Potential Impacts of Ecosystem Degradation on the Reproductive Biology and Behavior of Malawian Cichlids

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Abstract

The Rift Valley is a tropical region of eastern Africa characterized by its complex geological makeup consisting of tectonic plates that have driven the formation of some of the largest lakes in the world being Lake Malawi, Victoria, and Tanganyika. In turn, the formation of these amazing freshwater ecosystems has enabled the evolution, and radiation of thousands of species of fish from the family ***Cichlidae***, which constitutes the most diverse group of vertebrates on the globe. However, because these ecosystems are also in regions with a high prevalence of anthropogenic activities they are threatened by biodiversity loss. In particular, Lake Malawi is a notable example as it is an extremely delicate ecosystem that is home to the greatest number and diversity of African cichlids while also being surrounded by countries with severe anthropogenic pressures associated with climate change and increased agricultural activity. With that being said, by conducting an extensive literature review and experimental data collection in the Cruz Lab this study looked at the potential impacts of ecosystem degradation on the reproductive biology and behavior of Malawian cichlids. In doing so, I found that ecosystem degradation could have a negative impact on the reproductive biology and behavior of Malawian cichlids by disrupting aspects of sexual selection, courtship, spawning, and juvenile development and rearing. These finding are significant as they imply that continued ecosystem degradation in Lake Malawi could lead to a reduction in the fitness of Malawian cichlids that could substantially reduce the size and diversity of the largest family of vertebrates in the world.

Keywords: African Rift Valley Lakes, African Cichlids, Biodiversity loss, Lake Malawi, Malawian Cichlids, Ecosystem degradation, Cichlid Reproduction

Introduction

The earth is currently experiencing a mass loss of biodiversity due to increases in anthropogenic activity that began with the advent and habitual use of fossil fuels (Christian, 2012; Dirzo, 2014). While these losses in biodiversity are occurring at a global scale, tropical regions are afflicted more than others because their high percentage of delicate ecosystems and endemic species make them extremely vulnerable to anthropogenic pressures in these areas (Brooks, 2002; Kricher, 1999; Wilson, 1998). In particular, Lake Malawi of the African Rift Valley is a notable example as it is located in a region with severe anthropogenic pressures associated with climate change and increased agricultural activity, which are now threatening the lake and the many endemic fish from the family ***Cichlidae*** within it (Wood, 2005; Odada, 2006;Sturmbauer, 2011). As these anthropogenic pressures have led to the degradation of Lake Malawi's ecosystem and are projected to lead to further degradation this could significantly impact Malawian cichlid populations as their biology, physiology, and behavior is highly dependent on the environmental conditions in which they evolved (Chafota, 2005; Duponchelle, 2000, 2008; Genner, 2005; Kocher, 2000; Sturmbauer, 2011).

With that in mind, the goal of this study was to characterize the impacts of regional anthropogenic pressures on the fitness of Malawian cichlids by determining how deteriorating ecosystem conditions in Lake Malawi could impact their reproductive success by negatively influencing biological, and behavioral characteristics of their reproduction. In order to do so, the project was broken down into three parts. In Part I, an extensive literature review was conducted in order to familiarize myself with the project by establishing an understanding of how current global biodiversity loss relates to the

African Rift Valley. This was done by looking at the influences of regional anthropogenic pressures on the degradation of Lake Malawi's ecosystem and the resulting impact that these deteriorating ecosystem conditions could have fish biodiversity in general. In Part II, a literature review was used to identify novel trait's of Malawian cichlids that were significant in their evolutionary success and vulnerable to deteriorating ecosystem conditions in Lake Malawi due to the role that ecological selection played in their formation. Once Malawian cichlid reproduction was determined to be a novel trait in their evolutionary success and vulnerable to ecosystem degradation, experimental data collection and a literature review were used to try and identify the degree to which reproductive traits are shared across species of the Malawian flock so that I could begin to consider the potential influences of deteriorating ecosystem conditions on Malawian cichlid reproduction. In doing so, the Malawian Cichlid ***Labidochromis caeruleus*** (Electric Yellow) was used as a model organism in the Cruz Lab to collect qualitative and quantitative baseline data associated with characteristics of its reproductive biology, and behavior, which were then compared to information on Malawian cichlid reproduction gathered in a literature review in order to highlight similarities in sexual selection, courtship, spawning, and juvenile development and rearing. In Part III, an extensive analysis comparing the results from Part's I and II was conducted in order to describe how deteriorating ecosystem conditions in Lake Malawi could impact the fitness of Malawian cichlids by negatively influencing their reproductive success through changes in their reproductive biology, and behavior.

Objectives

In this study I will address the following:

Will degraded ecosystem conditions in Lake Malawi associated with increases in hypoxia, turbidity, sedimentation, and warm nutrient poor waters negatively impact the fitness of Malawian cichlids by negatively influencing their reproductive biology, and behavior? Based on this question, I predict that deteriorating ecosystem conditions could negatively impact the fitness of Malawian cichlids by potentially influencing aspects of their reproductive biology, and behavior associated with sexual selection, courtship, spawning, and juvenile development and rearing.

Part I – Global Biodiversity Loss and Tropical Ecosystems – Lake Malawi as a Case Study

In Part I of the project I consider the relationship between global biodiversity loss and the African Rift Valley. I then characterize the impact that regional anthropogenic pressures are having on the Rift Valley ecosystem of Lake Malawi by considering their influence on ecosystem degradation. Based on this information, I then characterize the potential impact of ecosystem degradation on the lake's fish biodiversity by researching the impacts of described ecosystem degradation on the biology, physiology, and behavior of fish in general.

Background

Biodiversity Loss in the Tropics

The earth is currently moving out of the Holocene epoch and entering the Anthropocene epoch, which has initiated a wave of global biodiversity extinctions, threats, and population declines comparable to past mass extinctions (Christian, 2012; Dirzo, 2014). Although the projected global rate of biodiversity loss is unprecedented, it is believed that the tropical latitudes will experience an even greater rate of loss as their long complex evolutionary history has led to the formation of delicate ecosystems that support a vast number of specialized endemic species (Kricher, 1999; Oakleaf, 2013). The fact that tropical ecosystems are extremely delicate has made them susceptible to biodiversity loss as slight fluctuations in environmental conditions can lead to ecosystem degradation by negatively influencing the flow of nutrients, energy, and water throughout biotic and abiotic pools of the ecosystem (Chapin, 2011). Moreover, the prevalence of highly specialized endemic species is significantly increasing rates of biodiversity loss in theses regions as their evolutionary history has made them extremely sensitive to ecosystem degradation. For example, because species in tropical latitudes represent those that have small, specialized home ranges that cannot easily be recreated or substituted, once a species loses its original habitat its chances of survival decrease significantly (Brooks, 2002). Furthermore, within these small home ranges species are scarce, so losing one individual has a significant impact on the rest of the population in terms of community interactions and genetic variability (Brooks, 2002). Finally, there is a high prevalence of coexistence between different species in tropical latitudes, so the loss of one species due to ecosystem degradation can significantly impact other species that may have co-evolved with it by disrupting ecosystem interactions associated with biotic symbioses and mutualisms or trophic energy transfer (Brooks, 2002).

