Mercury in African freshwater fishes:
A continent-wide review and a case study of Nile perch (*Lates niloticus*)

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Abstract

The methylated form of mercury (MeHg) is a potent neurotoxin that can have devastating effects on both wildlife and human health. Despite the critical importance of inland fisheries to food and economic security in many areas of Africa, information on Hg contamination and trends of these fisheries is scarce and scattered in the literature. In this thesis, I conduct a quantitative review of Hg levels in African freshwater fish, and I characterize variation in mercury contamination in a key fish stock in East Africa, the large piscivorous Nile perch (*Lates niloticus*). In the first chapter, I gather published data on total mercury (THg) concentrations in 166 different species of fish distributed across 31 waterbodies in 12 African countries and use these data to describe broad patterns and identify critical gaps. MeHg generally accounts for over 90% of THg, which can be used as a proxy to estimate Hg toxicity. Across locations, THg concentration averaged 140.7 ± 316.7 ng/g ww (SD) and ranged from 0.8 to 1865.0 ng/g ww. Only locations with nearby artisanal small-scale gold mining operations (ASGM) had mean THg levels above the WHO/FAO's recommended guideline for fish (500 ng/g ww), highlighting the need for both more extensive monitoring and regulations of Hg in areas with AGSM. Using mixed models, I demonstrated that mass, trophic level, and latitude are all positive predictors of THg levels. My results thus reveal overall low Hg concentrations in African fishes, but confirm the presence of bioaccumulation and biomagnification. In the second chapter, I quantified THg concentrations of Nile perch in Lake Nabugabo, Uganda: an important fishery for which, until now, there was no published information on Hg concentrations. I also investigate the effects of habitat use on Hg concentrations in this fishery and demonstrate the discrepancies in Hg accumulation between the open water and ecotonal Nile perch in this system. Open-water fish had the lowest Hg concentrations when small but also the highest rate of Hg accumulation, resulting in large open-

water fish with the most elevated Hg concentrations in the lake. Nile perch from a wetland ecotone had the highest levels of Hg in small fish, yet the lowest rates of Hg accumulation. Differences in acidity and dissolved oxygen detected among habitats might play a role in their Hg availability. Stomach content analysis suggested that diet was also a driver of Hg differences in Nile perch, whereby individuals from habitats with cannibalism had the highest Hg accumulation rates. Despite differences across habitats and sizes (range 6 -130 cm) Hg concentrations of Nile perch in Lake Nabugabo were all well below the WHO/FAO recommended guideline of 500 ng/g (mean: 13.6 ± 0.4 ng/g wet weight; range: 4.9 and 29.3 ng/g wet weight). Overall, this thesis explored patterns and predictors of Hg concentrations in African freshwater fishes and focused in particular on habitat has a predictor of these concentrations. Results show generally low levels of Hg in African fish.

Résumé

Le format méthyle du mercure (MeHg) est un contaminant qui peut avoir des effets dévastateurs sur la santé des animaux et des humains. Malgré l'importance critique des pêches continentales pour la sécurité alimentaire et économique de plusieurs régions de l'Afrique, l'information par rapport à la contamination du Hg autour du continent est minime et éparpillée à travers la littérature. Dans cette thèse, je fais une revue de la littérature afin de quantifier les niveaux de Hg dans les poissons d'eau douce africaine et je caractérise la variation dans la contamination de Hg de la perche du Nile (*Lates niloticus*), un poisson d'importance critique pour l'économie et la sécurité alimentaire en Afrique de l'est. Dans le premier chapitre de cette thèse je rassemble les données publiées sur les concentrations de mercure total (THg) de 166 différentes espèces de poissons qui viennent de 31 différents cours d'eau situés dans 12 pays africains. Généralement, le MeHg est composé de plus de 90 % du THg, qui peut être utilisé pour approximer la toxicité du Hg. La concentration moyenne de mercure total (THg) à tous ces endroits était 140.7 ± 316.7 ng/g ww (SD) et variait entre 0.8 et 1865.0 ng/g ww. Seuls les lieux avec des mines d'or à proximité avaient des concentrations moyennes de Hg au-dessus du niveaux recommandé par le FAO/WHO pour les poissons (500 ng/g ww), ce qui sousligne le besoin de réglementation et d'une surveillance plus extensive dans les endroits avec des mines d'or. À l'aide de modèles mixtes, je démontre que le poids, le niveau trophique et la latitude ont tous une relation positive avec les concentrations de Hg. Ce chapitre démontre donc de bas niveaux de Hg chez les poissons Africains et confirme la présence de biomagnification et de bioaccumulation. Dans le deuxième chapitre de la thèse j'évalue les concentrations de THg dans la perche du Nil du lac Nabugabo, en Ougada; une pêcherie importante qui n'a jamais été évaluée pour le Hg auparavant. Ensuite, je fais une investigation sur l'effet de l'utilisation de différents habitats sur

les concentrations de Hg et je démontre une différence en accumulation de Hg entre les écotones du lacs et celle de la région au large de la berge. Les poissons pêchés au large de la berge avaient les concentrations de Hg les plus basses lorsqu'ils étaient petits, mais avaient le plus haut taux d'accumulation de Hg, donnant lieux aux grands poissons avec les plus hautes concentrations de Hg. Les poissons pêchés dans un des écotones de marais avaient les plus hautes concentrations de Hg observées chez des petits poissons, mais le niveau d'accumulation de Hg le plus bas. Des différences dans l'acidité et le DO des habitats pourraient jouer un rôle dans la disponibilité de Hg. L'analyse du contenue des ventres suggère que la diète est également un facteur qui contribue aux différences de Hg entres les perches du Nil des différents habitats du lac Nabugabo. Par ce fait, les habitats avec de tendances cannibales avaient les plus hauts taux d'accumulation de Hg. Malgré les différences entres les habitats et les tailles de poissons (6 à 130 cm), les concentrations de Hg dans les perches du Nil du Lac Nabugabo ne surpassaient jamais la concentration recommandée par le WHO/FAO de 500 ng/g ww (concentration moyenne : 13.6 ± 0.4 ng/g ww; étendue des concentrations: 4.9 à 29.3 ng/g ww). Globalement, cette thèse a exploré la contamination de Hg dans les poissons Africains d'eau douce avec une attention particulière portée sur le lien entre l'habitat et le Hg. Les résultat ont généralement montrées des concentrations de Hg basses ches les poissons Africains d'eau douce.

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First, I would especially like to thank my advisor, Lauren Chapman, who has provided unconditional support over the course of this project. Her availability, enthusiasm, encouragement, curiosity, generosity, open-mind and mostly, her undying positive and constructive attitude, have taught me a great deal and made this experience nothing but positive. I would also like to thank my committee members, Chris Solomon and David Buck, who provided time, ideas, a good kick for learning to use R, and very appreciated fresh critical eyes. Thank you to Amanda Poste, who shows undying enthusiasm about mercury.

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Thank you to my family, your unconditional support and curiosity about all the different things I do is of the most important value to me. Thank you to my friends from Boyer, who have shared their diverse views and experiences with me night after night, and always been there to show me

a good time, no matter the conditions. Thank you to Louis, for bringing me back and forth from the woods time after time and keeping my mind fresh.

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Preface

Thesis format

This thesis has been written in the manuscript-based format, as permitted by McGill University regulations. The titles of the two manuscripts included in the thesis are listed below:

1. A review of mercury concentrations in African freshwater fishes: Patterns and predictors

2. Effects of habitat on Hg concentration: a case study of Nile perch (*Lates niloticus)* in Lake Nabugabo, Uganda

Chapter 1 was submitted to *Environmental Toxicology and Chemistry* in July 2014 and accepted with minor revisions in October 2014 (manuscript ID: ETCJ-Jul-14-00542). For Chapter 2, in the fall of 2014 I plan submitting this manuscript to *Freshwater Biology* after inclusion of pending isotope and prey mercury and methylmercury data. The general introduction, connecting statement, and general conclusion of the thesis help explain the logical progression between these two chapters and how they are linked. For form, references were incorporated throughout the thesis using the citation style required by *Freshwater Biology* and all referenced literature is compiled at the end of the thesis in one list.

Contributions of authors

This thesis, conducted under the supervision of Dr. Lauren J. Chapman in the Department of Biology at McGill University, is the product of my own independent research. For chapter 1, I carried out the development of the project idea, data collection, analysis, and writing. I also received guidance for the development of the project from David Buck, and a great deal of guidance regarding research design, statistical analysis, and writing from Chris Solomon. Amanda Poste provided guidance regarding for writing and the interpretation of results. Lauren Chapman helped throughout all these stages. As such, all these researchers are included as co-authors on the Chapter 1 manuscript. For chapter 2, I carried out the development of the project idea, field research, most data analysis in the lab, statistical analysis, and writing. Some samples were sent to the Norwegian Institute of Water Research and the University of Florida for analysis due to funding sources and infrastructure. Lauren Chapman also collected some of the associated environmental data with Ugandan field assistants and provided a great deal of guidance throughout this entire process, as such, she is included as a co-author on this manuscript. David Buck helped with the development of ideas and data analysis in the lab for this chapter and is thus also included as a co-author on this manuscript.

General introduction

Aquatic habitats are uniquely susceptible to contaminant loading due to their landscape position as major receivers of effluents (Ritter *et al*., 2002; Burger *et al*., 2004). This places aquatic organisms at risk of exposure to high contaminant concentrations that can have a number of negative health impacts. For example, chronic exposure to lead (Pb) can lead to anemia in fish (Alves *et al*., 2006); exposure to cadmium (Cd) can cause sensory blockage (Faucher *et al*., 2006); and exposure to the methylated form of mercury (MeHg), a potent neurotoxin, can lead to reproductive impairments in fishes (see review in Crump & Trudeau, 2009), as well as, a number of health problems in all fish-consuming species, such as humans (EPA, 2014). Mercury (Hg) is a pollutant of global importance, and its concentrations in the environment have increased approximately 3-fold as a result of anthropogenic activities over the past 150 years (Swain *et al*., 1992; Mason *et al*., 2012). Thus, understanding factors regulating the distribution of Hg in the environment and monitoring its concentrations is an extremely important task in maintaining ecosystem, wildlife and human health.

Background on mercury toxicity and movement in the environment

There are a number of effects, detected in laboratory and field studies, caused by long-term dietary exposure of fish to significant levels of methylmercury (MeHg) (Wiener *et al*., 2003), which is available for uptake by organisms. Because the costs of assessing THg are much lower than those of measuring MeHg, historically, numerous studies have only evaluated THg in organisms as it represents a large portion MeHg (generally over 90% of THg) and can thus be used as a proxy to estimate Hg toxicity (Bloom, 1992). The MeHg form is of particular importance as it is often stored in tissues and can thus be biomagnified through the food web, thereby leading to potentially toxic levels of Hg in organisms at higher trophic levels (Wiener *et*

al., 2003). Documented impacts of Hg on fishes include the inability to feed, diminished behavioural responsiveness, and reduced predator avoidance (Wiener *et al*., 2003). The reduction of the individual fitness of fish can scale up to population and community level responses, leading to negative repercussions on wildlife and human health due to the importance of fish as a food supply. In fact, Hg is most commonly exposed to humans through fish consumption (Clarkson *et al*., 2003), and has had devastating impacts on human health. In the United States alone, annually, numerous children are exposed to MeHg levels in the womb that are associated with impaired neurological development (Birch *et al.,* 2014). Effects are not limited to children: research has established links between blood pressure problems in adults and their exposure to MeHg via fish consumption (Valera *et al.,* 2011).

Multiple pathways transport Hg into aquatic ecosystems (Wiener *et al*., 2003). Groundwater discharge (Laurier *et al*., 2007), soil erosion (Caron *et al*., 2008), volcanic eruptions (Nriagu & Becker 2003), and forest fires (Sigler *et al.,* 2003) are all examples of natural phenomena via which Hg can be cycled through ecosystems. A number of anthropogenic activities can also transport Hg through ecosystems. For example, the burning of biomass (e.g., crop residue burning, biofuel combustion, coal fired power plants) releases Hg assimilated via plants into the atmosphere (Friedli *et al*., 2003). The creation of reservoirs is also known to increase MeHg production and contamination in aquatic ecosystems (Schetagne *et al*., 2000; Wiener *et al*., 2003). In developing countries, gold ore processing practices still commonly use liquid Hg. The mixing of gold ore and Hg dissolves the gold into the Hg, after which the gold can be recovered by burning the Hg-gold amalgam. This process releases Hg vapours into the atmosphere, which can have direct negative repercussions on health via inhalation or distribution in the environment (Van Straaten, 2000; Bensefa-Colas *et al*., 2011). Once in the atmosphere, Hg

can remain in movement there for a year, thus allowing it to be transported over long ranges and to remote areas. The atmospheric deposition of particulate and dissolved Hg into waterways is one of the major pathways via which Hg finds its way into aquatic ecosystems (Waite *et al*., 2002). In addition to this, both current and historic mine tailings from these processes are transported and redistributed throughout watersheds. Even once buried, these contaminated sediments can later be reintroduced into aquatic ecosystems via flooding or erosion (Domagalski, 1998; Conaway *et al*., 2004). This emphasizes the potentially ubiquitous effects of Hg on aquatic ecosystems.

Background on Hg availability in aquatic ecosystems

A number of abiotic and biotic factors influence the quantity of Hg found in aquatic ecosystems and its availability for uptake by aquatic organisms. Major abiotic factors include acidity, temperature, dissolved organic carbon (DOC), and trophic state. Waite *et al*. (2002) showed that in waters of high and low pH levels, significantly more Hg is absorbed than in waters with a pH close to neutral. Lake acidity (pH) and Hg methylation are correlated, thus allowing acidic lakes to have higher Hg bioaccumulation rates (Miskimmin *et al*., 2002; Shastri & Diwekar, 2008). In addition, Hg methylation rates are positively correlated with water temperature (Ramlal *et al*., 2003). However, water temperature is also correlated with the rate of Hg elimination from, which can counter temperature effects on Hg availability (Trudel & Rasmussen, 1997). DOC plays an important role in the photoreduction of Hg, which produces dissolved gaseous Hg. This gaseous form of Hg can in turn volatize from the water into the atmosphere, acting as an important mechanism via which the Hg pool of aquatic ecosystems can be reduced (O'Driscoll *et al*., 2004). The trophic state (e.g. oligotrophic, eutrophic) of lakes is also known to influence Hg bioaccumulation. Biodilution caused by a large amount of plankton

in eutrophic lakes is thought to lead to lower levels of Hg in organisms from these lakes than those observed in oligotrophic lakes (Chen & Folt, 2005; Pickhardt & Fisher, 2007; Miller *et al*., 2012).

Among all species, trophic position is a main factor influencing Hg contamination. Species higher in the trophic chain have higher concentrations of Hg in their systems due to biomagnification (Weiner *et al*., 2003). Among individuals of a given species, size, age, sex, growth rate, and diet all influence Hg concentrations. Larger and older individuals generally have higher tissue Hg levels because growth occurs at a faster rate than Hg is eliminated (Huckabee *et al*., 1979). Hg elimination rate is also negatively correlated with body size, emphasizing the age and size related trend among individuals (Trudel & Rasmussen, 1997). The relatively higher energetic requirements of females can in some cases lead to higher Hg levels (Lange *et al*., 1994; Stafford *et al*., 2004; Kojadinovic *et al*., 2006; Gewurtz *et al*., 2011). Growth rate also influences Hg uptake. At a given length fish that grew at faster rates will have lower concentrations of Hg than will slow growing fish (Stafford *et al*., 2004; Simoneau *et al*., 2005). This same phenomenon is observed throughout the trophic chain (Karimi *et al.*, 2007). Diet is the main pathway via which fish uptake Hg (Wiener *et al*., 2003). Variation and changes in feeding regiments influence Hg uptake. For example, during starvation, Hg concentration in fish increases, and is likely associated with muscle catabolism in undernourished fish. Muscle mass in starved fish is reduced faster than is Hg in the tissues, resulting in an increased tissue Hg concentration (Cizdziel *et al.*, 2002). Ontogenetic diet shifts can also alter tissue Hg levels (Szczebak & Taylor, 2011).

Thesis objectives

Although Hg has received significant attention over the past few decades there is still little information available on Hg concentrations and trends in developing countries, many of which rely on fish for protein (Hassanien & EL Shahawy, 2011). In Africa, almost 4 million people are engaged in fishing-related activities, and fish contribute on average 32% of animal protein intake and up to 70% intake in some countries (FAO, 2012). Fish are thus a resource that is of vital importance for both food and economic security in Africa. Contaminant loading is also of concern for inland, small-scale fisheries as they are important contributors to fish catches in Africa (FAO, 2011). Further research on Hg in African fishes is thus important, and could help in the creation of consumption guidelines to allow both local and international consumers to diminish Hg intake. Moreover, Hg research could help develop fisheries' management strategies and policies to strategically decrease Hg concentrations in aquatic ecosystems, and in fishes used for human consumption. In this thesis, I explore Hg contamination and trends in African fishes using both a meta-analytical approach and a case study of East Africa's most economically important harvested species. The thesis is presented in two chapters. In the first, I review the literature to compile available information on Hg contamination in African freshwater ecosystems and to explore patterns and potential predictors of Hg contamination in fishes. In the second chapter of this thesis, I evaluate Hg concentrations of the Nile perch (*Lates niloticus*) fishery from Lake Nabugabo, Uganda, for which no published information was previously available on Hg content. This information is critical, as the Nile perch is a species with important commercial and sustenance value in Africa. I then assess the effect of habitat of capture on Nile perch Hg concentrations, exploring the role of habitat specific diets and environmental conditions on Hg concentrations and accumulation trends.

Chapter 1

Title: A review of mercury concentrations in freshwater fishes of Africa: Patterns and predictors

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Abstract
The methylated form of mercury (MeHg), a potent neurotoxin, is a contaminant of concern for fisheries because of its potential negative effects on fish and human health. In Africa, inland fisheries are a crucial component of food and economic security, yet little information is available on mercury (Hg) contamination and trends. We compiled published data on Hg contamination in African freshwater fishes, invertebrates and plankton, as well as data on potential drivers of Hg levels in these organisms. From 30 identified studies we assembled 407 total Hg concentrations from 166 fish species, 10 types of invertebrates, and various plankton, distributed across 31 waterbodies in 12 countries. The total Hg concentration in fishes, expressed as mean per site, ranged from 0.8-1865.0 ng/g wet weight (ww), with a mean of 141.9 ± 316.5 ng/g ww (± SD). Only locations with nearby artisanal small-scale gold mining operations (ASGM) had mean Hg levels above the WHO/FAO's recommended guideline for fish (500 ng/g ww), highlighting the need for more extensive monitoring and regulations in areas with AGSM. Locations without ASGM generally had Hg levels well below guidelines, supporting previous work suggesting that Hg contamination is anomalously low throughout Africa. We used mixed models to detect relationships between fish Hg concentrations and trends previously established in temperate zones, which included trophic level, mass, latitude and chlorophyll *a*. Mass, trophic level, and latitude were all positive predictors of Hg levels. Our results thus confirmed the presence of Hg bioaccumulation and biomagnification in African fishes. This study also highlights the relative lack of data on Hg concentrations in African fishes and the need for a thorough assessment of Africa's freshwater Hg concentrations to further investigate and better understand low Hg levels.
Keywords: Total Mercury, Biomagnification, Bioaccumulation, Aquatic, and Contaminants

Introduction

In Africa, commercial and subsistence fisheries play a critical role in food and economic security, with almost 4 million people engaged in fishing-related activities (Béné & Friend, 2009; FAO, 2012; Heck, Béné & Reyes-Gaskin, 2007). Contributing on average 32% of animal protein intake and up to 70% in some African countries (FAO, 2012), fish provide essential micronutrients, minerals, and fatty acids. As in other regions, contaminants are of growing concern for African fisheries, as they can diminish recruitment and marketability of stock (Richardson, 2003). As important contributors to fish catches in Africa, inland, small-scale fisheries are of particular concern because of their susceptibility to contaminant loading both through localized and global sources (FAO & WHO, 2011; Ritter *et al*., 2002; Streets, Zhang & Wu, 2009; Wiener *et al*., 2003).

