value of 1 for species presence and 0 for species absence. All rasters were converted to TIF format for ease of manipulation in R in further steps.

A.1.4.2 Calculating temperature and precipitation variables

We were able to calculate estimates of environmental tolerance for all species in our dataset following methods outlined by Foden et al. (2013). This was done by calculating statistics of absolute change and change in variability in temperature and precipitation over the entire study area with climate data downscaled to 20-km resolution. To find the averages within each species ranges, zonal statistics were applied using clipped species ranges as zonal boundaries.

Ten-minute downscaled climate change projections for temperature and precipitation prepared by Worldclim (Fick and Hijmans, 2017) were downloaded from the Nelson Institute Center for Climatic Research, University of Wisconsin Madison (<http://nelson.wisc.edu/ccr/resources/10-minute.php>). These data were derived from four different global circulation models (UKMO HadCM3, MPIM ECHAM5, CSIRO MK3.5 and GFDL CM2.1) for the IPCC emission scenarios A2 (high emissions), A1B (moderate emissions), and B1 (low emissions). Climate data were originally in .asc format, and were converted into raster to improve computing speed. First, the data for four different models were averaged to obtain an ensemble dataset. The data were initially referenced to the unprojected coordinate system WGS84, and then projected to the Africa Albers Equal Area Conic projection. The climate projection data, extent, and resolution were adjusted to be the same as the species ranges.

Average absolute change in temperature and precipitation was calculated as the absolute difference between average temperatures in 1975 and average projected temperatures for 2050 or 2090. Change in variability was estimated through calculations of average absolute deviation (AAD) across species ranges for the same years. AAD is a variable that

represents the tolerance to temperature and precipitation variability across time (months) and space (species ranges) for each species (Foden et al., 2013). AAD was calculated for the dataset $\{x_1, x_2, \dots, x_n\}$ using the formula

$$\frac{1}{n} \sum_{i=1}^n |x_i - m(X)|$$

where each x represents a monthly mean for a cell within a species' range, and $m(X)$ refers to the central tendency of the data, in this case the average of all cells within a range over all months (Foden et al. 2013; Böhm et al., 2016). Lastly, to determine *tolerance to temperature and precipitation changes* for in SV4 and SV5 we used the AAD of historical (1975) climatic data, calculated as described above, to estimate the amount of historical variability experienced by each species.

In summary, the following calculations were performed for the extent covering the entire African continent for each emission scenario of A2, A1B, and B1:

- a. Difference in average temperature between 1975-2050 and 1975-2090;
- b. Difference in average precipitation between 1975-2050 and 1975-2090;
- c. Difference in AAD of temperature between 1975-2050 and 1975-2090;
- d. Difference in AAD of precipitation between 1975-2050 and 1975-2090;
- e. Historical AAD of temperature for 1975;
- f. Historical AAD of precipitation for 1975.

This resulted in 30 rasters with each statistic calculated for all cells in the entire working extent.

A.1.5 Creating univariate and bivariate maps

Univariate maps and bivariate maps were created in R studio v. 3.4.1 (R Core Team, 2017) to identify regions with high concentrations of climate change-vulnerable species and species of high conservation value. We used univariate maps to show the spatial distributions of species with high scores in the different vulnerability dimensions

(*sensitivity*, *LAC*, and *exposure*) and bivariate maps to explore the spatial relationship among dimensions and between climate change vulnerability and conservation value.

To create univariate maps we first created a separate raster layer for every species in our dataset denoting presence or absence in every 20 km x 20 km grid cell across Africa. We then created a file containing scores of the vulnerability and conservation value dimensions for all species based on all the different climate change and threshold scenarios. Species ranges were then stacked, and each grid cell was assigned a value indicating the number of species occupying that grid cell with high scores in the various categories. Each grid cell was assigned a colour that graduated from blues (to signify low species richness) to reds (to signify high species richness). We created univariate maps to show overall species richness (Fig. 1.2B) and to show distributions of fish that score high in each dimension (*sensitivity*, *LAC*, *exposure*), overall vulnerability (Fig. A1ACEG), and conservation value (Fig. 1.4, Fig. A1I).

To create bivariate maps, values of species richness for univariate layers of interest (e.g., climate change vulnerability and conservation value) were split into 10 quantiles based on Jenks' natural breaks. These layers were then overlaid, and bivariate plots were produced by assigning each grid cell a score based on the overlap in quantile scores. Each grid cell was assigned a colour on a bivariate colour scheme where cells with low frequencies were given duller colours and cells with higher frequencies were given more saturated colours, with tones approaching blue on the y-axis, tones approaching yellow on the x-axis, and tones approaching maroon where the two traits overlap strongly (e.g., Fig. 1.3). These maps thereby show where there is high spatial covariation between two variables of interest. We created bivariate maps that overlay biological susceptibility (i.e., species with high scores for both sensitivity and low adaptive capacity; y-axis) with exposure (x-axis; Fig. 1.3) and that overlay conservation value (y-axis) with vulnerability to climate change (x-axis; Fig. 1.4CD). See Script A1 for code for creating maps.

A.1.6 Dealing with uncertainties

A.1.6.1 Unknown data and optimistic vs. pessimistic scenarios

Many of the traits included in our dataset had missing data for at least some species (Table A1). For some traits, we were able to fill in missing data based on trait similarities with congeners (e.g., SV8 and LACV3, Section 1.8), however this was not always possible, especially when there were many (>2000) unknowns (e.g., SV1, SV13, LACV4, Section 1.8). Using a large number of trait variables to determine scores for the *sensitivity* and *LAC* dimensions can mitigate the uncertainty in species scores by increasing the diversity of traits considered, and reducing incidences where all the traits in a given dimension are by default ‘low’ or ‘unknown’ for a given species.

To address the potential effects of unknown data in our analysis, we calculated the overall scores for *sensitivity* and *LAC* under both optimistic and pessimistic scenarios (Foden et al., 2013). In the optimistic scenario all unknowns were coded as low, so fewer species got high scores for *sensitivity* and *LAC* (Table A1), and consequently fewer species qualified as being vulnerable to climate change (Fig. 1.2). In the pessimistic scenario, all unknowns were coded as high, so more species received high scores for *sensitivity* and *LAC*, and more species were qualified as being vulnerable to climate change (Fig. 1.2). The only exception to this rule was when there were >2000 (~70%) unknowns in a trait, as was the case for SV1, SV13, and LACV4. In these cases, unknowns were coded as low in both scenarios (see Section 1.8, SV1 for further explanation).

We used the optimistic scenario for the main analyses in this study. However, we compared differences in numbers of species that qualify under each category in Fig. 1.2 and in Table A1. In addition we mapped the absolute and proportional differences in numbers of species that are highly vulnerable under the optimistic and pessimistic scenarios as a way of visualizing where there were the highest concentrations of species with unknown data (Fig. A2), and we mapped differences in the optimistic and pessimistic scenarios combined with differences in climate change emissions scenarios and years (Fig. A3).

A.1.6.2 Uncertainty in climate change predictions

Climate change predictions generated by general circulation models (GCMs) are inherently uncertain. The IPCC publishes 20 general circulation models that are calculated for three potential greenhouse gas emissions scenarios (high; A2, moderate; A1B, and low; B1) and over two timeframes (2046 – 2065; avg. = 2050, and 2081 – 2100, avg. = 2090).

We calculated climate change projections for the three emissions scenarios over both timeframes resulting in a total of six climate change estimates (2050-A2, 2050-A1B, 2050-B1 and 2090-A2, 2090-A1B, 2090-B1). We calculated *vulnerability* scores based on all six of these scenarios and combined them with the optimistic and pessimistic scenarios described above. Species vulnerability distributions were mapped for spatial comparison under the different scenarios with 2050 data combined with the optimistic scenario, and 2090 data combined with the pessimistic scenario to show the best-case and worst-case extremes. The total number of highly climate change vulnerable species ranged from 1036 (37.1%) under 2050-B1-OPTIMISTIC to 2609 (93.4%) under 2090-A2-PESSIMISTIC (Fig. A3, Table A10).

A.1.6.3 Uncertainty in threshold cut-offs

A third layer of uncertainty in our data is deciding where high and low threshold cut-off points should be for continuous trait variables. We used arbitrary thresholds for the SV15, SV16, SV18, and SV19 and for all four *exposure* variables. To circumvent uncertainties associated with these thresholds we defined multiple thresholds for these traits, and classified these thresholds as either ‘strict’ (pessimistic) or ‘lenient’ (optimistic). In the case of the *exposure* variables we also had a moderate threshold. In all scenarios we define the ‘strict’ threshold as the one which qualifies more species to have high scores in that trait, and the ‘lenient’ threshold as the one which qualifies fewer species to have high scores. For example, for SV15: Range Size (EOO), species with narrower distributions were classified as highly *sensitive* to climate change. We used two thresholds (5000 km² and 20000 km²) for comparison. Using the 20000 km² qualified more species as highly *sensitive* (601 spp.), so this is defined as the ‘strict’ threshold

whereas fewer species qualified as highly *sensitive* under the 5000 km² cut-off (350 spp.), so this is defined as the 'lenient' threshold. The same logic is applied to all threshold situations.

As mentioned above, we used the lenient (optimistic) scenario for the main analyses in this study. However, we compare differences in numbers of species that qualify under each category under the different thresholds in Fig. 1.2 and in Table A1. In addition we mapped the absolute and proportional differences in numbers of species that are highly vulnerable under the lenient (optimistic) and strict (pessimistic) scenarios as a way of visualizing where there were the highest concentrations differences among traits (Fig. A2), and mapped difference in the lenient (optimistic) and strict (pessimistic) scenarios combined with differences in climate change emissions scenarios and years (Fig. A3, Table A10).

For the climate data, thresholds were arbitrarily set (based on Foden et al., 2013) at 25% (see Table A1). To investigate the effect of these thresholds, we recalculated vulnerability using 15% and 35% thresholds. We compared the effect of manipulating these thresholds by mapping the concentrations of vulnerable species under each threshold within the moderate (A1B) emissions scenario for 2050 (Fig. A4).

A.1.7 Data exploration

A.1.7.1 Taxonomic analysis

We explored which families of African freshwater fish were more likely to be susceptible to climate change, which dimensions of *vulnerability* (*sensitivity*, *LAC*, *exposure*) they were most likely to get high scores in, and which families were most likely to be classified as high *conservation value*. A summary of these data are presented in Table A11 and Fig. A5.

A.1.7.2 Trait analysis

We explored which traits contributed the most to climate change vulnerability for African freshwater fishes. First, we calculated which traits had the highest number of high

scores in each *vulnerability* dimension (Table A1, Fig. A6). Second, we carried out a sensitivity analysis to determine how many species qualified as high for the three *vulnerability* dimensions and for *conservation value* based exclusively on one trait (Fig. 1.5).

A.1.8 Caveats, threshold descriptions, and unknowns

Trait-based CCVAs require good data availability in order to be able to come up with scores for each trait considered. Often, high quality data are only available for a small number of well-studied species, and these are biased towards species that are common, of commercial importance, easy to access/catch, or those that are easy to maintain in laboratory situations. As a result, there are many species for which little is known, particularly for understudied taxonomic groups such as African freshwater fishes.

There were 492 (17.6%) species in our data set that were listed as ‘data deficient’ by the IUCN. While this lack of knowledge on some species can hinder our ability to make assessments, it is important that we do not allow lack of information prevent conservation-based decision making. Assessments such as this can help to understand where gaps exist in terms of traits, families, and regions, and can help to guide research effort in the future. In this study, the use of many traits allows us to catch small details, hopefully mitigating issues around lack of data. However, it is important to be aware of how these knowledge gaps may affect our interpretation. Below we acknowledge issues with data deficiencies in trait collection, and discuss some techniques used to overcome these deficiencies.

A.1.8.1 Sensitivity

SV 1. Depth

Estimates of a species average depth or depth range were provided by IUCN and fishbase. In some cases depth estimates were based on single observations of a population, whereas in other cases they were based on averages of multiple observations. Some estimates of species average depth or depth range were therefore more accurate than

others, however we included all estimates of depth in our dataset since there were high numbers of unknowns for this trait.

Unknowns: Our data set had a 2235 unknowns for this trait (80%; Table A1). Traits that had >2000 (~70%) unknowns complicated our comparison of the ‘optimistic’ (unknowns low) and ‘pessimistic’ (unknowns high) scenarios, because classifying all unknowns as ‘high’ flooded the data set with a seemingly unreasonable number of high scores. This would cause many species to be given a high score in a given vulnerability dimension based exclusively on that trait. Using depth as an example: We had 2235 species with unknown depth ranges. When all unknowns are classified as *low* there are only 5 species that are given a high *sensitivity* score based exclusively on depth. However, when all unknowns are classified as *high*, this number jumps to 378. This is a rather high number of species to be classified as highly sensitive based solely on one trait, especially since most of them are actually unknown. To avoid this, when we calculated the ‘pessimistic’ scenario for *sensitivity*, we did not include these high scores for depth, or for other traits that had > 2000 unknowns. Instead the unknowns were classified as low for both the ‘optimistic’ and ‘pessimistic’ scenarios.

SV 2. Habitat specialization

We had very good representation of habitat use data for the majority of species in our data set. However, IUCN habitat data are largely based on the expert opinions of assessors, which is likely to introduce bias to these data as some assessors may apply more detail to their categorization than others (i.e., selecting microhabitats within lakes instead of just selecting lakes as a whole). To accommodate this possible bias, we checked habitat data against information from FishBase to gather more details about fishes’ habitat use. In addition, we assigned habitat specialization data based not only on number of habitats occupied, but also on the rarity or vulnerability of those habitat types. In addition, we made assumptions (based on available information) about which habitats were likely to be under threat from climate change without having specific data for each habitat type; it is possible that not all sites will be equally badly-off.

Unknowns: There were 183 species with no information on habitat preference in our dataset (Table A1). For these species we performed the *sensitivity* calculation for both optimistic (all unknowns assumed low) and pessimistic (all unknowns assumed high) scenarios. The main results for this paper present the optimistic scenario. Differences between the optimistic and pessimistic scenarios are presented in Table A10 and Figs. A2 and A3).

SV 3. Microhabitat specialization / site affinities

Data on microhabitat specialization and site affinities are not systematically collected by the IUCN or FishBase, and were therefore gleaned from comments sections from both datasets where assessors and experts provide descriptions of unique ecological or biological traits of species. While this information is highly relevant for climate change assessments, these data are prone to bias towards well-studied species. It is likely that understudied species have high site affinities and were missed in this assessment. Where we had high certainty that all species in a given genus possessed the same traits in this category, we filled in the traits of all species with a genus. For example, all species in the genus *Melanochromis* (a well-known rock-dwelling group) were given a high score for affinities to rocky habitats.

SV 4 & 5. Tolerance to changes in temperature and precipitation

Scores in these categories are based on the assumption that species' tolerances to temperature and precipitation variation can be determined from historical exposure to climatic variables rather than from *in situ* measures of temperature and precipitation fluctuations in the species' actual habitats. There is increasing evidence that this is not always the case for fish species (Seebacher et al., 2015), and preferred temperatures do not always match those that maximize growth and reproduction in their native habitat (Gräns et al., 2014). To test whether there is validity in this assumption for our dataset we investigated the relationship between historical AAD in temperature, and known temperature ranges for 31 species with available data. There was a significant positive correlation between temperature AAD and in-situ temperature range (Fig. A7) for this subset of species, suggesting that AAD is likely to provide fairly robust estimates of

species tolerances. We did not have data available to perform similar analyses on precipitation tolerances.

SV 6 & 7. Tolerance to changes in turbidity (mating and food location)

Data on tolerance to changes in turbidity are not collected systematically by the IUCN or FishBase, and were therefore gleaned from comments sections from both datasets. While this information is highly relevant for climate change assessments, these data may be biased towards well-studied species. In addition, we assumed that all species that are visual hunters and that use breeding colouration will be negatively affected by turbidity even though it is possible that other signals (e.g., scent) can compensate for loss of visual stimuli. However, it is likely that fish that are known to use primarily vision for mating and food location suffer declines in fitness regardless of whether there are other signals.

SV 8. Dependence on precipitation activated trigger

Data on precipitation activated triggers are not collected systematically by the IUCN or Fishbase, and therefore likely to be biased towards well-studied species. Where we had high certainty that all species in a given genus possessed the same traits in this category, we filled in the traits of all species within that genus. For example, all species in the genus *Nothobranchius* were given a high score for dependence on precipitation activated trigger even if not specifically pointed out to have diapausing eggs.

SV 9. Prey specificity

We were able to obtain good data on prey specificity for over half of the species in our dataset. Again, the IUCN data are based on categories so bias may arise based on the assessor's level of detail, as discussed for SV2. However, the main difficulty in assigning prey specificity scores arose from determining the level of specificity within a prey group. For example, if a species was said to eat 'insects', and no other detail was given, it was not determined to be a prey specialist because of the diversity of insects available. Insects as a whole are likely to tolerate a broad range of environmental conditions, and a fish species that preys on a variety of insects is unlikely to have reduced food availability under climate change. A species was only given a high score for prey specialization if they

were documented to exclusively feed on (or strongly prefer) one to two types of insects within this classification. However, if a species specialized on zooplankton, for example, they were given a high score even though there is also a wide variety of zooplankton, mostly because distinctions among the different types of zooplankton were very rare in the data set. While this decision may be arbitrary, it helped to streamline the categorization process, and is similar to techniques for diet categorization in other studies (Bohm et al., 2016).

Unknowns: There were 1240 species with no information on prey specificity in our dataset (Table A1). For these species we performed the *sensitivity* calculation for both optimistic (all unknowns assumed low) and pessimistic (all unknowns assumed high) scenarios. The main results for this paper present the optimistic scenario. Differences between the optimistic and pessimistic scenarios are presented in Table A10 and Figs. A2 and A3).

SV 10. Interspecific interactions

Data on tolerance to changes in turbidity are not collected systematically by the IUCN or FishBase, and were therefore gleaned from comments sections from both datasets, so these data are prone to bias towards well-studied species. In addition, there are likely to be many more subtle interdependences within communities (e.g., competition and predation keeping communities in balance) that are unknown or very difficult to detect, and therefore not recorded. These subtler interactions are missing from this dataset.

SV 11 & 12. Complexity of life history

These data are not systematically collected by either IUCN or FishBase, and were therefore gleaned from comments sections in both databases, so any species that had little information on reproductive behaviours or egg and larvae requirements were given a low score. It is likely we missed recording complex reproductive strategies or early life history requirements of understudied species. These categories were included to encompass highly specific life history requirements that were highlighted in the comments sections from both datasets, but low scores for these traits are not totally

accurate (i.e., many likely missing). We therefore did not include the unknowns as ‘high’ in the pessimistic scenario calculation, as described for SV1.

SV 13. Spawning cycle

These data are systematically collected by FishBase, but were relatively rare in our dataset. Data in this category are therefore biased towards well-studied species.

Unknowns: There were 2411 species with no information on spawning cycle in our dataset (Table A1). Because there were >2000 unknowns in this category, these were not included in the ‘pessimistic’ scenario as described for SV1.

SV 14. Population abundance

These scores were derived from expert estimates of whether the taxon was common or rare, narrowly distributed or widespread, and decreasing or increasing in population size. Although we had data for the majority of species for this trait, scores are again based on opinions of assessors. To mitigate potential biases, we error checked these data with estimates from FishBase. Where the sites disagreed we took the more conservative estimate. These data are also backed and corrected by the range size estimates (EOO and AOO) that are calculated in a less arbitrary manner, and across similar spatial scales.

Unknowns: There were 303 species with no information on population abundance in our dataset. For these species we performed the *sensitivity* calculation for both optimistic (all unknowns assumed low) and pessimistic (all unknowns assumed high) scenarios. The main results for this paper present the optimistic scenario. Differences between the optimistic and pessimistic scenarios are presented in Table A10 and Figs. A2 and A3).

SV 15 & 16. Range size (EOO & AOO)

EOO and AOO were calculated directly from species distribution maps from the IUCN species information service, so we have estimates of range size for every species in our data set. For these traits, we assume that the species distribution ranges published by the IUCN are accurate. To ensure that we had reliable data for area of occupancy (AOO), we

trimmed the IUCN species distribution ranges to regions of the landscape where there were habitable fresh waters. We adapted protocols described in Foden et al., 2013 to trim ranges (see Section 1.4). We used two different thresholds set by the IUCN to define large or small ranges.