Because of these evolutionary constraints on endemic species and the ecosystems that they inhabit, the tropical latitudes are disproportionally threatened by biodiversity loss as they face high rates of ecosystem degradation due to sever anthropogenic pressures originating from lack of intuitional management in the economic and societal sectors of government (Charles Darwin University, 2015). For example, as local governments have failed to diversify local economies and educate the public, poverty and inequality have increased in these areas, which has significantly increased the number of malnourished and zero-income individuals (Charles Darwin University, 2015; Wilson, 1998). However, this has led to a rise in the rate of natural resource extraction, especially as it pertains to agricultural expansion, which has resulted increased rates of land conversion in highly sensitive ecosystems (Charles Darwin University, 2015; Wilson, 1998). As a result, this has significantly altered environmental conditions, which has led to the degradation of both terrestrial and aquatic components of these ecosystems resulting in high rates of biodiversity loss in these areas (Wilson, 1998). Moreover, because the high degree of inequality and poverty often influences the effectiveness of government institutions, there is no proper framework for sustainable management and conservation of tropical ecosystems, which intensifies their degradation and the loss of biodiversity as the negative impacts associated with independent anthropogenic activities often combine to pose a much more severe threat (Charles Darwin University, 2015; Wilson, 1998). With that being said, the tropical region of eastern Africa known as the Rift Valley is no exception as it is a region characterized by and incredible evolutionary history that has given rise to a array of delicate terrestrial and freshwater ecosystems that support a vast number of endemic species (Chafota, 2005; Sturmbauer, 2011; Wood, 2005). However, theses ecosystems and the species inhabiting them are threated by severe anthropogenic pressures due to high rates of poverty and inequality resulting from lack of institutional management in the region (Odada, 2006).

The African Rift Valley

The Rift Valley stretches more than 6,416 km from Jordan to Mozambique. The Rift Valley is characterized by its complex geological makeup consisting of the Arabian, Nubian, and Somalian tectonic plates, which have driven the formation of incredible landscapes (Wood, 2005). For example, as the Nubian, Somalian, and Arabian plates have gradually been separating over millions of years this has led to a fracturing of earth's crust, which has driven the uplift and collapse of the Rift Valley's landscape, resulting in the formation of long mountain ranges and large valley basins (Frommers, 2014; Wood, 2005). In the process of their formation, these landscapes have given rise to an amazing diversity of freshwater and terrestrial ecosystems, most notably of which are the Ancient Rift Valley Lakes (Frommers, 2014; Wood, 2005). The formation of the Rift Valley Lakes can be attributed to wetter climatic conditions that led to increased precipitation, resulting in the accumulation of massive amounts of water in low-lying areas of the valley basins formed by the geologic uplift and collapse of earth's crust (Frommers, 2014; Wood, 2005). As a result of this process we now have Lakes Tanganyika, Malawi, and Victoria, which are three of the largest and deepest lakes in the world as they encompass eleven countries and reach depths close to 700 meters (Hecky, 1993). Moreover, because of their massive size, the Ancient Lakes of the Rift Valley have an incredible diversity of ecological niches that have allowed the evolution, and radiation of thousands of species of fish from the family ***cichlidae***, especially in Lake Malawi (Kocher, 2000; Genner, 2005; Sturmbauer, 2011).

Lake Malawi

Lake Malawi represents the ninth largest and third deepest lake in the world with an area of 28,000 km^2 and depth of 700 m, and is bordered by the steep mountains, woodlands, and rocky and sandy coastlines of Tanzania, Mozambique, and Malawi (Bootsma, 2005). In terms of biophysical features, Lake Malawi is separated into three stratified layers know as the epilimnion, the metalimnion, and the hypolimnion layer, which are categorized based on water density (Bootsma, 2005; Vollmer, 2005). The epilimnion is characterized as the clear, least dense, top, warm layer of the lake between 40 and 100 m where a high percentage of the lake's biodiversity resides and where most algal growth occurs that supports the lake's food web (Bootsma, 2005). The metalimnion is characterized as the second densest, middle, cool layer ranging from the bottom of the epilimnion layer to 220 m where there is a strong vertical gradient of dissolved nutrients and oxygen (Bootsma, 2005). The hypolimnion is characterized as the densest, bottom, cold layer ranging from the bottom of the metalimnion to the bottom of the lake where no fish are present as result of anoxic conditions and high concentrations of dissolved nitrogen, phosphorus, and silica (Bootsma, 2005). Moreover, in addition to being permanently stratified, the lake has an extremely slow flushing rate as only 16% of the 68 km^3 of water entering the lake flows directly out through the connecting Shire River, while a very small percentage is loss to evaporation at the lake's surface (Bootsma, 2005). With that being said, because of the lake's large size and complexity of biophysical features it is composed of an array of micro-niches that not only support the greatest diversity of freshwater lake fish in the world, but also the greatest diversity of African cichlids with over 500 different endemic species present in the lake (Kocher, 2000; Carvalho, 2004).

Impacts of Regional Anthropogenic Pressures on Lake Malawi

As Lake Malawi represents a delicate ecosystem with high rates of endemic species it is highly susceptible to biodiversity loss from ecosystem degradation due to the abundance of anthropogenic activities in the area associated with land conversion and climate change. For example, since the countries that border Lake Malawi (Malawi, Mozambique, and Tanzania) are rich in natural resources, but poor in terms of government structure and economic development, the majority of their regional population lives in rural settings and are dependent on natural resources for their survival (Bootsma, 2005). This has been detrimental to Lake Malawi's ecosystem as growing populations and lack of economic resources has led to the unsustainable use and management of marginal lands (Bootsma, 2005). In fact, as populations have continued to grow and poverty has become more pronounced, there has been an increased instance of land conversion for the extraction of natural resources as well as the development of agricultural land (OECD, 2009.) In particular, there has been a significant increase in the amount of biomass burning and deforestation as locals try and extract timber and clear land for plantations and livestock grazing in response to socioeconomic pressures (Bootsma, 2005; OECD, 2009.) As a result, the prevalence of regional soil erosion and run-off has increased significantly, which has had negative implications for Lake Malawi's ecosystem as it has led to increased inputs of sediment and nutrients in the Lake (Bootsma, 2005). Additionally, recent fluctuations in regional temperature, precipitation, and evaporation rates associated with local land conversion and global climate change are contributing to increases in the lake's surface temperature, which has already increased by 1.45 degree Celsius in the last century and is projected to increase by 0.13 degrees Celsius per decade in the coming years (McSweeny, 2010; Vollmer, 2005.)