Mercury (Hg) is a contaminant of great concern for fisheries because of the toxicity of its methylated form (MeHg), which can have impacts on fish and human health (Clarkson *et al*., 2003; Munthe *et al*., 2007). Hg can cause complications with human foetal brain development, and has the potential to lead to several problems in adults and children, including headaches, emotional changes, insomnia and cognitive function deficits (EPA, 2014). A number of negative effects of Hg have also been observed in fishes, including reproductive impairment and change in important behavioural traits such as predator escape (see review in: (Depew *et al.* 2013). Reduced fitness of individual fish associated with Hg contamination can scale up to population and community level responses, which could have dramatic consequences for fish stocks. Because it is more expensive to monitor MeHg than total mercury (THg) and MeHg generally accounts for 90-95% of THg (Bloom *et al*. 1992), THg is often used as a proxy to determine the toxicity of Hg contamination in fishes.

Hg can be released to aquatic ecosystems through multiple sources. In Africa, Hg emissions are approximately 330 tonnes per year, with model estimates ranging from 172 to 555 tonnes per year (UNEP, 2013). Emissions across the continent are concentrated within the countries of western Africa, the East African rift valley region, and South Africa, with different emission sources types within and between these regions (AMAP & UNEP, 2013; UNEP, 2013). Artisanal and small-scale gold mining (ASGM) accounts for more than 70% of the emissions on the continent, with Ghana, Sudan, Tanzania, and Burkina Faso accounting for two-thirds of all emissions from the ASGM sector. South Africa is considered the largest emitter of Hg in Africa with emissions originating primarily from coal combustion and large-scale gold mining (UNEP, 2013). Other emission sources on the continent include cement production, biomass burning, and improper disposal of Hg-containing waste (AMAP & UNEP, 2013; Crutzen & Andreae, 1990; Foster, 1996; Friedli *et al*., 2003).

Hg deposition across Africa is comparable to other regions and continents (Selin *et al*., 2008; Travnikov *et al*., 2010). However, previous work on the fate and transport of Hg in aquatic ecosystems in Africa suggests that Hg concentrations in aquatic organisms are generally low. In a review of 11 published studies on fish Hg from Africa, these concentrations are considered 'anomalously' low because Hg levels in the water are not always as low as expected given the concentrations of Hg in fish (Black *et al*., 2011). Hg concentrations in fish ultimately depend on both the amount of Hg available for uptake into the aquatic food web as well as the efficacy with which Hg is taken up at the base of the food web and transferred through the consumer trophic levels. As such, Hg concentrations in any given fish are primarily determined by four key parameters: the concentration of bioavailable Hg in the water, the degree of Hg uptake at the base of the food web, the rate of Hg biomagnification through the food web, and the trophic level

of the fish. In addition, fish size and age can be important determinants of Hg concentrations since older, and therefore larger fish tend to accumulate mercury in their tissues as they grow (Wiener *et al*., 2003).

In turn, there are several environmental factors that can indirectly influence Hg concentrations in fish by affecting these key parameters. For example, Hg methylation rates, pH, dissolved organic carbon (DOC) concentrations and Selenium (Se) concentrations can affect the bioavailability of Hg (Ullrich, Tanton & Abdrashitova, 2001; Wiener *et al*., 2003), while total phytoplankton biomass and phytoplankton growth rates influence the uptake of Hg at the base of the food web through bloom dilution and growth biodilution (Pickhardt *et al*., 2002). Several environmental parameters are also thought to affect the biomagnification rate of Hg through a system, including growth rates of fish at consumer trophic levels (Wiener *et al*., 2003). These findings largely reflect research conducted in temperate zones; an exploration of these trends in Africa may help to shed light on the potential anomaly in Hg accumulation across the continent.

In Africa, the role of fisheries in food security and local income highlights the importance of monitoring concentrations of contaminants such as Hg. Understanding the mechanisms that control, and potentially limit Hg bioavailability in African freshwaters is important for the future long-term monitoring of African freshwater ecosystems and its fisheries. Yet, as many other areas in the developing world, data on Hg contamination and trends in Africa are limited and scattered across the literature (Hassanien & EL Shahawy, 2011; Lavoie *et al*., 2013). To address this disparity, we assembled published data on Hg concentrations to describe broad patterns and to identify critical gaps in available data. We predicted that Hg concentrations in fish will generally be low across Africa, in concordance with results from previous work on the topic (Black *et al*., 2011). We also used statistical models to test relationships between Hg

concentrations and environmental and biological factors that were available in our dataset. We predicted that Hg concentrations would increase with both fish size and trophic level, and that systems with high phytoplankton biomass would have overall lower Hg concentrations.

Materials and methods

We assembled data on Hg concentrations in tissue samples of African freshwater organisms from the literature, along with information about the individuals, species, and water bodies represented by the data. We summarized patterns in these data, and used mixed models to evaluate the importance of various biological traits and environmental parameters as predictors of Hg concentrations. Below we describe each element of our approach in more detail.

Mercury data collection

We conducted a search including all papers evaluating Hg concentrations of fishes in African inland freshwaters indexed in ISI Web of Science by March 2014. Using the keywords "Mercury AND Africa" we located 30 studies, evaluating Hg concentrations of aquatic organisms in 65 different locations, distributed across 31 different water bodies throughout Africa. The exact geographic position (latitude, longitude) of each study location was determined using Google Earth.

From each of these studies, we compiled information on total mercury concentrations in sampled species when available. The data set included information on Hg levels for 166 fish species, 10 different invertebrates, and a variety of plankton. Because data for non-fish species were very limited, we present them in the supplemental information (SI) but do not discuss or analyze them further. Total mercury (THg) concentration was the most widespread measurement reported in fish and is generally composed of approximately 90-95 % methylmercury (MeHg) in

temperate systems (Bloom, 1992), thus is likely to reflect the quantity of potentially toxic mercury stored in tissues in African systems as well. Most studies provided mercury levels per unit of fish wet weight in ng/g, and those that did not provided the conversion factor to transform data from dry weight to wet weight (ww). Units were all standardized to ng/g ww. When Hg concentrations were available only in figures, we obtained the data by contacting the authors or by reading them from the figures using DataThief software (Tummers, 2006). We also gathered other available biological and environmental information relevant to Hg concentrations in fish from each retrieved publication. Biological information included species, mass, and length of individuals, as well as the number of individuals used to create the presented mercury concentration and the associated standard error. Environmental data included chlorophyll *a* (chl-*a*) concentrations, water temperature, pH, dissolved organic carbon concentration (DOC), sulphate concentration, particulate and filtered Hg concentrations, lake volume, lake area, lake depth, Secchi depth, as well as, water body-type (river, lake or reservoir). The presence or absence of mining activities in each sampling location was determined by a search within each publication.

Determining trophic levels of organisms

The trophic level (TL) of each taxa was determined using FishBase (Froese & Pauly, 2011) when available. When not available, we gathered information about their diets and attributed a trophic level between 2 and 4, based on Lindeman's concept of ecosystem organization, in which primary consumers feeding on photosynthetic organisms are level 2, secondary consumers feeding on primary consumers are level 3, and top piscivores are level 4 (Gerking, 1994; Lindeman, 1942). Some fishes experience ontogenetic diet shifts including the heavily exploited Nile perch, which switch from invertebrate to piscivorous feeding habits at

approximately 15 cm in total length, although this can vary with habitat and across lakes (Paterson & Chapman, 2009). Because Nile perch were one of the more common species in our dataset, we separated them into two trophic level categories (one piscivorous, and one invertebrate feeding) based on a 15-cm criteria when length data were available. Although other African fishes may experience ontogenetic diet shifts, this was not considered in our dataset when attributing trophic levels.

Chlorophyll data collection

Due to recent interest in the potential relationship between environmental productivity and Hg in aquatic food webs, expressed by a relationship between chl-*a* and Hg bioaccumulation (Chen & Folt, 2005; Pickhardt *et al*., 2002), we also furthered our search for complimentary data on chl-*a* concentrations in all sampling site locations from which Hg data were available. This was accomplished using the key words "Chlorophyll AND x location" (e.g.: chlorophyll AND lake Ziway) on ISI Web of Science, Google Scholar, and Google. When we found two different sources with relevant chl-*a* data or a given study evaluated temporal differences in chl-*a* concentrations, we retained the data gathered closest to the date when Hg data were collected. For studies that only provided chl-*a* concentrations in figures, we contacted authors to attempt to acquire raw data. If this was not possible, we used Data Thief (Tummers, 2006) to extract chl-*a* concentrations from relevant figures.

Data analysis

For each location we calculated the median, standard deviation, and range of Hg concentrations in all aquatic organisms. Data on environmental variables collected from each Hg study are presented in Table 1 of the SI. All these variables, except chl-*a*, are not included in the

models below because they were only available for small subsets of the data, which were insufficient for statistical analysis.

To evaluate effects of mass, trophic level, and chl-*a* on mercury concentrations we used a multilevel varying intercept, mixed-effects model, implemented by the 'lmer' function of the R (version 3.0.2 for Mac OS X 10.8) package 'lme4' (Bates *et al.*, 2014). We fit this model to a subset of the data that included observations for which fish mass and lake chl-*a* data were available (n = 129 observations in analyzed dataset), and excluded locations near ASGM operations (n = 23 excluded locations) where atypically high mercury concentrations could potentially drive different Hg dynamics. We also re-ran the models described here including ASGM locations. Because our dataset spanned a large geographical range, we included latitude as a covariate in the deterministic portion of the model, as it was recently shown to be a significant predictor of Hg biomagnification (Lavoie *et al*., 2013). The (full) model can be written as:

[Eq. 1] $THg_{ijk} = \beta_{0j[i]} + \beta_{1k[i]} + \beta_{2j[i]}*TrophicLevel_i + \beta_{3j[i]}*Mass_i + e_i$

$e_i \sim N(0, \sigma^2_e)$

$\beta 0j \sim N(\mu\beta 1, \sigma^2\beta_0)$

$\beta 1k \sim \gamma o + \gamma 1*chla_k + \gamma 2*Latitude_k + \varepsilon_\beta 1$

$e1 \sim N(0,\sigma^2\beta_1)$

$\beta 2j \sim N(\mu\beta_2,\sigma 2\beta_2)$

$\beta 3j \sim N(\mu\beta_3,\sigma^2\beta_3)$

where the total mercury concentration in an individual or aggregate sample *i* of species *j* from location *k* is a function of a species- and location-specific intercept, the individual's trophic level and mass, and the trophic state (chl-*a*) and latitude of the sampled location. This model can also be written in the syntax of the lmer function in R as:

[Eq. 2] lmer(THg~Trophic Level + Mass + Chlorophyll *a* + Latitude + (1|Location) + (1|Species), data= AfricaHgdata)

Variables were log-transformed when necessary to improve normality, and all continuous covariates were standardized to Z scores.

We fit the entire suite of variations of the full model described above, using all possible combinations of the set of fixed predictors, through maximum likelihood (ML). To assess goodness of fit of these models we computed AIC values, as implemented in the R function 'anova' (Core Team, 2013). All models were re-fit through restricted maximum likelihood (REML) to obtain coefficient estimates as well as marginal and conditional R^2 values, where marginal R^2 represents variance explained by fixed factors and conditional R^2 represents variance explained by both fixed and random factors (Nakagawa & Schielzeth, 2013). The best fit model met all assumptions of linear mixed models.

Results

Mercury and chlorophyll-a concentrations

We located 30 studies that reported Hg concentrations in inland African aquatic organisms from 65 different locations distributed across 12 different countries in Africa (see Figure 1a for locations and Hg concentrations, and SI Table 1 for a complete list of studies used to compile data). From these studies, we gathered 380 total mercury (THg) concentrations in fishes from 59 of the locations that looked at a total of 166 different species. Each Hg concentration was based on individuals of the same species with sample size ranging from 1-53 (mean = 8, SD = 8), resulting in a dataset based on Hg measurements from 2986 individual fish. The total Hg concentration, expressed as mean per site, ranged from 0.8-1865.0 ng/g wet weight (ww), with a mean of 141.9 ± 316.5 ng/g ww (± SD) (Figure 1b). The highest Hg concentrations recorded (e.g., 1865 ng/g ww, 1330 ng/g ww) were from samples collected in the Hg amalgamation ponds in the Rwamagasa subarea of Tanzania (see SI Table 1). When locations

with nearby ASGM were removed, total mercury concentrations were available from 36 different locations and 136 different species. Across these locations, the mean concentration of Hg was 44.2 ± 52.3 ng/g ww (± SD) and the Hg upper range limit was 628.0 ng/g ww, which was documented in *Barbus intermedius* from Lake Awassa, Ethiopia. Small and large Nile perch (*Lates niloticus*) and *Tilapia zilli* , two species of important commercial and sustenance value in Africa, had THg concentrations of 38.2 ± 35.4 ng/g ww, 71.3 ± 73.6 ng/g ww, and 23.5 ± 29.2 ng/g ww (± SD), respectively (note that *Tilapia zilli* has a different common name across all African countries and will therefore be referred to by its scientific name).

We retrieved measurements of chl-*a* (1 chl-*a* concentration/location) for a total of 36 different locations (see SI Table 1). Of these, 30 were situated in areas without gold mining activities. Across these sites, chl-*a* concentrations ranged from 0.3- 64.3 ug/L.

Patterns in mercury concentrations

Predictors retained in the best fit model included trophic level, mass, and latitude. Relationships between Hg and the four fixed predictors evaluated in this study (chl-*a*, latitude, trophic level, and mass) are presented in Figure 2. The models discussed here were built using a subset of data from locations without mining in their vicinity that had both measures of chl-*a* and mass available. This resulted in a dataset with 129 Hg concentrations, which came from 20 different locations and 74 different species. From the full suite of the fitted models, those with ΔAIC values within 7 of the best fit models' ΔAIC are presented in Table 1. The best fit model included all fixed effects except chl-*a*, which exhibited only a weak positive slope with a 95% confidence interval that overlapped with 0 in all models in which it was retained. When evaluating fixed predictors in the best fit model, trophic level, mass, and latitude all showed positive relationships with Hg concentrations in African fishes, and confidence intervals that did

not overlap with 0. However, latitude's confidence interval was very close to overlapping with 0, demonstrating a weak relationship between this variable and Hg concentrations. Together, these fixed factors explained ~30% of the variation in Hg concentrations, and overall the best fit model explained ~85% of the variation (see marginal and conditional R^2 values in Table 1). The next best model, not included in this table, had a much higher ΔAIC value of 11.86, and did not include trophic level and chl-*a*. Although they are not presented here, in the models including ASGM locations all trends remained the same as those discussed above, further emphasizing the importance of trophic level and weight as predictors of Hg concentrations in fishes across Africa.

Discussion

This study provides an up to date review of patterns in Hg concentrations in African aquatic biota. Of the 833 inland waterbodies identified in Africa by the FAO (FAO & GeoNetwork, 2000) (which do not include rivers), our dataset indicates that only 26 lakes/reservoirs and 5 rivers have been evaluated for Hg contamination in fishes, though additional data may be available in non-published sources. Given the importance of fish for food and economic security of the continent (FAO, 2012) and the health risks associated with Hg contamination via fish consumption, which is the primary source of Hg contamination in humans (Clarkson *et al*., 2003; Hughner, Maher & Childs, 2008), additional research on Hg contamination throughout Africa would be important for ecosystem and human health. Given the limited amount of studies available, we did not consider quality control measures for individual studies, and thus the accuracy and precision of estimates may have varied among studies. However, the general patterns that emerged seem robust. Results suggest that Hg levels in African fishes are generally low, which supports results from the earlier study of Black *et al*. (2011), based on piscivorous and non-piscivorous fishes in 11 locations in Africa. Overall, Nile

perch and *Tilapia zilli,* the two most important commercial fishing species, had concentrations well below the FAO's lowest recommended limit for human consumption (500 ng/g) (FAO & WHO, 2011). In agreement with previous observations of Hg biomagnification in African aquatic food webs, *Tilapia zilli* had lower Hg concentrations than Nile perch, a species which typically occupies a higher trophic position. Small Nile perch also had lower Hg concentrations than large ones, highlighting the importance of both bioaccumulation and ontogenetic dietary shifts in this species. Among the 65 locations from which we retrieved data on total mercury in fish, only four had overall mean Hg concentrations above the WHO/FAO's recommended limit for fish. These four locations were found in the Rwamagasa ASGM area of northwest Tanzania and although not all species collected in this area had high Hg concentrations (see SI Table 1), for some species concentrations surpassed the FAO guideline by as much as 1365 ng/g. A recent study in Tanzania found that almost half of the people living and working in these areas were not aware of the potential health effects of Hg contamination (Charles *et al*., 2013), emphasizing the importance of increasing efforts to provide education on risks of Hg, continued and standardized Hg monitoring in ASGM hotspots, and implementing the use of cleaner technologies for the extraction of gold (UNEP, 2012).

While the Hg levels that we observed were low relative to established health guidelines, there are several concerns about Hg in Africa that indicate a need for caution and further research. Some studies suggest that there may be effects of levels of exposure to Hg that are below guidelines on neurochemical receptor-binding characteristics in animals and infant growth (Basu *et al*., 2005; Karagas *et al*., 2012). In fact, the upper range of Hg levels documented in this study in locations without mining (i.e. Lake Awassa, Ethiopia) can have certain effects on reproductive systems in fish (Crump & Trudeau, 2009). In addition to this, in a review published

in 2012 by Environmental Health Perspectives, Karagas *et al*. (2012) found evidence for negative effects of low Hg concentrations on neurological and other body systems in humans; although results were widely inconsistent, the review highlights the potential for negative effects of low-level exposure and the need further more detailed investigations. Furthermore, many waterbodies of inland Africa have not been evaluated for Hg contamination, making it impossible to confirm that levels of Hg are below levels of concern throughout the continent. This is of particular importance because Africa has been identified as a hotspot for future atmospheric Hg deposition (Streets *et al*., 2009). Given the low levels of Hg in aquatic biota observed across Africa, it has been argued that the discrepancy between Hg atmospheric deposition and contamination in Africa could be indicative of an anomaly in Hg accumulation across the continent (Black *et al*., 2011). Our results are consistent with this idea of low levels, but clearly a more exhaustive examination of Hg levels and trends in Africa is required to draw strong inferences regarding a continental Hg anomaly.

Our results demonstrated a weak, positive relationship between latitude and Hg concentrations. In their global review of Hg biomagnification in aquatic foodwebs, Lavoie *et al*. (2013) reported a positive relationship between latitude and Hg trophic magnification factors. They suggested that the trend primarily reflected decreasing temperatures from South to North, which would drive lower biomagnification rates due to differences in Hg assimilation and excretion associated with temperature (See review in: Wiener *et al*., 2003). With increasing biomagnification rates along this gradient, increasing Hg concentrations in fish might also be expected, as observed in this study. Interestingly, our results do not suggest that temperature decrease is the main driver of the observed Hg concentration gradient, because water and air temperatures actually increase between the South of Africa and the northern most African

regions sampled in this study (FAO & GeoNetwork, 2005). This suggests the possibility of alternative drivers regulating the latitudinal gradient in Hg concentration that we detected in African inland waters. Some examples of potential latitudinal differences include geology, acidity, or atmospheric deposition patterns which could affect the bioavailability of Hg. However, the trend between Hg and latitude in African aquatic organisms was weak at best, and clearly, further examination of the trend and drivers of the relationship will be informative.