Thresholds: To account for uncertainty in using arbitrary cut-off points we calculated these traits with two different thresholds representing optimistic (fewer species given a high score) and pessimistic (more species given a high score) scenarios. For the optimistic scenario, all species were classified as highly *sensitive* if their EOO was below 5000 km² and in their AOO as below 500 km². For the pessimistic scenario all species were classified as highly *sensitive* if their EOO was below 20000 km² and if their AOO was below 200 km² (Table A1). Optimistic and pessimistic scenarios are compared in Table A10 and Figs. A2 and A3.

SV 17. Population fragmentation

Data on population fragmentation of fish species are not collected systematically by the IUCN or FishBase, and were therefore gleaned from comments sections from both datasets. These data are therefore prone to bias towards well-studied species. To make up for this bias we assumed that a population was not fragmented if it existed in a large river system or water body where the system was *a priori* understood not to be fragmented (e.g., a large contiguous river system). This assumption may introduce some uncertainty into our data set because populations living in these large systems might still be fragmented if, for example, they only exist in a particular pool within these greater systems.

Unknowns: There were 1718 species with no information on population fragmentation in our dataset (Table A1). For these species we performed the *sensitivity* calculation for both optimistic (all unknowns assumed low) and pessimistic (all unknowns assumed high) scenarios. The main results for this paper present the optimistic scenario. Differences between the optimistic and pessimistic scenarios are presented in Table A10 and Figs. A2 and A3.

SV 18. Fishing pressure

We had very good data on the degree of fishing pressure on each species. However, fishery classification as artisanal, commercial, or industrial may be subjective. As with estimates of abundance, there are no pre-defined thresholds for determining how to assign a fishery to one of these categories. In addition, artisanal fisheries can contain a broad range of intensity.

Thresholds: To account for this uncertainty we calculated fishing pressure scores using two thresholds representing optimistic (fewer species given a high score) and pessimistic (more species given a high score) scenarios. In the optimistic scenario, only species that were classified as being harvested in commercial or industrial fisheries were given a high score for *sensitivity*, whereas in the pessimistic scenario fish that were part of any fishery were given a high score (Table A1). Optimistic and pessimistic scenarios are compared in Table A10 and Figs. A2 and A3.

SV 19 & 20. Other threats / threats intensified by climate change

We had good representation of exposure to threats for the species in our dataset as these data are systematically collected by the IUCN redlist. IUCN threat data are based on expert opinion, which may introduce bias as some assessors may apply more detail to their threat categorization. For example, they might select the main stressor (e.g., water management) without selecting specific subcategories of that threat (e.g., groundwater abstraction). To overcome this potential bias we filled in missing threats from expert comments from both databases. Freshwater fish species that are already affected by other stresses are likely be using physiological, genetic, and behavioural resources to respond, and are therefore predicted to have especially acute responses to the additional impacts of climate change (Hare et al., 2016). Many CCVAs do not incorporate the effects of other stressors in analyses of vulnerability, primarily because they are not based on species' intrinsic biological or ecological traits. We included them because exposure to these threats is likely to increase sensitivity to climate change for reasons outlined above. We examined the degree to which incorporating exposure to other threats changed our findings. By removing the 'other stressors' trait set from the *sensitivity* dimension, the

number of species sensitive to climate declined by 174 species (2201 species qualify as sensitivity as opposed to 2375,) and the number of species vulnerable declined by 75 species (984 species qualify as highly vulnerable instead of 1059) under an optimistic, moderate emissions scenario for 2050. This indicates that exposure to other disturbances is likely to be a component that will be very important in species abilities to adjust to climate change.

Thresholds: We summed threats for each species creating a continuous variable of the number of threats experienced by each species. To account for uncertainty associated with assigning arbitrary cut-off points to determine which species should be considered highly threatened we calculated threat scores using two thresholds representing optimistic (fewer species given a high score) and pessimistic (more species given a high score) scenarios. In the optimistic scenario, species in the highest 25% of threats (≤ 7 threats) were given a high score, and in the pessimistic scenario species in the top 50% of number of threats (≤ 3 threats) were given a high score (Table A1). Optimistic and pessimistic scenarios are compared in Table A10 Figs. A2 and A3.

A.1.8.2 Low Adaptive Capacity

LACV 1: Intrinsic low probability of dispersal

Data on species' intrinsic probability of dispersal were limited, so we based these scores on an index derived from a recent study (Comte and Olden, 2018) that showed how various life-history traits are correlated with dispersal ability. This allowed us to incorporate a number of traits that were well represented in our dataset (e.g., degree of parental care) with some traits that were less well represented (e.g., longevity) to create an index describing dispersal capacity. While none of the traits in this index directly measure intrinsic dispersal ability, combining multiple traits that have been shown to correlate to dispersal capacity increases the accuracy of these estimates (Table A6).

LACV 2: Barriers to dispersal

Data on biogeographical dispersal barriers are not collected systematically by the IUCN or FishBase, and were therefore gleaned from comments sections from both datasets with

heavier representation of well-studied species. For this trait, we inferred barriers to dispersal primarily based on habitat types occupied by the species (i.e., those that are difficult to disperse from) and whether species are unable to transverse large areas of unsuitable habitat. We inferred which habitats would be hard to disperse from based on Carr et al. 2013, 2014 and Hare et al., 2016. Habitats that had the potential to limit dispersal are listed in Table A2. There is some overlap between these habitats, and those that gave species high scores for microhabitat specialization / site affinities. Although assessments often include altitudinal restrictions in this trait, we were not able to include altitude because of the limited data available for African freshwater fishes.

LACV 3: Dispersal of early life history stages

Direct information on the locations and pelagic stages of eggs and larvae were rare, so dispersal capacity of early life stages were inferred from the spawning behaviour of adults. To account for high levels of unknowns in this trait, spawning behaviour was inferred from congeners. If at least three species in a genus were documented to have the same spawning style, and no species in that genus had a different spawning style, all species within that genus were denoted to have the same spawning style. For example, because 8 out of 25 species in the genus *Maylandia* were documented to spawn in caves or rocky crevices, and none of them were reported to be pelagic spawners, the remaining 17 species were also assumed to spawn in caves or crevices.

Unknowns: There were 1808 species with no information on dispersal of early life-history stages. For these species we performed the LAC calculation for both optimistic (all unknowns assumed low) and pessimistic (all unknowns assumed high) scenarios. The main results for this paper present the optimistic scenario. Differences between the optimistic and pessimistic scenarios are presented in Table A10 Figs. A2 and A3).

LACV 4: Low reproductive capacity

Data on relative fecundity were very rare for species in this study, and were much too low to infer based on congeners without introducing too much error. Furthermore, here we assume that fishes with low fecundity will be more prone to climate change because of

lower reproductive rates, however some of the traits that go along with low relative fecundity might actually increase survival of some species, particularly if species are near carrying capacity limits, and if there are high levels of parental care for early life stages when survival is more difficult (Willi and Hoffmann, 2008). In general, however, there is evidence that species with higher reproductive rates will fare better in stressful conditions (Purvis et al., 2000; Williams et al., 2008; Pacifici et al., 2017).

Unknowns: There were 2693 species with no information on relative fecundity in our dataset. Because we had >2000 unknowns for this trait we did not assess unknowns as high for the optimistic scenario, as discussed in SV1.

LACV 5: Low population growth

Actual population growth rate and generation time is not measured in many fish species, particularly in tropical latitudes. Population growth rate was inferred from life history traits that categorize species as r-selected or k-selected (Table A7). We assumed that r-selected species will have high population growth (and therefore low *LAC*) and k-selected species will have low population growth (and therefore high *LAC*). Traits included in this assessment are longevity, generation time, size and age at maturity, absolute (as opposed to relative) fecundity, and body length (as a close correlate to all the above traits; Table A8). Although there are high levels of uncertainty in calculating population growth based on any one of these traits alone, by basing it on many different traits we were able to overcome some of this uncertainty (Hare et al., 2016). In addition, recent research has shown that for marine fishes, fast population growth rates increased the risk of collapse under climate change adding uncertainty to our assumptions (Pinsky and Byler, 2015); however it is unknown whether the same trend exists for freshwater fishes.

Unknowns: There were 55 species with no information on population growth in our dataset. For these species we performed the *LAC* calculation for both optimistic (all unknowns assumed low) and pessimistic (all unknowns assumed high) scenarios. The main results for this paper present the optimistic scenario. Differences between the optimistic and pessimistic scenarios are presented in Table A10 Figs. A2 and A3).

A.1.8.3 Exposure

EV 1 - 4: Changes in mean and variability in temperature and precipitation

Estimates of changes in mean temperature and precipitation and changes in variability in temperature and precipitation were derived by averaging values across species ranges following the methods of Foden et al. (2013; Section 1.4). For these estimates to be accurate we relied on accurate range distributions for the species and on accurate climate projections. To ensure accuracy of range distributions, we trimmed the IUCN range data to existing water bodies (Section 1.4). To ensure accuracy of climate change projections, we used the most current versions of the downscaled data, and averaged estimates across four models. We also performed calculations across three different emissions scenarios (high, moderate, and low) and two different years (2050 and 2090; Section 1.4).

Thresholds: Because climate change projections are continuous measures, we used arbitrary cut-off points following Foden et al. (2013) and Böhm et al. (2016) to determine whether species were given high or low scores in these traits. For the main analyses we used the 25% threshold where species with the highest 25% projected change were given a high score. To account for uncertainty associated with assigning arbitrary thresholds we also calculated scores based on the top 15% and top 35%. Differences among these thresholds and between years and emissions scenarios are shown in Table A10 and Figs. A3 and A4)

A.1.9 References

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A.2 Supplementary Tables

Table A1 Detailed descriptions of trait sets, variables, and thresholds qualifying species as high or low for three *vulnerability* dimensions (*sensitivity*, *low adaptive capacity*, and *exposure*) and for *conservation value*. The number of species classified as ‘high’, ‘low’, and ‘unknown’ for each trait set, variable, dimension, and threshold are provided. The last three columns indicate the numbers and proportions of species that were given a high score in a vulnerability dimension based exclusively on one variable, and the rank of importance of that variable within each dimension, based on the optimistic scenario and A1B emissions for 2050 (Fig. 1.5). Numbers and proportions of species qualifying for overall *sensitivity*, *low adaptive capacity*, *exposure*, *vulnerability* and *conservation value* in table headings, and numbers qualifying within each trait set (column 1) are also based on the optimistic scenario and A1B emissions for 2050.

Trait set	Variable	Description	Threshold / Definition	Classification	Number species	# sp. w/ high scores from only one variable	Percentage susceptible spp.	Rank
DIMENSION 1: SENSITIVITY (n = 2375; 84.8% of all species in dataset)								
I. Specialized habitat or microhabitat requirements (n = 727; 26.0% of all spp.)	1. Depth range	taxon is restricted to shallower habitats or shallow depths	restricted to shallow depths (< 3 m)	high	78	5	0.2105263	17
			not restricted to shallow depths	low	480			
			no information	unknown	2235			
	2. Habitat specialization	taxon is a habitat generalist or specialist	restricted to 1- 2 rare or climate change-vulnerable habitats Table A2)	high	79	6	0.2526316	16
			diverse or very common, widespread habitats	low	2531			
			no habitat information	unknown	183			
	3. Microhabitat specialization / site affinities	taxon is restricted to one rare or vulnerable habitat for at least part of life cycle	restricted to temporary pools, mountain rivulets, rapids, flooded areas, forest streams, submerged roots, mangroves, estuaries, lagoons, freshwater springs and oases, regions below waterfalls, or to specific temp., DO, bottom types	high	652	124	5.2210526	3
			all other taxa	low	2141			

Trait set	Variable	Description	Threshold / Definition	Classification	Number species	# sp. w/ high scores only from this trait	Percentage susceptible spp.	Rank
II. Narrow environmental tolerances (n = 1449; 51.2% of all spp.)	4. Tolerance to changes in precipitation	historical variability in precip. across the taxon's range	lowest 25% in AAD of precip. (≤ 56.1 mm)	high	691	84	3.5368421	4
			highest 75% in AAD of precip. (> 56.1 mm)	low	2102			
	5. Tolerance to changes in temperature	historical variability in temp. across the taxon's range	lowest 25% in AAD of temp. (≤ 0.66 °C)	high	682	200	8.4210526	1
			highest 75% in AAD of temp. (> 0.66 °C)	low	2111			
	6. Sensitivity to increases in turbidity: mating	taxon's mate recognition system affected by changes in turbidity	uses breeding colouration to attract mates, hybridization is a threat (e.g., haplochromine mouthbrooding cichlids)	high	267	19	0.8	7
			all other taxa	low	2526			
	7. Sensitivity to increases in turbidity: food collection	taxon's food gathering or prey selection affected by changes in turbidity	exclusive or nearly exclusive zooplanktivores feeding from water column (e.g., sardines), visual hunters	high	137	13	0.5473684	12
			all other taxa	low	2656			
	8. Dependence on precipitation activated trigger	Category 1	requires rainfall to migrate to breeding/spawning grounds	high	154	17	0.7157895	10
		Category 2	eggs develop in dry mud following rains (e.g., <i>Nothobranchius</i> spp.), requires rain to allow resubmergence (e.g., <i>Protopterus</i> spp.)	high	47			
		Category 3	juveniles require waters to retreat to migrate (e.g., some <i>Enteromius</i> spp.)	high	24			
			categories combined	total high	207			
			none of the above	low	2586			
III. Dependence on interspecific interactions (n = 316; 11.3% of all spp.)	9. Prey specificity	taxon is a prey generalist or specialist	specific to one type of prey (e.g., dependence on rocks with biocover). A taxon that relies on a whole group (e.g. 'insects') is given a low score unless they strongly prefer 2-3 specific taxa within that group (e.g., chironomids) (Table A3)	high	266	23	0.9684211	6
			consumes a wide variety of prey items	low	1287			
			no information	unknown	1240			
	10. Dependence	relies on another for some aspect of survival	relies on another for food, protection, or habitat (Table A4)	high	77	9	0.3789474	14
			not documented to rely on another species	low	2716			

Trait set	Variable	Description	Threshold / Definition	Classification	Number species	# sp. w/ high scores only from this trait	Percentage susceptible spp.	Rank
IV. Complexity of life history strategy (n = 307; 11.0% of all spp.)	11. Complexity in reproductive strategy	taxon relies on precise environmental / social cues, or rare habitats for reproduction	taxon relies on precise temps, seasons, aggregations, or rare habitats to spawn or breed (e.g., dependent on gravel or coarse sand for breeding).	high	242	19	0.8	8
			taxon is not documented to rely on precise cues or rare habitats for reproduction	low	2551			
	12. Complexity in early life history requirements	taxon's larvae or eggs rely on precise environmental cues, water conditions, or habitats for survival	larvae depend on specific environmental cues (e.g., temp.), environmental conditions (e.g., clear water) or habitats for survival, hatching, or settlement.	high	49	2	0.0842105	19
			larvae are not documented to be dependent on specific environmental cues, conditions, or habitats for survival of eggs and/or larvae	low	2744			
	13. Spawning cycle	number and duration of a taxon's spawning events	spawns only once, spawns a few times but over a short period of time (< 2 months)	high	70	5	0.2105263	18
			several spawnings throughout the year, more than one season, duration of > 2 months	low	312			
			no information	unknown	2411			
	14. Taxon abundance	taxon is rare or common	rare, narrow distribution (< 3 locations), declining (at least 2 of these)	high	455	28	1.1789474	5
			common, widespread, increasing (at least 1)	low	2035			
			no information	unknown	303			
V. Rarity continued (n = 774; 27.7% of all spp.)	15. Range size: extent of occurrence	taxon's extent of occurrence	strict : < 20000 km ²	high	601	15	0.6315789	11
			lenient : < 5000 km ²	high	350			
			strict : > 20000 km ²	low	2192			
			lenient : > 5000 km ²	low	2443			
	16. Range size: area of occupancy	taxon's area of occupancy	strict : < 2000 km ²	high	738	19	0.8	9
			lenient : < 500 km ²	high	397			
			strict : > 2000 km ²	low	2055			
			lenient : > 500 km ²	low	2396			
	17. Population fragmentation	taxon's populations are fragmented or very small	populations fragmented or very small	high	47	2	0.0842105	20
			populations are large and contiguous	low	1028			
			no information	unknown	1718			

Trait set	Variable	Description	Threshold / Definition	Classification	Number species	# sp. w/ high scores only from this trait	Percentage susceptible spp.	Rank
VI. Exposure to other disturbances (n = 1012; 36.2% of all spp.)	18. Fishing pressure	taxon is harvested for human consumption	strict: artisanal, commercial, or highly commercial	high	1078	145	6.1052632	2
			lenient: fishery is commercial or highly commercial	high	684			
			strict: taxon is not harvested	low	1715			
			lenient: taxon is not harvested or fished artisanally	low	2109			
	19. Other threats	number of threats currently affecting the taxon	strict : 4+ threats	high	686	7	0.2947368	15
			lenient : 7+ threats	high	135			
			strict : 0-3 threats	low	2107			
			lenient : 0-6 threats (Table A5)	low	2658			
	20. Threats intensified by climate change	number of threats	2 - 9 threats	high	371	11	0.4631579	13
			0 - 1 threats	low	2422			

DIMENSION 2: LOW ADAPTIVE CAPACTIY (n = 2000; 71.6% of all species in dataset)								
VII. Low potential for dispersal (n = 1263; 45.2% of all spp.)	1. Intrinsic low probability of dispersal	taxon has traits that lead to low dispersal syndromes (low disp. = high LAC)	taxon has a combination of: low fecundity, small body size, short generation, small length at maturity, short-lived, parental care, prey / habitat specialist (Table A6)	high	386	59	2.95	4
			all other taxa	low	2407			
	2. Barriers to dispersal	taxon's dispersal limited by ecological barriers /habitat affinities as adults	site-dependent adults restricted to high elevations, crater lakes, rapids, caves, mountain rivulets, rocks, freshwater springs, karst (Table A6)	high	539	207	10.35	3
			all other taxa	low	2254			
	3. Dispersal of early life stages	ability for taxon's eggs and larvae to disperse	eggs or larvae are benthic	high	774	255	12.75	2
			eggs or larvae are pelagic	low	211			
			no information	unknown	1808			
VIII. Low potential to evolve (n = 1211 43.4% of all spp.)	4. Reproductive capacity	taxon's mean annual relative fecundity	low relative fecundity of < 200 eggs / gram (lowest 75%)	high	23	18	0.9	5
			high relative fecundity of > 200 eggs / gram (highest 25%)	low	77			
			no information	unknown	2693			
	5. Population growth	taxon's potential for population growth based on life history characteristics (low pop. growth = high LAC)	species has no life history traits that correspond to high population growth (see Table A7)	high	1188	719	35.95	1
			species has at least one life history trait that corresponds to high population growth	low	1550			
			no information	unknown	55			

Trait	Variable	Description	Threshold / Definition Trait set	Classi- fication	Number of species	H-score exclusively on this trait	% of all susceptible spp.	Rank
DIMENSION 3: EXPOSURE (n = 1510; 54.1% of all species in dataset)								
IX. Predicted exposure to the effects of climate change (n = 1510; 54.1% of all spp.)	1. Changes in mean temperature	Average change in mean temp. (1975 - 2050) across range	strict : highest 35% (≥ 3.45 °C)	high	980	112	7.4172185	3
			mod : highest 25% (≥ 3.14 °C)	high	538			
			lenient : highest 15% (≥ 2.72 °C)	high	420			
			strict : lowest 65% (< 3.45 °C)	low	1813			
			mod : lowest 75% (< 3.14 °C)	low	2255			
			lenient : lowest 85% (< 2.72 °C)	low	2373			
	2. Changes in temperature variability	Average change in temp. AAD (1975 -2050 across taxon's range	strict : highest 35% (≥ 3.37 °C)	high	1108	258	17.086093	1
			mod : highest 25% (≥ 3.64 °C)	high	834			
			lenient : highest 15% (≥ 4.34 °C)	high	420			
			strict : lowest 65% (< 3.37 °C)	low	1685			
			mod : lowest 75% (< 3.64 °C)	low	1959			
			lenient : lowest 85% (< 4.34 °C)	low	2373			
	3. Changes in mean precipitation	Average change in mean precip. (1975 - 2050) across taxon's range	strict : highest 35% (≥ 25.5 mm)	high	987	134	8.8741722	2
			mod : highest 25% (≥ 26.2 mm)	high	929			
			lenient : highest 15% (≥ 34.5 mm)	high	420			
			strict : lowest 65% (< 25.5 mm)	low	1806			
			mod : lowest 75% (< 26.2 mm)	low	1864			
			lenient : lowest 85% (< 34.5 mm)	low	2373			
	4. Changes in precipitation variability	Average change in precip. AAD (1975 - 2050) across taxon's range	strict : highest 35% (≥ 18.0 mm)	high	981	107	7.0860927	4
			mod : highest 25% (≥ 21.0 mm)	high	527			
lenient : highest 15% (≥ 24.3 mm)			high	418				
strict : lowest 65% (< 18.0 mm)			low	1812				
mod : lowest 75% (< 21.0 mm)			low	2266				
lenient : lowest 85% (< 24.3 mm)			low	2375				
VULNERABILITY (n = 1059; 37.9% of all species in dataset)								

Trait	Variable	Description	Threshold / Definition Trait set	Classi- fication	Number of species	H-score exclusively on this trait	% of all susceptible spp.	Rank
CONSERVATION VALUE (n = 1714, 61.4% of all species in dataset)								
I. Endemism (n = 1267, 45.4%)	1. Endemism	taxon is endemic to a region	endemic	high	1267	571	33.313886	1
			not endemic	low	1526			
II. IUCN redlist status (n = 585; 20.9%)	2. Level of endangerment	taxon's listing under the IUCN vulnerability assessment	critically endangered (CR), endangered (EN), vulnerable (VU)	high	585	171	9.9766628	3
			least concern (LC), not threatened (NT)	low	1680			
			data deficient (DD)	unknown	528			
III. Importance for human use (n = 712, 25.5% of all spp.)	3. Fishing pressure	taxon is harvested for human consumption	strict :artisanal, commercial, or highly commercial	high	1078	207	12.077013	2
			lenient : fishery is commercial or highly commercial	high	684			
			strict : taxon is not harvested	low	1715			
			lenient : taxon is not harvested or fished artisanally	low	2109			
	4. Other uses	taxon is used by humans in other ways (see table A9)	strict 1+ use	high	949	24	1.4002334	4
			lenient : 2+ uses	high	69			
			strict : 0 uses	low	1844			
			lenient : ≤ 1 use	low	2724			

Table A2 Habitat classifications used to determine habitat or micro-habitat specialization.