Ecosystem Degradation in Lake Malawi

Because the rate of climate change and the prevalence of regional poverty show no signs of decreasing in the near future, increases in sediments, nutrients, and water temperature in Lake Malawi will likely continue. As a result, this will lead to the continued degradation of the lake's ecosystem in a number of ways (Bootsma, 2005.)

Impacts of Nutrient Loading

Nutrient loading has led to and will continue to lead to the degradation of Lake Malawi's ecosystem as increases in the amount of nitrogen and phosphorus entering the lake have led to increased instances of eutrophication, which has resulted in the more common occurrence of hypoxia, turbidity, and decreased nutrient availability at the lake's surface (Bootsma, 2005; Hecky, 1993). The occurrence of hypoxia at the lake's surface has been on the rise because increases in the amount of nitrogen and phosphorus entering the lake have enabled massive phytoplankton blooms, which has resulted in increasingly anoxic conditions at the bottom of the lake as bottom dwelling bacteria utilize incredible amounts of oxygen in order to decompose the larger loads of biomass (Hecky, 1993). As a result, this has increased the instance of hypoxic conditions across upper layers of the lake as upwelling has lead to the dispersal of this extremely oxygen poor water from the lake's depths to its surface (Hecky, 1993; Vollmer, 2005). Moreover, the occurrence of nutrient poor surface waters has risen because increases in the amount of nitrogen entering the lake have enabled massive cyanobacteria blooms, which have been detrimental as cyanobacteria are considered to be a poor source of energy and nutrients in the lake. As a result, large increases in their density and abundance has significantly disrupted the transfer of energy to higher trophic levels, resulting in decreased nutrient availability at the lake's surface (Hecky, 1993). Finally, the occurrence of turbid conditions at the lake's surface has been on the rise because the amount of phosphorus and nitrogen entering the lake has increased the abundance and concentration of suspended solids and algae/microalgae, respectively. As a result, this has decreased the intensity of light penetration in the lake, leading to decreased amounts of visible light in the water column and rocky and sandy niches of the lake's surface waters (Bootsma,2005; Hecky, 1993; Gray, 2011).

Impacts of Sediment Loading

Sediment loading has led to and will continue to lead to the degradation of Lake Malawi's ecosystem as increases in the amount of sediments entering the lake have resulted in the more common occurrence of turbidity, and the sedimentation of habitats in the lake's surface waters (Bootsma, 2005; Hecky, 1993). The occurrence of turbidity in the lake's surface waters has been on the rise because increases in the amount of sand, silt, and clay entering the lake have lead to a significant increase in the concentration and abundance of suspended solids at the lake's surface (Bootsma, 2005; Hecky, 1993). Additionally, the occurrence of the sedimentation of habitat has been on the rise as increases in the amount of sand, silt, and clay entering the lake has lead to a significant intensification in the concentration and abundance of sediments settling on biotic and abiotic components of the lake's ecosystem at its surface waters (Bootsma, 2005).

Impacts of Increased Water Temperature

Increased water temperature has lead to and will continue to lead to the degradation of Lake Malawi's ecosystem by leading to warm, nutrient poor water at the lake's surface. For example, when the surface waters of Lake Malawi have warmed more than its deeper waters it influences the lakes stratification by disrupting the density gradient, leading to decreased vertical mixing (Bootsma, 2005; Vollmer, 2005). As a result, this significantly disrupts primary productivity and the upwelling of nutrients from deeper layers of the lake, resulting in decreased nutrient availability for higher trophic levels at the lake's surface (O'Reilly, 2003).

Methods - Characterizing the Impact of Described Ecosystem Degradation In Lake Malawi on Fish (in general)

In methods Part I, I characterize the impacts of ecosystem degradation on fish in general so that these impacts could then be analyzed in relation to Malawian Cichlid reproductive trends in Part III of the project. In doing so, an extensive review of scientific literature was used in order to identify how ecosystem degradation in Lake Malawi as described above could influence fish biology, physiology, and behavior.

Results - Impact of Described Ecosystem Degradation In Lake Malawi on Fish (in general)

Impacts of Hypoxia

Hypoxia as observed in Lake Malawi can have a significant impact on biological characteristics of fish. For example, when trying to maintain oxygen levels in hypoxic conditions fish undergo a number of physiological changes associated with increasing the amount of water flowing over their gills, the diffusion capacity of their gills, and their hemoglobin binding capacity in addition to reducing their metabolism, rate of protein synthesis, and regulation of enzymes in aerobic pathways (Wu, 2002). As a result, these physiological changes reduce the amount of available energy for them, which can lead to a reduction in their size and growth rate as they move farther from their biological optimum equilibrium (Wu, 2002). Additionally, hypoxia can impact biological characteristics of spawning and juvenile development in fish. For example, hypoxia often reduces the number of spawning attempts, fertilization success, and the number of eggs laid, because a reduction in oxygen puts extra pressure on the mating pair while also acting as an endocrine disrupter (Pollack, 2007; Wu, 2003). Moreover, hypoxic conditions interfere with the growth and development of juveniles as decreased oxygen levels often lead to increased mortality rates of eggs while reducing the viability of juvenile offspring (many eggs never hatch or juveniles are deformed) (Pollack, 2007). Additionally, increases in hypoxia as observed in Lake Malawi can have a significant impact on fish behavior (Wu, 2002). For example, hypoxic conditions cause fish to abandon their territories and migrate to areas with higher concentrations of oxygen, which disrupts territoriality and feeding habits as these changes in behavior lead to a loss in community structure (Pollack, 2007; Wu, 2002).

Impacts of Turbidity

Increases in turbidity as observed in Lake Malawi can have a significant affect on behavioral characteristics of fish. For example, increased turbidity degrades fish habitat, which causes fish to change their behaviors in order to disperse to non-turbid areas, resulting in a reduction of community structure and the disruption feeding habits (Gray, 2011). Moreover, increases in turbidity can reduce courtship behaviors among fish as decreases in visibility disrupt the visual cues (displays) associated with courting an individual (Gray, 2011; Seehausen, 1997). Additionally, increases in turbid conditions as observed in Lake Malawi can have a significant affect on the biological characteristics of fish. For example, increased turbidity can lead to a reduction in the effectiveness of the biological mechanism of sexual selection as decreased visibility disrupts visual cues associated with higher fitness in mate choice, which can lead to less fit offspring and a reduction in species diversity (Seehausen, 1997). Moreover, because turbidity disrupts feeding it can lead to a reduction in the body condition of fish (Dupponchelle, 2000).

Impacts of Sedimentation

Increases in sedimentation as observed in Lake Malawi can have a significant affect on the behavioral characteristics of fish. For example, sedimentation can lead to the degradations of fish habitat, which causes a change in fish behavior as they disperse to new habitats and compete for spawning grounds, resulting in a reduction in community structure and the number of spawning attempts (Jamu, 2009; Rusuwa, 2006). Additionally, increases in sedimentation as observed in Lake Malawi can affect biological characteristics of fish. For example, increased sediment loading degrades or prevents access to available food sources, leading to reduced energy availability, which can result in reduced growth rate and body condition. (Jamu, 2009; Rusuwa, 2006).