We searched for measures of a suite of potentially important environmental correlates of Hg concentrations in fish including: pH, Secchi depth, DOC, and other variables (see methods for complete list). However, information on these variables was not available in many of the retrieved Hg studies (see SI, Table 1). Thus, it was not possible to include these variables in our mixed models. Nonetheless, it was an informative line of inquiry, demonstrating that it is not yet the norm in studies evaluating Hg concentrations in African inland waters to document this suite of environmental factors, despite their potential role in regulating Hg concentrations in aquatic ecosystems. We recommend that future studies document these environmental factors to provide a more comprehensive understanding of global Hg cycling and patterns, and insight on a potential African Hg accumulation anomaly.

Some studies in temperate and subtropical regions have demonstrated a negative relationship between chl-*a* and Hg accumulation (e.g. Chen & Folt, 2005; Wang *et al.*, 2011). The proposed mechanism is that high phytoplankton biomass reduces the dissolved Hg available for uptake (biomass dilution), and the rapid rate of phytoplankton production does not allow dividing cells to completely equilibrate with available dissolved Hg (growth dilution) (Pickhardt *et al*., 2002). Both these phenomena would lead to lower levels of Hg in individual phytoplankton and consequently in organisms throughout the food chain when comparing

systems with similar concentrations of bioavailable Hg (Chen *et al*., 2005; Karimi *et al*., 2007). Based on the results of a survey of 20 lakes in the northeastern United States, Chen & Folt, (2005) suggest that plankton density may be an effective predictor of fish Hg concentrations. As such, the relationship between Hg concentrations in fish and trophic state is of particular interest because chl-*a* requires less resources to measure than Hg in both water and fish. Current technology to monitor Hg is expensive and necessitates infrastructure that is often inaccessible in developing countries (Hassanien & EL Shahawy, 2011). If chl-*a* were to be a robust indicator of Hg concentrations in fish, it could be used as a proxy measurement for Hg concentrations, increasing the economic viability of more regular and extensive monitoring. However, we did not detect an important relationship between chl-a and Hg levels in African freshwater fishes, and the observed trend (albeit weak) was positive. In temperate systems, where this trend has gained significant attention, the relationship between chl-*a* and Hg in fish is not always robust among different species (Simonin *et al.*, 2008). Thus, this relationship might not be likely to occur across the scope of species we assessed in this study might. The fact that we did not document a relationship could also reflect geographic variation in the effects of primary production on Hg between Africa and other locations where this trend has been documented. This could also be due to limited availability of data for African aquatic biota. We did not have access to data on aqueous Hg concentrations in different locations, making it difficult to disentangle the effects of chl-*a* and Hg bioavailability. Also, our chl-*a* data often came from single measurements that may not be representative of a given system and seasonal fluctuations in chl-*a* concentrations (Witte *et al*., 2011; Zinabu, 2002). Overall, these results suggest that chl-a would not serve as an appropriate proxy measurement to estimate Hg concentrations in African

fish. More detailed studies are needed to assess the effect of lake trophic status on Hg trophodynamics in tropical systems.

As expected, our compilation supports strong patterns between trophic level, mass, and Hg concentrations reported for many systems. Globally, species at higher trophic levels, such as piscivorous fish, have higher Hg concentrations due to biomagnification through food webs. Within species, larger fish also typically have higher Hg concentrations due to bioaccumulation (See summary in Wiener *et al*., 2003; see also examples from various geographic locations: Cheng *et al*., 2011; Chumchal *et al*., 2011; Gentès *et al*., 2013; Kidd *et al*., 2012; Molina *et al*., 2010). To date, biomagnification and bioaccumulation have been evaluated in only a handful of studies in Africa. Generally, the expected trends have remained robust (e.g. Campbell *et al.*, 2004; Campbell *et al.*, 2008; Poste, Hecky & Muir, 2008), yet some studies have demonstrated contrasting results, with organisms from low trophic levels that have high Hg concentrations (Campbell, Dixon & Hecky, 2003), and species that do not seem to accumulate Hg as they increase in size (Kwaansa-Ansah, Agorku & Nriagu, 2011). Our results, which integrate across a wide range of data, suggest that these two traits are important and robust positive predictors of Hg concentrations in aquatic organisms throughout Africa. While there is certainly observation error in our estimate of trophic level due to the use of FishBase and the unexplored importance of ontogenetic diet shifts, this does not obscure a strong relationship between trophic level and Hg. The presence of these patterns is an important finding across the geographic scale and range of species evaluated in this study, as trophic position and size are factors that can be easily identified by Africans who consume fish regularly and could be used to help individuals minimize Hg intake. Adequately communicating the principles of biomagnification and bioaccumulation in community and classroom settings could provide a cost effective method to

help consumers determine which fish are likely to contain relatively higher levels of Hg, and potentially encourage them to vary the types and sizes of fish they consume. Although not feasible in all contexts, such strategies could reduce exposure to Hg, particularly in at risk communities.

Overall, our results demonstrate low mercury concentrations in fishes throughout Africa and that globally established trends of biomagnification and bioaccumulation are robust across Africa. In spite of low levels, Hg contamination is an important issue in Africa as fish are a primary food source, and both long and short term health effects of exposure low mercury concentrations are not yet properly understood. This study also highlights the relative lack of data on Hg concentrations in African fishes and the need for a thorough assessment of Hg concentrations across the continent's freshwater ecosystems.

Figure and table captions

Figure 1. Mercury concentrations in inland aquatic fish across Africa documented in published peer-reviewed studies. Waterbodies are represented in blue, as per (FAO & GeoNetwork, 2000). a) Locations of retrieved studies. Red dot size indicates which range bracket mean total mercury concentrations each location fell into (see in-map legend for details). In locations with no available data studies presented Methylmercury concentrations but did not evaluate Total mercury concentrations. b) Box and whisker plots showing the median, the lower and upper quartiles (25% and 75%), and the minimum and maximum values of total mercury concentrations at each different location. Locations appear West to East, from left to right. The red line indicates the FAOs guideline of recommended maximal mercury concentrations in fish for consumption. See SI for a complete list of studies, location names, and the mean Total mercury concentrations of all species at each location.

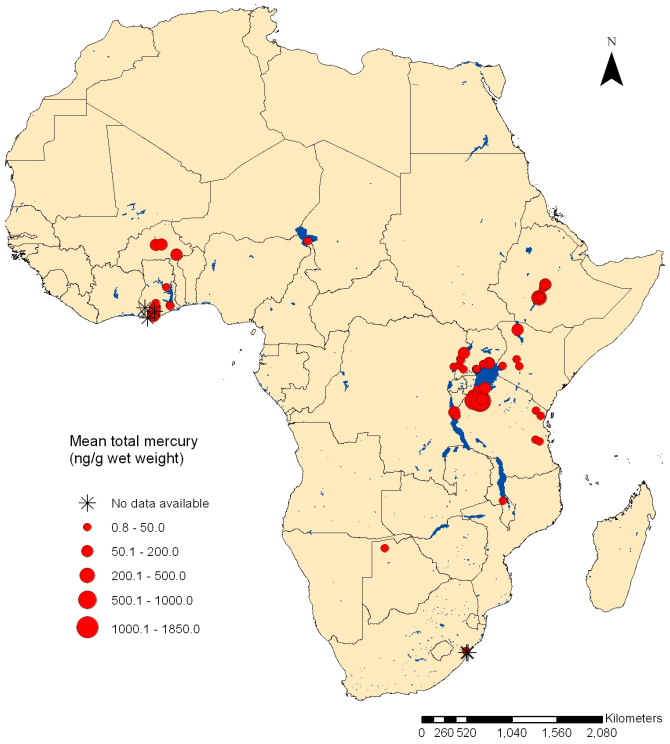
Figure 2. Total mercury concentrations in African freshwater fishes in relation to evaluated biological and environmental factors (n = 129 Hg concentrations, from 74 different species and 20 locations).

Table 1. Models evaluating mercury concentrations in African freshwater fishes with AIC values within seven of the best fit model. Models are placed, top-down, one per row, in order from best to worst. In addition to fixed factors indicated in the table, all models included random species and location effects. The slope of each parameter is followed by its respective confidence interval in parenthesis. Marginal and conditional R^2 values indicate variance explained by the models' fixed effects, and by both fixed and random effects, respectively. Models were fit through maximum likelihood to compute ΔAIC values and through restricted maximum likelihood to compute other presented information.

Figures

Figure 1.

a)



b)

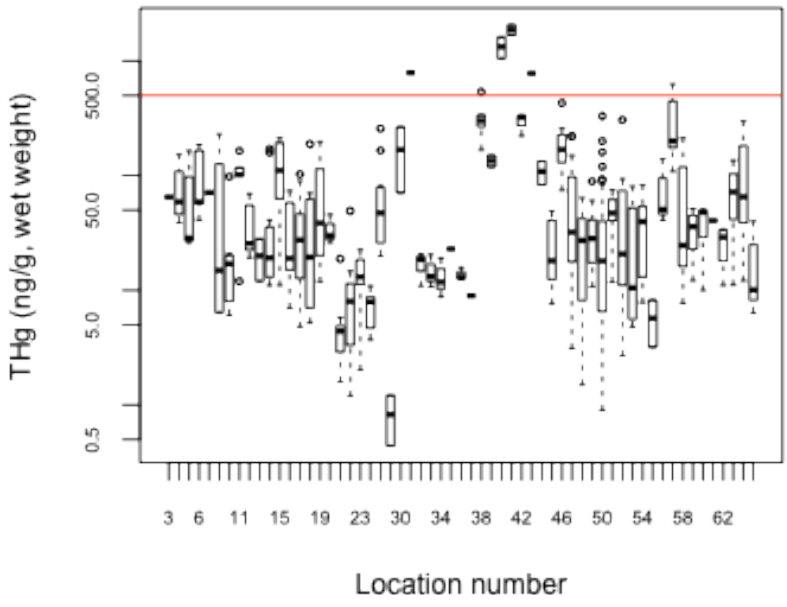


Figure 2.

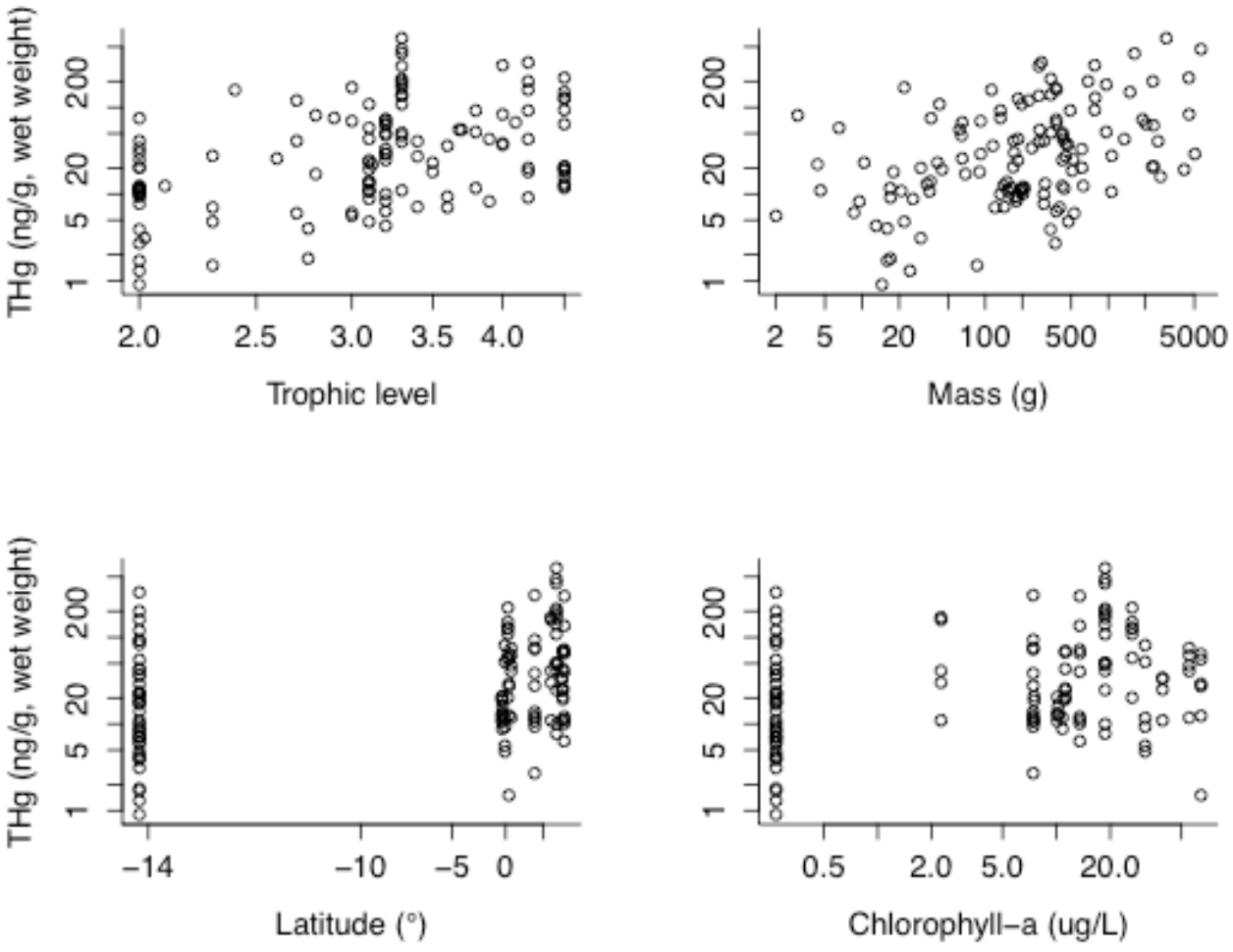

THg (ng/g, wet weight)
1
5
20
200
2.0
2.5
3.0
3.5
4.0
Trophic level
2
5
20
100
500
5000
Mass (g)
−14
−10
−5
0
Latitude (°)
0.5
2.0
5.0
20.0
Chlorophyll−a (ug/L)

Table 1.

Model number	Trophic level	Weight	Latitude	Chlorophyll *a*	Marginal R^2 (%)	Conditional R^2 (%)	ΔAIC
1	0.46 (0.25-0.69)	0.20 (0.04-0.36)	0.48 (0.02-0.94)	-	30.55	84.93	0
2	0.47 (0.25-0.69)	0.20 (0.04-0.36)	0.45 (-0.07-0.97)	0.09 (-0.41-0.59)	31.81	85.49	1.81
3	0.45 (0.23-0.67)	0.21 (0.05-0.37)	-	-	18.51	82.86	2.35
4	0.46 (0.24-0.68)	0.20 (0.04-0.36)	-	0.27 (-0.19-0.73)	22.87	83.65	2.85
5	0.59 (0.41-0.77)	-	0.51 (0.03-0.99)	-	29.16	84.31	4.21
6	0.59 (0.41-0.77)	-	0.44 (-0.06-0.94)	0.14 (-0.34-0.62)	32.04	85.07	5.82
7	0.58 (0.40-0.76)	-	-	-	20.25	83.23	6.78
8	0.58 (0.40-0.76)	-	-	0.19 (-0.15-0.53)	21.38	82.89	6.86

Acknowledgments

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Connecting statement

In the first chapter of this thesis I compiled published data on Hg concentrations in African fishes and explored patterns and predictors of Hg. I demonstrated that Hg concentrations throughout Africa are generally low, except in certain areas with ASGM. There was also considerable variability in Hg concentrations, which was in large part predicted by the trophic position and size of fish. Given the importance of trophic position and size as predictors of Hg across African fishes, in the second chapter of this thesis I further explored how variation in diet and in size of individuals influences Hg contamination. In particular, I evaluated how Hg concentrations vary in different individuals of a species found in distinct habitat types within a lake system characterized by varying environmental conditions and different prey bases. I was interested in this question because previous work on Hg shows that Hg concentrations in fish vary between different habitat types (Castro *et al.*, 2007; Chételat, Amyot & Garcia, 2011; Chételat, Cloutier & Amyot, 2013; Chumchal *et al*., 2011; Rypel, 2010; St. Louis *et al*., 1994). However, most of these studies were conducted by comparing different systems, and those within one system concentrated primarily on interspecific differences between littoral and pelagic fish. In this study, I concentrated on intraspecific differences between open-water water and ecotonal fish to assess the presence of robust trends in Hg concentrations across these specific habitat types. I used Nile perch (*Lates niloticus*), a predatory fish that is an important component of people's diets, as a model species. I thus compiled data on mercury concentrations from the Nile perch in Lake Nabugabo, Uganda. I characterized Hg contamination trends in the ecotonal and open-water habitats among individuals of varying body size, and then related patterns to variation in diet and environmental characteristics.

Chapter 2

Title: Effects of habitat on mercury concentrations in fish: a case study of Nile perch (*Lates niloticus*) in Lake Nabugabo, Uganda

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Abstract

The methylated form of mercury (MeHg), a potent neurotoxin, is of particular concern in aquatic ecosystems as fish are the primary source of mercury (Hg) contamination in humans. Biological, chemical and physical factors can drive divergence in Hg contamination among varying aquatic habitat types and their fish inhabitants. For example, wetlands and watersheds with larger proportions of forest in their catchment areas are typically characterized by heightened Hg concentrations. As such, in lakes that intersect with wetlands and forests, fish from the habitats along the lake periphery might also have heightened Hg concentrations relative to the open-water region of a lake. Here, we explore patterns of Hg concentrations in Nile perch (*Lates niloticus*), a large piscivore which is one of East Africa's most important fisheries. Nile perch show strong patterns of habitat-associated divergence in a suite of ecological traits that might correlate with variation in Hg contamination. Total mercury (THg) content was quantified in 152 Nile perch four different habitat types in Lake Nabugabo, Uganda: open-water, forest ecotone, *Miscanthidium violaceum* dominated wetland ecotone and *Vossia cuspidata* dominated wetland ecotone in the summer of 2013. Both habitat of capture and body size were important predictors of THg. Open-water fish had the lowest Hg concentrations when small and the highest concentrations when large. Nile perch from the *M. violaceum* wetland ecotone had the highest levels of Hg in small fish, yet, the lowest rates of Hg accumulation as they increased in size. Observed differences in acidity, as well as, dissolved oxygen among habitats might play a role in their Hg availability. Stomach content analysis suggested that diet was also a potential driver of Hg differences because Nile perch from habitats with cannibalism had the highest Hg accumulation rates. Despite differences across habitats and sizes (range 6 -130 cm), Hg concentrations were all well below the WHO/FAO recommended guideline of 500 ng/g (mean: 13.6 ± 0.4 ng/g wet weight; range: 4.9 and 29.3 ng/g wet weight).

Introduction

The methylated form of mercury (MeHg) is a potent neurotoxin that is of particular concern in aquatic ecosystems because of their susceptibility to mercury (Hg) loading (Ritter *et al*., 2002) both through anthropogenic and natural sources (Caron *et al*., 2008; Friedli *et al*., 2003; Laurier *et al*., 2007; Schetagne *et al*., 2000). Fish are the primary source of Hg contamination in humans (Clarkson *et al*., 2003). Therefore, understanding factors driving variation in Hg concentrations within and among fish species is important in informing fisheries policies and, more generally, in maintaining human and ecosystem health. This is particularly critical in many developing countries where fish are essential to economic and food security.