(A) IUCN habitat classifications and codes and (B) common micro-habitats determined in this study, along with their frequency of occurrence in our dataset, whether the habitat is considered rare or climate-change threatened, and whether the habitat is difficult to disperse from. Habitats include some coastal and marine environments (i.e., habitats in categories 9.x, 10.x and 12.x) because we included all species that use freshwaters for any portion of their life cycle including diadromous, anadromous, and estuarine species. (C) Habitat types from the Global Lakes and Wetlands Database (GLWD) used to determine the rarity of habitat types in Africa based on the proportion of all freshwater pixels contained in a raster map of freshwater habitat types. Stars in the rarity column indicate that they were designated as rare based on GLWD habitat data.

A. IUCN habitat types in this study					
Code	Description	Freq.	Rare	Climate-change threatened	Restrict dispersal
1.8	Subtropical/tropical swamp	1			
4.6	Subtropical/tropical seasonally wet/flooded	2		prone to temperature change, seasonal	
5.1	Permanent rivers/streams/creeks (incl. falls)	1767			
5.2	Seasonal/intermittent/irregular rivers/streams/creeks	1190		prone to temperature change, seasonal	yes
5.3	Shrub dominated wetlands	30			
5.4	Bogs, marshes, swamps, fens, peatlands	368		prone to temperature change	yes
5.5	Permanent freshwater lakes (≥ 8 ha)	1364			
5.6	Seasonal/intermittent freshwater lakes (≥ 8 ha)	410		prone to temperature change, seasonal	
5.7	Permanent freshwater marshes/pools (≤ 8 ha)	1003			
5.8	Seasonal/intermittent freshwater marshes/pools (under 8ha)	899		prone to temperature change, seasonal	
5.9	Freshwater springs and oases	21	yes	prone to temperature change	yes
5.11	Alpine wetlands (incl. waters from snowmelt)	1	yes	prone to temperature change, seasonal	
5.13	Permanent inland deltas	108			
5.14	Permanent saline, brackish or alkaline lakes	20	yes*	seasonal	yes
5.15	Seasonal saline, brackish, alkaline lakes	18	yes*		yes
5.16	Permanent saline, brackish, alkaline marshes	33	yes*		yes
5.17	Seasonal/ saline, brackish or alkaline marshes	30	yes*	prone to temperature change, seasonal	yes
5.18	Karst and subterranean hydrological systems	4			yes
7.1	Caves and subterranean habitats	1			yes
9.1	Estuaries	68	yes*	prone to temperature change	yes
9.2	Subtidal rock and rocky reefs	2		prone to temperature change	yes
9.3	Subtidal loose rock/pebble/gravel	2			
9.4	Subtidal sandy	3			
9.5	Subtidal sandy-mud	3			
9.6	Subtidal muddy	4			
9.7	Macro-algae/kelp	2			
9.8.4	Lagoon	13	yes*	prone to temperature change	yes
9.9	Seagrass (submerged)	6		prone to temperature change	
10.1	Epipelagic (0-200m)	6			
10.2	Mesopelagic (200-1000m)	4			

10.3	Bathypelagic (1000-4000m)	1		
12.1	Intertidal rocky shoreline	2		prone to temperature change
12.2	Intertidal sandy shoreline, beach, sand bars	2		prone to temperature change
12.3	Intertidal shingle, pebble shoreline beaches	1		prone to temperature change
12.4	Intertidal mud flats and salt flats	6		prone to temperature change
12.5	Intertidal salt marshes (emergent grasses)	5		prone to temperature change
12.6	Intertidal tidepools	5		prone to temperature change
12.7	Intertidal mangrove submerged roots	24		prone to temperature change
13.4	Coastal brackish/saline lagoons/marine lakes	26	yes*	prone to temperature change
13.5	Coastal freshwater lakes	18	yes*	
15.1	Water storage areas (over 8ha)	56		
15.11	Marine anthropogenic structures	1		
15.13	Marine/brackish culture ponds	1		
15.2	Ponds (below 8ha)	35		
15.3	Aquaculture ponds	22		
15.4	Salt exploitation sites	1		
15.5	Excavations (open)	1		
15.6	Wastewater treatment areas	2		
15.7	Irrigated land (includes irrigation channels)	19		
15.8	Seasonally flooded agricultural land	15		
15.9	Canals and drainage channels, ditches	42		
* Habitats deemed rare according to the GLWD habitat data				

B. Common microhabitats and site affinities				
Description		Rare	Climate-change threatened	Restrict dispersal
Specific do and t conditions	63	yes		yes
Specific soil type	21	yes		
Temporary pools	103	yes	prone to temperature change	yes
Mountain rivulets	44	yes	prone to temperature change	yes
Small rapids/creels	135	yes	prone to temperature change	yes
Flooded areas	19	yes	prone to temperature change, seasonal	
Rainforest gallery streams	143	yes		yes
Submerged roots	50	yes		yes
Below waterfalls	16	yes		yes
Springs and spring-fed streams, oases	12	yes		yes
Rock-dwellers	35			
Dense stands of plants	5			
Estuaries/lagoons	65	yes	prone to temperature change	yes
Mangroves	44	yes	prone to temperature change	yes

C. GLWD habitat types			
Description	Pixel count	Proportion	Area (km²)
Freshwater marsh / floodplain	862559	41.06796056	741800.74
Intermittent wetland	333311	15.86952661	286647.46
Lake + river	355919	16.9459335	306090.34
Swamp forest, flooded forest	209646	9.981617096	180295.56
Pan, Brackish/Saline wetland	155168	7.387823099	133444.48
Coastal wetland	129822	6.181055182	111646.92
Reservoir	53797	2.561370381	46265.42
Bog / fen	99	0.004713565	85.14

Table A3 Summary of 16 diet categories included in SV9, and their frequency in our dataset.

Diet category	Frequency
Fish	418
Insect juvenile	656
Insect adult	94
Crustaceans	211
Molluscs	156
Other macroinvertebrates	259
Macrophyte	205
Mud/detritus	195
Fish eggs	34
Fish scales/fins	22
Zooplankton	232
Seeds	13
Phytoplankton	174
Algae	257
Rock biocover	215
Other	53

Table A4 Summary of 11 categories of interspecific interactions included in SV10, and their frequency in our dataset.

Interspecific interactions	Frequency
Parasite cleaner	2
Specialized paedophage	3
Brood parasite	3
Kleptoparasite	4
Scale/fin eater	3
Relies on another to stir up sediments	4
Food source provided by another (other)	26
Shell dweller	12
Habitats provided by another (other)	5
Mutualisms	12
Other	3

Table A5 Threat classifications used by the IUCN, their frequency of occurrence in our dataset, and whether the threat is likely to be directly intensified by climate change. Bolded values represent totals within broader categories, but do not necessarily represent the sum of the sub-categories as some species were classified only under broad categories.

Category	Threat	Frequency	Intensified?
1. Residential & commercial development	1.1 Housing & urban areas	95	
	1.2 Commercial & industrial areas	39	
	1.3 Tourism & recreation areas	21	
2. Agriculture & aquaculture	2.1 Annual & perennial non-timber crops	315	
	2.1.2 Small-holder farming	240	
	2.1.3 Agro-industry farming	75	
	2.2 Wood & pulp plantations	26	
	2.2.1 Small holder plantations	12	
	2.2.2 Agro-industry plantations	14	
	2.3 Livestock farming & ranching	26	
	2.3.2 Small-holder grazing, ranching or farming	18	
	2.3.3 Agro-industry grazing, ranching or farming	8	
3. Energy production & mining	2.4 Marine & freshwater aquaculture	58	
	3.1 Oil & gas drilling	65	
	3.2 Mining & quarrying	357	
4. Transportation & service corridors	3.3 Renewable energy	2	
	4.1 Roads & railroads	51	
	4.2 Utility & service lines	5	
5. Biological resource use	4.3 Shipping lanes	50	
	5.2 Gathering terrestrial plants	32	
	5.3 Logging & wood harvesting	381	
	5.3.1 Intentional use: subsistence/small scale	374	
	5.3.2 Intentional use: large scale	7	
	5.4 Fishing & harvesting aquatic resources	1084	
6. Human intrusions & disturbance	5.4.1 Intentional use: subsistence/small scale	690	
	5.4.2 Intentional use: large scale	394	
	6.1 Recreational activities	8	
7. Natural system modifications	6.2 War, civil unrest & military exercises	31	
	6.3 Work & other activities	4	
	7.2 Dams & water management/use	814	
	7.2.1 Abstraction of surface water (domestic use)	10	yes
	7.2.2 Abstraction of surface water (commercial / agricultural use)	130	yes
	7.2.5 Abstraction of ground water (domestic use)	2	yes
	7.2.6 Abstraction of ground water (commercial / agricultural use)	198	yes
	7.2.9 Small dams	197	
	7.2.10 Large dams	277	
	7.3 Other ecosystem modifications	11	
8. Invasive & problem species	8.1 Invasive non-native/alien species/diseases	281	
	8.2 Problematic native species/diseases	175	
9. Pollution	9.1 Domestic & urban waste water	390	
	9.1.1 Sewage	177	
	9.1.2 Run-off	7	
	9.2 Industrial & military effluents	433	
	9.2.1 Oil spills	76	
	9.2.2 Seepage from mining	106	
	9.3 Agricultural & forestry effluents	988	
9. Pollution	9.3.1 Nutrient loads	78	yes
	9.3.2 Soil erosion, sedimentation	941	yes
	9.3.3 Herbicides and pesticides	79	yes
	9.4 Garbage & solid waste	5	
	9.5 Air-borne pollutants	3	

	9.5.1 Acid rain	1	
	9.6 Excess energy	1	
	9.6.2 Thermal pollution	1	
10. Geological	10.1 Volcanoes	25	
11. Climate change & severe weather	11.1 Habitat shifting & alteration	167	
	11.2 Droughts	107	yes
	11.3 Temperature extremes	2	yes
	11.4 Storms & flooding	2	yes
12. From FishBase	1 deoxygenation	127	yes
	2 crater lake burping CO2 gas	25	yes
	3 blockages to spawning migration	44	yes

Table A6 Scoring regime for intrinsic dispersal ability including traits used to develop scores for low and high intrinsic probability of dispersal, each trait's relationship to dispersal ability according to Comte and Olden (2018), how points were awarded, and the number of species with estimates for each trait.

Trait	Relationship to dispersal	Low dispersal	High dispersal	Species w/ estimates
Habitat specificity	-	very specific (H) = 2 points	not specific (L) or unknown = 0 points	2616
Prey specificity	-	very specific (H) = 2 points	not specific (L) or unknown = 0 points	2793
Depends on biocover	-	depends on rocks with biocover (H) = 2 points	does not depend on rocks with biocover or unknown (L) = 0 points	2793
Temperature specificity	-	not variable (L) = 2 points; slightly variable = 1 point	highly variable (H, VH) = 0 points	2793
Precipitation specificity	-	not variable (L) = 2 points; slightly variable = 1 point	highly variable (H, VH) = 0 points	2793
Parental care	-	high levels of parental care (H) = 1 point	no parental care (L) or unknown = 0 points	2793
Combination of life history parameters (see below)		≤ 3 LH parameters that lead to low dispersal rates = 2 points	> 3 LH parameters that lead to high dispersal rates = 0 points	2747
Scoring system		> 5 LOW DISPERSAL POINTS = HIGH SCORE (low probability of dispersal)	≤ 5 LOW DISPERSAL POINTS = LOW SCORE (high probability of dispersal)	
Life history traits combined		Life history parameters that lead to low dispersal rates	Life history parameters that lead to high dispersal rates	
Longevity	+	short lived (< 2 Y); lowest 10%	long lived (> 2 Y)	57
Years to maturity	+	young age at maturity (< 1 Y); lowest 25%	older age at maturity (> 1 Y)	83
Length at maturity	+	small length at maturity (< 7 cm); lowest 25%	large length at maturity (> 7 cm)	204
Mean fecundity	+	low fecundity (< 3000 eggs); lowest 75%	high fecundity (> 3000 eggs)	210
Relative fecundity	+	low relative fecundity (< 200 eggs/g); lowest 75%	high relative fecundity (> 200 eggs/g)	100
Body size (TL)	+	small body size (< 12.5 cm); lowest 75%	large body size (> 12.5 cm)	2747

Table A7 Scoring regime for population growth rate including traits used to develop scores for low and high population growth rate, their relationship to dispersal ability according to Musick et al. (1999), how points were awarded, and the number of species with estimates for each trait.

Trait	High population growth	Low population growth	Species w/ estimates
Life history traits	Life history parameters that lead to high pop gr (r-selected)	Life history parameters that lead to low pop gr (k-selected)	
VonBertalanffy growth (K)	high K (> 0.50); highest 50%= 1 POINT	low K (< 0.50) = 0 POINTS	53
longevity	short lived (< 10 Y); lowest 10% = 1 POINT	long lived (> 10 Y) = 0 POINTS	57
years to maturity	young age at maturity (< 3 Y); lowest 25% = 1 POINT	older age at maturity (> 3 Y) = 0 POINTS	83
length at maturity	small length at maturity (< 20 cm); lowest 25% = 1 POINT	large length at maturity (> 20 cm) = 0 POINTS	204
mean fecundity	high fecundity (> 3000 eggs); highest 25% = 1 POINT	low fecundity (< 3000 eggs) = 0 POINTS	210
body size (TL)	small body size (lowest 25%) = 1 POINT	large body size (highest 75%) = 0 POINTS	2747
Scoring	2+ population growth points = high therefore low score for LAC	≤1 population growth points = low therefore high score for LAC	

Table A8 Pearson's correlations and sample sizes (N) showing relationships between average adult body length (total length) and the life-history traits (longevity, age at maturity, length at maturity, and fecundity) used to develop scores for high and low population growth rates in this study. * indicates significance at $\alpha \leq 0.01$

Life-history variables	N	Pearson's correlations				
		Total length	Longevity	Age at maturity	Length at maturity	Fecundity
Longevity (mo)	34	0.697*	1			
Age at maturity (mo)	52	0.753*	0.843*	1		
Length at maturity (cm)	112	0.841*	0.676*	0.620*	1	
Fecundity (# eggs)	125	0.479*	0.145	-0.056	0.159	1

Table A9 Summary of the 6 categories of human uses included in CV4, and their frequency in our dataset.

Human use categories	Frequency
Aquaculture	54
Bait fish	28
Aquarium trade	839
Game fish	79
Biocontrol agent	15
Other uses	15

Table A10 Numbers and proportions of species that were classified as being highly vulnerable under various combinations of three emissions scenarios (low [B1], moderate [A1B], and high [A2]), years (2050 and 2090), and optimistic vs. pessimistic scenarios.

	2050-OPTIMISTIC		2050-PESSIMISTIC		2090-OPTIMISTIC		2090-PESSIMISTIC	
B1	1036	(37.1%)	1384	(49.6%)	1293	(46.3%)	1802	(64.5%)
A1B	1059	(37.9%)	1440	(51.6%)	1691	(60.5%)	2533	(90.6%)
A2	1202	(43.0%)	1607	(57.5%)	1734	(62.1%)	2609	(93.4%)

Table A11 Numbers and proportions of species within families that were classified as: *sensitive, low adaptive capacity, exposed, vulnerable*, and of high *conservation value*. Orange bars indicate families comprised of ≥ 9 species with over 50% high scores in each category. These values are based on the optimistic scenario of the A1B emissions scenario for 2050. Not all families are included in this table due to uncertain taxonomic resolution.

Order	Family	Total	Sensitive		Exposed		LAC		Vulnerable		Cons. Value	
			#	%	#	%	#	%	#	%	#	%
Anguilliformes	Anguillidae	3	3	100	0	0	3	100	0	0	3	100
	Ophichthidae	3	2	67	2	67	3	100	1	33	0	0
Characiformes	Alestidae	108	90	83	35	32	33	31	8	7	49	45
	Citharinidae	6	4	67	1	17	6	100	1	17	3	50
	Distichodontidae	90	70	78	24	27	32	36	5	6	30	33
	Hepsetidae	1	1	100	0	0	1	100	0	0	1	100
Clupeiformes	Clupeidae	24	18	75	4	17	7	29	1	4	9	38
	Denticipitidae	1	1	100	0	0	1	100	0	0	1	100
Cypriniformes	Balitoridae	1	0	0	1	100	0	0	0	0	0	0
	Cobitidae	1	1	100	1	100	1	100	1	100	1	100
	Cyprinidae	502	391	78	262	52	255	51	117	23	243	48
Cyprinodontiformes	Cyprinodontidae	4	4	100	4	100	1	25	1	25	4	100
	Nothobranchiidae	213	209	98	151	71	175	82	127	60	160	75
	Poeciliidae	59	51	86	28	47	30	51	14	24	31	53
Elopiformes	Elopidae	1	1	100	1	100	1	100	1	100	1	100
	Megalopidae	1	1	100	0	0	0	0	0	0	1	100
Gonorynchiformes	Kneriidae	30	26	87	14	47	10	33	3	10	12	40
	Phractolaemidae	1	1	100	0	0	1	100	0	0	0	0
Lepidosireniformes	Protopteridae	7	7	100	0	0	7	100	0	0	2	29
Mugiliformes	Mugilidae	3	3	100	0	0	3	100	0	0	3	100
Osmeriformes	Galaxiidae	1	1	100	0	0	1	100	0	0	0	0
Osteoglossiformes	Arapaimidae	1	1	100	0	0	0	0	0	0	1	100
	Gymnarchidae	1	1	100	0	0	1	100	0	0	1	100
	Mormyridae	172	145	84	66	38	113	66	39	23	49	28
Perciformes	Notopteridae	3	2	67	0	0	3	100	0	0	1	33
	Pantodontidae	1	1	100	0	0	0	0	0	0	1	100
	Anabantidae	26	21	81	7	27	10	38	1	4	12	46
	Channidae	2	1	50	0	0	2	100	0	0	0	0
	Cichlidae	920	823	89	651	71	862	94	579	63	807	88
	Eleotridae	12	8	67	5	42	6	50	2	17	2	17
	Gobiidae	19	17	89	9	47	9	47	4	21	4	21
	Kuhliidae	1	1	100	0	0	1	100	0	0	1	100
	Latidae	7	7	100	2	29	6	86	2	29	7	100
	Polycentridae	1	1	100	0	0	1	100	0	0	1	100
	Soleidae	1	0	0	0	0	1	100	0	0	0	0
	Polypteridae	11	9	82	3	27	11	100	3	27	3	27
Polypteriformes	Salmonidae	3	3	100	2	67	3	100	2	67	2	67
Salmoniformes	Amphiliidae	70	59	84	35	50	30	43	18	26	26	37
Siluriformes	Ariidae	2	2	100	1	50	2	100	1	50	2	100
	Austroglanididae	3	3	100	3	100	2	67	2	67	3	100
	Bagridae	9	9	100	4	44	8	89	4	44	6	67
	Clariidae	73	60	82	31	42	64	88	24	33	38	52
	Claroteidae	73	59	81	25	34	60	82	16	22	40	55
	Malapteruridae	16	14	88	7	44	16	100	6	38	2	13
	Mochokidae	189	154	81	94	50	131	69	52	28	100	53
	Schilbeidae	31	23	74	8	26	17	55	5	16	12	39
	Mastacembelidae	35	28	80	10	29	33	94	8	23	24	69
	Synbranchidae	2	2	100	2	100	2	100	2	100	0	0
	Syngnathidae	7	7	100	3	43	6	86	3	43	5	71
	Tetraodontidae	6	5	83	3	50	5	83	2	33	3	50
Synbranchiformes												
Syngnathiformes												
Tetraodontiformes												

Table A12 Numbers and proportions of species within families that were classified as high latent risk (Sens & LAC), potential adapters (Sens & Exp), potential persisters (Exp & LAC) and that did not score high for any vulnerability dimension. These values are based on the optimistic scenario of the A1B emissions scenario for 2050. Not all families are included in this table due to uncertain taxonomic resolution.