Impacts of Warm and Nutrient Poor Water

Warn Nutrient poor water can have a significant affect on biological characteristics of fish by reducing the amount of energy available to them. For example when independent of one another, increased water temperature and decreased nutrient availability both can significantly decrease the growth rate of fish (Kim, 2011). Moreover when combined, increased water temperature and decreased nutrient availability can cause growth of fish to stop altogether (Kim, 2011).

Part II – Characterizing Malawian Cichlid Reproductive Biology and Behavior – *L. caeruleus* as a Case Study

In Part II of the project I consider the relationship between African cichlid evolutionary history and the various environmental, sexual, and genetic pressures shaping it. I then describe Malawian cichlid evolution and radiation in relation to African cichlid evolutionary history in order to identify reproduction as novel trait of the Malawian flock that is vulnerable to deteriorating ecosystem conditions in Lake Malawi due to the indirect and direct role that ecological selection played in shaping it. Based on these relationships, I then identify similarities in the novel trait of reproduction through a literature review and experimental data collection with a model organism so that I could begin to consider the potential influences of deteriorating ecosystem conditions on Malawian cichlid reproduction.

Background

African Rift Valley Cichlids

The teleost fish of the family ***cichlidae*** represent the most diverse group of vertebrates in the world as two initial global diversification events 160 million years ago and 90 million years gave rise to an estimated 3,000 species of cichlids endemic to an array of freshwater ecosystems found in Sri Lanka, India, Africa, South America, Central America, and the southern most region of North America (Kocher, 2000; Sturmbauer, 2011). However, the East African Rift Valley is the hotspot for cichlid diversity and abundance as ten million years of evolution in Lakes Tanganyika, Malawi, and Victoria has given rise to 60% of the global population of cichlids through explosive adaptive radiation (Kocher, 2000; Sturmbauer, 2011).

Primary Radiation

As one of the earliest lake formations and the oldest lake in the Rift Valley, the radiation of African cichlids began in Lake Tanganyika and later spread to Lakes Victoria and Malawi (Sturmbauer, 2011). The primary radiation of cichlids in Lake Tanganyika began about five to six million years ago with seven seeding lineages consisting of mouthbrooders and substrate-breeders, which quickly grew into several new lineages through a number of diversification events in the lake. In particular, two seeding lineages known as the substrate breeding ***lamprologine*** and mouthbrooding ***c-lineage*** underwent successive divergence events, which gave rise to a new species of cichlid known as the mouthbrooding ***haplochromine*** (Sturmbauer, 2011). After their formation, the mouthbrooding haplochromines were able to leave Lake Tanganyika and colonize surrounding rivers as geologic and climatic pressures caused massive fluctuations in the lake's level. Once established in surrounding river basins, the mouthbrooding haplochromines further diversified into six new lineages known as the ***haplochromis***, the ***astatoreochromis***, the ***pseudocrenilabrus***, the ***serranochromis***, the modern mouthbrooding ***haplochromines***, and an un-described lineage, that would all go on to ultimately colonize Lakes Malawi, Victoria, and Tanganyika, leading to the evolution and radiation of the modern cichlid lineages found in each lake (Sturmbauer, 2011).

The Role of Novel Traits

The initiation of the process of adaptive radiation that ultimately led to the divergence of cichlid species from their ancient riverine ancestors to the modern seeding lineages of the Rift Valley Lakes was dependent on two conditions. Firstly, the formation of new novel habitats such as the Rift Valley Lakes, which gave ancient riverine cichlids a new territory to inhabit. Secondly, the presence of novel traits such as broodcare and the possession of two sets of jaws, which allowed ancient riverine cichlid species to successfully colonize the newly formed lake habitats by ensuring high rates of survival and reproduction through increasing the rate of juvenile survivorship and the efficiency of food acquisition (Sturmbauer, 2011). In particular, broodcare was significant for increasing the rate of survival and reproduction among cichlids because it is a reproductive method associated with a high survivorship of juveniles. For example, substrate breeders protect their eggs and fry by laying and rearing them in isolated and sheltered areas, while mouthbrooders protect their eggs and fry by holding them in the buccal cavity of their mouth. Additionally, broodcare is associated with a high degree of community density, territoriality, and paternal investment, which in combination worked in deterring predators (Sturmbauer, 2011). Moreover, the possession of two sets of jaws significantly increased rates of survival and reproduction among cichlids by giving them access to a greater range of nutrient sources as the oral jaw served as a specialized tool for food acquisition and manipulation, while the pharyngeal jaw served as specialized tool for food processing before swallowing, (Sturmbauer, 2011).

Divergence Through Adaptive Radiation

After the initial colonization of the Great Rift Valley Lakes by ancient cichlid species was complete, pressures associated with ecological selection, sexual selection, and genetic isolation further drove radiation events most closely associated with the divergence of the modern flock of African cichlids (Sturmbauer, 2011; Kocher, 2000). While ecological selection played a large role in the early stages of the diversification of ancient riverine cichlid species to the modern African flock, sexual selection, and genetic isolation played a much larger role in the latter stages of radiation (Kocher, 2000). For example, after the initial colonization of the Rift Valley Lakes by ancient riverine cichlid species was complete, adaptive radiation of the modern African flock began through habitat divergence as generalist cichlids colonized the various niches of each lake's ecosystem in the absence of specialized competitors (Sturmbauer, 2011). Once established, further diversification of cichlids took place based on their preferred modes of food acquisition, which gave rise to separate species based on novel trophic morphologies. Moreover, once cichlids had radiated into separate populations based on acceptable trophic morphologies for a particular niche, they experienced further diversification as ecological selection led to the formation of niche partitioning behaviors, enabling many different species to inhabit the same niche (Kocher, 2000; Sturmbauer, 2011). Because the trait of niche partitioning led to niches characterized by denser communities of cichlids, sexual selection led to further divergence events as females began selecting for males that were the most colorful, ornamental, largest in terms of body size, and that had a specific color pattern, resulting in the rise of hundreds of new species of cichlids based on sexual traits that ensured assertive mating and prevented hybridization of individuals within these niches (Kocher, 2000). Finally, once cichlids had diversified into hundreds of new species through ecological and sexual selection, diversification from genetic isolation associated with cichlid's lack of dispersal at any life stage (no pelagic larval stage in juveniles and adults have high degree of territoriality) led to the formation of distinct populations within these densely populated communities based on preferences in sexual traits and ecological niches (Genner, 2005; Kocher, 2000; Sturmbauer, 2011.) As a result, the formation of these genetically isolated populations further drove divergence events through allopatric speciation, ultimately resulting in the formation of the thousands of species of cichlids that we now consider to be part of the modern cichlid flock of the African Rift Valley Lakes (Sturmbauer, 2011).