The concentrations of Hg in aquatic ecosystems and organisms can be influenced by a number of interrelated biological, chemical, and physical factors. Methylmercury (MeHg) is the biologically available form of Hg that tends to accumulate through food webs (Wiener *et al*., 2003). The bioavailability of MeHg is determined by a wide range of factors including, as examples, microbially mediated methylation rates, pH, and dissolved organic carbon (DOC) (Ullrich *et al*., 2001). The uptake of Hg at the base of the food web can in turn be affected by growth rates of phytoplankton (Pickhardt *et al*., 2002). Within fish species, individuals that are larger, older, and/or of higher trophic level tend to have higher MeHg concentrations due to bioaccumulation and biomagnification (Wiener *et al*., 2003). Together, these factors can drive divergence in mercury contamination among habitats. For example, ecosystems with large wetlands typically have organisms with heightened concentrations of Hg (Rypel 2010; Simonin *et al*., 2008; St. Louis *et al*. 1994; Warner *et al*. 2005), and lakes with a relatively higher percentage of leaf litter or forest in their catchment areas have higher MgHg concentrations in the water (Tsui & Wang, 2004; Wang *et al*., 2009). When the periphery of a lake intersects with

forest and wetlands, the water of its ecotonal habitats might have higher MeHg concentrations than the open-water due to its proximity to wetlands and forests, where MeHg is typically higher. These differences in Hg availability could in turn influence Hg in aquatic organisms and lead to intra and interspecific habitat-associated divergence in Hg contamination. Previous work does indeed show that Hg concentrations in fish vary between different aquatic habitat types (Castro *et al.*, 2007; Chételat, Amyot & Garcia, 2011; Chételat, Cloutier & Amyot, 2013; Chumchal *et al*., 2008; Rypel, 2010; Stafford *et al*., 2004; St. Louis *et al*., 1994; Warner *et al*. 2005). However, most of these studies were conducted by comparing different systems, and those within one system concentrated primarily on interspecific differences among fish feeding in benthic, littoral and pelagic zones. In this study, we concentrate on intraspecific differences between open-water water and ecotonal fish to assess the presence of robust trends in Hg concentrations across these specific habitat types. We explore patterns of Hg concentrations in Nile perch (*Lates niloticus*), a large piscivore that shows strong patterns of habitat-associated divergence in a suite of morphological and ecological traits that might correlate with variation in Hg contamination. We focus on THg concentrations because the costs of assessing THg are much lower than those of measuring MeHg. Nonetheless, MeHg generally represents over 90 % of THg in fish, allowing THg to be used as a proxy to estimate Hg toxicity (Bloom, 1992).

Nile perch were introduced into Lake Victoria, East Africa, the largest tropical lake in the world, and other lakes in the basin (Nabugabo, Kyoga) in 1950s and 1960s to compensate for depleting commercial fisheries and to promote sport fishing (Balirwa *et al*., 2003; Pringle, 2005) The exponential growth of the Nile perch population in the 1980s in Lake Victoria resulted in the development of a new fishing industry and a very lucrative export market for the three countries (Uganda, Kenya, Tanzania) that share Lake Victoria (Balirwa *et al*., 2003). Although Hg levels

in small Nile perch (<10 kg) have been reported as below the WHO's (World Health Organization) recommended limits (Campbell, Dixon & Hecky, 2003), Hg bioaccumulation has been a concern for the introduced Nile perch because it is a piscivore reaching over 100 kg in mass, which might contribute to high biomagnification and bioaccumulation effects. In addition, there are important sources of Hg in Lake Victoria, including the processing of gold ore in artisanal and small-scale gold mines (ASGM) on the southern shore of the lake (Campbell, Dixon & Hecky, 2003). Quantifying effects of body size and habitat on Hg concentrations in Nile perch is a critical next step to understanding drivers of Hg contamination in this important stock.

Lake Nabugabo, Uganda, a small satellite lake of Lake Victoria has over the years served as a useful model for understanding dynamics of the larger Lake Victoria, since introduced Nile perch are intensively harvested both lakes, and lacustrine wetlands that are dominated by *Miscanthidim violaceum* and *Vossia cuspidata* are extensive in both systems. The wetlands that surround Lake Nabugabo, as well as, those in the Lake Victoria basin might play an important role in Hg concentrations of Nile perch. In Lake Nabugabo, Nile perch show habitat-associated divergence in diet (Chapman *et al*., 2003; Paterson & Chapman, 2009; Schofield & Chapman, 1999), gill size (Paterson, Chapman, & Schofield, 2010), body shape (Nyboer & Chapman, 2013a), and colour (Nyboer, Gray & Chapman, In press). And, they exhibit a relatively small home range size that may reflect tight habitat associations (Nyboer & Chapman, 2013b). Here, we test for habitat-specific patterns in Hg contamination of Nile perch by (a) quantifying total Hg (THg) concentrations of Nile perch from the distinct ecotonal and open-water habitats of Lake Nabugabo, (b) characterizing the diet of sampled Nile perch, and (c) assessing habitat-

associated variation in a suite of physico-chemical variables that might influence Hg concentration.

Methods

Study System

Lake Nabugabo, Uganda (S 00°21'07.8'', E031°52'42.9'') is a small (33 km^2) satellite lake of the larger Lake Victoria that is approximately 5 km long and wide with a mean depth of 4.5 m. This lake became separated from Lake Victoria about 5000 years ago (Stager *et al.*, 2005) and is surrounded by dense wetlands and forest along its periphery. Three distinct ecotonal habitat types are found around the lake. The north-western region is bordered by forest. The remainder of the lake is surrounded by wetland dominated by the macrophyte *Miscanthidium violaceum* at the wetland/open-water ecotone, or by the grass *Vossia cuspidata* (Paterson & Chapman, 2009). We characterize the off-shore regions of the lake as the open-water habitat type. In Lake Nabugabo, Nile perch feed on a combination of invertebrates and other fish, tending to switch from mainly invertebrate-feeding to piscivory over the course of their lives. The size of the ontogenetic diet shift has been shown to differ between habitat types, with the switch to piscivory occurring at a smaller size in wetland ecotones (< 15 cm) than in the forest edge habitat (> 35 cm) (Paterson & Chapman, 2009).

Data collection

We collected 184 Nile perch from the four different habitat types (forest edge, *Miscanthidium violaceum*, *Vossia cuspidata*, open water) in Lake Nabugabo between June and August 2013. Within each habitat type Nile perch were sampled from three randomly selected sites located at least 2 km apart (approximately 2 x the mean home range size of Nile perch in

this system, Nyboer & Chapman 2013). We sequentially visited one of these 12 sites every second morning or when weather permitted to set gill nets. Six 30 m experimental gill nets (4 panels each: 25.4, 50.8, 76.2, 101.6 mm stretched mesh) were joined and set within 30 m of the shoreline for ecotonal sites and otherwise offshore. Nets were checked the following morning, and all captured fish were indentified and measured (total length) as part of long-term monitoring in the Lake Nabugabo system. Nile perch were euthanized with a sharp blow to the head and kept on ice until processing and other live fish were returned to the lake.

To ensure a broad size range in Nile perch samples, we collected a minimum of three individuals from each of six size brackets (8-14 cm, 15-24 cm, 25-34 cm, 35-44 cm, 45-54 cm and > 55 cm). When necessary, sample sizes were supplemented by returning to sites of a given habitat type and/or purchasing fish from local fishers. In order to identify site and habitat where fish were captured, fishers were asked to indicate at which of the 27 fishing sites (Vaccaro *et al*., 2014) in Lake Nabugabo they had captured the Nile perch and the distance from shore. Environmental data (surface pH and conductivity, depth, Secchi depth, water temperature and dissolved oxygen (DO) profiles at 50-cm intervals) were also collected at each sampling site using a DO/water temperature meter (YSI Pro DO, professional series) and a waterproof combo pH and EC meter (Hanna). To measure chlorophyll *a* concentrations (an estimate of trophic state) in different habitat types we collected 450 mL of water from the euphotic zone (1.7 x the Secchi depth) using a tube sampler. This water was filtered using 47 mm Whatman GF/C Glass microfiber filters (nominal pore size 1.2 μm) and was manually pumped for a maximum of 30 minutes. Filters were then stored frozen until analysis. The 12 sampling sites were re-visited in March of 2014 and sampled for THg and MeHg in the water as well as DOC and Total Nitrogen (TN). For DOC and TN, 1 L of water was collected from the euphotic zone using a tube sampler.

For DOC, 20 mL of this water was filtered into clear scintillation vials syringe filters (0.45 um pore size and 2.5cm diameter). For TN, 20 mL of water was transferred into new polyethylene scintillation vials and kept cool until analysis. Water samples for Hg analyses were collected by lowering certified trace-metal clean 250 mL fluoropolymere (FLPE) bottles to ~15 cm below surface and opening, filling and re-sealing at depth. Water from these bottles was poured into a second 250 mL FLPE bottle that contained 1 mL of trace metal clean concentrated HCl (to yield a 0.4 % solution). The acidified sample was then sealed, double bagged, and kept in a cold and dark environment (~4ºC) until analysis.

Nile perch

Nile perch were weighed and measured for total and standard length. Approximately 1 g of tissue was collected from the dorsal musculature (fillet) of each fish for Hg content analysis. When fish were too small to obtain sufficient tissue from the dorsal musculature, external tissues (scales) were kept in the samples (See Appendix for further details on all steps of fish processing). Samples were weighed using a portable milligram scale (Gemini-20), frozen, transported back to the USA and later analyzed for THg (see details below). During dissection, gender and stage of maturity were determined following staging criteria established for Nile perch (Nkalubo, 2012). Stomach contents (diet) were analyzed following the methods used in previous studies (e.g., Paterson & Chapman 2009), and used to assess overall diet trends among habitats.

Tissue mercury and analysis

All Nile perch tissue samples were analyzed for THg at the Biodiversity Research Institute's (BRI) Wildlife Hg Research Laboratory in Gorham, Maine, USA, using direct combustion/trapping atomic absorption (AA) method on a Milestone DMA 80. Moisture content

of tissue samples were determined, and all total Hg concentrations are presented as ng/g wet weight. We used an approach that has been incorporated by the U.S. Environmental Protection Agency (EPA) in EPA SW-846 Method 7473. A blank and two standard reference materials (DORM-3 and DOLT-4) were used in each of the two detector cells to calibrate the instrument. Response was evaluated immediately following calibration, and thereafter, following every 20 samples and at the end of each analytical run by running the two standard reference materials and a check blank. Instrument detection limit is approximately 0.050 ng.

Water chemistry

Chl-*a* concentrations were analyzed at the National Fisheries Resource Research Institute (NaFIRRI) lab in Jinja, Uganda, using a spectrophotometric method (SFS 5772, 1993). DOC and TN were analyzed in the Department of Geography at McGill University using a TOC-TN analyzer (TOC-VCSN, Simadzu Corp., Kyoto, Japan). Detection limit was of 0.35 mg/L for DOC and 0.05 mg/L for TN. Particulate MeHg and THg concentrations were analyzed at the Norwegian Institute for Water Chemistry (NIVA) following the protocol described in Braaten *et al*. (2014).

Stomach content characterization

Non-empty stomach contents were examined under a dissecting microscope and divided into 11 prey type categories adapted from Schofield & Chapman (1999) and Paterson & Chapman (2009). These categories included fishes (*Barbus sp*., cichlids, *Aethieomastacembelus frenatus* (a mastacembelid eel), haplochromine cichlids, *Lates niloticus*, *Rastrineobola argentea*, and unidentified fishes)), and invertebrates (Family Chironomidae, Order Odonata, Order Ephemeroptera, and unidentified insect remains). Each identifiable prey item was counted and weighed to the nearest 0.01 g. We assessed dietary patterns of Nile perch using the same indices

as in previous studies of this system (Paterson & Chapman, 2009; Schofield & Chapman, 1999) that included: (1) relative prey abundance (%N): a percentage representing the number of times each prey type is found in relation to all food items; (2) frequency of occurrence (%F): number of Nile perch containing each prey taxon in divided by the total number of non-empty stomachs; (3) relative prey mass (%M): the mass of each prey type expressed as a percentage of the total mass of stomach contents; (4) Index of Relative Importance (IRI): a single overarching measure of dietary importance of each prey type that combines all other measures and can be calculated as:

Eq. 1: IRI = %F x [%N + %M] (Hyslop, 1980)

and; (5) Percent Index of Relative Importance (% IRI) that is calculated as:

Eq. 2: $\%IRI_i = 100 * [IRI_i / \sum_{i=1}^{n} IRI_i]$

and provides a more robust measure to changes in other dietary measures while also allowing for comparisons among studies (Cortés, 1997).

Variation in diet with Nile perch body size was explored by quantifying diet indices for three size classes of Nile perch: 0-15 cm, 15-40 cm, and >40 cm. Size classes were determined based on previously established trends of habitat-dependent ontogenetic dietary shift size of Nile perch in Lake Nabugabo, whereby wetland individuals typically make this shift before they reach 15 cm in total length, and forest-edge fish do not make this shift until they reach ~ 35 cm (Paterson & Chapman, 2009; Schofield & Chapman, 1999). We also evaluated these same parameters by categorizing prey types into the larger groupings of invertebrates and fish and then examining trends across all fish from each habitat type.

Statistical analysis

To evaluate the effect of habitat and mass on THg concentration in Nile perch we used mixed-effects models, implemented by the 'lmer' function of the R (version 3.0.2 for Mac OS X 10.8) package 'lme4' (Bates *et al*., 2014). The deterministic portion of the model included habitat type and mass as fixed effects, and mass was allowed to interact with habitat type to account for potential differences in bioaccumulation trends among habitats. The random portion of the model included capture site of individual fish. The full model can thus be written as: [Eq. 1] $THg_{ij} \sim$ Habitat $Type_i * Mass_i + (1 | Site)$, where i represents individual fish, and j represents different sites. Variables were log-transformed when necessary to improve normality of residuals.

To determine the importance of various terms in the model we fit, through maximum likelihood, the full model as described above, and reduced models with all possible permutations of fixed factors. These models were compared using AIC values, as implemented in the R function 'anova' (R Core Team, 2013). Models were also re-fit through restricted maximum likelihood to estimate parameter coefficients and produce pseudo R^2 values. The marginal R^2 describes the proportion of variance explained by the models' fixed factors, and the conditional R^2 describes that explained by the fixed and random factors (Nakagawa & Schielzeth, 2013). Finally, we conducted post-hoc analyses to evaluate differences in the slopes and THg concentrations of each habitat type using the 'mcposthoc.fnc' function in the 'LMERConvenienceFunctions' R package (Tremblay & Ransijn, 2013). We also calculated weight adjusted mean THg concentrations (least square means) within each of the three Nile perch size classes described above using the 'lsmeans' function in the 'lsmeans' R package (Lenth, 2014).

ANOVA was used ('aov' function in R: (R Core Team, 2013) to detect differences among habitats in environmental characteristics (temperature, pH, DO, Chlorophyll-a, Secchi depth, DOC, TN, as well as, total and methyl mercury in the water). Tukey's post-hoc test ('TukeyHSD' in R) was employed for pairwise comparisons when the main habitat effect was significant (R Core Team 2013). Where multiple samples were taken for a site (within habitat), the average value was used in the ANOVA model. This included water column averaging for temperature and DO values. For all relevant tests the significance threshold was set at 0.05.

Results

THg concentrations and habitat use

THg concentration was determined for 45 Nile perch from the forest ecotone, 54 from the *M. violaceum* ecotone, 39 from the *V. cuspidata* ecotone, and 47 from the open-water, with fish ranging between 8.4 and 130 cm in length (mean ± SE: 24.7 ± 1.3 cm) and 5.6 and 31000.0 g in mass (mean ± SE: 529.0 ± 89.8 g). THg concentration averaged 13.6 ± 0.4 ng/g ww and ranged between 4.9 and 29.3 ng/g ww (13.6 ± 0.4 ng/g ww). All replicates were within a 5% margin of each other.

Both size and habitat were important predictors of THg concentrations in Nile perch. The best fit model included both mass and habitat type, as well as, the interaction between these two variables. In this model, fixed factors explained 53% of variation in THg concentrations of Nile perch, and overall, the model accounted for 59% of variation (Table 1). THg concentration increased with Nile perch body size (Figure 1), however, the relationship varied across habitats. The most striking pattern was the lower slope in Nile perch captured from the *M. violaceum* ecotone relative to all other habitats (post-hoc results: forest: $p = 0.003$; open water: $p < 0.001$; *V. cuspidata*: $p = 0.029$) indicating a lower rate of increase in THg with body size in this habitat.

The Hg accumulation slope was also lower in the *V. cuspidata* ecotone relative to the open-water habitat ($p = 0.0463$) (Figure 1). Given the difference in slopes across habitats, we also tested for habitat effects within the three size categories of Nile perch using the same mixed model approach described above. Within each size class the best fit-model suggested that habitat and mass were important predictors of THg, and slopes did not differ across habitats. Post-hoc analyses demonstrated that within smaller Nile perch THg concentrations were lowest in fish captured in the open-water, whereas, in larger Nile perch fish captured near *M. violaceum* had the lowest THg concentrations (Figure 2).

Nile perch stomach contents

Fifty percent of the Nile perch sampled had non-empty stomachs. Of the 93 stomachs we assessed, 28 of the fish came from the forest ecotone, 13 from the open water, 30 from the *M. violaceum* wetland ecotone, and 22 from the *V. cuspidata* wetland ecotone. When assessing differences in fish and invertebrate consumption, Nile perch from the *V. cuspidata* ecotone had the highest relative abundance of fish in their stomachs, followed by those from the open water, the forest ecotone and the *M. violaceum* ecotone (respectively, %N: 96.0%, 86.7%, 71.4%, 67.67%). Trends were similar for the frequency of occurrence of prey (%F: 100.0%, 92.3%, 72.4% and 67.7%, respectively). With respect to fish prey mass, however, values were more similar across habitat types (%M: 99.4%, 99.4%, 98.0%, and 95.9%, for *V. cuspidata*, open water, forest, *M. violaceum*, respectively), and similarly for the Index of Relative Importance (% IRI: 99.89%, 98.76%, 92.09% and 88.61%, respectively), indicating a high degree of piscivory in Nile perch across habitats (Figure 3).

We used the integrative index, %IRI, to explore variation in diet across Nile perch size classes among habitat types. Generally, small Nile perch had consumed a high proportion of

invertebrate prey, with the exception of Nile perch from the *V. cuspidata* ecotone, where only fish prey were found in smaller Nile perch (Table 1; see SI Tables 1-3 for %N, %F and %M measures across size classes). Invertebrate prey were most important in the diet of small fish from the forest edge habitat. Cannibalism, although rare, was only evident in the forest ecotone and open-water habitats. In Nile perch <40 cm, the most important fish prey was *R. argentea* in the forest edge, while cichlids were the dominant fish prey in the wetland ecotones and open water habitats (Table 1; see SI Tables 1-3 for %N, %F and %M).

Environmental Data

Most environmental parameters did not differ significantly among habitat types with the exception of DO and pH (Figure 4). DO and pH were higher in the forest-edge than in *M. violaceum* and *V. cuspidata* ecotones (Figure 4). The pH of the open-water was also higher than in the *M. violaceum* and *V. cuspidata* ecotones (Figure 4). All recorded mean MeHg concentrations, except one, were below detection (0.02 ng/L) (SI Figure 1), indicating very low levels of MeHg in all habitats sampled.

Discussion

The documented levels of Hg concentrations in Nile perch from Lake Nabugabo, Uganda, were well below the WHO/FAO's lowest recommend guideline of 500 ng/g (FAO & WHO, 2011). Our results thus suggest that humans can regularly consume Nile perch from Lake Nabugabo without experiencing adverse health effects associated with Hg contamination. Although Nile perch from Lake Victoria generally have slightly higher Hg concentrations than those from Lake Nabugabo, they too rarely exceed this consumption guideline (Campbell, Dixon & Hecky, 2003). In Lake Nabugabo, Nile perch are one of the only piscivorous species alongside the catfish *Clarias gariepinis,* which comprises a very small component of the lakes fish catch.