Order	Family	Sens & LAC		Sens & Exp		Exp & LAC		No high score	
		Count	%	Count	%	Count	%	Count	%
Anguilliformes	Anguillidae	3	100	0	0	0	0	0	0
	Ophichthidae	1	33	0	0	1	33	0	0
	Alestadidae	19	17	24	22	0	0	10	9
Characiformes	Citharinidae	3	50	0	0	0	0	0	0
	Distichodontidae	23	25	14	15	2	2	12	13
	Hepsetidae	1	100	0	0	0	0	0	0
Clupeiformes	Clupeidae	4	17	2	8	1	4	4	17
	Denticipitidae	1	100	0	0	0	0	0	0
	Balitoridae	0	0	0	0	0	0	0	0
Cypriniformes	Cobitidae	0	0	0	0	0	0	0	0
	Cyprinidae	93	18	107	21	18	4	45	9
	Cyprinodontidae	0	0	3	75	0	0	0	0
Cyprinodontiformes	Nothobranchiidae	47	22	23	11	1	0	3	1
	Poeciliidae	15	25	13	22	0	0	7	12
	Elopidae	0	0	0	0	0	0	0	0
Elopiformes	Megalopidae	0	0	0	0	0	0	0	0
	Kneriidae	7	23	9	30	0	0	2	7
Gonorynchiformes	Phractolaemidae	1	100	0	0	0	0	0	0
Lepidosireniformes	Protopteridae	7	100	0	0	0	0	0	0
Mugiliformes	Mugilidae	3	100	0	0	0	0	0	0
Osmeriformes	Galaxiidae	1	100	0	0	0	0	0	0
	Arapaimidae	0	0	0	0	0	0	0	0
	Gymnarchidae	1	100	0	0	0	0	0	0
Osteoglossiformes	Mormyridae	54	30	19	11	8	4	4	2
	Notopteridae	2	67	0	0	0	0	0	0
	Pantodontidae	0	0	0	0	0	0	0	0
	Anabantidae	9	35	4	15	0	0	3	12
	Channidae	1	50	0	0	0	0	0	0
	Cichlidae	207	22	27	3	42	5	13	1
	Eleotridae	4	33	2	17	0	0	3	25
Perciformes	Gobiidae	5	24	4	19	1	5	1	5
	Kuhliidae	1	100	0	0	0	0	0	0
	Latidae	4	57	0	0	0	0	0	0
	Monodactylidae	0	0	1	100	0	0	0	0
	Polycentridae	1	100	0	0	0	0	0	0
	Soleidae	0	0	0	0	0	0	0	0
Pleuronectiformes	Polypteridae	7	50	0	0	0	0	0	0
Salmoniformes	Salmonidae	1	33	0	0	0	0	0	0
	Amphiliidae	8	11	15	21	0	0	5	7
	Ariidae	1	50	0	0	0	0	0	0
	Austroglanididae	0	0	1	33	0	0	0	0
	Bagridae	4	44	0	0	0	0	0	0
	Clariidae	28	38	2	3	4	5	0	0
	Claroteidae	34	46	6	8	2	3	2	3
Siluriformes	Malapteruridae	8	47	0	0	1	6	0	0
	Mochokidae	52	27	28	15	11	6	4	2
	Schilbeidae	10	32	1	3	1	3	5	16
	Mastacembelidae	18	50	1	3	1	3	0	0
	Synbranchidae	0	0	0	0	0	0	0	0
Synbranchiformes	Synbranchidae	0	0	0	0	0	0	0	0
Syngnathiformes	Syngnathidae	3	43	0	0	0	0	0	0
Tetraodontiformes	Tetraodontidae	2	33	1	17	0	0	0	0

A.3 Supplementary Figures

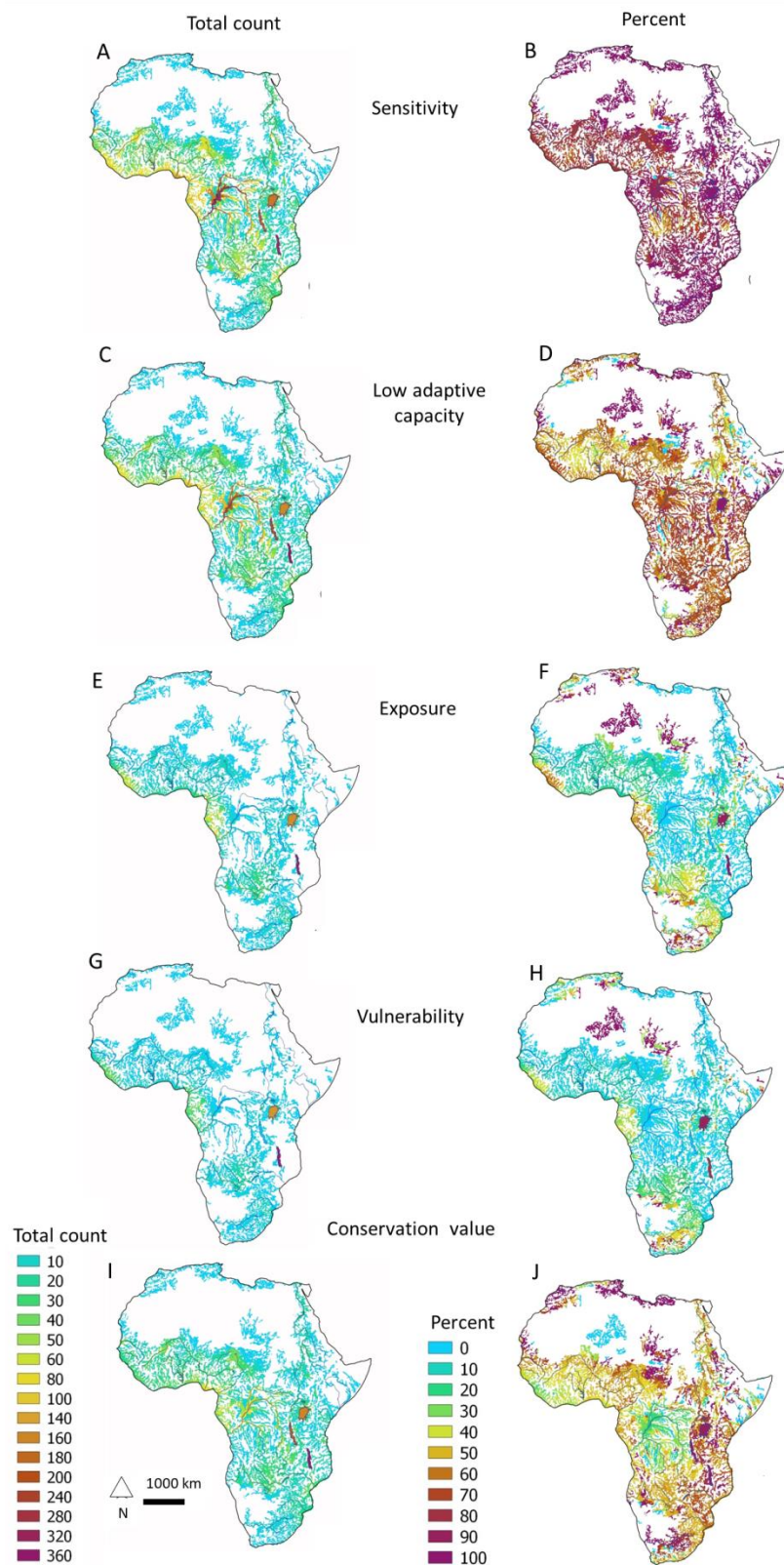


Figure A1 Geographic concentrations of freshwater fish species that are highly sensitive (AB), of low adaptive capacity (CD), exposed (EF), highly climate change vulnerable (GH) and of high conservation value (IJ). The left-hand column (Figs. A, C, E, G, and I) represents the total count of all species, while the right-hand column (Figs. B, D, F, H, and J) represents the proportion of total species. These values are based on the optimistic scenario of the A1B emissions scenario for 2050.

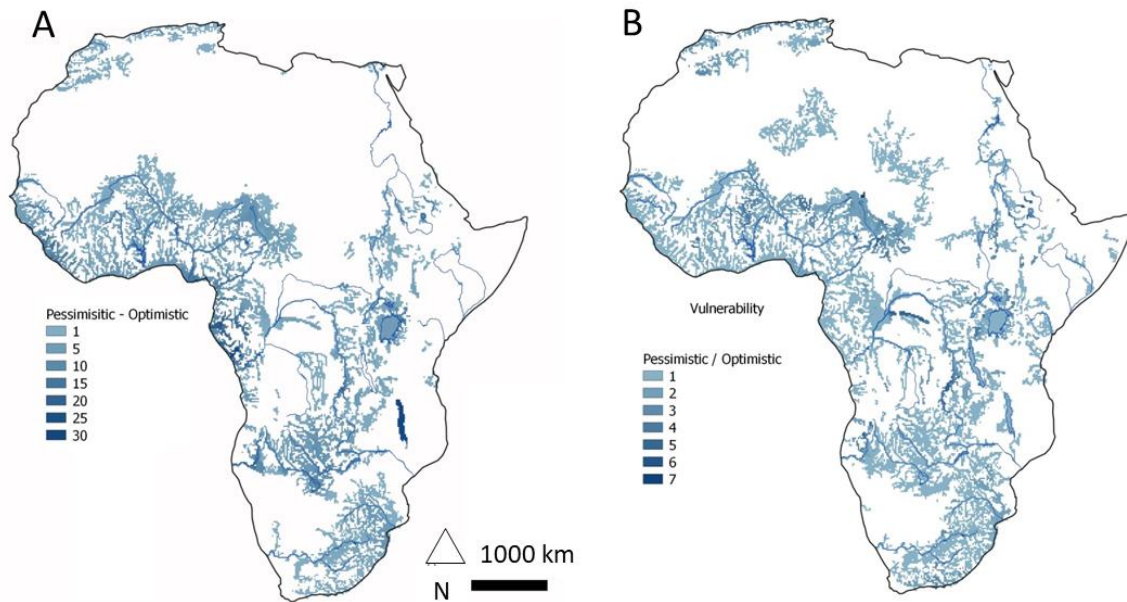


Figure A2 Geographic concentrations of freshwater fish species that are highly vulnerable to climate change under a pessimistic scenario (unknowns = high, strict thresholds) relative to the optimistic scenario (unknowns = low, lenient thresholds). (A) The absolute difference between the optimistic and pessimistic scenarios (pessimistic – optimistic) representing the total number of extra species that would be vulnerable under the pessimistic situation. A score of 10 indicates that 10 more species would be vulnerable in that region. (B) The relative difference between the optimistic and pessimistic scenarios (pessimistic / optimistic) indicating the proportionate increase in species vulnerability in a given region. A score of 7 indicates that there are 7x more vulnerable species in that region. These calculations are based on the A1B climate change emission scenario for 2050.

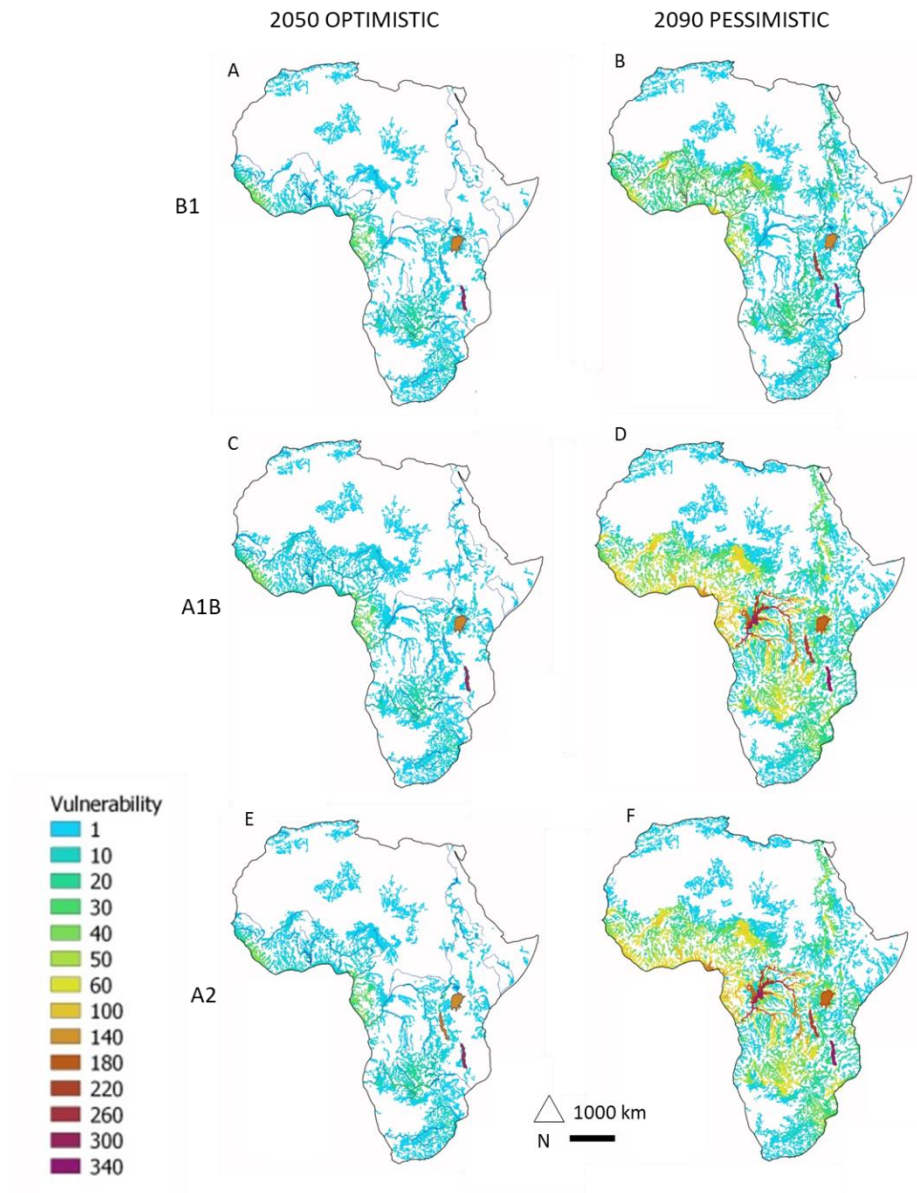
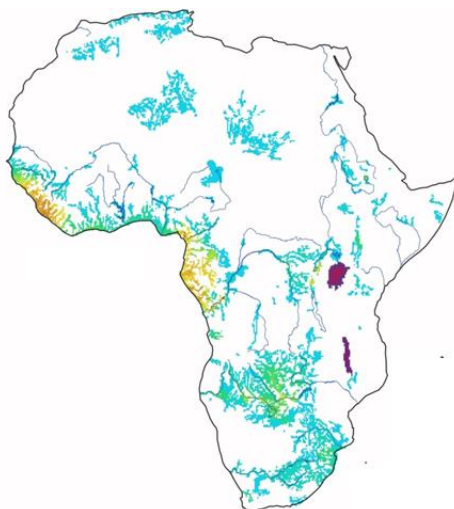


Figure A3 Geographic concentrations of vulnerable freshwater fish species under three different emissions scenarios: low (B1, panels AB), moderate (A1B, panels CD), and high (A2, panels EF). Panels on the left show data for 2050 under the optimistic scenario (unknowns = low, lenient thresholds), while panels on the right show data for 2090 under the pessimistic scenario (unknowns = high, strict thresholds). Total numbers of species qualifying as vulnerable in each scenario are presented in Table A10.

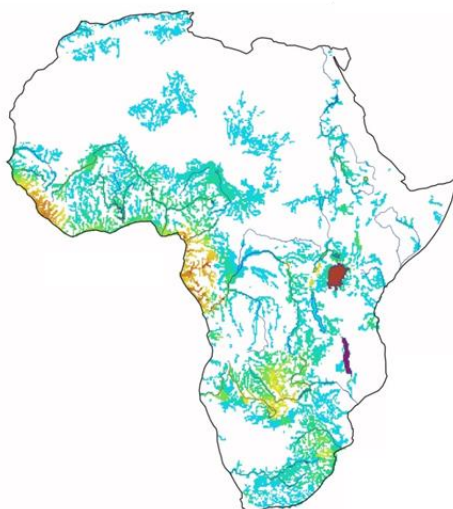
A 15%

894, 32.0%



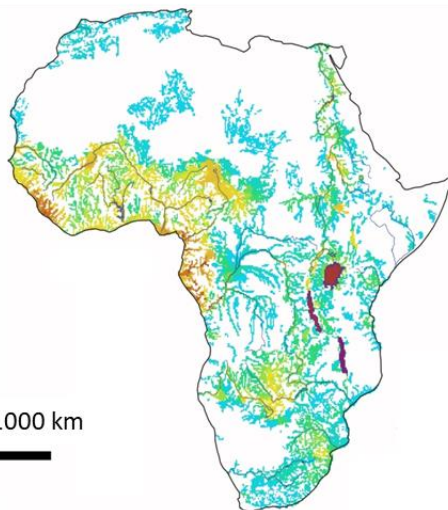
B 25%

1059, 37.9%

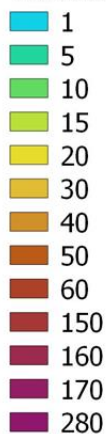


C 35%

1340, 48.0%



Vulnerability



1000 km
N

Figure A4 Geographic

concentrations of vulnerable species under three climate change thresholds. (A) Lenient threshold: species in regions with the highest 15% of climatic changes are considered vulnerable. (B) Moderate threshold: species in the highest 25% of climate change are considered vulnerable. (C) Strict threshold: species in the highest 35% of climate change are considered vulnerable. All figures are based on an optimistic scenario under the A1B emission scenario for 2050. Total numbers and percentages of species qualifying as vulnerable in each scenario are presented to the left of each map.