Malawian Cichlid Evolution and Diversity

The initial colonization events of cichlids in Lake Malawi are associated with two categories of ancient riverine cichlids known as the mouthbrooding ***haplochromines*** and the substrate breeding and mouthbrooding ***tilapiines***. From these two lineages five modern lineages of sand and rock dwelling Malawian cichlids arose through explosive adaptive radiation driven by ecological selection, sexual selection, and genetic isolation (Genner, 2005; Smith, 2000; Sturmbauer, 2011).

The processes of selection associated with the divergence of ***haplochromines*** and ***tilapiines*** in Lake Malawi can be attributed to the colonization of the lake's fundamental niches by a generalist species from each lineage in the absence of specialized competitors, the subdivision of the fundamental niches by niche partitioning behaviors based on specialized morphological adaptions and spawning site preference, the divergence of sexual characteristics within each preferred micro-niche based on sexual selection, and then the divergence of community characteristics (sexual and ecological preference) through genetic isolation. For example, in the first stage of explosive adaptive radiation a generalist riverine ***haplochromine*** and ***tilapiine*** entered Lake Malawi and colonized the lake's fundamental niche's of rocky and sandy habitat in the absence of any specialized competitors by increasing their rates of survival and reproduction through the utilization of the novel traits of two oral jaws and broodcare (Genner, 2005; Sturmbauer, 2011). Once established in the rocky and sandy habitats of Lake Malawi, the second stage of adaptive radiation led to further diversification of the rock and sand dwelling ***haplochromines*** and ***tilapiines*** through the subdivision of their preferred niche as ecological selection led to specialized trophic structures and reproductive traits based on niche preference (Genner, 2005; Sturmbauer, 2011). This led to a high degree of habitat specialization among ***haplochromine*** and ***tilapiine*** species, resulting in niche partitioning behaviors associated with preferred food sources and sites for spawning and rearing of juveniles based on morphological adaptions for feeding and specialized broodcare traits (Genner, 2005; Kocher, 2000; Sturmbauer, 2011). As a result, these partitioning behaviors significantly increased the rate of coexistence among Malawian cichlids, enabling them to further diversify in the absence of competition as the third stage of adaptive radiation led to the parallel evolution of reproductive characteristics through the mechanism of sexual selection (Genner, 2005). In this process reproductive isolation associated with sexual preferences in courtship behaviors, and body shape, size, color pattern, and color intensity led to the formation of more distinct populations as individuals began choosing mates based on a very specific criteria of traits that were associated with high fitness (Genner, 2005; Sturmbauer, 2011). Moreover, because the stages of explosive adaptive radiation associated with ecological and sexual selection led to the formation of distinct populations this significantly reduced interactions among different species resulting in genetic isolation that enabled further divergence of the rock and sand dwelling cichlids (Genner, 2005; Sturmbauer, 2011).

Because of these many divergence events, Lake Malawi now holds 800 species of morphologically distinct, but reproductively similar rock and sand dwelling ***haplochromines*** and ***tilapiines*** that compose 85% of the lakes fish diversity (Duponchelle, 2008; Genner, 2005; Kocher, 2000; Smith, 2000). Among the ***haplochromines*** are the mouthbrooding astatotilapia group (one nonendemic species), the haplochromis group (multiple endemic species) and mbuna group (multiple endemic species), which make up 99% of the lake's cichlid diversity (Smith, 2000). Among the ***tilapiines*** are two groups composed of substrate breeders and endemic mouthbrooders, which contribute to only 1% of the lake's cichlid diversity (Smith, 2000).

Methods – Characterizing Malawian Cichlid Reproductive Biology and Behavior

In Part II of methods, an extensive experiment was conducted in the Cruz Lab using the mouthbrooding, rock dwelling, Malawian cichlid ***L. caeruleus*** (mbuna group) as model organism in order to establish trends in its reproductive biology and behavior that could later be applied to the whole Malawian flock based on similarities in reproductive traits identified through review of literature. When carrying out this experiment I used thirty ***L. caeruleus*** within the size range of 15-80 mm, which were divided up between two 378-liter tanks. Within each tank there were two adult males, three adult females, and multiple juveniles of both sexes in order to replicate community density and structure associated with Malawian cichlid populations. With the fish separated in their respective tanks I then collected quantitative and qualitative data in order to identify trends in ***L. caeruleus*** reproductive biology and behavior associated with sexual selection, courtship, spawning, and juvenile development. This was done so that reproductive trends identified could then be compared and analyzed in relation to the results from Part I of the project in order to give insight into the degree to which deteriorating ecosystem conditions in Lake Malawi could impact the fitness of Malawian cichlids by negatively influencing their reproductive biology and behavior.

Sexual Selection

Quantitatively, I was interested in looking at male mate choice of females by observing the relationship between female length and how often they were brooding eggs over the study period. When collecting data, I would check each tank every day for females that were holding, and if there were, I would remove them, measure them in standard length, and then record that length. These data were then sorted into five categories that ranged from 18-30 mm, 30-42 mm, 42-54 mm, 54-66 mm, and 66-78 mm. Data from each category was then analyzed in Excel through the creation of a histogram and scatter plot, and by running a regression.

Courtship

Qualitatively, I was interested in looking at male displays and aggression as well as female receptiveness to different males during the courtship process. In order to collect these data I recorded tank activity twelve hours a day over the course of the semester (Fall 2014), saving all relevant footage. This footage was then analyzed through a careful viewing in order to establish trends in the above aspects of ***L. caeruleus*** reproduction.

Spawning

Qualitatively, I was interested in looking at the spawning ritual overall, but especially as it pertains to spawning ground preferences, the role that male and female egg-spots play in the dispersal and fertilization of eggs, and the time spent spawning. In order to collect these data I recorded tank activity twelve hours a day over the course of the semester, saving all relevant footage. This footage was then analyzed through a careful viewing in order to establish trends in the above aspects of ***L. caeruleus*** reproduction.

Quantitatively, I was interested in observing fecundity by looking at the relationship between female length and brood size over the study period. In collecting data, I would remove females that were holding from their tank, measure them in standard length, strip them of their eggs, count those eggs, and then record the number of eggs. These data were then analyzed in Excel through a regression and the creation of a scatter plot.

Juvenile Development and Rearing

Quantitatively, I was interested in looking at the average growth rate of individuals over the course of development, changes in the average growth rate of individuals over the course of development, and differences in the growth rate of individuals between each consecutive three day period over the course of development. To collect data I would first strip females of their eggs the day of fertilization and then add those eggs to an egg tumbler. Development of the eggs was then documented day by day (including the day of fertilization) through pictures taken on a digital microscope. After all the pictures were taken, the juveniles portrayed in them were then measured in standard length by using a micrometer to establish a scale of length in millimeters for each magnification level. Once measurements were made, I then identified trends in the growth rate of individuals over the course of development. These data were then analyzed in Excel through the creation of bar graphs, scatter plots and the running of a regression and paired t-test.