Most other piscivores were extirpated from Lake Nabugabo with the upsurge of Nile perch (e.g., *Bagrus docmac, Prognathochromis venator*) (Ogutu-Ohwayo, 1993). Because Nile perch are top predators in Lake Nabugabo and Hg tends to bioaccumulate through aquatic food chains (Lavoie *et al*., 2013), it is likely that other fish species in this system are also safe for regular consumption. However, further studies of fishes captured for consumption in Lake Nabugabo will be required to confirm low levels of Hg across species in the lake. In addition, some recent studies suggest that there may effects of exposure to low Hg levels (Basu *et al*., 2005; Karagas *et al*., 2012), emphasizing the need for continued research and monitoring of mercury levels in the fisheries of the Lake Victoria basin.

The low concentrations of Hg in Nile perch from Lake Nabugabo are consistent with the low concentrations found in a number of other African aquatic systems and species (Black *et al*., 2011; Hanna *et al.*, In review), and could be due to a number of factors. High temperatures such as those observed in the tropics typically lead to higher growth rates in fishes (Buesa, 1987), and faster rates of Hg elimination (Trudel & Rasmussen, 1997), both of which might lead to lower levels of Hg (Harris & Bodaly, 1998; Simoneau *et al*., 2005). Alternatively, low concentrations of Hg in fish could be attributable to low concentrations of bioavailable Hg. Indeed, our assessment of MeHg levels in the water column of Lake Nabugabo suggested that the concentrations of bioavailable Hg were also low (< 0.02 ng/L), which is similar to results observed in other East-African lakes (A. Poste, personal communication). High DOC levels of the lake could be playing a role in these low MeHg concentrations in the water. In a study evaluating DOC concentrations and Hg bioaccumulation in 26 tundra lakes, DOC concentrations below 8.6 mg/L were found to increase THg and MeHg bioaccumulation, whereas, systems with DOC concentrations above this lowered bioaccumulation through its effect on Hg bioavailability

(French *et al*., 2014). Tropical systems might have different types of interactions between DOC and MeHg than tundra ecosystems, but similar processes could be at play in Lake Nabugabo, potentially playing a part in the low Hg concentrations observed. Interestingly, Black *et al*. (2011) suggested that low Hg levels in Africa might actually be due to an anomaly in Hg accumulation, leading to overall low concentrations in aquatic organisms across the continent in spite of variable conditions in Hg availability. Clearly, further investigation into cycling processes will be necessary to better understand low African Hg concentrations like those documented in Lake Nabugabo.

Our results suggest habitat of capture Nile perch in Lake Nabugabo is an important predictor of their Hg concentrations, and that the relationship between habitat and Hg is size dependent. These habitat-associated differences are likely explained by a combination of interrelated environmental and biological factors. Although most environmental characteristics that we quantified did not differ among habitat types, the water was more acidic in both wetland ecotones than in the forest ecotone and the open water, and DO was lower in wetland ecotones than in the forest ecotone. Acidity and DO are known to affect the amounts of bioavailable Hg (MeHg) in the water, which can in turn affect Hg concentrations in aquatic organisms. Typically, increased acidity is correlated with higher Hg concentrations in aquatic organisms due to increased bioavailability of Hg (Simonin *et al*., 2008). Thus acidity may have contributed to heightened concentrations of Hg in small Nile perch from wetland ecotones relative to the open-water habitat. However, differences in acidity were weak, and might therefore not be such an important driver of differences in Hg in fish. When considering DO, previous work has shown that the water solubility of MeHg increases under anoxic conditions (Regnell *et al*., 1996). This might explain, in part, why small Nile perch from the *M. violaceum* ecotone, where DO was

lowest, had the highest Hg concentrations. Although these environmental factors might play a part in regulating Hg concentrations in Nile perch, it is difficult to confirm their role in Hg bioavailability given the undetectable differences in MeHg in the water among habitats and the variation between the sites of each habitat type. Furthermore, environmental conditions interact with biological factors that can also mediate habitat associated differences in Nile perch Hg concentrations.

Size and diet are likely among the most important biological factors at play regulating Hg concentration in Nile perch from Lake Nabugabo. Nile perch size is an important predictor of Hg concentrations across all habitat types. This is in line with expectations, because as fish increase in size they tend to bioaccumulate Hg (Wiener *et al*., 2003). In Nile perch, this accumulation of Hg may also reflect size related dietary changes, whereby individuals tend to switch from invertebrate to piscivory feeding over the course of their lives (Paterson & Chapman, 2009), theoretically leading to increased biomagnification of Hg in larger individuals and thus, higher Hg concentrations. Our analysis of stomach content does indeed confirm a shift from invertebrate toward piscivorous feeding as Nile perch size increased across all habitat types, expect in the *V. cuspidata* ecotone where even the smallest fish were piscivorous. The differences in both the mean THg levels of Nile perch among habitats and the relationships (i.e. slopes) between size and THg might also reflect, at least in part, habitat-associated differences in diet and ontogenetic diet shifts. Previous work in Lake Nabugabo shows that forest ecotone and off-shore Nile perch tend to eat higher in the food chain than those from the wetland ecotones, and also shows that their shift to piscivory occurs at a larger size (Paterson & Chapman, 2009). Considering these diet differences, wetland ecotonal Nile perch would be expected to have higher Hg concentrations at a small size relative to forest ecotone and open-water Nile perch, but

not at a larger size. Although our results do not fully support this pattern, we did observe lower Hg concentrations in small Nile perch from the open-water relative to all other habitat types. As Nile perch increased in size, this was inversed, with open-water Nile perch having the highest Hg concentrations, followed by forest-edge fish. Cannibalism might be a factor explaining these higher concentrations of Hg. Stomach content analysis suggests that only forest and open-water Nile perch prey on other Nile perch, potentially explaining why Hg accumulation slopes are steeper in these habitat types than in wetland ecotonal habitats. The particularly shallow Hg accumulation slope documented in the *M. violaceum* ecotone could also be related to the percentage of invertebrates in Nile perch diet of this habitat, which is the highest among all habitats. The occurrence of cannibalism in forest Nile perch below 15 cm in length might contribute to the relatively higher Hg concentrations in small fish from this habitat type in relation to small fish from the open-water, where cannibalism was only documented in individuals above 15 cm. Thus, there we found some evidence to suggest a link between diet and THg levels in Nile perch; however, clearly, there are unexplored factors other than stomach content driving the observed habitat-associated patterns. Alternative factors might include, for example, varying MeHg concentrations in the water, which we were unable to accurately measure due to extremely low levels, or differences in growth rates between habitat types, which we did not measure. If Nile perch are growing faster in a given habitat type, this could lead to lower Hg accumulation slopes in this habitat. In addition, a more intensive study on the diet of Nile perch integrating stable isotopes will be necessary to improve our understanding of the interactions of long-term diet trends, habitat, and THg levels of Nile perch. It would also be interesting to obtain information on the THg levels of prey items to better understand how Hg is moving through the food web and how this might differ between habitat types.

In summary, Hg concentrations in Nile perch of Lake Nabugabo are low, but these concentrations differ across the habitat types in the lake, as well as, individuals of different sizes. Our results suggest that habitat associated THg discrepancies are driven by a combination of environmental factors and Nile perch diet, including variation in ontogenetic diet shifts. This work contributes to a growing awareness of intra-lake divergence in Nile perch, as well as, divergence in Hg concentrations between varying aquatic habitat types.

Figure and table captions

Figure 1. Total mercury concentrations in Nile perch from the four main habitat types of Lake Nabugabo, Uganda. Intercepts and slopes represent the fitted linear mixed effect model. Habitat types that do not share the same letters indicated beside the legend had significantly different slopes according to post-hoc analyses.

Figure 2. Least square adjusted mean total mercury concentrations of Nile perch from the different habitat types in Lake Nabugabo, Uganda. Each panel shows Nile perch from different size classes. The left panel shows fish below 15 cm, the center panel shows those between 15 and 40 cm and the right panel shows fish above 40 cm in length. Within each panel habitat types that do not share the same letters indicated on top of the bars had significantly different THg concentrations according to post-hoc analyses of the associated linear mixed model.

Figure 3. Relative importance of invertebrates and fish in the diet of Nile perch from Lake Nabugabo, Uganda. The amount of evaluated stomachs, in each habitat type, from left to right, was: 28, 13, 30, and 22.

Figure 4. Mean environmental conditions in 12 sites from four different habitat types of Lake Nabugabo, Uganda. Significant differences were only observed in panels with letters, where habitat types that do not share the same letters on top of the points had significantly different values. Results were not available for chlorophyll *a* concentration from one of the 12 sites which was located in the open-water habitat.

Table 1. AIC values of linear mixed models evaluating the importance of habitat type and mass as predictors of total mercury concentrations in Nile perch from Lake Nabugabo, Uganda. One model is presented on each row and terms included in that model are indicated using a check mark. Models were fit through maximum likelihood to estimate AIC values and then re-fit through restricted maximum likelihood to estimate marginal and conditional pseudo R^2 values, and coefficients (not presented here).

Table 2. Percent Index of Relative Importance (%) of prey types in the stomachs of Nile perch from Lake Nabugabo, Uganda.

Figures

Figure 1.

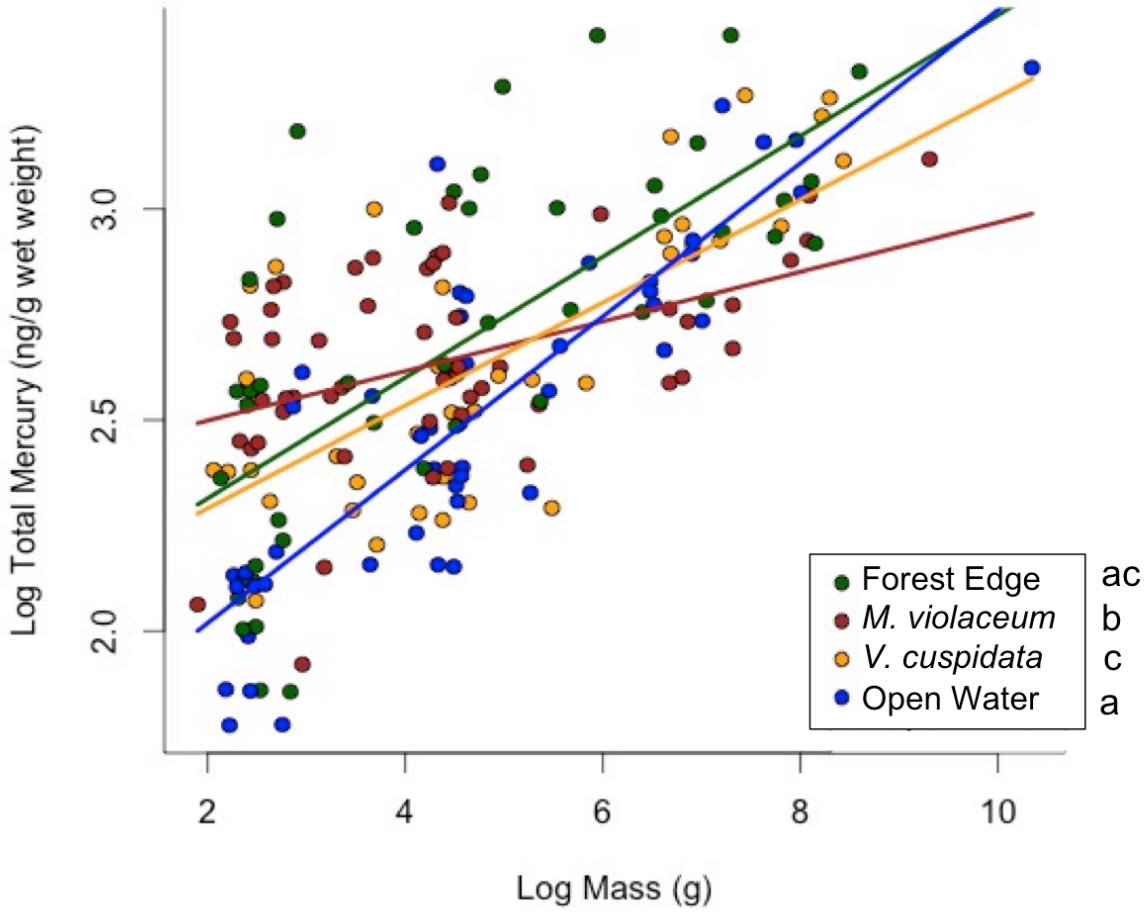


Figure 2.

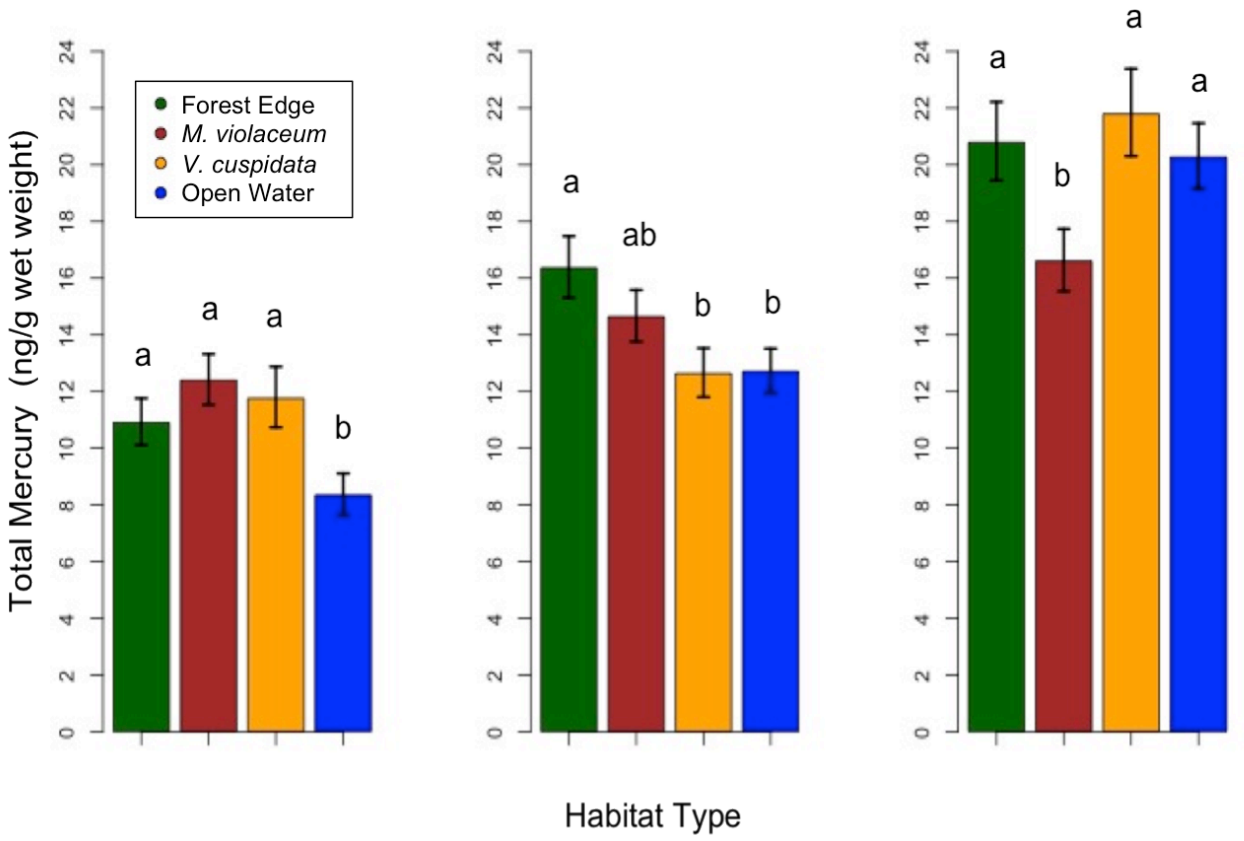

Forest Edge
M. violaceum
V. cuspidata
Open Water
Total Mercury (ng/g wet weight)
0 2 4 6 8 10 12 14 16 18 20 22 24
a a a b
a ab b b
a b a a
Habitat Type

Figure 3.

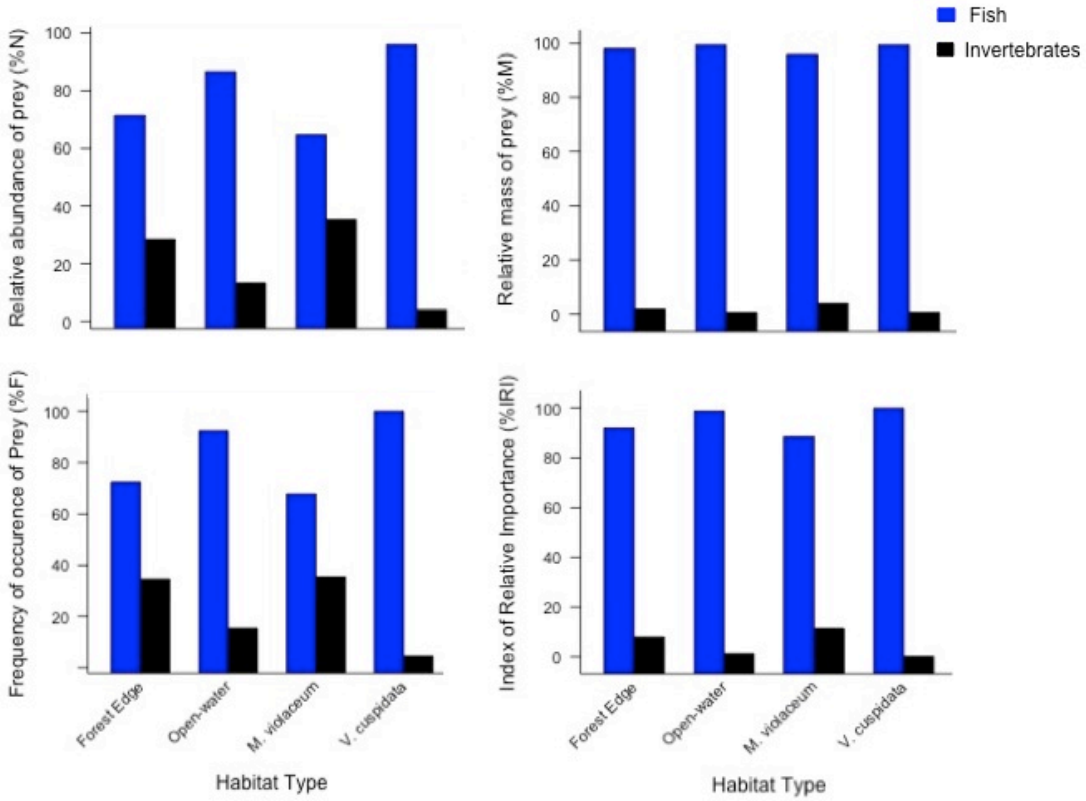
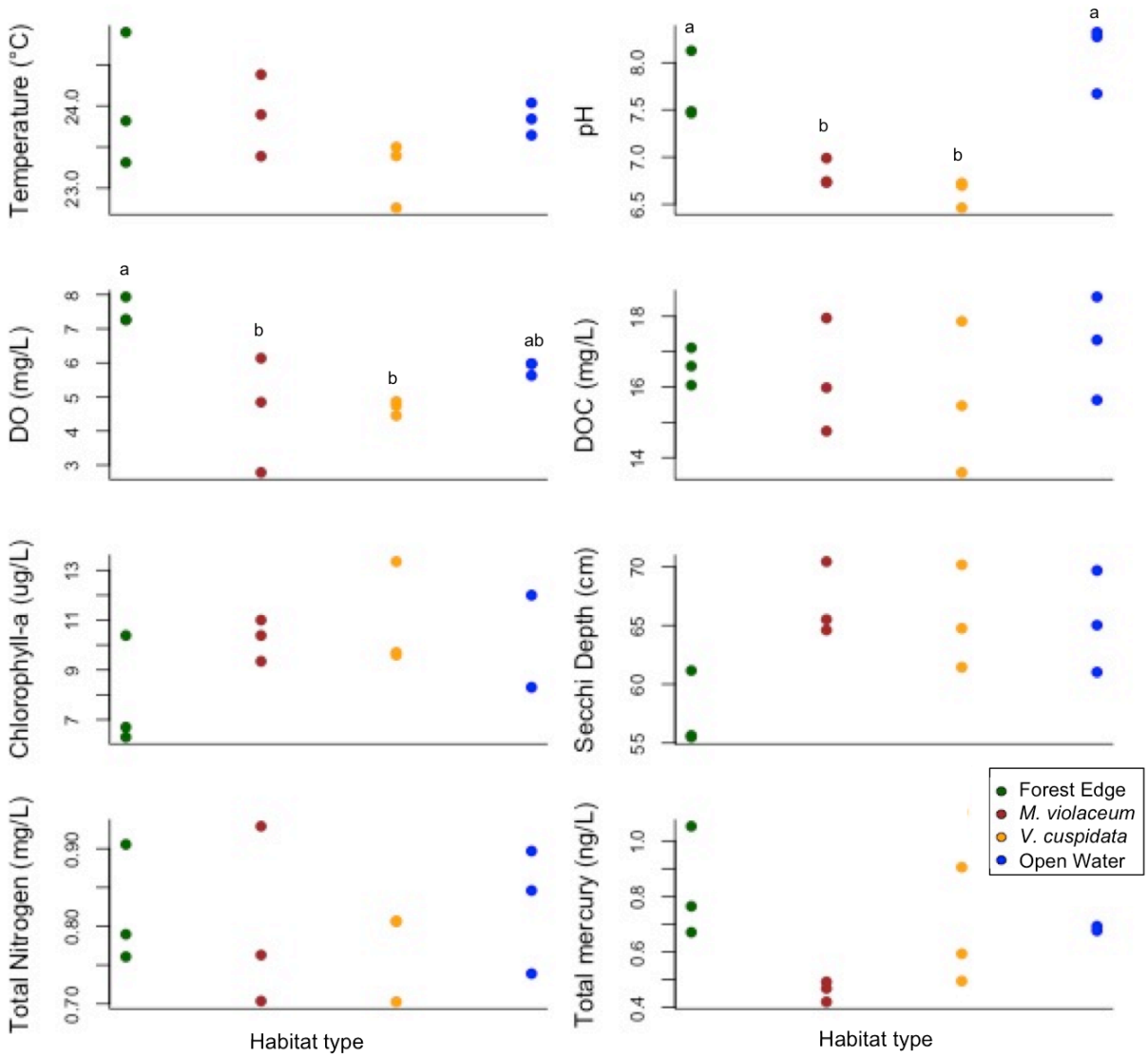