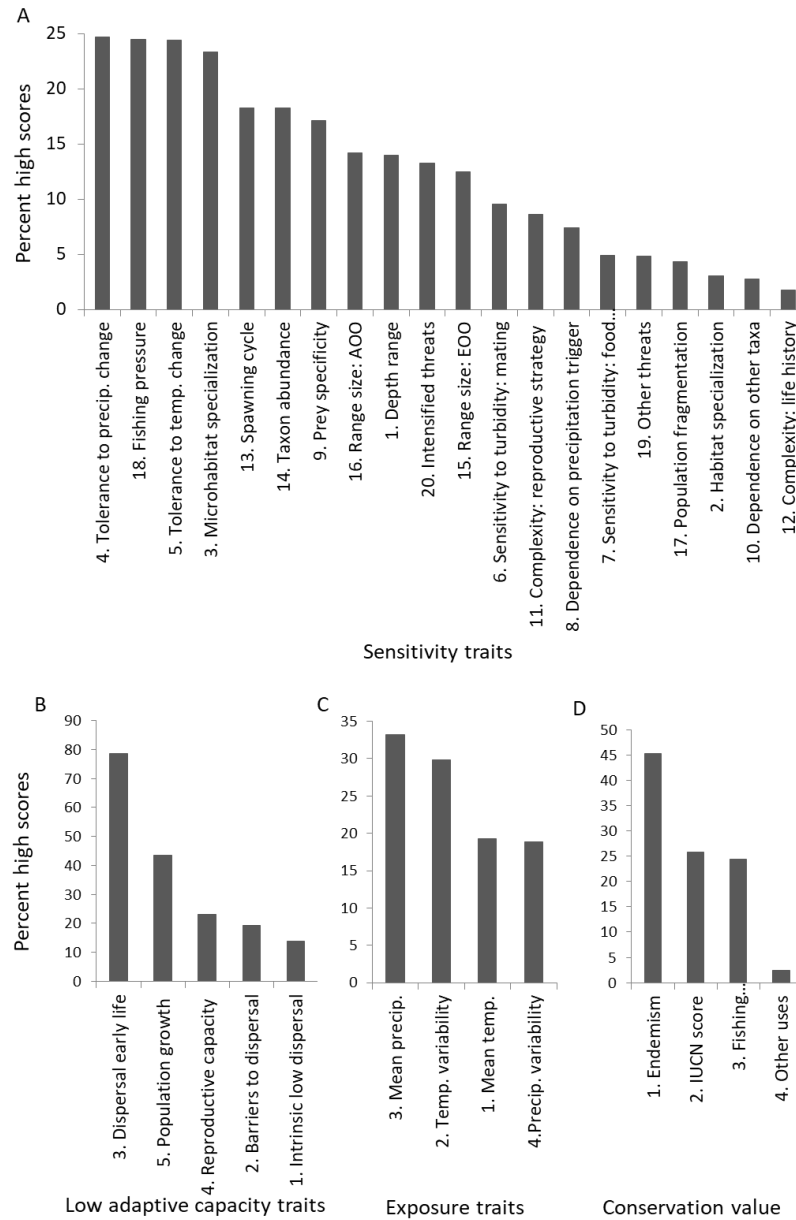


Figure A6 Summary of the proportion species with high scores for each variable within each vulnerability dimension: A) *sensitivity*, B) *low adaptive capacity* and C) *exposure*, and the number of species with high scores for each variable within D) *conservation value*. Proportions are calculated from known traits only (unknowns excluded). Traits are ranked by importance (from largest impact to smallest) within each dimension. Data are based on an optimistic scenario under the A1B emission scenario for 2050.

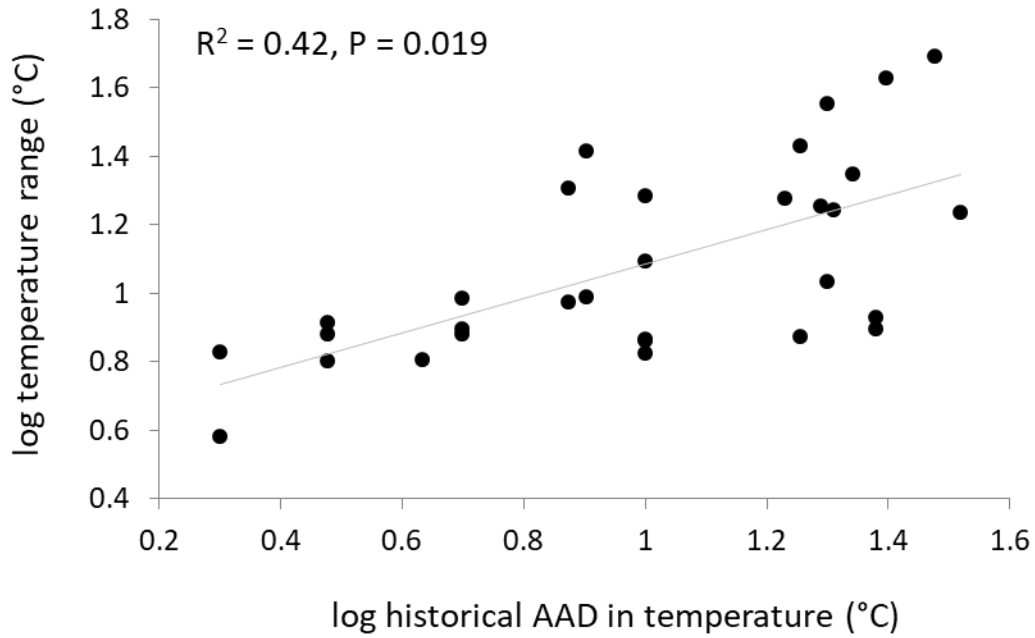


Figure A7 Pearson's correlation between absolute average deviation (AAD) of historical (1960 - 1990) temperatures across a species' range, versus species-specific temperature range data. Values were \log_{10} transformed to meet assumptions of this statistical test.

A.4 Supporting Scripts

Script A1 Creating univariate and bivariate maps (R studio)

LOAD NECESSARY LIBRARIES

```
library(devtools)
library(classInt)
library(raster)
library(rgdal)
library(dismo)
library(XML)
library(maps)
library(sp)
library(sf)
library(colorspace)
library(rasterVis)
library(foreign)
library(rio)
library(dplyr)
library(tidyr)
library(spatialEco)
library(Hmisc)
library(rgeos)
library(ggplot2)
library(tidyverse)
library(mapedit)
library(mapview)
library(leaflet.extras)
library(ggmap)
library(maps)
library(mapdata)
library(broom)
library(stringi)
library(qdap)
```

ADD ALL SPECIES RASTER LAYERS TO MAKE TOTAL COUNTS FOR UNIVARIATE MAPS

```
##load the data with all the scores including the fish IDs
spec.data<-(read.csv("C:/... scores.csv"))
```

```
##set the working directory to be the file where the individual presence/absence species rasters are
stored
setwd("C:/...speciesrasters")
```

```
## create a list of all the .tif files in the working directory
```

```
id <- dir(pattern = "*.tif$")
```

```
## create a baser file that is all 0s (repeat for each new trait)
```

```
baser<-raster("C:/...anyspeciesraster.tif")
```

```
baser[baser>-1]<-0
```

```
baser[is.na(baser)]<-0
```

```
plot(baser)
```

```
##loop to create the univariate raster layer for richness, vulnerability dimensions, etc.
```

```
for(i in 1:length(id)){
```

```
  r <- raster(id[i])
```

```
  r[is.na(r)]<-0
```

```
  spname <- id[i]
```

```
  spname <- gsub(spname, pattern = "*.tif", replacement = "")
```

```
  uniraster <- spec.data[spec.data$id==spname,"traitofinterest"]
```

```
  baser <- baser + uniraster*r
```

```
}
```

```
#plot and write raster
```

```
#colours and breakpoints can be adjusted
```

```
my.colors = colorRampPalette(c("cadetblue1", "seagreen1", "green3",
```

```
  "yellowgreen", "yellow2", "orange",
```

```
  "orangered1", "red", "magenta", "magenta1"))
```

```
breakpoints<-c(1,2,5,10,20,50,100,150,200,250,300,350,400)
```

```
plot(baser, col = my.colors(13), breaks=breakpoints, legend.shrink = 2)
```

```
writeRaster(baser,"C:/...uniraster.tif" )
```

```
#load and plot new univariate raster files for visualization
```

```
uniraster <- raster("C:/...uniraster.tif")
```

```
plot(uniraster, col = my.colors(13), breaks=breakpoints, legend.shrink = 2 )
```

```
# raster calculations (after creation of different raster layers following the steps above)
```

```
# calculate proportions
```

```
percent_uniraster <- uniraster/speciesrichnessraster*100
```

```
# pessimistic vs optimistic
```

```
pessminusopt <- pessimisticraster – optimisticroaster
```

```
pessdivopt <- pessimisticraster / optimisticroaster
```

##CODE FOR CREATING BIVARIATE MAPS: <http://rfunctions.blogspot.com/2015/03/bivariate-maps-bivariatemap-function.html/>

```
##colour matrix function
```

```
colmat<-function(nquantiles=10, upperleft=rgb(0,150,235, maxColorValue=255),
```

```
upperright=rgb(130,0,80, maxColorValue=255), bottomleft="white", bottomright=rgb(255,230,15,
```

```
maxColorValue=255), xlab="x label", ylab="y label"){
```

```
  my.data<-seq(0,1,.01)
```

```

my.class<-classIntervals(my.data,n=nquantiles,style="quantile")
my.pal.1<-findColours(my.class,c(upperleft,bottomleft))
my.pal.2<-findColours(my.class,c(upperright, bottomright))
col.matrix<-matrix(nrow = 101, ncol = 101, NA)
for(i in 1:101){
  my.col<-c(paste(my.pal.1[i]),paste(my.pal.2[i]))
  col.matrix[102-i,]<-findColours(my.class,my.col)}
plot(c(1,1),pch=19,col=my.pal.1, cex=0.5,xlim=c(0,1),ylim=c(0,1),frame.plot=F, xlab=xlab,
ylab=ylab,cex.lab=1.3)
for(i in 1:101){
  col.temp<-col.matrix[i-1,]
  points(my.data,rep((i-1)/100,101),pch=15,col=col.temp, cex=1)}
seqs<-seq(0,100,(100/nquantiles))
seqs[1]<-1
col.matrix<-col.matrix[c(seqs), c(seqs)]}

col.matrix <- colmat(nquantiles=10, xlab = "")

```

##bivariate map function

```

bivariate.map<-function(rasterx, rastery, colormatrix=col.matrix, nquantiles=10){
  quanmean<-getValues(rasterx)
  temp<-data.frame(quanmean, quantile=rep(NA, length(quanmean)))
  brks<-with(temp, unique (quantile(temp,na.rm=TRUE, probs = c(seq(0,1,1/nquantiles)))))
  r1<-within(temp, quantile <- cut(quanmean, breaks = brks, labels = 2:length(brks),include.lowest =
TRUE))
  quantr<-data.frame(r1[,2])
  quanvar<-getValues(rastery)
  temp<-data.frame(quanvar, quantile=rep(NA, length(quanvar)))
  brks<-with(temp, unique(quantile(temp,na.rm=TRUE, probs = c(seq(0,1,1/nquantiles)))))
  r2<-within(temp, quantile <- cut(quanvar, breaks = brks, labels = 2:length(brks),include.lowest = TRUE))
  quantr2<-data.frame(r2[,2])
  as.numeric.factor<-function(x) {as.numeric(levels(x))[x]}
  col.matrix2<-colormatrix
  cn<-unique(colormatrix)
  for(i in 1:length(col.matrix2)){
    ifelse(is.na(col.matrix2[i]),col.matrix2[i]<-1,col.matrix2[i]<-which(col.matrix2[i]==cn)[1])}
  cols<-numeric(length(quantr[,1]))
  for(i in 1:length(quantr[,1])){
    a<-as.numeric.factor(quantr[i,1])
    b<-as.numeric.factor(quantr2[i,1])
    cols[i]<-as.numeric(col.matrix2[b,a])}
  r<-rasterx
  r[1:length(r)]<-cols
  return(r)}

```

##use the bivariate.map function to create maps

```

bivmap<-bivariate.map(rasterX, rasterY , colormatrix=col.matrix, nquantiles=10)

```

```
## write bivariate map
writeRaster(bivmap,"C:/...bivraster.tif" )

#load and plot new bivariate raster files for visualization
bivraster <- raster("C:/...bivraster.tif")
plot (bivraster, frame.plot=F,axes=F,box=F,add=F,legend=F,col=as.vector(col.matrix))
```

##THE FOLLOWING CODE IS FOR MAKING THE FINAL BIVARIATE MAPS FOR PUBLICATION

```
##set the working directory
setwd("C:/...BivMaps")

##import the Africa map outline (created in QGIS) and simple water layer; plot together
africa_outline <-readOGR("C:/....Africa_Natural_Earth.shp")
water <- readOGR("C:/...Africa_major_rivers_lakes.shp")

##set margins
par(mar=c(2,2,2,2))

##plot the different layers to a high resolution .tif file
tiff("bivraster.tiff", height = 6, width = 6, units = 'in', res=1000)
plot(bivraster, frame.plot=F,axes=F,box=F,add=F,legend=F,col=as.vector(col.matrix))
plot(africa_outline, border= "black", lwd = 1, add = TRUE)
plot(water, col = "navy", lwd = 0.3, add = TRUE)
dev.off()
```

##THE FOLLOWING CODE IS FOR MAKING THE FINAL UNIVARIATE MAPS FOR PUBLICATION (same except for the colour scheme used)

```
##set the working directory
setwd("C:/...UniMaps")

##import the Africa map outline and simple water layer; plot together
africa_outline <-readOGR("C:/....Africa_Natural_Earth.shp")
water <- readOGR("C:/...Africa_major_rivers_lakes.shp")

##set margins
par(mar=c(2,2,2,2))

##plot the different layers to a high resolution .tif file
tiff("uniraster.tiff", height = 6, width = 6, units = 'in', res=1000)
plot(uniraster, col = my.colors(13), breaks=breakpoints, legend.shrink = 2)
plot(africa_outline, border= "black", lwd = 1, add = TRUE)
plot(water, col = "navy", lwd = 0.3, add = TRUE)
dev.off()
```

Appendix B: Supplementary materials for Chapter 2

B.1 Supplementary tables

Table B1. Time (min) for fish to reach standard metabolic rate (SMR) estimated through visual inspection of recovery curves and through statistical analysis of breakpoints after the chase protocol (C) and after transfer (T) without chasing. For the breakpoint analysis, Chow tests were used to determine whether the coefficient of the slope before and after the breakpoint differ from one another. The last breakpoint at which slopes differ was taken as the point at which the fish can be said to have achieved SMR. These were compared to points selected through visual assessment of raw Mo_2 values. Differences between Chow tests and visual estimates, and differences in recovery time for C vs T were calculated.

Stressor	Fish ID	Visual (min)	Breakpoint (min)	Difference between estimates	Difference between C and T (visual)	Difference between C and T (breakpoint)
Chase (C)	1	200	200	0	60	70
	2	240	190	50	40	50
	3	200	140	40	0	20
	Mean	213	177	30	33	46
Transfer (T)	1	140	130	10		
	2	200	140	60		
	3	200	160	40		
	Mean	180	143	37		

B.2 Supplementary figures

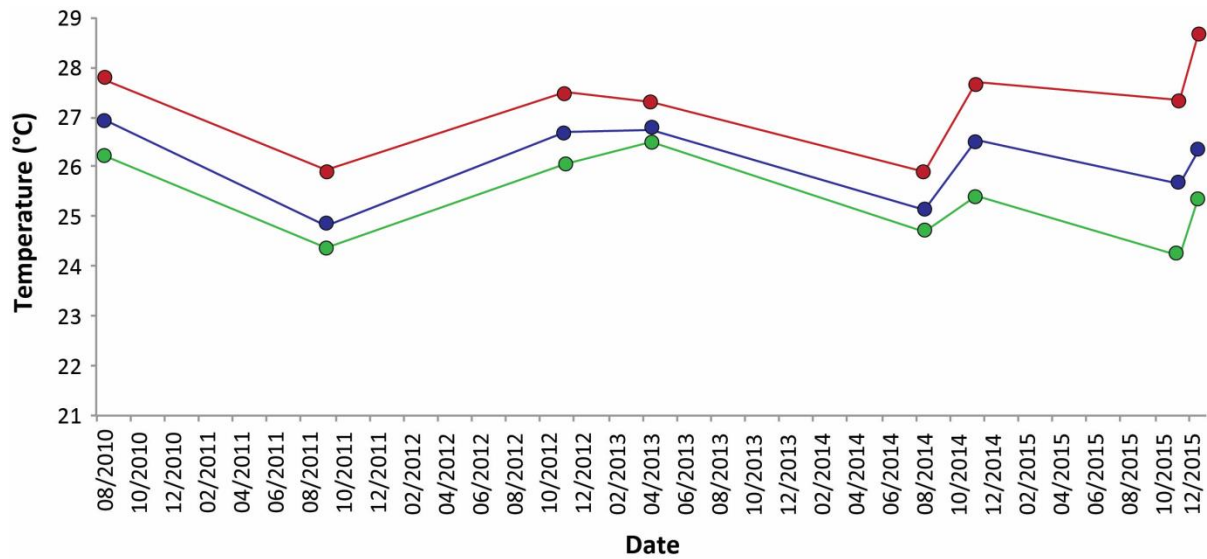


Figure B1. Maximum (red), average (blue), and minimum (green) monthly temperatures at near-shore locations around Entebbe Bay, Lake Victoria, Uganda, taken from August 2010 to December 2015. Data were compiled by E. Nyboer from 4 temperature-monitoring projects including the Sonfish Survey Project (NaFIRRI, 2013, 2015), the Lakewide Survey Project (LVEMP, 2011, 2012 & 2015), the ARDC Survey Project (Kajjansi, 2014), and the PhD research of W. Nkalubo (NaFIRRI, 2010).

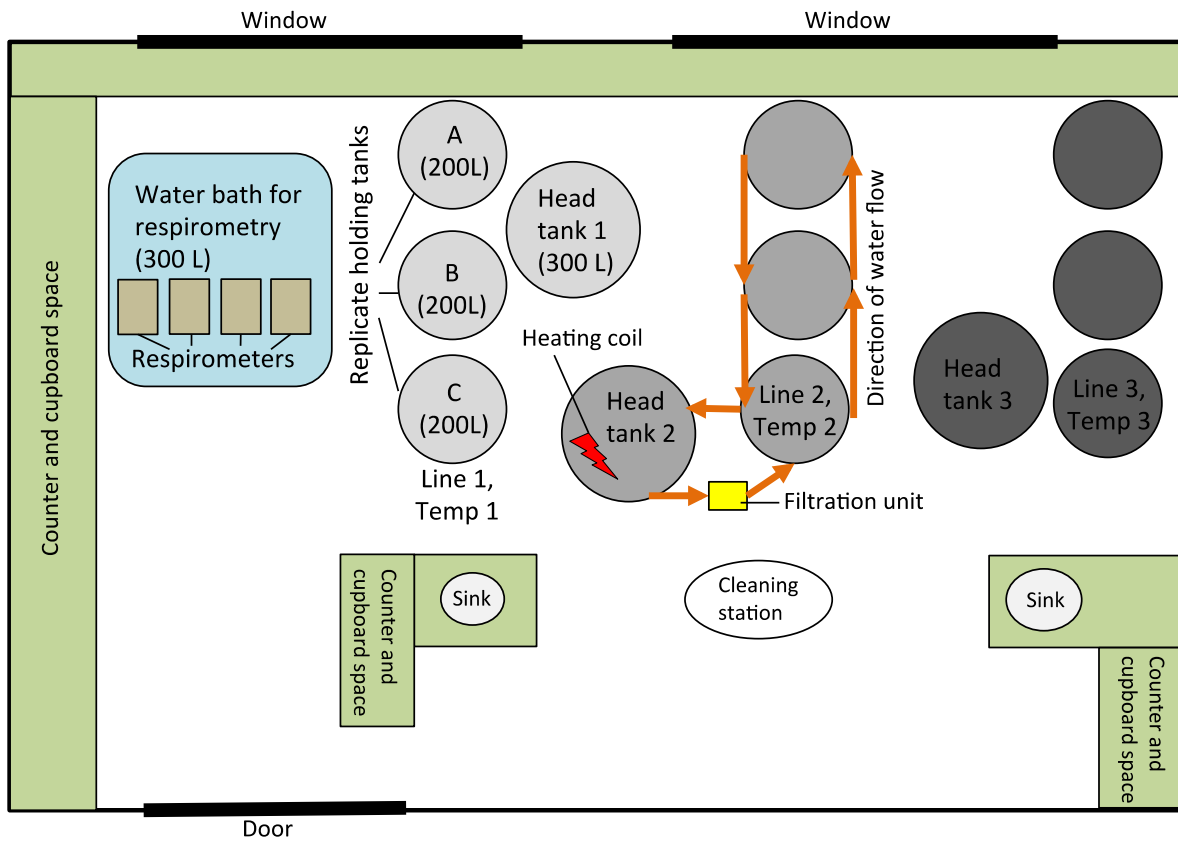


Figure B2. Schematic diagram of the respirometry laboratory at the Aquaculture Research and Development Center in Kajjansi, Uganda.