Qualitatively, I was interested in characterizing the stages of juvenile development as well as female behavior during the brooding period. In order to collect these data I recorded tank activity twelve hours a day over the course of the semester, in addition to taking pictures after each day of development (above methods). This footage and the pictures taken were then analyzed through a careful viewing in order to establish trends in the above aspects of ***L. caeruleus*** reproduction.

Results – Similarities in Malawian Cichlid Reproductive Biology and Behavior

Sexual Selection

After analyzing quantitative data associated with trends in sexual selection as they relate to mate choice, I found that males preferred larger females on average. For example, I found that males selected zero females within the size range of 18-30 mm, one female within the size range of 30-42 mm, two females within the size range of 42-54 mm, ten females within the size range of 54-66 mm, and twenty-seven females within the size range of 66-78 mm (see figure 1). Moreover, based on these frequencies it is evident that there is a positive relationship between female size and the number of times selected for and that this relationship is significant (see figure 2).

Figure 1: Differences in the number of times females were brooding over the study period based on their length

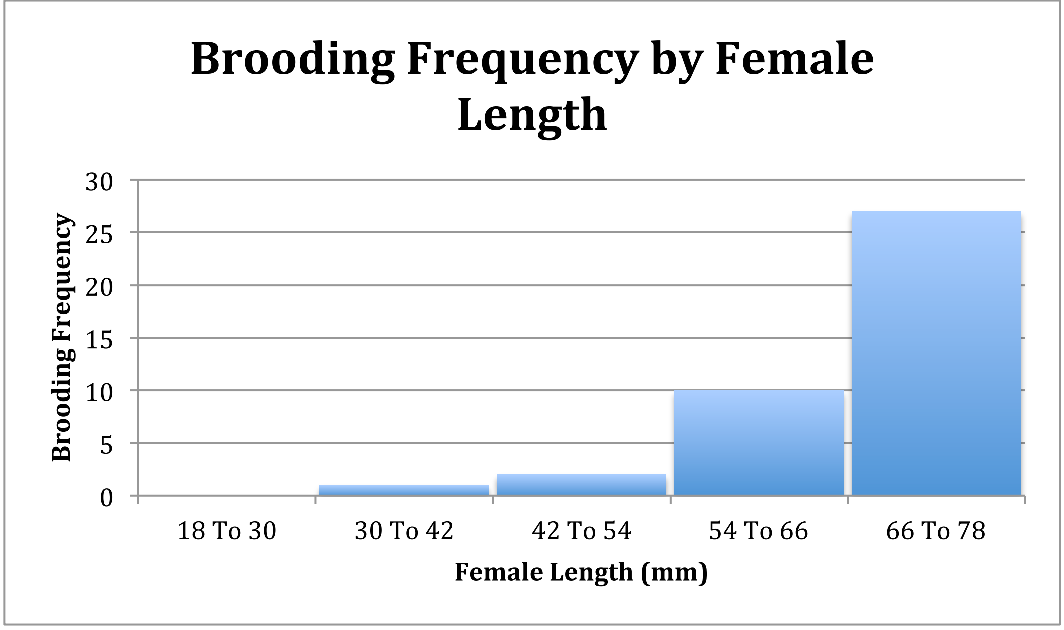
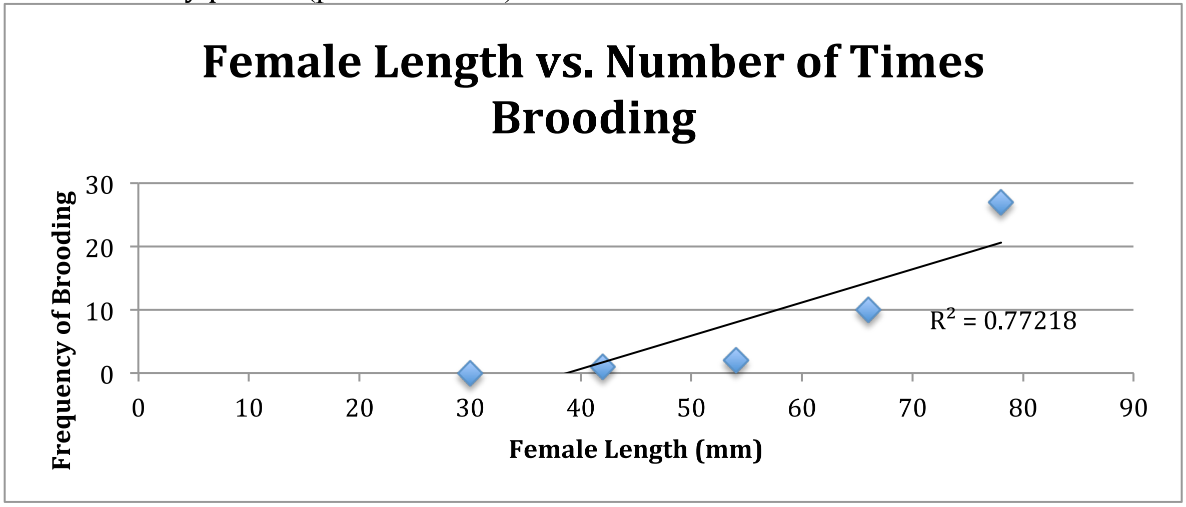


Figure 2: Rleationship bewtween female length and the number of times brooding over the study period (p-value=<0.05)



While these findings are consistent with trends identified in a literature review of Malawian cichlid reproduction, the literature review also highlighted the role of territory quality and the shape and size of sandcastle bowers in sexual selection. For example, in female's larger body size is associated with higher fitness because it corresponds to a greater reproductive capacity, while in male's larger body size is associated with higher fitness because it corresponds to their occupation of a more robust and higher quality territory (Duponchelle, 2008; Sturmbauer, 2011). Moreover, the size of sandcastle bowers is an indicator of male fitness as more fit males often construct much larger and more impressive bowers compared to those individuals with lower fitness because an incredible amount of energy is needed (Sturmbauer, 2011).