Fish
Invertebrates
Relative abundance of prey (%N)
Relative mass of prey (%M)
Frequency of occurence of Prey (%F)
Index of Relative Importance (%IRI)
0
20
40
60
80
100
Forest Edge
Open-water
M. viduceum
V. cuspidata
Habitat Type
Habitat Type

Figure 4.


Temperature (°C)
23.0
24.0
pH
6.5
7.0
7.5
8.0
a
b
b
a
DO (mg/L)
3
4
5
6
7
8
a
b
b
ab
DOC (mg/L)
14
16
18
Chlorophyll-a (ug/L)
7
9
11
13
Secchi Depth (cm)
55
60
65
70
Total Nitrogen (mg/L)
0.70
0.80
0.90
Total mercury (ng/L)
0.4
0.6
0.8
1.0
Habitat type
Habitat type
Forest Edge
M. violaceum
V. cuspidata
Open Water

Tables

Table 1.

Model Number	Habitat type and mass interaction term	Habitat type	Mass	AIC value	Marginal R^2 (%)	Conditional R^2 (%)
1	√	√	√	10.18	53.05	59.04
2		√	√	24.86	45.70	53.79
3		√		118.53	1.04	47.86
4			√	23.55	43.08	54.00

Table 2.

Index of relative importance (% IRI)	Habitat type											
	Forest			Open water			M. violaceum			V. cuspidata		
Size class	< 15 cm	15 - 40 cm	> 40 cm	< 15 cm	15 - 40 cm	> 40 cm	< 15 cm	15 - 40 cm	> 40 cm	< 15 cm	15 - 40 cm	> 40 cm
Sample size	11	14	3	3	9	1	14	10	4	8	9	5
Invertebrate prey												
Family Chironomidae	59.28	0.00	0.00	39.84	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Order Ephemeroptera	0.00	0.00	0.00	0.00	0.00	0.00	24.07	0.00	0.00	0.00	0.00	0.00
Order Odonata	0.00	8.18	0.00	0.00	0.00	0.00	4.10	2.45	0.00	0.00	0.00	5.29
Unidentified insect remains	0.00	0.00	0.00	0.00	0.00	0.00	0.73	0.00	0.00	0.00	0.00	0.00
All invertebrates	59.28	8.18	0.00	39.84	0.00	0.00	28.89	2.45	0.00	0.00	0.00	5.29
Fish prey												
Barbus sp.	0.00	1.68	0.00	0.00	0.00	0.00	0.00	0.00	17.18	0.00	0.00	0.00
Cichlids	6.13	22.18	95.24	0.00	32.72	100.00	0.00	23.27	20.14	70.32	40.98	35.19
Eels	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.42	0.00	0.00	0.00	0.00
Haplochromine cichlids	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.53	47.56	6.06	14.65	22.51
Lates niloticus	2.41	0.00	0.00	0.00	2.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rastrineobola argentea	29.30	37.20	0.00	0.00	5.18	0.00	0.00	12.62	0.00	0.00	3.13	28.74
Unidentified fishes	2.88	30.76	4.76	60.16	59.90	0.00	71.11	51.71	15.12	23.62	41.24	8.28
All fish	40.72	91.82	100.00	60.16	100.00	100.00	71.11	97.55	100.00	100.00	100.00	94.71

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General conclusion

In this thesis, I reviewed the literature for Hg concentrations in freshwater aquatic ecosystems across Africa, and I evaluated the effects of habitat on Hg concentrations in Nile perch. In the first chapter, I showed that Hg concentrations in African freshwater fishes are generally low, which is consistent with the earlier study of Black *et al*. (2011). However, my study captures a much larger number of studies, species, and locations. Only areas with artisanal and small-scale gold mining (ASGM) had mean Hg concentrations above the WHO/FAO's recommended consumption guideline of 500 ng/g (FAO/WHO 2011). This finding does not mean that levels of Hg are low in the rest of the continent, as I was unable to find published data on Hg for the majority of inland African waterbodies. Furthermore, several studies that present data on Hg in fishes do not present data on relevant environmental conditions or ecological traits. As such, there is a suite of factors not assessed in this meta-analysis that might be drive the low Hg concentrations in fishes, which limits our ability to offer an explanation for the overall low Hg levels. One important example is the MeHg concentrations in the water. It would be important to have this information as it could explain low Hg levels in fish and help understand if there is indeed an African Hg accumulation anomaly taking place. The data I gathered did allow me to explore the relationships between THg in fish and size, trophic level, latitude and chlorophyll *a*. Linear mixed models demonstrated strong positive relationships between Hg concentrations and size and trophic level, supporting the roles of bioaccumulation and biomagnification of Hg in African fishes across the continent. Latitude shared a weak positive relationship with Hg concentrations in fishes. However, this could not be explained by a temperature gradient that might typically drive this type of relationship (Lavoie *et al*., 2013). My data indicate that chlorophyll *a* is not a good predictor of Hg concentrations in African fishes.

This suggests that relationships documented between trophic state and Hg in other areas of the world are not widespread across locations and species, or that there are differences in the role of trophic state in Hg accumulation between Africa and other areas. It is important to note that the data collected on chlorophyll *a* were not all gathered at the same time as the Hg data and we could thus not account for potential roles of temporal variation on the trends observed. The results from this chapter of my thesis clearly emphasize the need for more comprehensive and continued monitoring of Hg in African inland waters, particularly in areas with ASGM. Additional research will be required to understand factors driving low levels of Hg in Africa and how Hg cycling in the continent might differ from other locations in the world.

In the second chapter of my thesis, I explored patterns of Hg concentrations in Nile perch (*Lates niloticus*), an important commercial and sustenance fishery in East-Africa. This large piscivore shows strong habitat-associated divergence in a suite of ecological traits (e.g. Paterson & Chapman, 2009) and inhabits both open-water and ecotonal regions of Lake Nabugabo, Uganda, providing a unique opportunity to evaluate the relationship between Hg concentrations in fish and these varying habitat-types. In particular, I examined variation in Hg contamination among fish from wetland ecotones, the forest ecotone and the open-water region of the lake. My analysis demonstrated that habitat of capture is an important predictor of THg in Nile perch, and that the relationship between habitat and THg is size dependant. Open-water fish had the lowest THg concentrations when small and the highest concentrations when large. Nile perch from the *M. violaceum* wetland ecotone had the highest levels of Hg in small fish, yet, the lowest rates of Hg accumulation as they increased in size. Differences in acidity, as well as, dissolved oxygen detected among habitats might play a role in their Hg availability. Stomach content analysis suggested that diet was also a driver of Hg differences, whereby individuals from habitats with

cannibalism had the highest Hg accumulation rates. Differences in growth rates of Nile perch among habitats might also explain differences in habitat trends. These data are not yet available in this system, but represent a critical avenue for future studies. Despite differences, across habitats and sizes (range 6 -130 cm), Hg concentrations were all well below the WHO/FAO recommended guideline of 500 ng/g (mean: 13.6 ± 0.4 ng/g wet weight; range: 4.9 and 29.3 ng/g wet weight).

The results of my thesis highlight several areas in which future research on Hg should focus. Additional research on habitat-use and Hg in fish evaluating open-water and ecotonal habitat types would further help understand the role of these habitats, their environmental conditions, and variation in diet in predicting Hg concentrations in fish over the course of their lives. Although there might not be a robust consistent trend in Hg concentrations across aquatic habitat types, understanding the variation in individual systems can help regular consumers diminish their daily intake of Hg and further understand details of Hg cycling that are essential to improve monitoring and regulation of Hg in aquatic ecosystems. Future research on Hg in Africa should focus on characterizing Hg concentrations in fishes from locations that have not yet been evaluated for Hg. These missing data would allow for a more comprehensive assessment of continent wide trends, which may help shed light on the supposed African mercury anomaly (Black *et al*., 2011). This is an important topic for both wildlife and human health at a global scale, as Africa's low Hg concentrations might provide interesting insight into processes that prevent mercury from being assimilated into food chains. Measuring the differences between Methylmercury and Total mercury in the water and fishes of multiple African aquatic ecosystems would be an excellent route to begin further assessing this anomaly, as too little data are currently available to assess the hypothesis Black *et al.* (2011) made regarding discrepancies

between Africa and other places at this stage of Hg cycling. Future studies should measure environmental and biological characteristics associated with variation in fish Hg concentrations, because, as my review shows, it becomes difficult to assess continent wide trends when information is unavailable or inconsistent across studies. Given the fact that I did not document a relationship between THg concentrations in fishes and the trophic state of aquatic ecosystems, it would be particularly interesting to further evaluate the role of trophic state (chlorophyll *a*) on Hg concentrations in Africa. Differences in phytoplankton and zooplankton Hg accumulation between Africa and other areas of the world might be one of the differing aspects of Hg cycling, but further research will be required to adequately assess this question. Given of the high Hg concentrations documented in areas with artisanal small-scale gold mining (ASGM), I recommend that mining operations be required to monitor Hg concentrations in aquatic ecosystems nearby their mines and to post and explain consumption advisories so that people inhabiting areas surrounding the mine avoid health problems. Because this type of monitoring and communication is not yet widespread in African mines, NGO initiatives can help act as watchdogs around these mines and could facilitate programs to increase the awareness of local people regarding mercury contamination, which is low (Charles *et al*., 2013). Furthermore, if mining companies were obliged to invest in research for alternative 'greener' technologies to extract gold then Hg could eventually be entirely removed from the ASGM process, which would be ideal.

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Chapter 1: Supplemental information

Table caption

Table 1. Summary of located peer-reviewed studies evaluating mercury concentrations in African freshwater organisms and the information they contained on environmental factors that may influence mercury concentrations the water and fish. Individual locations found within each study are listed and numbered, as in Figure 1 of the manuscript. Studies used for chlorophyll-a concentrations are also numbered. Full references, indicated with the same numbers as in this table, can be found in the SI reference list. All environmental factors for which we looked for information are included except non-particulate total mercury and sulphate concentrations in the water, for which we found one data point or less.

Supplemental Information

Table 1.

Hg/ Chl-a Study[i]	Location Number and Name[ii]	Country	Water Body Type	Latitude (y) /Longitude (x)	Mean THg (ng/g wet weight)/ AGM present	Chl-a (ug/L)	DOC (umol/ L)	pH	Secchi Depth (m)	Water Temp. (°C)	Part. THg (ng/L)	Mean Depth (m)	Lake Vol./ Area (km^2)	Water Body Max Depth (m)	List of Species Present at each location[iii]	Species Trophic Level	Species mean THg (ng/g wet weight)
1/NA	(1) Tano River basin	Ghana	River	5.994/-2.562	NA/Yes	NA	NA	NA	NA	NA	NA	NA	NA/NA	NA	*NA*	NA	NA
1/NA	(2) Ankobra River Basin	Ghana	River	4.923/-2.271	NA/Yes	NA	NA	NA	NA	NA	NA	NA	NA/NA	NA	*NA*	NA	NA
2/NA	(3) Twifo Mampong Pra River Basin	Ghana	River	5.512/-1.617	65.0/Yes	NA	NA	NA	NA	NA	NA	NA	NA/NA	39	*Tilapia multifasciata*	2.0	65.0
2/NA	(4) Beposo Pra River Basin	Ghana	River	5.12/-1.616	77.5/Yes	NA	NA	NA	NA	NA	NA	NA	NA/NA	37	*Alestes affinis*	2.9	65.0
															Chrysichthys spp.	2.8	153.0
															Labeo coubie	2.0	39.0
															Tilapia multifasciata	2.0	53.0
2/NA	(5) Daboase Pra River Basin	Ghana	River	5.312/-1.598	62.3/Yes	NA	NA	NA	NA	NA	NA	NA	NA/NA	38	*Chrysichthys spp.*	2.8	166.0
															Labeo coubie	2.0	29.0
															Tilapia multifasciata	2.0	26.0
															Tilapia zilli	2.0	28.0
2/NA	(6) Twifo Praso Pra River Basin	Ghana	River	5.617/-1.549	101.8/Yes	NA	NA	NA	NA	NA	NA	NA	NA/NA	45	*Alestes affinis*	2.9	41.0
															Chrysichthys spp.	2.8	187.0
															Heterobranchus longifillis	3.7	165.0
															Labeo coubie	2.0	57.0
															Tilapia zilli	2.0	59.0
3/NA	(7) South-Africa Review	South-Africa	Several	5.617/-1.549	NA/Yes	NA	NA	NA	NA	NA	NA	NA	NA/NA	NA	NA	NA	NA
2/NA	(8) Awisam Pra River Basin	Ghana	River	5.946/-1.489	71.0/Yes	NA	NA	NA	NA	NA	NA	NA	NA/NA	46	*Labeo coubie*	2.0	71.0

4/NA	(9) Loumbila	Burkina Faso	Reservoir	12.513/-1.415	66.6/Yes	NA	NA	NA	NA	NA	NA	NA	NA/NA	41	*Auchenoglanis occidentalis*	2.9	23.4
															Clarias anguillaris	3.4	6.4
															Oreochromis niloticus	2.0	6.4
															Schilbe intermedius	3.6	230.0
5/31	(10) Lake Bosomtwe	Ghana	Lake	6.504/-1.414	17.5/Yes	10.3	NA	NA	NA	NA	0.51	NA	NA/NA	78	*Chromidotilapia guentheri*	2.4	97.9
															epiphytic algae	1.0	7.1
															Hemichromis fasciatus	3.2	20.1
															invertebrates	2.0	11.6
															macrophytes	1.0	1.6
															periphyton	1.0	4.5
															Sarotherodon galilaeus multifasciatus	2.0	6.0
															Tilapia busuma	2.3	17.7
															Tilapia discolor	2.2	9.8
															Zooplankton	2.0	5.4
6/31	(10) Lake Bosomtwe	Ghana	Lake	6.504/-1.414	17.5/No	10.3	NA	NA	NA	NA	0.51	NA	NA/NA	86	*Tilapia busuma*	2.3	21.0
															Tilapia discolor	2.2	17.0
															Tilapia multifasciata	2.0	8.0
4/NA	(11) Ziga	Burkina Faso	Reservoir	12.588/-0.827	99.2/Yes	NA	NA	NA	NA	NA	NA	NA	NA/NA	42	*Bagrus bayad*	4.0	101.0
															Clarias anguillaris	3.4	117.0
															Oreochromis niloticus	2.0	12.0
															Schilbe intermedius	3.6	102.0
															Synodontis membranaceus	3.1	164.0
7/32	(12) Lake Volta: Upper	Ghana	River	8.133/-0.328	38.5/No	11.19	NA	NA	NA	NA	NA	NA	NA/NA	NA	*Bagrus docmac*	4.1	67.0
															Chrysichthys nigrodigitatus	2.6	25.7

	Volta Basin at Yeji														*Distichodus rostratus*	2.0	20.5
															Marcusenius senegalensis	3.1	19.2
															Synodontis gambiesis	3.0	69.5
															Synodontis membranaceus	3.1	43.2
															Synodontis ocellifer	3.1	24.5
6/NA	(13) Akosombo Reservoir	Ghana	Reservoir	6.28/0.063	20.0/No	NA	NA	NA	NA	NA	NA	NA	NA/NA	36	*Synodontis granulosus*	2.9	28.0
															Tilapia zilli	2.0	12.0
6/32	(14) Kpong reservoir	Ghana	Reservoir	6.167/0.086	45.9/No	2.3	NA	NA	NA	NA	NA	NA	NA/NA	NA	*Amphilius grammatophorus*	3.0	170.0
															Apistogramma trifasciata	3.3	11.0
															Chromidotilapia guentheri	2.4	159.0
															Chrysichthys auratus	2.7	41.0
															Tilapia zilli	2.0	30.0
8/32	(14) Kpong Reservoir	Ghana	Reservoir	6.167/0.086	45.9/No	2.3	NA	NA	NA	NA	NA	NA	NA/NA	NA	*Bagrus bayad*	4.0	13.2
															Chrysichthys auratus	2.7	12.9
															Clarias ebriensis	3.4	19.2
															Clarotes laticeps	3.1	20.1
															Mormyrops anguilloides	3.6	16.0
															Oreochromis niloticus	2.0	11.9
4/NA	(15) Kompienga	Burkina Faso	Reservoir	11.508/0.741	121.0/Yes	NA	NA	NA	NA	NA	NA	NA	NA/NA	40	*Auchenoglanis occidentalis*	2.9	74.0
															Bagrus bayad	4.0	213.0
															Clarias anguillaris	3.4	197.0