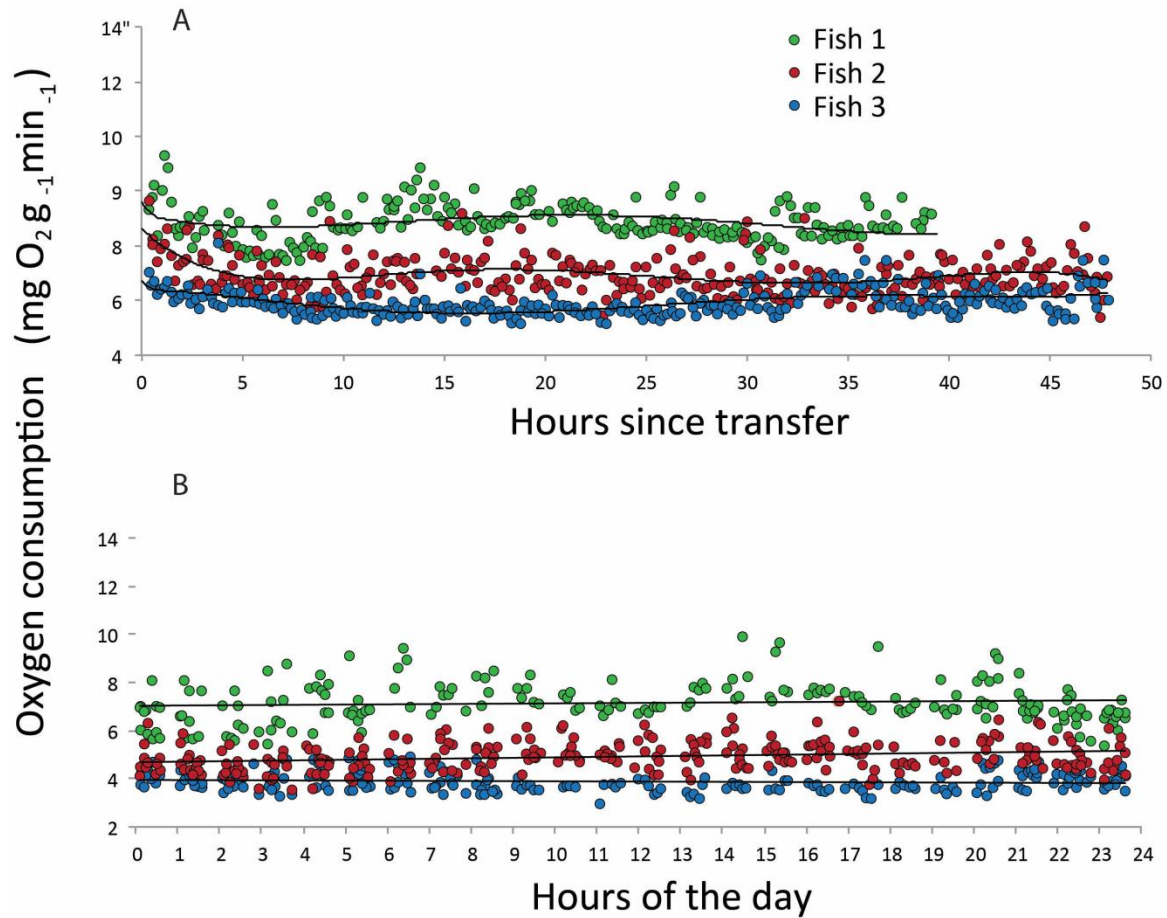


Figure B3. Raw oxygen consumption (Mo_2) values of three Nile perch plotted against hours since transfer (A) and hours of the day (B) to detect diel cycles of metabolic activity over 48 hours. In panel A, T_0 corresponds to the time the fish were put into the respirometers (~9am) showing that there are no major changes in Mo_2 over 48 hours in SMR after the fish have settled. In panel B, T_0 corresponds to midnight and data are averaged across the two 48-h cycles showing that there are no changes in Mo_2 at particular times of day.

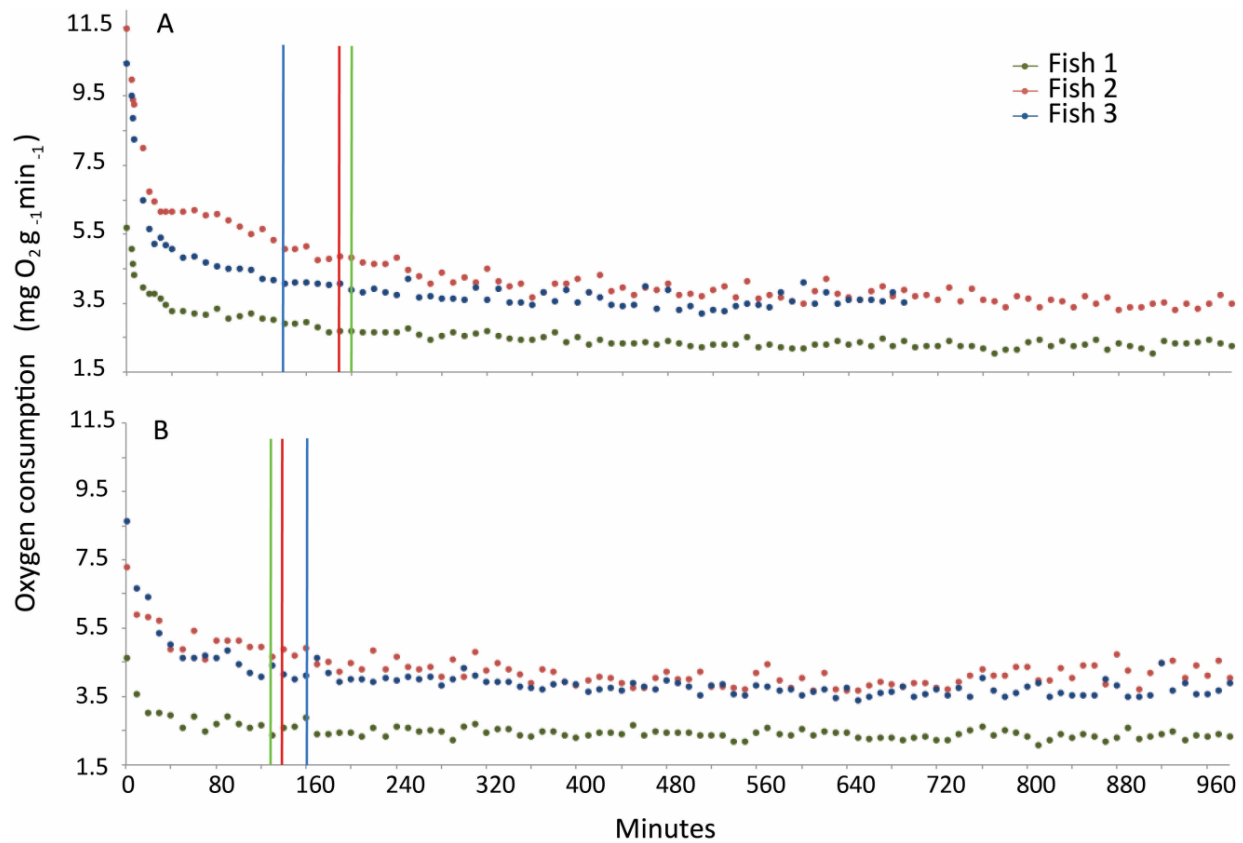


Figure B4. Recovery times of three Nile perch after experiencing the chase protocol (A) and transfer to the respirometer without chasing (B). Vertical lines represent breakpoints after which the change in slope of a given curve is no longer significant as determined by Chow tests. These breakpoints were compared to visual estimates of recovery time to estimate the point at which the fish can be said to have reached SMR after experiencing a stressor.

Appendix C: Supplementary materials for Chapter 3

C.1 Supplementary tables

Table C1. Sample sizes (N) and means \pm s.e.m. of body mass (Mb), standard length (SL) and total length (TL) of wild juvenile Nile perch stocked into 3 replicate blocks of containing among 2 rearing regimes: T_{avg} ($\sim 25^{\circ}\text{C}$) representing current average temperatures in Lake Victoria and T_{warm} ($\sim 29^{\circ}\text{C}$) representing conditions predicted under climate change. The average age of Nile perch stocked in the rearing ponds was estimated to be ~ 2 months based on the von Bertalanffy length-at-age growth equation calculated using previously published growth parameters for Lake Victoria Nile perch (Nkalubo et al., 2012).

Rearing Regime	Block	N	Mb (g)	SL (cm)	TL (cm)
T_{avg}	1	100	17.76 ± 0.60	10.16 ± 0.29	12.33 ± 0.46
	2	100	19.41 ± 0.74	10.30 ± 0.29	12.42 ± 0.47
	3	100	21.64 ± 0.74	10.24 ± 0.25	12.31 ± 0.44
T_{warm}	1	100	18.45 ± 0.65	10.28 ± 0.26	12.46 ± 0.42
	2	100	19.83 ± 0.65	10.37 ± 0.26	12.55 ± 0.43
	3	100	19.31 ± 0.56	10.28 ± 0.24	12.57 ± 0.39
TOTAL		600	19.41 ± 6.69	10.27 ± 1.16	12.42 ± 1.39

Table C2. Means \pm s.e.m. for water quality variables: maximum and minimum temperature, lux (luminosity), dissolved oxygen (DO), pH, and turbidity (Secchi depth), across rearing regimes (T_{avg} and T_{warm}) and among replicates (blocks) within a rearing regime.

Rearing regime	Block	Max. temp. (°C)	Min. temp. (°C)	Lux (lm m ⁻²)	Avg. DO (mg L ⁻¹)	pH	Secchi (cm)
T_{avg}	mean	24.5 \pm 0.70	23.0 \pm 0.62	85.8 \pm 55.0	4.253 \pm 1.56	6.965 \pm 0.62	51.9 \pm 9.92
	1	24.4 \pm 0.66	22.9 \pm 0.63	82.5 \pm 56.3	4.081 \pm 1.49	7.018 \pm 0.63	51.75 \pm 10.69
	2	24.5 \pm 0.74	22.9 \pm 0.62	96.5 \pm 57.2	4.352 \pm 1.52	6.95 \pm 0.64	51.25 \pm 9.80
	3	24.5 \pm 0.71	23.0 \pm 0.57	78.1 \pm 53.3	4.325 \pm 1.68	6.933 \pm 0.60	52.71 \pm 9.32
T_{warm}	mean	28.6 \pm 1.41	27.1 \pm 1.53	112.587 \pm 63.4	4.358 \pm 1.60	6.86 \pm 0.60	50.81 \pm 10.59
	1	29.1 \pm 1.56	27.7 \pm 1.79	114.222 \pm 65.1	4.261 \pm 1.82	6.928 \pm 0.65	49.57 \pm 10.52
	2	28.6 \pm 1.38	27.2 \pm 1.34	94.592 \pm 54.1	4.411 \pm 1.55	6.793 \pm 0.55	50.47 \pm 10.53
	3	28.2 \pm 1.04	26.4 \pm 1.02	128.039 \pm 66.0	4.403 \pm 1.43	6.857 \pm 0.60	52.37 \pm 10.70

Table C3. Sample sizes (N) and means \pm s.e.m. of body mass (Mb), standard length (SL), and total length (TL) for juvenile Nile perch in each rearing regime used in analyses of critical thermal maximum (CT_{max}), relative ventricular mass (RVM), percent compact myocardium (%CM), gill metrics, relative brain mass (RBM), and hepatosomatic index (HSI). Sample sizes were selected to ensure adequate power based on known levels of variability in the traits measured.

Trait	Rearing regime	N	Mb (g)	TL (cm)	SL (cm)
CT_{max}	Tavg	9	29.14 \pm 2.00	15.34 \pm 0.31	12.76 \pm 0.28
	Twarm	10	31.40 \pm 3.64	15.99 \pm 0.56	13.25 \pm 0.48
RVM	Tavg	19	34.73 \pm 3.19	15.03 \pm 0.37	12.79 \pm 0.31
	Twarm	18	39.11 \pm 3.89	15.78 \pm 0.45	13.13 \pm 0.39
%CM	Tavg	19	34.73 \pm 3.19	15.3 \pm 0.37	12.79 \pm 0.31
	Twarm	17	40.39 \pm 3.89	15.92 \pm 0.46	13.25 \pm 0.39
Gills	Tavg	9	37.21 \pm 3.23	15.58 \pm 0.41	13.03 \pm 0.33
	Twarm	10	36.96 \pm 3.47	15.65 \pm 0.42	12.96 \pm 0.35
Brains	Tavg	11	39.35 \pm 4.41	15.83 \pm 0.52	13.23 \pm 0.43
	Twarm	12	41.31 \pm 3.35	16.13 \pm 0.42	13.44 \pm 0.36
HSI	Tavg	19	34.73 \pm 3.19	15.3 \pm 0.370	12.79 \pm 0.31
	Twarm	13	38.21 \pm 4.65	15.68 \pm 0.49	13.08 \pm 0.42

Table C4. Results of 2-way ANCOVA on raw organ masses and percent of complex myocardium among two rearing temperatures (T_{avg} vs. T_{warm}) and among replicates (block) with body mass (Mb) as a covariate.

Variables		Rearing regime	Block	Mb	$Mb \times RR$
Ventricle mass (g)	$F_{(1, 31)}$	11.933	0.475	203.411	31.831
	P	0.002	0.627	<0.001	<0.001
	η^2	0.278	0.030	0.868	0.507
Liver mass (mg)	$F_{(1, 27)}$	24.828	0.303	85.008	
	P	<0.001	0.741	<0.001	
	η^2	0.479	0.022	0.759	
% Compact myocardium	$F_{(1, 31)}$	10.306	0.888	3.114	
	P	0.003	0.442	0.087	
	η^2	0.250	0.054	0.091	
Brain mass (mg)	$F_{(1, 19)}$	0.146	0.012	14.380	
	P	0.706	0.988	0.001	
	η^2	0.008	0.001	0.431	

Table C5. Eigenvalues, percent variance explained, and correlation of each gill metric on the components extracted in the PCA analysis. Gill traits are total hemibranch area (THA), total gill filament length (TGFL), average gill filament length (AGFL), total filament number (TFN), and filament base length (FBL). Filament density (D) was not included in the PCA analysis because it did not correlate with the other traits.

	PC1	PC2
Eigenvalue	3.327	1.346
% Variance	66.5	26.9
THA (mm²)	0.890	0.428
TGFL (mm)	0.881	0.440
AGFL (mm)	0.991	-0.108
TFN (mm)	0.203	0.915
FBL (mm)	0.115	0.918

C.2 Supplementary figures

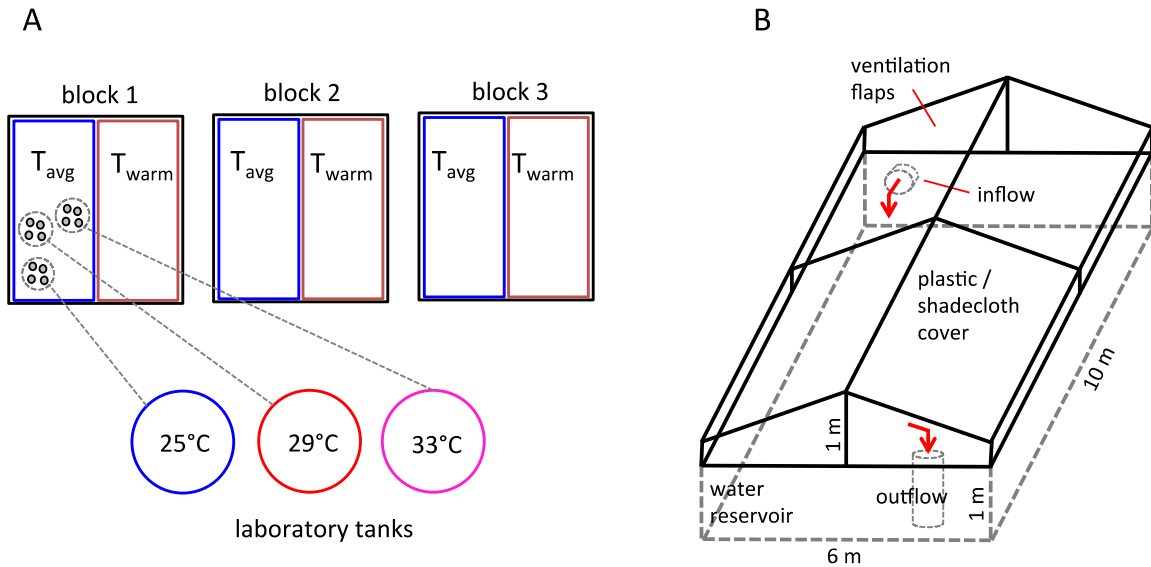


Figure C1. A schematic diagram of the experimental layout. Panel A shows 3 blocks containing one replicate of the T_{warm} and one replicate of the T_{avg} rearing ponds. 2 - 4 fish (represented by grey dots) from each rearing pond were exposed to each of the 3 laboratory temperatures, as represented by the dashed grey lines from the T_{avg} pond in block 1. Panel B is a diagram of one plastic- or shade cloth-covered rearing pond highlighting key components of the heating and cooling design.

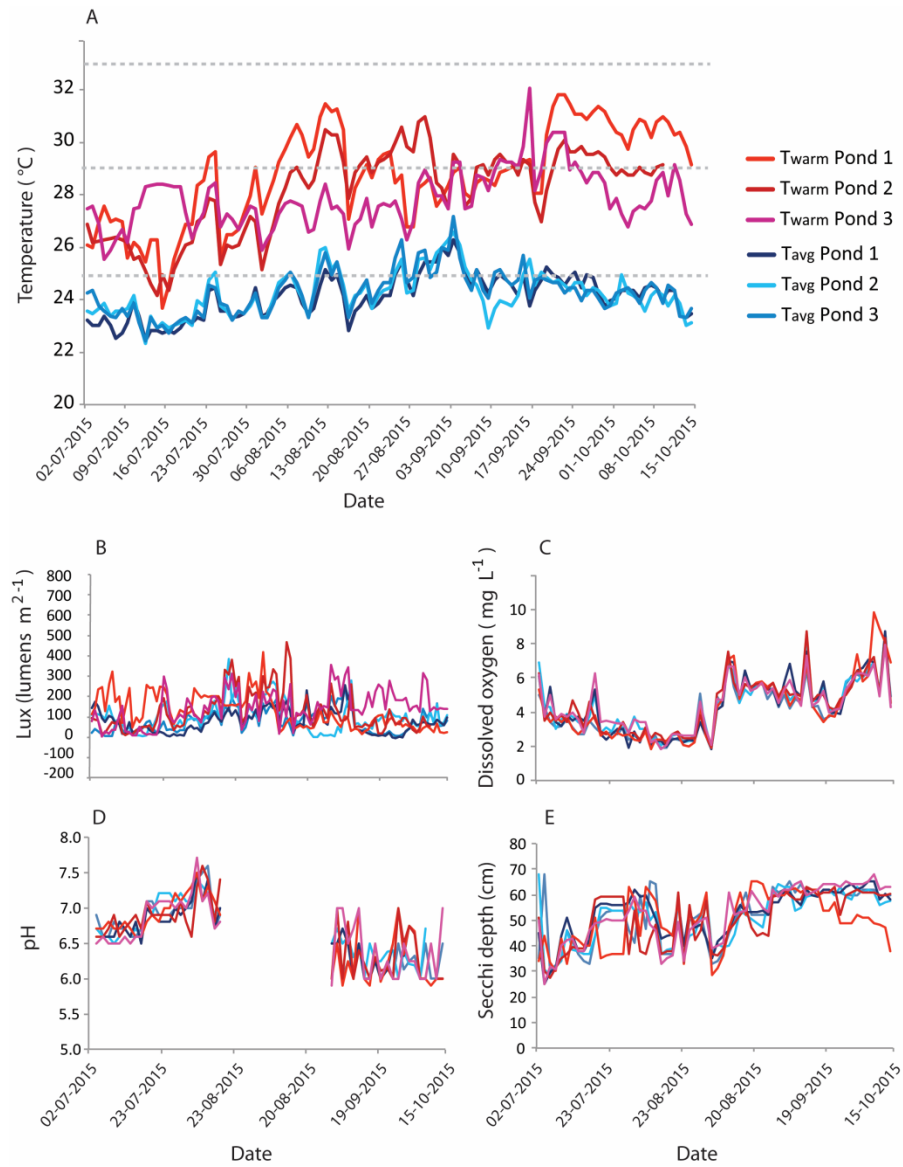


Figure C2. Plots of raw pond water quality data over the 3-month rearing period (19-Jul. –25-Oct., 2015). In all panels each line represents a pond replicate, with T_{warm} tanks in red tones and T_{avg} tanks in blue tones. Panel A shows daily average maximum temperatures. Grey dotted lines represent the 3 experimental temperatures (25, 29 and 33°C) used in the laboratory for respirometry tests. Panels B - E show daily averages for Lux (B), dissolved oxygen (DO) concentrations (C), pH (D), and turbidity as measured by Secchi depth (E).