Courtship

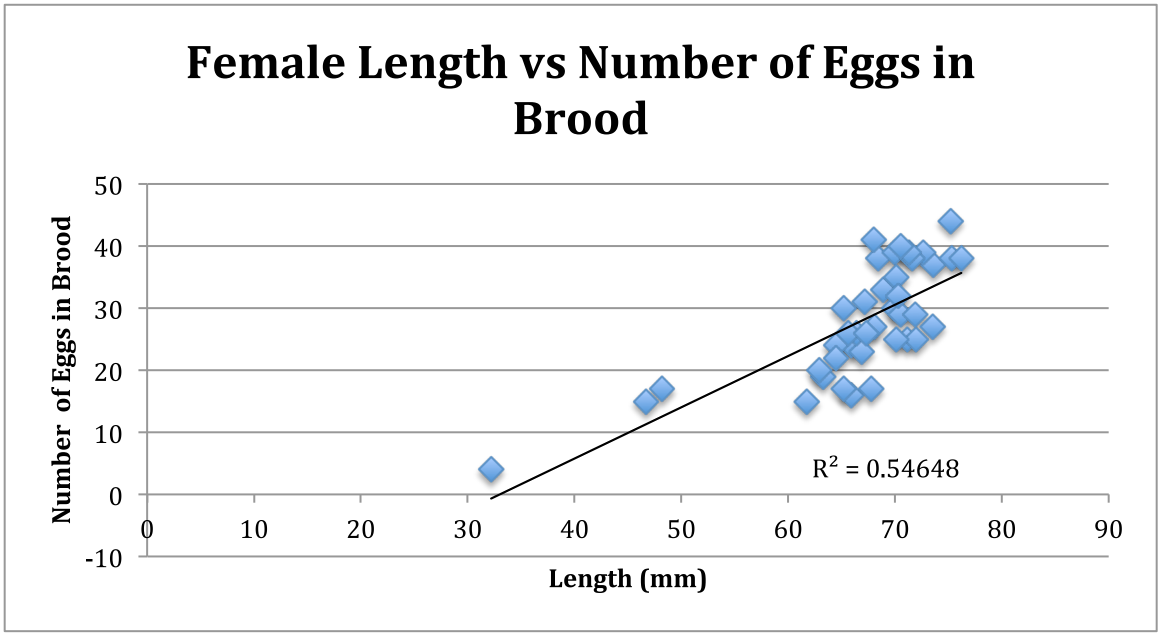
After analyzing qualitative data associated with trends in courtship, I found that it is an energy intensive process mostly associated with males where they aggressively establish a spawning territory and then swim up to a female in order to display by way of a horizontal quivering motions followed by lead swimming and quick circle backs to ensure that the female is still interested. Moreover, male aggression was also evident in the courtship process itself as they would go after other males that got to close to the female of interest or the female herself if she was not receptive to the male's displays. Moreover, I noticed that female's seemed to be the most receptive to courtship attempts from the dominant male.

These findings are consistent with trends described in a literature review of Malawian cichlid reproduction, as it was evident that all Malawian cichlids partake in an elaborate, energy intensive courtship ritual in order to attract a mate for spawning. For example, in sand dwelling species of Malawian cichlids courtship begins with the construction of elaborate sandcastle bowers by male cichlids in order to try and attract a female mate, while in rock dwelling species of Malawian cichlids courtship begins with a dominant male using aggressive behavior to secure a high quality spawning ground in order to try and attract a female (Genner, 2005; Kocher, 2000; Sturmbauer). The courtship ritual then commences when a female enters the males territory causing him to swim in front her while he begins to perform a lateral quivering display in an attempt to grab her attention (Genner, 2005; York, 2015). Once the male has gotten the females attention he then attempts to lead the female into his preferred spawning site (sand-castle bower or rocky shelter) through a series of exaggerated wiggling movements know as lead swimming (Genner, 2005; York, 2015). If the female is interested in these displays she will follow the male into his preferred spawning site, leading them to partake in the spawning ritual (Genner, 2005).

Spawning

After analyzing quantitative data associated with fecundity in spawning, I found that larger females carry more eggs on average. For example, my data show that there is a positive relationship between female size and the number of eggs carried and that this relationship is significant (see figure 3). Moreover, after analyzing qualitative data associated with the spawning process I found that spawning was an energy intensive process that lasted around 120 minutes, that male and female egg spots play a large role in egg dispersal/fertilization, and that flowerpots turned on their sides were the preferred location for spawning due to the shelter that they provide.

Figure 3: Relationship between female length and the number of eggs brooded (p=<0.05.)



These findings are consistent with trends identified in a literature review of Malawian cichlid reproduction, as it was evident that all Malawian cichlids are mouthbrooders that are subject to an elaborate, energy intensive spawning ritual in sheltered areas where egg spots play a large role in fertilization success (with the exception of one substrate brooding species) (Duponchelle, 2008; Genner, 2005; Kocher, 2000; Sturmbauer, 2011). For example, the spawning ritual begins after a successful courtship attempt when a female enters male's preferred spawning ground (sandcastle bower or rocky shelter) leading them to take part in intermittent cycles of circling each other with each cycle ending with the pair in the shape of a T. When the female is perpendicular to the male in this cycle she flashes her egg spots causing the male to rub up against her, which stimulates the releases of one or two of her eggs. The female then quickly circles around and picks up the eggs in her mouth leading her to occupy the male's old position, while the male takes her old position. With the female now perpendicular to the male, he then flashes his egg spots causing the female to nip at his backside (because she thinks the males egg spots are eggs she missed picking up), which stimulates the fertilization of the eggs in the female's mouth. (Genner, 2005; Theis, 2012). The size of the female is highly important in this process as larger females produce more eggs, and thus have larger broods (Duponchelle,2008).

Juvenile Development and Rearing

After analyzing quantitative data associated with trends in juvenile development, I found that the average growth rate of individuals was 0.322 mm/three days but that the unaveraged growth rate of individuals differed between each consecutive three-day period over the course of development (figure 4, and 5). Moreover, I found that there is a negative relationship between average growth rate and the number of days passed and that this relationship is significant (figure 6). Additionally, I found that there is a significant difference in the average growth rate of juveniles between days 0-15 and days 15-30 and that the average growth rate between days 0-15 is significantly larger (see figure 7).