															Lates niloticus	3.1	190.0
															Oreochromis niloticus	2.0	11.0
															Schilbe intermedius	3.6	111.0
															Synodontis membranaceus	3.1	51.0
															Alestes baremoze	3.1	13.0
9/33	(16) Lake Chad	Chad	Lake	12.947/14.377	31.5/No	32.5	NA	NA	NA	NA	NA	NA	NA/NA	NA	*Auchenoglanis occidentalis*	2.9	19.0
															Bagrus sp.	3.9	58.0
															Clarias gariepinus	3.2	33.0
															Etheria elliptica	2.0	19.0
															Hydrocynus forskahlii	4.0	74.0
															Lates niloticus	4.5	60.0
															Oreochromis niloticus	2.0	7.0
															Polypterus bichir	4.5	15.0
															Syndontis schall	2.9	17.0
10/NA	(17) Okavango Delta (Ngarange, Seronga, Guma and Chanoga)	Botswana	River	-19.002/22.401	35.4/No	NA	NA	NA	NA	NA	NA	NA	NA/NA	40	*Barbus poechii*	3.4	28.9
															Brycinus lateralis	3.5	27.4
															Clarias gariepinus	3.2	102.9
															Clarias ngamensis	4.3	36.3
															Hepsetus odoe	4.5	45.7
															Hydrocynus vittatus	4.4	76.9
															Marcusenius macrolepidotus	3.2	25.5
															Mormyrus lacerda	3.7	25.2
															Oreochromis andesonii	2.0	5.1
															Oreochromis macrochir	2.2	9.1
															Pharyngochromis acuticeps	3.3	12.8
															Sargochromis carlottae	3.6	9.7
															Sargochromis condringtonni	3.1	12.6
															Sargochromis giardi	3.5	89.6
															Schilbe intermedius	3.6	59.7
															Serranochromis altus	4.2	83.0
															Serranochromis angusticeps	4.5	46.8
															Serranochromis macrocephalus	4.2	29.4
															Serranochromis	3.7	14.3

															thumbergi		
															Synodontis nigromaculatus	3.1	37.0
															Synodontis spp.	3.0	24.6
															Tilapia rendalli	2.2	4.8
															Tilapia sparrmanii	2.7	7.3
11/34	(18) Lake Edward	Uganda/ Congo	Lake	-0.13/29.53	37.7/No	43.8	NA	NA	0.75	26	NA	4.5	NA/NA	NA	*Bagrus docmac*	4.1	70.7
															Barbus bynni	3.1	11.6
															Clarias gariepinus	3.2	53.7
															Haplochromine spp	3.0	27.3
															Haplochromis squamipinnis	3.2	188.3
															Oreochromis leucostictus	2.3	5.6
															Oreochromis niloticus	2.0	8.4
															Phytoplankton-nearshore	1.0	2.9
															Phytoplankton-offshore	1.0	3.1
															Protopterus aethiopicus	3.4	5.2
12/35	(19) Kigoma Bay area, Lake Tanganyika	Tanzania	Lake	-4.876/29.611	61.3/Yes	0.7	NA	NA	NA	NA	NA	NA	NA/NA	1.5	*Boulengerochromis microlepis*	4.5	115.7
															Chrysichthys stappersii	3.3	197.9
															Clarias theodorae	4.4	117.5
															Grammatotria lemairii	2.7	37.9
															Gthochromis permaxillaris	3.3	31.1
															Lamprichthys tanganicanus	3.3	26.1
															Lates mariae	4.2	115.0
															Lates stappersii	4.2	11.9
															Limnotilapia dardenni	3.1	20.0
															Oreochromis tanganicae	2.0	16.8
															Platythelphusa armata	3.0	54.2
															Plecodus paradoxus	4.4	57.7
															Stolothrissa tanganicae	2.7	17.4

															Synodontis multipunctatus	3.4	39.2
13/36	(20) Uvinza, Malagarasi River	Tanzania	River	-5.223/29.828	34.0/Yes	0.001	NA	NA	NA	NA	NA	NA	NA/NA	NA	*Barbus tropidolepis*	2.8	30.0
															Distochodus spp.	2.0	26.0
															Oreochromis tanganicae	2.0	46.0
11/34	(21) Lake George	Uganda	Lake	0/30.11	5.2/No	138.0	NA	NA	0.37	26.4	NA	2.8	0.5/250	NA	*Bagrus docmac*	4.1	4.9
															Clarias gariepinus	3.2	4.9
															Haplochromine spp	3.0	5.8
															Haplochromis squamipinnis	3.2	18.8
															Oreochromis esculentus	2.5	2.9
															Oreochromis leucostictus	2.3	3.3
															Oreochromis niloticus	2.0	1.6
															Phytoplankton	1.0	2.6
															Protopterus aethiopicus	3.4	4.4
															Tilapia zilli	2.0	2.9
14/37	(22) Lake Saka	Uganda	Lake	0.698/30.239	9.1/No	117.8	NA	7.7	0.5	23	0.81	NA	NA/0.15	NA	*Astatoreochromis alluaudi*	3.6	11.4
															Barbus neumayeri	3.0	14.8
															Benthic algae	1.0	1.2
															Blue red Chest	3.0	3.3
															blue small eye	3.0	4.9
															blue unknown	3.0	7.2
															brassy large eye	3.0	3.0
															brassy unknown	3.0	8.4
															Lates niloticus	4.5	14.0
															Oreochromis niloticus	2.0	2.8
															Pelagic algae	1.0	1.1
															Yellow red chest	3.0	2.6
11/37	(22) Lake Saka	Uganda	Lake	0.698/30.239	9.1/No	9.8	NA	8.2	3.25	23	0.45	NA	NA/0.15	NA	*Astatoreochromis alluaudi*	3.6	9.7
															Barbus neumayeri	3.0	49.2
															Haplochromine spp	3.0	9.1
															Lates niloticus	4.5	8.0
															Oreochromis niloticus	2.0	7.8
															Phytoplankton	1.0	1.3
															Tilapia zilli	2.0	12.9
14/37	(23) Lake	Uganda	Lake	0.525/30.301	8.7/No	9.8	NA	8.2	3.25	23	0.45	NA	NA/0.03	NA	*Anisoptera*	3.0	3.1

	Nkuruba														*Chironomidae*	2.8	1.5
															Hirudinea	3.5	9.2
															Oreochromis niloticus	2.0	13.1
															Rhamphochromis spp.	3.2	12.3
															Tilapia zilli	2.0	16.9
															Zygoptera (damselfly)	3.0	3.2
11/37	(23) Lake Nkuruba	Uganda	Lake	0.525/30.301	8.7/No	9.8	NA	8.2	3.25	23	0.45	NA	NA/0.03	38	*Zooplankton*	2.0	2.1
															Oreochromis leucostictus	2.3	10.8
															Phytoplankton	1.0	3.1
															Rhamphochromis spp.	3.2	20.1
															Tilapia zilli	2.0	11.7
11/34	(24) Lake Mburo	Uganda	Lake	-0.39/30.56	6.5/No	48.6	NA	NA	0.48	24.7	NA	3.2	0.325/13	NA	*Bagrus docmac*	4.1	7.9
															Clarias gariepinus	3.2	10.9
															Haplochromine spp	3.0	9.1
															Oreochromis esculentus	2.5	3.7
															Oreochromis leucostictus	2.3	5.4
															Oreochromis niloticus	2.0	4.0
															Phytoplankton	1.0	2.7
															Protopterus aethiopicus	3.4	8.4
11/38	(25) Lake Albert, Tutiaba/Kaiso	Uganda/ Congo	Lake	1.31/30.58	67.6/No	19.2	NA	NA	NA	NA	NA	NA	NA/5600	NA	*Alestes baremoze*	3.1	79.9
															Bagrus bayad	4.0	29.0
															Barbus bynni	3.1	39.4
															Brycinus nurse	2.4	81.4
															Hydrocynus forskahlii	4.0	20.0
															Labeo horie	2.1	62.7
															Lates macrophthalamus	3.9	165.6
															Lates niloticus	4.5	257.5
															Neobola bredoi	3.0	37.9
															Oreochromis leucostictus	2.3	20.7
															Oreochromis niloticus	2.0	19.9
															Schilbe intermedius	3.6	51.3
															Thoracochromis mahagiensis	3.3	62.7
															Tilapia zilli	2.0	22.7

15/39	(26) Inanda Dam	South-Africa	Reservoir	-29.676/30.836	0.8/Yes	4.4	NA	NA	NA	NA	NA	NA	NA/NA	NA	*Clarias gariepinus*	3.2		1.2
															Cyprinus carpio	3.0		0.4
16/NA	(27) Pra River	Ghana	River	-29.838/30.879	NA/Yes	NA	NA	NA	NA	NA	NA	NA	NA/NA	NA	*NA*	NA		NA
17/NA	(28) Mungcewe ni River	South Africa	River	-29.838/30.879	NA/No	NA	NA	NA	NA	NA	NA	NA	NA/NA	NA	*NA*	NA		NA
17/NA	(29) Umgeni River	South Africa	River	-29.855/31.017	NA/No	NA	NA	NA	NA	NA	NA	NA	NA/NA	NA	*NA*	NA		NA
13/NA	(30) Nikonga R.; Rwamagasa subarea	Tanzania	River	-3.13/31.546	125.3/Yes	NA	NA	NA	NA	NA	NA	NA	NA/NA	56	*Clarias alluaudi*	3.2		71.0
															Gastropoda	3.0		40.0
															Synodontis victoriae	3.3		265.0
13/NA	(31) Tembomine ; Rwamagasa subarea	Tanzania	River	-3.7/31.59	792.0/Yes	NA	NA	NA	NA	NA	NA	NA	NA/NA	50	*Clarias gariepinus*	3.2		792.0
18/18	(32) ForestEdge Habitat, Lake Nabugabo	Uganda	Lake	-0.367/31.868	16.8/No	7.5	NA	7.75	0.58	24.19	NA	1.05	NA/25	1.5	*Lates niloticus*	3.1		10.8
															Lates niloticus	4.5		19.7
18/18	(33) Mixed-Wetland habitats, Lake Nabugabo	Uganda	Lake	-0.391/31.895	14.8/No	10.1	NA	6.57	0.6417	23.29	NA	1.67	NA/25	3.5	*Lates niloticus*	3.1		10.7
															Lates niloticus	4.5		16.9
18/18	(34) Open-Water habitats, Lake Nabugabo	Uganda	Lake	-0.365/31.896	13.2/No	10.8	NA	7.89	0.6296	23.86	NA	2.68	NA/25	3	*Lates niloticus*	3.1		8.8
															Lates niloticus	4.5		15.5
19/18	(35) Lake Nabugabo	Uganda	Lake	-0.358/31.9	23.0/No	9.3	NA	7.62	0.63	23.76	NA	4.5	NA/25	NA	*Lates niloticus*	4.5		23.0
18/18	(36) Miscanthidi um habitat, Lake Nabugabo	Uganda	Lake	-0.341/31.914	13.8/No	10.2	NA	6.57	0.6417	23.29	NA	1.67	NA/25	2.2	*Lates niloticus*	3.1		13.0
															Lates niloticus	4.5		14.1
13/NA	(37) Lake Victoria (purchased Rwamagasa market)	Tanzania	Lake	-2.517/31.975	9.0/Yes	NA	NA	NA	NA	NA	NA	NA	NA/NA	47	*Oreochromis niloticus*	2.0		9.0
13/NA	(38) Pond	Tanzania	Pond	-3.73/32.05	322.2/Yes	NA	NA	NA	NA	NA	NA	NA	NA/NA	55	*Barbus spp.*	3.0		301.0

	6; Rwamagasa subarea														*Brycinus spp.*	3.0	338.0
															Clarias alluaudi	3.2	267.0
															Clarias gariepinus	3.2	538.0
															Haplochromine spp	3.0	167.0
13/NA	(39) Munekesi; Rwamagasa subarea	Tanzania	River	-3.5/32.1	134.5/Yes	NA	NA	NA	NA	NA	NA	NA	NA/NA	48	*Clarias gariepinus*	3.2	134.5
13/NA	(40) Pond 1; Rwamagasa subarea	Tanzania	Pond	-3.67/32.25	1330.0/Yes	NA	NA	NA	NA	NA	NA	NA	NA/NA	51	*Barbus spp.*	3.0	1050.0
															Clarias gariepinus	3.2	1610.0
13/NA	(41) Pond 2; Rwamagasa subarea	Tanzania	Pond	-3.71/32.25	1865.0/Yes	NA	NA	NA	NA	NA	NA	NA	NA/NA	52	*Clarias gariepinus*	3.2	1670.0
															Haplochromine spp	3.0	2060.0
13/NA	(42) Pond 4; Rwamagasa subarea	Tanzania	Pond	-3.75/32.27	293.7/Yes	NA	NA	NA	NA	NA	NA	NA	NA/NA	53	*Clarias gariepinus*	3.2	279.0
															Haplochromine spp	3.0	323.0
13/NA	(43) Pond 5; Rwamagasa subarea	Tanzania	Pond	-3.7/32.27	779.0/Yes	NA	NA	NA	NA	NA	NA	NA	NA/NA	54	*Clarias gariepinus*	3.2	779.0
13/NA	(44) Nyamsenga ; Rwamagasa subarea	Tanzania	River	-3.45/32.45	108.5/Yes	NA	NA	NA	NA	NA	NA	NA	NA/NA	49	*Clarias alluaudi*	3.2	108.5
20/20	(45) Murchison Bay, Lake Victoria	Uganda	Lake	0.16/32.615	20.9/No	96.5	NA	NA	0.72	25.6	1.3	3.2	NA/NA	NA	*Chironomidae*	2.8	14.3
															Clarias gariepinus	3.2	17.3
															Ephemeroptera	2.0	5.9
															Haplochromine spp	3.0	18.9
															Hirudinea	2.5	10.7
															Lates niloticus	4.5	42.0
															Oreochromis leucostictus	2.3	11.0
															Oreochromis niloticus	2.0	14.1
															Protopterus aethiopicus	3.4	7.6
															Rastrineobola argentea	3.4	49.1
															Synodontis afrofischeri	3.4	40.8
															Synodontis victoriae	3.3	27.9
															Tilapia zilli	2.0	12.4
21/40	(46) Lake	Tanzania	Lake	-2.379/32.795	197.9/Yes	6.9	NA	NA	NA	NA	0.2	NA	NA/NA	NA	*Lates niloticus*	4.5	197.9

22/41	Victoria (southern) (47) Napoleon Bay, Lake Victoria	Uganda	Lake	0.257/33.18	60.8/No	25.6	6.95	7.88	NA	21.63	2.92	2.8	NA/NA	NA	*Caridi nilotica* *Haplochromine spp* *Lates niloticus* *Lates niloticus* *Oreochromis niloticus* *Rastrineobola argentéa*	2.0 3.0 3.1 4.5 2.0 3.4	21.2 65.8 76.0 152.0 25.6 16.3
23/41	(47) Napoleon Bay, Lake Victoria	Uganda	Lake	0.257/33.18	60.8/No	25.6	6.95	7.88	NA	21.63	2.92	2.8	NA/NA	NA	*Lates niloticus* *Lates niloticus* *Oreochromis niloticus*	3.1 4.5 2.0	83.4 156.2 20.1
20/20	(47) Napoleon Gulf, Lake Victoria	Uganda	Lake	0.257/33.18	60.8/No	25.6	6.95	7.88	NA	21.63	2.92	2.8	NA/NA	NA	*Astatoreochromis alluaudi* *Bagrus docmac* *Brycinus sadleri* *Chironomidae* *Haplochromine spp* *Lates niloticus* *Mormyrus kannume* *Oreochromis leucostictus* *Oreochromis variabilis* *Protopterus aethiopicus* *Rastrineobola argentea* *Synodontis afrofischeri* *Synodontis victoriae* *Tilapia zilli*	3.6 4.1 3.2 2.8 3.7 4.5 3.2 2.3 2.0 3.4 3.4 3.4 3.3 2.0	7.3 27.9 85.3 17.1 30.4 34.8 31.7 3.1 12.8 3.2 7.1 17.0 28.6 111.5
24/42	(48) Thruston Bay, Lake Victoria	Uganda	Lake	0.382/33.298	27.7/No	64.3	NA	NA	NA	NA	NA	5	NA/NA	11	*Clarias gariepinus* *Haplochromine spp* *Lates niloticus* *Oreochromis leucostictus* *Oreochromis niloticus* *Protopterus aethiopicus* *Tilapia zilli*	3.2 3.7 4.5 2.3 2.0 3.4 2.0	29.0 55.5 64.1 1.5 12.4 27.2 3.9
22/43	(49) Winam	Kenya	Lake	-0.021/34.609	33.0/No	17.2	2.85	7.85	NA	26.8	3.576	2.4	NA/NA	NA	*Ephemeroptera* *Haplochromine spp*	2.0 3.0	19.1 14.4

	Gulf, Lake Victoria														*Lates niloticus*	3.1	28.6
															Lates niloticus	4.5	62.8
															Oreochromis niloticus	2.0	17.5
															Protopterus aethiopicus	3.4	20.3
															Schilbe intermedius	3.6	45.8
															Synodontis afrofischeri	3.4	60.9
25/44	(50) Monkey Bay, Lake Malawi	Malawi	Lake	-14.066/34.65	38.4/No	0.27	NA	NA	NA	NA	NA	NA	NA/28800	700	*Alticorpus mentale*	2.7	120.0
															Aulonocara guentheri	3.5	23.0
															Bagrus spp.	3.9	43.0
															Barilius spp	3.1	22.0
															Bathyclarias gigas	4.0	83.0
															Bathyclarias nyasensis	3.7	55.0
															Bellamya ecclesi	3.0	44.0
															Buccochromis lepturus	4.2	43.0
															Buccochromis Nototaenia	4.0	37.0
															Chaoborus edulis	3.0	34.0
															Clarias sp	3.2	10.0
															Copadichromis spp	3.1	4.8
															Crab	3.0	42.0
															Ctenopharynx nitidus	3.5	18.0
															Ctenopharynx pictus	3.0	6.1
															Dimidiochromis kiwinge	4.2	18.0
															Diplotaxodon greenwoodi	4.2	330.0
															Diplotaxodon limnothrissa	3.1	14.0
															Diplotaxodon macrops	3.6	36.0
															Engraulicypris sardella	3.1	11.0
															Labeotropheus fuelleborni	2.0	1.7
															Lethrinops gossei	3.2	29.0
															Melanoides nodicincta	3.0	34.0
															Mussel	2.5	56.0
															Mylochromis cf. mola	3.6	7.0
															Opsaridium	3.8	92.0

															microlepis		
															Oreochromis karongae	2.0	3.9
															Oreochromis lidole	2.3	7.0
															Oreochromis squamipinnis	2.7	6.0
															Petrotilapia fuscous	2.0	3.1
															Petrotilapia gelutea	2.0	1.3
															Protomelas taeniolatus	3.2	4.3
															Pseudotropheus tropheops lilac	2.8	1.8
															Pseudotropheus tropheops maleri yellow	2.8	4.0
															Pseudotropheus xanstomachus	2.0	0.9
															Rhamphochromis esox	4.2	160.0
															Rhamphochromis ferox	4.2	200.0
															Rhamphochromis leptosoma	4.2	92.0
															Rhamphochromis macrophthalmus	4.2	20.0
															Rhamphochromis spp.	3.9	8.2
															Sponge	2.5	11.0
															Synodontis njassae	3.1	23.0
															Taeniolethrinops furcicauda	2.8	17.0
															Taeniolethrinops praeorbitalis	3.2	8.3
															Trematocranus microstoma	3.4	7.1
															Tyrannochromis nigriventer	4.2	9.1
															Zooplankton	2.0	3.0
26/45	(51) Lake Baringo	Kenya	Lake	0.643/36.058	47.3/No	55.3	NA	7	0.15	NA	NA	NA	160 x 10-9/NA	NA	*Barbus intermedius australis*	3.3	47.2
															Clarias gariepinus	3.2	62.0
															Labeo cylindricus	2.0	75.0
															Oreochromis niloticus	2.0	11.8
															Protopterus aethiopicus	3.4	40.6
26/46	(52) Lake Turkana	Kenya	Lake	3.702/36.15	56.2/No	7.4	NA	9.7	1	28.3	NA	NA	204/NA	NA	*Alestes baremoze*	3.1	13.8
															Bagrus bayad	4.0	38.4