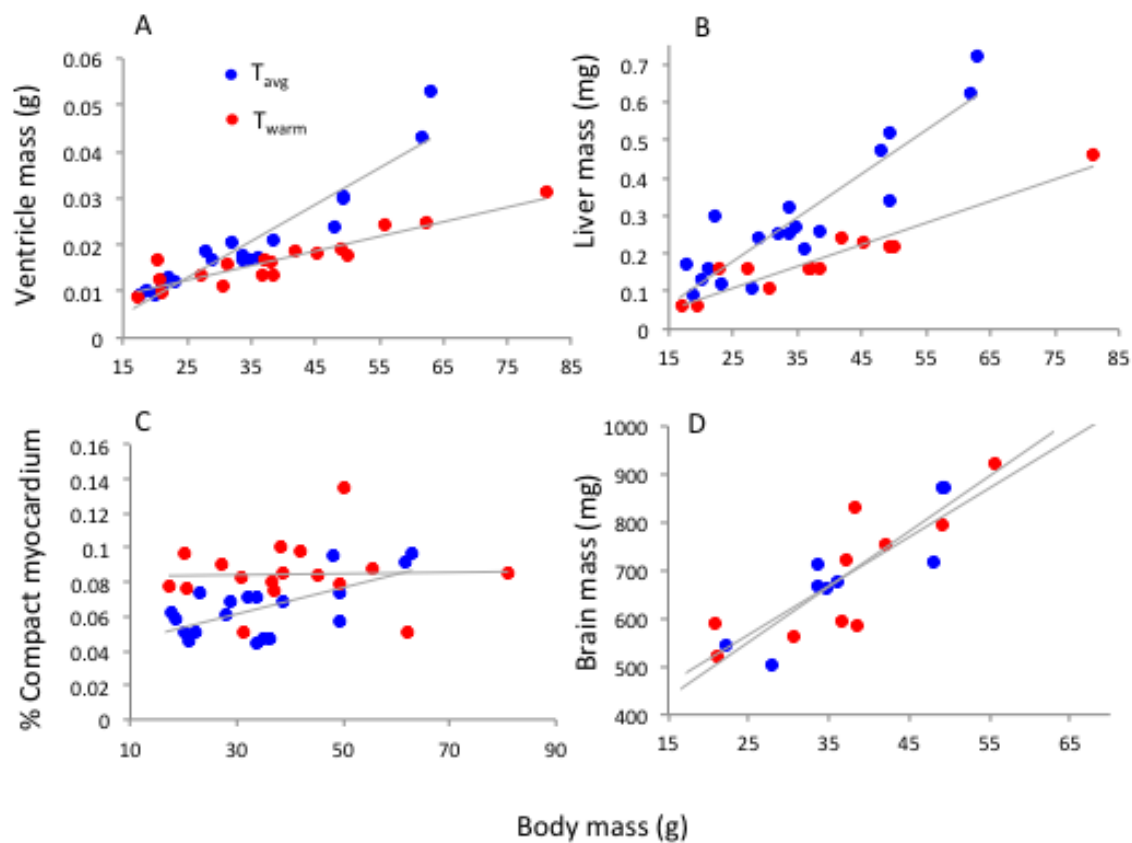


Figure C3. Linear relationships between body mass and ventricle mass (A), liver mass (B), % compact myocardium (C), and brain mass (D) raised under T_{warm} and T_{avg} conditions for 3 months.

Appendix D: Supplementary materials for Chapter 4

D.1 Survey, focus group, and interview tools

Document D.1.1 Household survey

McGill University and the National Fisheries Resources Research Institute of Uganda

Livelihood Survey: Climate change perceptions and adaptations

The purpose of this survey is to assess the social, economic, and ecological impacts of climate variability and change on fishing-dependent households in Lake Victoria Basin in Uganda

Date: _____

Survey administrator: _____

Survey number: _____

I. GENERAL INFORMATION

A. Household Demographics

1. Village: _____ 2. Tribe: _____ 3. Landing site used: _____
4. Gender: (M) (F) _____ 5. Age: _____
6. Number of children: _____ 7. Total number of household members: _____

B. Involvement in the fishery

How many years?

- 1 () Fishing in own boat _____
2 () Fishing in hired boat _____
3 () Boat crew _____
4 () Boat manager _____
5 () Boat owner (renting only) _____
6 () Boat building _____
7 () Renting gear _____
8 () Net repairing _____
9 () Net cleaning/arranging _____
10 () Preparing meals _____
11 () Fish trading _____
12 () Fish processing _____
13 () Other Specify: _____

C. Marital status

- 1 () Married
2 () Single
3 () Separated/Divorced
4 () Widowed
5 () No response

D: Education and Skills

1. To what level have you been educated?

- 1 () None
2 () Primary Level: _____
3 () Secondary Level: _____
4 () University
5 () Vocational Training Specify: _____
6 () Functional Adult Literacy (FAL)
7 () Other Specify: _____
8 () No response

2. What skills do you have?

- 1 () construction
2 () fishing
3 () net mending
4 () sewing
5 () brick making
6 () gardening
7 () teaching
8 () nursing
9 () mechanic
10 () carpenter
11 () weaving
12 () livestock peasant
13 () Other Specify: _____

E. Residence and Assets

1. Where is your permanent residence?

- 1 () In this village
- 2 () Within the subcounty
- 3 () Within this district
- 4 () Another district
- 5 () Outside of Uganda Specify: _____
- 6 () Other Specify: _____
- 7 () No response

2. How long have you lived in this village?

- 1 () less than 1 year
- 2 () 1 - 5 years
- 3 () 5 - 10 years
- 4 () 10 - 20 years
- 5 () 20 - 30 years
- 6 () 30 - 40 years
- 7 () 40+ years

3. What kind of a house do you live in?

- 1 () Permanent
- 2 () Semipermanant
- 3 () Grass-thatched

4. How many rooms do you have in the house

- 1 () 1 room
- 2 () 2 rooms
- 3 () 3+ rooms

5. Does your house have the following?

- 1 () solar panel
- 2 () hydro-thermal electricity
- 3 () latrine
- 4 () Other Specify: _____
- 5 () No response

6. How far is your house from the following (m)?

- 1 Water source _____
- 2 School _____
- 3 Health center _____
- 4 Market _____
- 5 Banking facilities _____
- 6 Church _____
- 7 Refridgeration facilities _____

7. Do you own any of these assets?

	Quantity (acres or no.)	Approximate present value
1 () Land	_____	_____
2 () Plot	_____	_____
3 () Bicycle	_____	_____
4 () Vehicle	_____	_____
5 () Motorcycle	_____	_____
6 () Radio	_____	_____
7 () Mobile phone	_____	_____
8 () Television	_____	_____
9 () Boat	_____	_____
10 () Garden	_____	_____
12 () Other Specify: _____	_____	_____
12 () No response		

8. Do you own fishing gear? (Y) (N)

Type	Quantity	Approximate value
_____	_____	_____
_____	_____	_____
_____	_____	_____
_____	_____	_____

F: Social capital indicators

1. Are you a member of any of the following social groups or committees?

Please specify your involvement [leader (1), member (2)]

- | | |
|------------------------------------|----------------------------|
| 1 () Credit and savings groups | Specify involvement: _____ |
| 2 () Social groups Specify: _____ | Specify involvement: _____ |
| 3 () Labour-exchange groups | Specify involvement: _____ |
| 4 () Agricultural groups | Specify involvement: _____ |
| 5 () Religious groups | Specify involvement: _____ |
| 6 () Political groups | Specify involvement: _____ |
| 7 () Women's groups | Specify involvement: _____ |
| 8 () Craft groups | Specify involvement: _____ |
| 10 () Water user committee | Specify involvement: _____ |
| 11 () Village council | Specify involvement: _____ |
| 12 () Other Specify: _____ | Specify involvement: _____ |
| 13 () No response | |

2. Do you participate in any of the following communal tasks in the village:

(activities that friends and neighbours help each other with; labour exchange; friend in need)

- | | |
|-----------------------|------------------------------|
| 1 () Ploughing | 6 () Brick making |
| 2 () Weeding | 7 () House building |
| 3 () Planting | 8 () Water pump maintenance |
| 4 () Crop harvesting | 9 () Other Specify: _____ |
| 5 () Child care | 10 () No response |

3. Do you have a leadership role in the village (e.g. LC1, BMU chairperson, elder): _____

4. Do others in your community come to you for advice? (Y) (N)

If yes, what do they usually come to you for?

- | | |
|-----------------------------------|-----------------------------|
| 1 () Health | 7 () Income generation |
| 2 () Agriculture | 8 () Savings |
| 3 () Home / property improvement | 9 () Skills training |
| 4 () Family issues | 10 () Other Specify: _____ |
| 5 () Conflict resolution | 11 () No response |
| 6 () Fishing advice | |

5. When you are in need of assistance, are you usually able to access help from neighbours? (Y) (N)

6. What kind of help do people give?

- | | |
|-------------------------|----------------------------|
| 1 () Money | 5 () Education/Training |
| 2 () Food | 6 () Employment |
| 3 () Advice | 7 () Other Specify: _____ |
| 4 () Emotional support | 8 () No response |

II: PERCEPTIONS OF CLIMATE VARIABILITY AND CHANGE

1. Are you aware of climate variability and change?

- 1 () Yes
- 2 () No
- 3 () Don't know
- 4 () No response

2. Normally, what are the wet months of the year

- | | | |
|----------------|--------------|-----------------|
| 1 () January | 5 () May | 9 () September |
| 2 () February | 6 () June | 10 () October |
| 3 () March | 7 () July | 11 () November |
| 4 () April | 8 () August | 12 () December |

3. Normally what are the dry months of the year

- | | | |
|----------------|--------------|-----------------|
| 1 () January | 5 () May | 9 () September |
| 2 () February | 6 () June | 10 () October |
| 3 () March | 7 () July | 11 () November |
| 4 () April | 8 () August | 12 () December |

4. Has the timing of the dry an wet seasons changed?

- 1 () Yes ----->
- 2 () No
- 3 () Don't know
- 4 () No response

If so, how?

- 1 () Earlier rains
- 2 () Later rains
- 3 () Unpredictable

5. Has the length of the wet and dry seasons changed?

- 1 () Yes ----->
- 2 () No
- 3 () Don't know
- 4 () No response

If so, how?

- 1 () Longer rains / shorter dry
- 2 () Shorter rains / longer dry
- 3 () Unpredictable

6. Has the intensity of the wet and dry seasons changed?

- 1 () Yes ----->
- 2 () No
- 3 () Don't know
- 4 () No response

If so, how?

- 1 () more intense rains
- 2 () less intense rains
- 3 () more intense heat/dryness
- 4 () less intense heat/dryness

7. Can you remember any major periods of drought since you've started fishing?

- | | | | |
|-------|-------------|-------|---------------------------|
| 1 () | Yes | ----> | If so, when (list years)? |
| 2 () | No | | _____ |
| 3 () | Don't know | | _____ |
| 4 () | No response | | _____ |

8. Can you remember any major periods with floods since you've started fishing?

- | | | | |
|-------|-------------|-------|---------------------------|
| 1 () | Yes | ----> | If so, when (list years)? |
| 2 () | No | | _____ |
| 3 () | Don't know | | _____ |
| 4 () | No response | | _____ |

9. Have the number of years with drought increased or decreased since you've started fishing?

- | | |
|-------|-----------------------|
| 1 () | Increased |
| 2 () | Decreased |
| 3 () | Stayed about the same |
| 4 () | Don't know |
| 5 () | No response |

10. Have the number of years with floods increased or decreased since you've started fishing?

- | | |
|-------|-----------------------|
| 1 () | Increased |
| 2 () | Decreased |
| 3 () | Stayed about the same |
| 4 () | Don't know |
| 5 () | No response |

11. Have you noticed other changes in the environment since you've started fishing?

- | | | | |
|-------|-------------|-------|------------------------|
| 1 () | Yes | ----> | If so, what were they? |
| 2 () | No | | _____ |
| 3 () | Don't know | | _____ |
| 4 () | No response | | _____ |

III: OTHER LIVELIHOOD ACTIVITIES

A. Please select the activities that are practiced by a member of your household

Category	Activity	Done in household?	Done by you?	Rank	Done when? wet season (1) dry season (2) year round (3)	Done where? on property (1) in village (2) out of village (3)	How many years?
Crops	Maize	()	()	_____	_____	_____	_____
	Coffee	()	()	_____	_____	_____	_____
	Pineapple	()	()	_____	_____	_____	_____
	Sorghum	()	()	_____	_____	_____	_____
	Sweet banana	()	()	_____	_____	_____	_____
	Matooke	()	()	_____	_____	_____	_____
	Cassava	()	()	_____	_____	_____	_____
	Sweet potatoes	()	()	_____	_____	_____	_____
	Tomatoes	()	()	_____	_____	_____	_____
	Ground nuts	()	()	_____	_____	_____	_____
	Beans	()	()	_____	_____	_____	_____
	Cabbages	()	()	_____	_____	_____	_____
	Oranges	()	()	_____	_____	_____	_____
	Watermelon	()	()	_____	_____	_____	_____
	Irish potatoes	()	()	_____	_____	_____	_____
	Sugar cane	()	()	_____	_____	_____	_____
	Lemons	()	()	_____	_____	_____	_____
	Cow peas	()	()	_____	_____	_____	_____
	Tangerines	()	()	_____	_____	_____	_____
	Bitter berries	()	()	_____	_____	_____	_____
	Other _____	()	()	_____	_____	_____	_____
	Other _____	()	()	_____	_____	_____	_____
	Other _____	()	()	_____	_____	_____	_____
	Other _____	()	()	_____	_____	_____	_____
	Other _____	()	()	_____	_____	_____	_____
	Other _____	()	()	_____	_____	_____	_____
	Other _____	()	()	_____	_____	_____	_____
Livestock	Chickens: no. _____	()	()	_____	_____	_____	_____
	Ducks: no. _____	()	()	_____	_____	_____	_____
	Goats: no. _____	()	()	_____	_____	_____	_____
	Pigs: no. _____	()	()	_____	_____	_____	_____
	Sheep: no. _____	()	()	_____	_____	_____	_____
	Cows: no. _____	()	()	_____	_____	_____	_____
	Other _____	()	()	_____	_____	_____	_____
Fishing-related	Fishing in own boat	()	()	_____	_____	_____	_____
	Fishing in hired boat	()	()	_____	_____	_____	_____
	Boat crew	()	()	_____	_____	_____	_____

Category	Activity	Household	you?	Rank	When?	Where?	How long?
Fishing related continued	Boat manager	()	()	_____	_____	_____	_____
	Boat owner (renting only)	()	()	_____	_____	_____	_____
	Boat building	()	()	_____	_____	_____	_____
	Renting gear	()	()	_____	_____	_____	_____
	Net repairing	()	()	_____	_____	_____	_____
	Net cleaning/arranging	()	()	_____	_____	_____	_____
	Preparing meals	()	()	_____	_____	_____	_____
	Fish trading	()	()	_____	_____	_____	_____
	Fish processing	()	()	_____	_____	_____	_____
	Other _____	()	()	_____	_____	_____	_____
Trade and Service	Shop: grocery	()	()	_____	_____	_____	_____
	Shop: household	()	()	_____	_____	_____	_____
	Shop: livelihood items	()	()	_____	_____	_____	_____
	Bar	()	()	_____	_____	_____	_____
	Driving	()	()	_____	_____	_____	_____
	Skilled trade / service	()	()	_____	_____	_____	_____
	Sewing	()	()	_____	_____	_____	_____
	Brewing local beer	()	()	_____	_____	_____	_____
	Other _____	()	()	_____	_____	_____	_____
Natural Resources	Charcoal	()	()	_____	_____	_____	_____
	Brick making	()	()	_____	_____	_____	_____
	Rock quarry	()	()	_____	_____	_____	_____
	Forestry	()	()	_____	_____	_____	_____
	Sand mining	()	()	_____	_____	_____	_____
	Hunting	()	()	_____	_____	_____	_____
	Other _____	()	()	_____	_____	_____	_____
Craft work	Basket weaving	()	()	_____	_____	_____	_____
	Mats	()	()	_____	_____	_____	_____
	Jewelry/beadwork	()	()	_____	_____	_____	_____
	Handicrafts	()	()	_____	_____	_____	_____
	Other _____	()	()	_____	_____	_____	_____
Non-income earning	Childcare	()	()	_____	_____	_____	_____
	Water fetching	()	()	_____	_____	_____	_____
	Cooking	()	()	_____	_____	_____	_____
	Cleaning	()	()	_____	_____	_____	_____
	Home repairs	()	()	_____	_____	_____	_____
	Home improvements	()	()	_____	_____	_____	_____
	Collection of firewood	()	()	_____	_____	_____	_____
	Other _____	()	()	_____	_____	_____	_____

B. Estimated income

1. What is the average weekly income earned from fishing activities? How many days per week?

- | | | | |
|----|---------------------------|-------|-------|
| 1 | Fishing in own boat | _____ | _____ |
| 2 | Fishing in hired boat | _____ | _____ |
| 3 | Boat crew | _____ | _____ |
| 4 | Boat manager | _____ | _____ |
| 5 | Boat owner (renting only) | _____ | _____ |
| 6 | Renting gear to others | _____ | _____ |
| 7 | Using rented gear | _____ | _____ |
| 8 | Net repairing | _____ | _____ |
| 9 | Net cleaning/arranging | _____ | _____ |
| 10 | Preparing meals | _____ | _____ |
| 11 | Fish trading | _____ | _____ |
| 12 | Fish processing | _____ | _____ |
| 13 | Boat building | _____ | _____ |
| 14 | Crew leader/boat manager | _____ | _____ |
| 15 | Other Specify: _____ | _____ | _____ |

2. What is the average income earned from other activities? How many days per week?

- | | | | | |
|---|-------------------|-------|----------|-------|
| 1 | Agriculture | _____ | (season) | _____ |
| 2 | Livestock | _____ | (yearly) | _____ |
| 3 | Trade and Service | _____ | (weekly) | _____ |
| 4 | Natural resources | _____ | (weekly) | _____ |
| 5 | Craft work | _____ | (weekly) | _____ |

3. Who controls the income in your household? [self (1) spouse (2) both (3)] _____

4. In your household what are the 5 most important areas of expenditure?

- Rank
- | | | |
|--------|-------|------------------------|
| 1 () | _____ | Food |
| 2 () | _____ | Clothing / shoes |
| 3 () | _____ | School fees |
| 4 () | _____ | Seed |
| 5 () | _____ | Fishing gear |
| 6 () | _____ | Fuel |
| 7 () | _____ | Charcoal |
| 8 () | _____ | Alcohol |
| 9 () | _____ | Leisure Specify: _____ |
| 10 () | _____ | Gambling |
| 11 () | _____ | Hygiene |
| 12 () | _____ | Medical fees |
| 13 () | _____ | Airtime |
| 14 () | _____ | Other Specify: _____ |
| 15 () | _____ | No response |

C: Fishery Related Livelihood activities

1. What fishing activities do you do more often in the dry season?

- 1 () Fishing in own boat Gill net
 Long line
 Seine
 Other _____
- 2 () Fishing in hired boat Gill net
 Long line
 Seine
 Other _____
- 3 () Boat crew
 4 () Boat manager
 5 () Boat owner (renting only)
 6 () Renting gear to others
 7 () Using rented gear
 8 () Net repairing
 9 () Net cleaning/arranging
 10 () Preparing meals
 11 () Fish trading
 12 () Fish processing
 13 () Boat building
 14 () Other Specify: _____

2. What fishing activities do you do more often in the wet season?

- 1 () Fishing in own boat Gill net
 Long line
 Seine
 Other _____
- 2 () Fishing in hired boat Gill net
 Long line
 Seine
 Other _____
- 3 () Boat crew
 4 () Boat manager
 5 () Boat owner (renting only)
 6 () Renting gear
 7 () Using rented gear
 8 () Net repairing
 9 () Net cleaning/arranging
 10 () Preparing meals
 11 () Fish trading
 12 () Fish processing
 13 () Boat building
 14 () Other Specify: _____

D: Fish species and changes in abundance

1. What are the most important target species?

- | Rank | | | |
|-------|-------|----------------------|--------------------------------------------|
| 1 () | _____ | Mputa (Nile perch) | 5 () _____ Nkeje (Haplochromines) |
| 2 () | _____ | Ngege (Nile tilapia) | 6 () _____ Enkolongo (Synodontis catfish) |
| 3 () | _____ | Mukene (Silverfish) | 7 () _____ Emale/Nzere (other catfish) |
| 4 () | _____ | Mamba (Lungfish) | 8 () _____ Other Specify: _____ |

2. Have the quantities of target species changed since you've started fishing?

- | | Ngege | Mputa | Mukene | Mamba | Nkeje | Enkolongo | Emale/Nzere | Other |
|----------------|-------|-------|--------|-------|-------|-----------|-------------|-------|
| (1) Increase | () | () | () | () | () | () | () | () |
| (2) Decrease | () | () | () | () | () | () | () | () |
| (3) No change | () | () | () | () | () | () | () | () |
| (4) Don't know | () | () | () | () | () | () | () | () |

3. Have the species that are targeted in this fishery changed since you've started fishing?

- | | Ngege | Mputa | Mukene | Mamba | Nkeje | Enkolongo | Emale/Nzere | Other |
|----------------|-------|-------|--------|-------|-------|-----------|-------------|-------|
| (1) Increase | () | () | () | () | () | () | () | () |
| (2) Decrease | () | () | () | () | () | () | () | () |
| (3) No change | () | () | () | () | () | () | () | () |
| (4) Don't know | () | () | () | () | () | () | () | () |

4. On average, how much fish is caught each fishing trip per species (specify units)?

a. Wet season

- 1 Mputa (Nile perch) _____
- 2 Ngege (Nile tilapia) _____
- 3 Mukene (Silverfish) _____
- 4 Mamba (Lungfish) _____
- 5 Nkeje (Haplochromines) _____
- 6 Enkolongo (Synodontis) _____
- 7 Emale/Nzere (other catfish) _____
- 8 Other Specify: _____

b. Dry season

- 1 Mputa (Nile perch) _____
- 2 Ngege (Nile tilapia) _____
- 3 Mukene (Silverfish) _____
- 4 Mamba (Lungfish) _____
- 5 Nkeje (Haplochromines) _____
- 6 Enkolongo (Synodontis) _____
- 7 Emale/Nzere (other catfish) _____
- 8 Other Specify: _____

IV: EFFECTS OF CLIMATE CHANGE ON FISHERY-BASED LIVELIHOODS

1. What were the most significant environmental events to impact your livelihood since you've started fishing?

- 1 () Droughts
- 2 () Floods
- 3 () Other Specify: _____

2. What were the major impacts of droughts on livelihoods?

- 1 () Crop failure
- 2 () Loss of pasture
- 3 () Disease outbreaks
- 4 () Crop disease
- 5 () Not having enough food
- 6 () Death of livestock
- 7 () Reduction in fisheries

3. What were the major impacts of floods on livelihoods?

- 1 () Crop failure
- 2 () Loss of pasture
- 3 () Disease outbreaks
- 4 () Crop disease
- 5 () Not having enough food
- 6 () Death of livestock
- 7 () Landslides
- 8 () Road blockages
- 9 () Reduction in fisheries

4. Do you think there are any positive impacts of droughts?

5. Do you think there are any positive impacts of floods?

6. How did floods impact fishery-based income?

- 1 () Reduced
- 2 () Increased
- 3 () No effect
- 4 () Don't know
- 5 () No response

7. How did droughts impact fishery-based income?

- 1 () Reduced
- 2 () Increased
- 3 () No effect
- 4 () Don't know
- 5 () No response

8. How did floods impact amount of fish eaten in your household?

- 1 () Reduced
- 2 () Increased
- 3 () No effect
- 4 () Don't know
- 5 () No response

9. How did droughts impact amount of fish eaten in your household?

- 1 () Reduced
- 2 () Increased
- 3 () No effect
- 4 () Don't know
- 5 () No response

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10. How did the floods impact fishing?

- 1 () Decrease in fish catches
- 2 () Increase in fish catches
- 3 () Decrease in fish size
- 4 () Increase in fish size
- 5 () Damage to landing sites
- 6 () Damage to boats
- 7 () Damage to gear
- 8 () Loss of lives
- 9 () Fewer fishers working
- 10 () More fishers working
- 11 () Migration to the fishery
- 12 () Migration away from the fishery
- 13 () Increased fishing effort
- 14 () Decreased fishing effort
- 15 () Other Specify: _____
- 16 () Don't know
- 17 () No response

11. How did the droughts impact fishing?

- 1 () Reduction in fish catches
- 2 () Increase in fish catches
- 3 () Decrease in fish size
- 4 () Increase in fish size
- 5 () Damage to landing sites
- 6 () Damage to boats
- 7 () Damage to gear
- 8 () Loss of lives
- 9 () Fewer fishers working
- 10 () More fishers working
- 11 () Migration to the Lake
- 12 () Migration away from the lake
- 13 () Increased fishing effort
- 14 () Decreased fishing effort
- 15 () Other Specify: _____
- 16 () Don't know
- 17 () No response

12. How did the quantities of target species change during floods?

	Ngege	Mputa	Mukene	Mamba	Nkeje	Enkolongo	Emale/Nzere	Other
(1) Increase	()	()	()	()	()	()	()	()
(2) Decrease	()	()	()	()	()	()	()	()
(3) No change	()	()	()	()	()	()	()	()
(4) Don't know	()	()	()	()	()	()	()	()
(5) Not applicable	()	()	()	()	()	()	()	()

13. How did the quantities of target species change during droughts?

	Ngege	Mputa	Mukene	Mamba	Nkeje	Enkolongo	Emale/Nzere	Other
(1) Increase	()	()	()	()	()	()	()	()
(2) Decrease	()	()	()	()	()	()	()	()
(3) No change	()	()	()	()	()	()	()	()
(4) Don't know	()	()	()	()	()	()	()	()
(5) Not applicable	()	()	()	()	()	()	()	()

14. How did droughts affect income from the following activities?

	forestry	charcoal	brickmaking	craft work	crops	livestock	rock quarry	sand mining	hunting
(1) Increase	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
(2) Decrease	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
(3) No change	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
(4) Don't know	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
(5) Not applicable	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

15. How did floods affect income from the following activities?

	forestry	charcoal	brickmaking	craft work	crops	livestock	rock quarry	sand mining	hunting
(1) Increase	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
(2) Decrease	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
(3) No change	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
(4) Don't know	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
(5) Not applicable	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

V: ADAPTATION STRATEGIES

A. Fishery specific adaptations

1. What have you practiced during floods?

- 1 ☐ Migrate
- 2 ☐ Change fishing gear Specify: _____
- 3 ☐ Use more nets
- 4 ☐ Change target species
- 5 ☐ Revert to non-fishing activities
- 6 ☐ Exit the fishery
- 7 ☐ Change fishing grounds
- 8 ☐ Increase time fishing
- 9 ☐ Do nothing
- 10 ☐ Other Specify: _____
- 11 ☐ Don't know
- 12 ☐ No response

2. What have you practiced during droughts?

- 1 ☐ Migrate
- 2 ☐ Change fishing gear Specify: _____
- 3 ☐ Use more nets
- 4 ☐ Change target species
- 5 ☐ Revert to non-fishing activities
- 6 ☐ Exit the fishery
- 7 ☐ Change fishing grounds
- 8 ☐ Increase time fishing
- 9 ☐ Do nothing
- 10 ☐ Other Specify: _____
- 11 ☐ Don't know
- 12 ☐ No response

3. What was the result of changing activities within the fishery? [increase (1) decrease (2) no change (3)]

	Droughts			Floods		
	Income	Food security	Employment	Income	Food security	Employment
Migrate						
Change fishing gear						
Use more nets						
Change target species						
Exit the fishery						
Change fishing grounds						
Increase time fishing						
Do nothing						
Other						
Don't know						
No response						

B. Non-fishery specific adaptations

1. During droughts, what non-fishing activities do you turn to?

- 1 () Crop Specify: _____ 5 () Other Specify: _____
 2 () Livestock Specify: _____ 6 () Don't know
 3 () Non-fishery trading Specify: _____ 7 () No response
 4 () Manual labour Specify: _____

2. During floods, what non-fishing activities do you turn to?

- 1 () Crop Specify: _____ 5 () Other Specify: _____
 2 () Livestock Specify: _____ 6 () Don't know
 3 () Non-fishery trading Specify: _____ 7 () No response
 4 () Manual labour Specify: _____

3. What were the main reasons for turning to other activities during drought or flood periods?

- 1 () Income 4 () Other Specify: _____
 2 () Food security 5 () Don't know
 3 () Employment 6 () No response

4. What was the result of turning to non-fishing activities?

[increase (1) decrease (2) no change (3)]

	Droughts			Floods		
	Income	Food security	Employment	Income	Food security	Employment
Crops						
Livestock						
Non-fishery trading						
Manual labour						
Other						

5. How do you survive when income, food security, and employment are low?

- 1 () Rent land
 2 () Harvest wild plants / animals
 3 () Provide labour for food
 4 () Sell livestock
 5 () Sell belongings / assets
 6 () Sell capital from shop/business
 7 () Borrow money from family and friends
 8 () Rely on village leaders for financial assistance
 9 () Turn to social groups
 10 () Government assistance (financial or food-aid)
 11 () Missions assistance (financial or food-aid)
 12 () Other Specify: _____
 13 () No response

6. In times of drought / flood do you receive assistance from the following external agencies?

- 1 () NAADS
- 2 () Community Based Organizations
- 3 () Microfinance/Credit
- 4 () Skills development and training outreach
- 5 () Financial education
- 6 () Church

7. Has the overall well-being of your household improved, stayed the same, since you started fishing? ____ [increase (1) decrease (2) no change (3)]

8. What have you done to protect your household from climate variability and change?

VI. CONSTRAINTS TO ADAPTATION

1. If you could pick something new to diversify to, what would it be?

2. What are the barriers preventing you from doing so?

- 1 () Lack of money
- 2 () Lack of appropriate planning materials
- 3 () Limited training on how to diversify
- 4 () Lack of community support
- 5 () Lack of support from the government
- 6 () Other Specify: _____
- 7 () Don't know
- 8 () No response

3. What would help you to overcome these barriers?

- 1 () Increased awareness
- 2 () Enforce laws and regulations
- 3 () Provide low interest credit
- 4 () Provide irrigation pumps
- 5 () Provide training
- 6 () Financial or asset-based support
- 7 () Other Specify: _____
- 8 () Don't know
- 9 () No response

Do you have any other comments on how climate variability and change have affected the fishery?

Document D.1.2 Focus group discussion annotated questionnaire

OPENING COMMENTS

Welcome to this discussion group and thank you for agreeing to take part

Introductions: Agnes & JB from NaFIRRI; Elizabeth from McGill University in Canada

Purpose: To understand whether people living in fishing communities are aware of the impacts of climate change on the fishery, and how changes in the environment affect their livelihoods, and how they can adapt to these changes through livelihood diversification and other measures like access to capital, cohesive communities, and effective governance.

Results used: To inform governments and policy makers on the best ways to support fishing communities as they are faced with the increasing impacts of climate variability and change.

You were selected because you are a _____ working at _____ landing site, and we want to know more details about your opinions on a few key things. Many of you participated in the survey, but some of you did not. It doesn't matter either way.

Disclaimer: You can choose whether or not to participate in the focus group and stop at any time. Although the focus group will be tape recorded, your responses will remain anonymous and no names will be mentioned in the report. Do you have any questions? Do you all agree to these terms?

Comfort and ground rules:

- There are no right or wrong answers to the focus group questions.
- We are here to listen: We want to hear many different viewpoints and would like to hear from everyone.
- We hope you can be honest even when your responses may not be in agreement with the rest of the group.
- In respect for each other, we ask that only one individual speak at a time in the group and that responses made by all participants be kept confidential.

Roles: My role as moderator will be to guide the discussion; _____ will be taking notes, and _____ will be interpreting for Elizabeth so that she can follow along as much as possible.

Introduction of participants: We would like to go around the circle and say our names and what we do

OPENER

Q1. What are your thoughts about how the fishery is doing these days?

- *This is just a broad question to get them talking; they can really go any direction they want, but try to keep the discussion on this question as short as possible*

LIVELIHOOD

Q2.

- (a) In your opinion, what are the most important environmental impacts on your life in terms of livelihood stability (*ability to maintain a comfortable level of existence – buy food, send kids to school*) and fishery productivity (*ability to catch enough fish*)? Explain / Give examples.
- (b) Do you think these impacts are affecting you MORE or LESS than they did in the past?
 - *I am trying to get a sense of whether the environmental impacts they mention above are increasing or decreasing with time.*
 - *Encourage them to think back to when they started fishing or when they were younger, and compare THEN to NOW*
- (c) Some people say that incomes increase during droughts. Do you agree? Why is this so?
- (d) Some people say that fish increase in number during floods, while others say they decrease. What are your thoughts on this?

Q3. What livelihood challenges do you face that are specific to you as _____?

- *(Women, Boat crew, Boat owners, Traders)*

Q4. (LAMBU ONLY)

- (a) Lambu has a lot of economic disparity among people. Are there any advantages or disadvantages to having very rich people (boat managers, large-scale traders) next to very poor people (boat crew, processors)?
- (b) (CREW ONLY) Why do some crew-members earn high amounts and other's earn little

DIVERSIFICATION

Q5.

- (a) Do you think diversification is important? Why or why not?
- (b) What are the main diversification options for you as _____?
- (c) Which one is the most appealing to you? Why?

Q6. Rank these items according to importance to livelihood stability and ability to diversify?

1. Education and skill training
2. Access to financial capital
3. Strong community cohesion
4. Easy access to facilities (*health centers, clean water source, good roads, power, daily life requirements*)
5. Steady environmental conditions (*predictable seasonality, no drought, no flood*)

How do these assets help you to achieve your goals?

ADAPTATION STRATEGIES

Q7.

- (a) It was indicated in the survey that droughts and floods impact fishing by changing fish quantities and income. Think about the things you or others have done in the past DURING times of drought and flood. What actions led to improved livelihood stability, increased diversification, or long-term improvement
- (b) Are there any adaptation actions that are specific to you as women/boat owners/crew/traders

Here I am looking for short-term responses to the fact that the flood or drought is happening right now. What are the immediate responses that are taken?

Q8. There are predictions that in the future there may be more years with floods or droughts than before. Since droughts or floods are likely to become more frequent, can you think of anything you or others can do in advance to mitigate the negative effects?

Here I am looking for long-term (planning ahead) responses to the fact that floods or droughts is will happen more and more frequently with time.

BARRIERS

Q9.

- (a) Results from the survey indicate that for most people (not necessarily YOU) during times of droughts and floods nothing is done to adapt or to protect households from their effects. Why is this so?
- (b) Other than JUST financial barriers, what are the main constraints preventing you from taking action to diversify or to protect your household from climate variability?
- (c) Are there any constraints that are specific to you as women/boat owners/crew/traders

GOVERNANCE

Q10.

- (a) In your opinion, is the management system in place effective in managing fisheries and protecting livelihood stability? Why or why not?
- (b) What are some of your thoughts on how to make it better?
- (c) Can you think of any specific actions that could be taken by the government to improve fishery livelihoods?

- *Here I am looking for the HOW. E.g. if they say "We need more enforcement" HOW should this enforcement be done? More officers on the ground? More fines? Jail time?*

GENDER

Q11. Are women supported and fairly treated by the men within the fishery?

CLOSING

We are done with our questions! Thank you very much for your participation. Is there anything you would like to add at this point?

Document D.1.3 Semi-structured interview questions for village leaders

- Q1. Village/Landing site demographics: Population size, number of fishers of Nile Tilapia Nile perch and mukene, number of women, number of migrants, fish trade routes, amounts of fish harvested.
- Q2. How do systems of land ownership impact livelihoods? Do you find the system fair?
- Q3. How do systems of tax collection at landing sites impact fishing livelihoods? Is the system fair?
- Q4. In your opinion do you think that BMUs were effective in managing fisheries? How has the dissolution of the BMU system impacted your livelihood?
- Q5. What recommendations would you make on how to improve the livelihoods of the people here?
- Q6. This village has: (BK) mostly residents (non-migrants) living and working here / (GN) a high proportion of migrants from around Uganda / (L) a high proportion of regional/national migrants. How do you think this affects your community? Do you think your community is strong?
- Q7. How do migrant fishers impact diversification and livelihood stability within a community? Are migrants more adaptable or less adaptable?
- Q8. What are the most important long-term solutions to poverty reduction and livelihood stability? Of the actions taken which ones actually lead to livelihood stability and which ones lead to increased diversification or long-term improvement?
- Q9. What infrastructure do you see as being the most important for the health and well-being your village? Electricity, Solar, Latrine, Roads, Clean water supply
- Q10. What facility do you see as being the most important for the health and well-being your village? Schools, Churches, Hospitals, Shops/markets
- Q11. What asset do you see as being the most important for the health and well-being your village? Mobile, Radio, Garden, Land, Bicycle, Boat, Fishing gear
- Q12. How important are changes in climate to fishery productivity and livelihood stability? What are the most important environmental impacts on your livelihood? What are the most important government impacts on your livelihood? Between government and climate, which one impacts your livelihood more?

Document D.1.4 Semi-structured interview questions for government employees

- Q1. Name, Job title, Time in post
- Q2. What are your thoughts about how the fishery is doing these days? What are the major problems?
- Q3. In your opinion, what are the most important environmental impacts on fisheries? Do you think these are changing with time?
- Q4. What are the main diversification options for fishermen? What do you think might be preventing them from diversifying?
- Q5. Why is land distributed the way it is? Do you think it would be possible for some land to be opened up around landing sites? How do you think it could or should be distributed?
- Q6. There is a general sense that I get that compared to other sectors in the agriculture department fisheries have been left behind and have not received government aid or attention for diversification or improving livelihoods. Do you think this is true? Why do you think this is? What can be done to improve this situation? What has been attempted at fish landing sites in the past? What has been successful and what has not?
- Q7. In your opinion, is the management system in place effective in managing fisheries? Why or why not? What are some of your thoughts on how to make it better?
- Q8. When asked what should be done to improve the situation on the lake, many fishers suggest that the government should ban the importation of illegal nets. Why has this not been done?
- Q9. Many fishers state that problems managing the fishery come from the fact that laws (though good) are not very well implemented on the ground. Why do you think there is such a problem with law enforcement? What can be done to improve this situation?
- Q10. Do you think it is possible for lines of communication and trust to be restored among enforcers, government, and the communities? If you could make any recommendations on how to improve governance what would they be?

D.2 Supplementary figures

Figure D1. Frequencies of diversification options that fishers (A) have already exploited, and (B) want to exploit, with the four major groupings of livestock, crops, business, and trade and service broken down into specific categories.