															Citharinus citharus intermedius	2.0	10.6
															Clarias gariepinus	3.2	72.6
															Distichodus niloticus	2.3	27.6
															Hydrocynus forskahlii	4.0	306.0
															Labeo horie	2.1	12.4
															Lates niloticus	4.5	93.4
															Oreochromis niloticus	2.0	11.6
															Sarotherodon galilaeus	2.0	2.7
															Syndontis schall	2.9	75.5
															Tetraodon lineatus	3.6	9.3
26/47	(53) Lake Naivasha	Kenya	Lake	-0.077/36.364	27.4/No	31.3	NA	NA	0.8	21.25	NA	NA	4.6/NA	NA	*Barbus paludinosus*	2.8	81.1
															Haplochromine spp	3.0	5.6
															Micropterus salmoides	3.8	52.0
															Oreochromis leucostictus	2.3	4.8
															Procambarus clarkii	3.8	11.7
															Tilapia zilli	2.0	9.3
27/NA	(54) Mtera (Great Ruaha River basin)	Tanzania	River	-7.693/38.03	39.5/No	NA	NA	NA	NA	NA	NA	NA	NA/NA	41	*Alestes affinis*	2.9	54.0
															Bagrus orientalis	3.9	36.0
															Clarias mossambicus	3.0	43.3
															Hydrocynus vittatus	4.4	82.8
															Synodontis maculipinna	2.9	13.0
															Tilapia urolepis	2.0	7.8
27/NA	(55) Nyumba ya Mungu	Tanzania	Reservoir	-4.695/38.095	5.7/No	NA	NA	NA	NA	NA	NA	NA	NA/NA	43	*Synodontis maculipinna*	2.9	8.2
															Tilapia urolepis	2.0	3.2
28/48	(56) Lake Awassa (open-water)	Ethiopia	Lake	7.03/38.418	77.2/No	18.7	NA	NA	NA	NA	NA	NA	NA/90	NA	*Barbus intermedius*	3.3	140.1
															Clarias gariepinus	3.2	50.6
															Oreochromis niloticus	2.0	41.0
29/48	(57) Lake Awassa	Ethiopia	Lake	7.036/38.423	311.0/No	18.7	NA	NA	NA	NA	NA	11	NA/90	22	*Barbus intermedius*	3.3	311.0
28/48	(58) Lake Awassa (near-shore)	Ethiopia	Lake	7.046/38.449	81.9/No	18.7	NA	NA	NA	NA	NA	NA	NA/90	NA	*Barbus intermedius*	3.3	213.2
															Clarias gariepinus	3.2	24.6
															Oreochromis niloticus	2.0	7.7

27/NA	(59) Kidatu (Great Ruaha River basin)	Tanzania	Reservoir	-7.881/38.468	33.9/No	NA	NA	NA	NA	NA	NA	NA	NA/NA	42	*Bagrus orientalis* *Hydrocynus vittatus* *Synodontis maculipinna* *Tilapia urolepis*	3.9 4.4 2.9 2.0	38.0 51.8 33.8 12.1
28/48	(60) Lake Awassa (river-head)	Ethiopia	Lake	7.089/38.479	36.3/No	18.7	NA	NA	NA	NA	NA	NA	NA/90	NA	*Barbus intermedius* *Clarias gariepinus* *Oreochromis niloticus*	3.3 3.2 2.0	50.8 48.0 10.0
27/NA	(61) Hale-Pangani (Pangani River basin)	Tanzania	Reservoir	-5.229/38.602	40.5/No	NA	NA	NA	NA	NA	NA	NA	NA/NA	44	*Synodontis maculipinna*	2.9	40.5
30/48	(62) Lake Ziway	Ethiopia	Lake	7.991/38.828	25.8/No	39.2	NA	7.5	NA	NA	NA	NA	1.8/490	NA	*Carassius auratus* *Clarias gariepinus* *Oreochromis niloticus* *Tilapia zilli*	2.0 3.2 2.0 2.0	25.0 33.0 11.0 34.0
28/49	(63) Lake Koka (nearshore)	Ethiopia	Lake	8.403/39.027	73.0/No	13.5	NA	NA	NA	NA	NA	NA	NA/200	NA	*Barbus intermedius* *Clarias gariepinus* *Oreochromis niloticus*	3.3 3.2 2.0	135.9 72.0 11.1
28/49	(64) Lake Koka (nearshore)	Ethiopia	Lake	8.413/39.046	125.4/No	13.5	NA	NA	NA	NA	NA	NA	NA/200	NA	*Barbus intermedius* *Clarias gariepinus* *Oreochromis niloticus*	3.3 3.2 2.0	298.9 65.3 12.1
28/49	(65) Lake Koka (open water)	Ethiopia	Lake	8.371/39.081	18.8/No	13.5	NA	NA	NA	NA	NA	NA	NA/200	NA	*Barbus intermedius* *Clarias gariepinus* *Oreochromis niloticus*	3.3 3.2 2.0	40.1 6.3 10.1

[i] The numbers are those presented in the reference list of the SI; they refer to a study used to compile data.
[ii] These are the numbers presented in Figure 1b of the manuscript., which refer to the locations listed here.
[iii] Species that are annotated with 'spp.' were documented as such in the studies from which information was retrieved. To estimate their trophic levels we collected trophic levels of 5-10 species from the same tribe or genus on FishBase and used an average.

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[2] The red line from this figure was used as data on Hg contamination was from the central part of the lake (Kalokol fish landing). Data dates back to 1988.

Chapter 2: Supplemental information

Figure and table captions

Figure 1. Methyl Mercury concentrations in 12 sites from the four different habitat types of Lake Nabugabo, Uganda. Concentrations were calculated based duplicates in 6 sites and unique measurements in other sites. All concentrations expect the highest documented value in the *M. violaceum* habitat were below the detection limit of the instrument used to measure concentrations (0.02 ng/L).

Table 1. Relative abundance prey (%N) of prey types in the stomachs of Nile perch from Lake Nabugabo, Uganda.

Table 2. Frequency of occurrence (%F) of prey types in the stomachs of Nile perch from Lake Nabugabo, Uganda.

Table 3. Percent mass (%M) of prey types in the stomachs of Nile perch from Lake Nabugabo, Uganda.

Figures and tables

Figure 1.

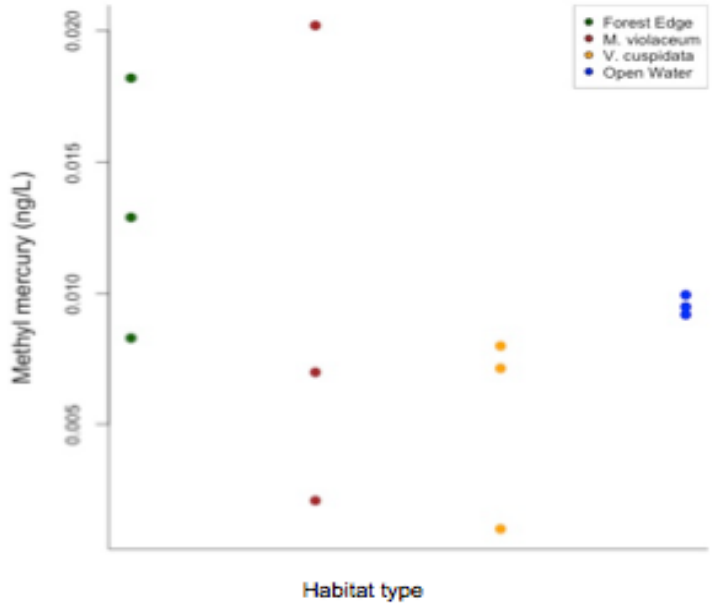


Table 1.

Relative prey abundance (% N)	Habitat type											
	Forest			Open water			M. violaceum			V. cuspidata		
Size class	< 15 cm	15 - 40 cm	> 40 cm	< 15 cm	15 - 40 cm	> 40 cm	< 15 cm	15 - 40 cm	> 40 cm	< 15 cm	15 - 40 cm	> 40 cm
Sample size	11	14	3	3	9	1	14	10	4	8	9	5
Invertebrate prey												
Family Chironomidae	50.00	0.00	0.00	50.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Order Ephemeroptera	0.00	0.00	0.00	0.00	0.00	0.00	33.33	0.00	0.00	0.00	0.00	0.00
Order Odonata	0.00	17.65	0.00	0.00	0.00	0.00	13.33	9.09	0.00	0.00	0.00	14.29
Unidentified insect remains	0.00	0.00	0.00	0.00	0.00	0.00	6.67	0.00	0.00	0.00	0.00	0.00
All invertebrates	50.00	17.65	0.00	50.00	0.00	0.00	53.33	9.09	0.00	0.00	0.00	14.29
Fish prey												
Barbus sp.	0.00	5.88	0.00	0.00	0.00	0.00	0.00	0.00	25.00	0.00	0.00	0.00
Cichlids	8.33	17.65	75.00	0.00	30.00	100.00	0.00	18.18	25.00	50.00	40.00	28.57
Eels	0.00	0.00	0.00	0.00	0.00	0.00	0.00	9.09	0.00	0.00	0.00	0.00
Haplochromine cichlids	0.00	0.00	0.00	0.00	0.00	0.00	0.00	9.09	25.00	12.50	10.00	14.29
Lates niloticus	8.33	0.00	0.00	0.00	10.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rastrineobola argentea	25.00	29.41	0.00	0.00	10.00	0.00	0.00	18.18	0.00	0.00	10.00	28.57
Unidentified fishes	8.33	29.41	25.00	50.00	50.00	0.00	46.67	36.36	25.00	37.50	40.00	14.29
All fish	50.00	82.35	100.00	50.00	100.00	100.00	46.67	90.91	100.00	100.00	100.00	85.71

Table 2.

Frequency of Occurance (%F)	Habitat type											
	Forest			Open water			*M. violaceum*			*V. cuspidata*		
Nile perch size class	< 15 cm	15 - 40 cm	> 40 cm	< 15 cm	15 - 40 cm	> 40 cm	< 15 cm	15 - 40 cm	> 40 cm	< 15 cm	15 - 40 cm	> 40 cm
Nile perch sample size (n)	11	14	3	3	9	1	14	10	4	8	9	5
Invertebrate prey												
Family Chironomidae	54.55	0.00	0.00	66.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Order Ephemeroptera	0.00	0.00	0.00	0.00	0.00	0.00	35.71	0.00	0.00	0.00	0.00	0.00
Order Odonata	0.00	21.43	0.00	0.00	0.00	0.00	14.29	10.00	0.00	0.00	0.00	20.00
Unidentified insect remains	0.00	0.00	0.00	0.00	0.00	0.00	7.14	0.00	0.00	0.00	0.00	0.00
Fish prey												
Barbus sp.	0.00	7.14	0.00	0.00	0.00	0.00	0.00	0.00	25.00	0.00	0.00	0.00
Cichlids	9.09	21.43	100.00	0.00	33.33	100.00	0.00	20.00	25.00	50.00	44.44	40.00
Eels	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.00	0.00	0.00	0.00	0.00
Haplochromine cichlids	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.00	25.00	12.50	11.11	20.00
Lates niloticus	9.09	0.00	0.00	0.00	11.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rastrineobola argentea	27.27	35.71	0.00	0.00	11.11	0.00	0.00	20.00	0.00	0.00	11.11	40.00
Unidentified fishes	9.09	35.71	33.33	66.67	55.56	0.00	50.00	40.00	25.00	37.50	44.44	20.00

Table 3.

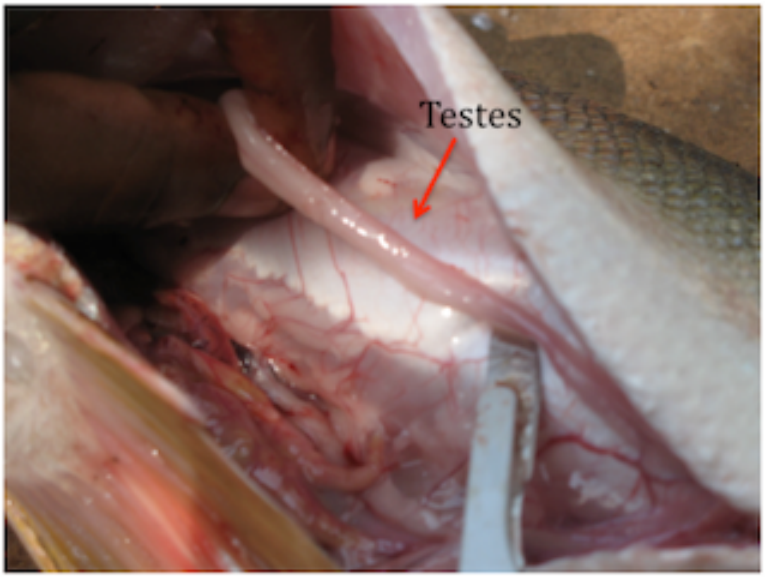
Percent Mass (% M)	Habitat type											
	Forest			Open water			M. violaceum			V. cuspidata		
Size class	< 15 cm	15 - 40 cm	> 40 cm	< 15 cm	15 - 40 cm	> 40 cm	< 15 cm	15 - 40 cm	> 40 cm	< 15 cm	15 - 40 cm	> 40 cm
Sample size	11	14	3	3	9	1	14	10	4	8	9	5
Invertebrate prey												
Family Chironomidae	13.61	0.00	0.00	29.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Order Ephemeroptera	0.00	0.00	0.00	0.00	0.00	0.00	20.90	0.00	0.00	0.00	0.00	0.00
Order Odonata	0.00	3.83	0.00	0.00	0.00	0.00	9.76	2.22	0.00	0.00	0.00	1.26
Unidentified insect remains	0.00	0.00	0.00	0.00	0.00	0.00	1.54	0.00	0.00	0.00	0.00	0.00
All invertebrates	13.61	3.83	0.00	29.67	0.00	0.00	32.20	2.22	0.00	0.00	0.00	1.26
Fish prey												
Barbus sp.	0.00	7.35	0.00	0.00	0.00	0.00	0.00	0.00	9.36	0.00	0.00	0.00
Cichlids	31.12	40.59	98.94	0.00	42.07	100.00	0.00	35.59	15.27	61.58	13.44	23.15
Eels	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.72	0.00	0.00	0.00	0.00
Haplochromine cichlids	0.00	0.00	0.00	0.00	0.00	0.00	0.00	21.10	70.12	25.95	66.44	51.87
Lates niloticus	7.20	0.00	0.00	0.00	4.58	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rastrineobola argentea	37.89	29.19	0.00	0.00	24.20	0.00	0.00	10.99	0.00	0.00	6.33	13.66
Unidentified fishes	10.18	19.04	1.06	70.33	29.16	0.00	67.80	23.38	5.24	12.47	13.78	10.05
All fish	86.39	96.17	100.00	70.33	100.00	100.00	67.80	97.78	100.00	100.00	100.00	98.74

Chapter 2 appendix: Fish processing

Section 1-Sexing and determining stage of maturity of Nile Perch

a) Cut incision on euthanized Nile perch from anus up to gills on the bottom side of the fish

b) Evaluate length and size of testes or ovaries to determine gender and stage of maturity. (See Nkalubo, 2012, for further details.)



Section 2- Analyzing stomach contents

a) Remove stomach from incised Nile perch body and cut off using a scalpel

b) Preserve stomach in formalin until ready for dissection. (The dissection can be completed from minutes to years after preservation; in the case of this study, dissections were completed 1-4 days after preservation.)

c) When ready for dissection, clean all dissection tools using ethanol (95%) and use clean scissors to open Nile perch stomach

d) Remove stomach contents and place in sterile petri dish

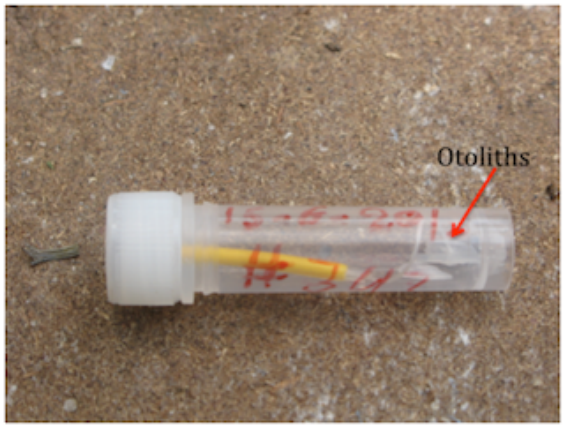
e) Identify each individual to the best possible level using key features such as presence of vertebrates, pharyngeal jaws, scales etc. Count and weigh individuals of each prey type.

Section 3- Removing otoliths for age analysis

a) Cut open fish head

b) Expose interior of skull

c) Remove otoliths from under brain matter and store in vial until ready for analysis



*Note that we did not conduct analysis of otoliths for this thesis, as this data was collected for future work only.

Section 4- Sampling of dorsal musculature for Hg tissue analysis

1) Small sized fish

a) Pre-weigh cryovials and then clean all dissection tools and cutting board covered with aluminum foil using kimwipes and ethanol (95%).

b) Place euthanized specimen of Nile perch on cutting board

c) Remove entire tail using dissection scissor

d) Remove entire head using dissection scissors

e) Remove entire abdomen and internal organs using dissection scissors

f) Section remaining mid-piece into 2 portions and remove scales if there is sufficient tissue

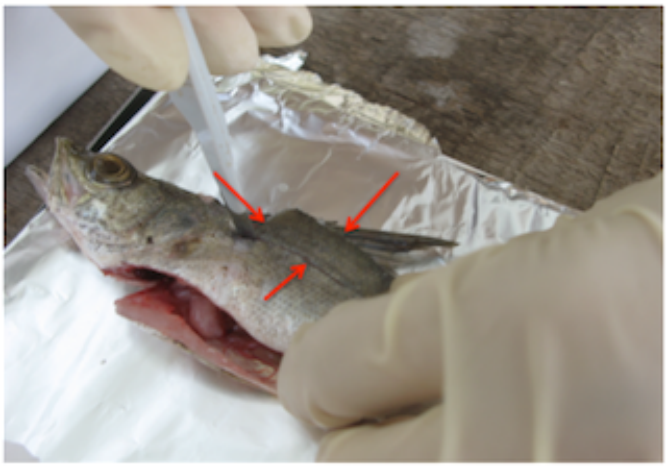
g) Place tissue samples into cryovial, weigh vial and freeze.

2) Medium to large sized fish

a) Pre-weigh cryovials and then clean all dissection tools and cutting board covered with aluminum foil using kimwipes and ethanol (95%).

b) When possible, place specimen on clean cutting board, if not, leave on cleared counter surface.

c) Using a scalpel, make 3 incisions across dorsal musculature.



d) Using forceps and scalpel, peal back external tissue with scales.

e) Using scalpel and forceps, slice dorsal musculature tissue into sizes that will fit into cryovials.

f) Place tissue samples into cryovial, weigh vial and freeze.