Figure 4: Average growth rate of juveniles over the course of development

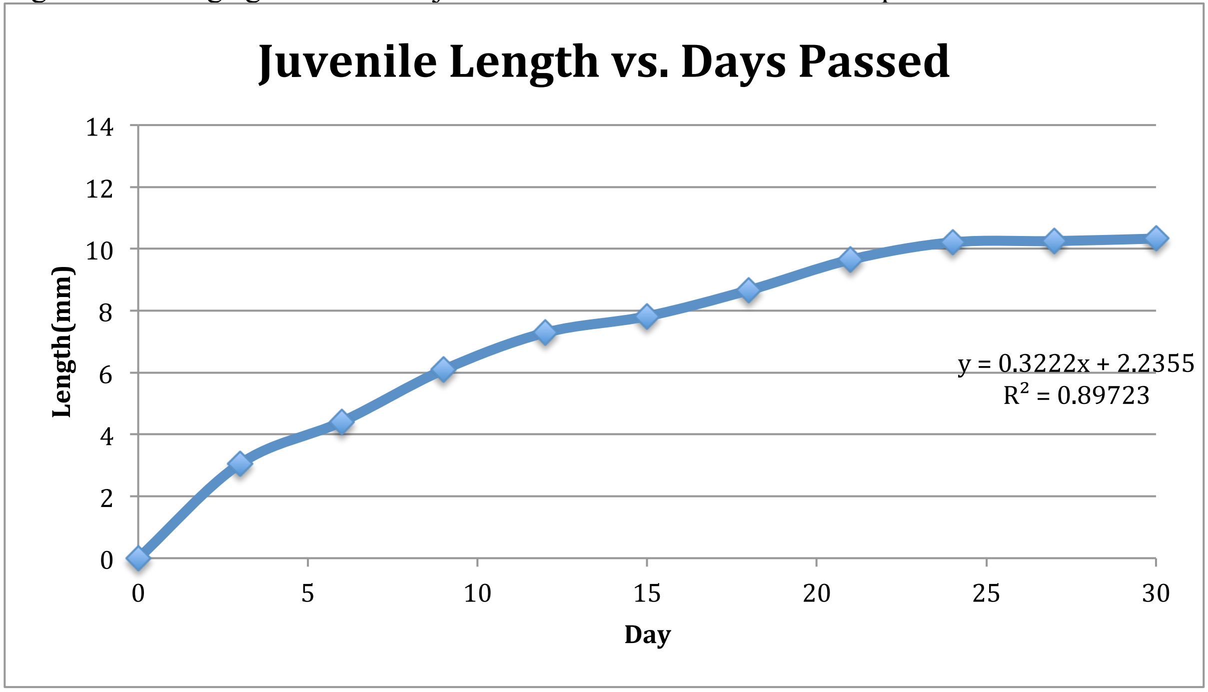


Figure 5: Differences in the growth rate of juveniles over the course of development

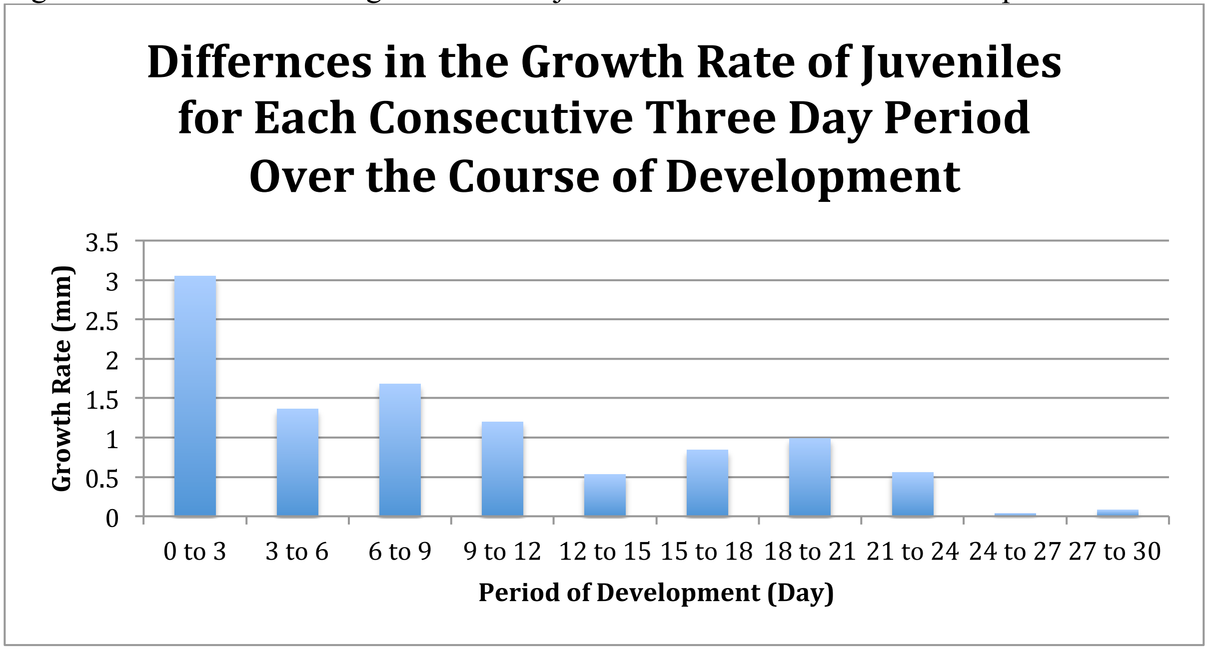


Figure 6: Relationship between cumulative growth rate and time passed (p-value=<0.05)

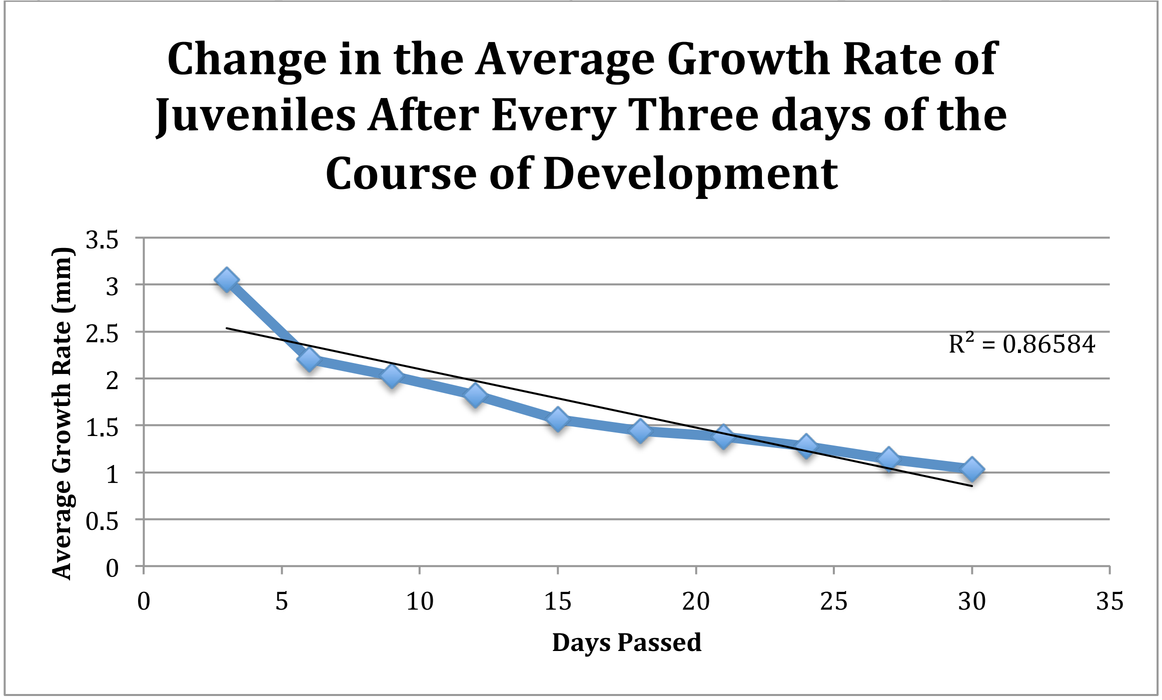
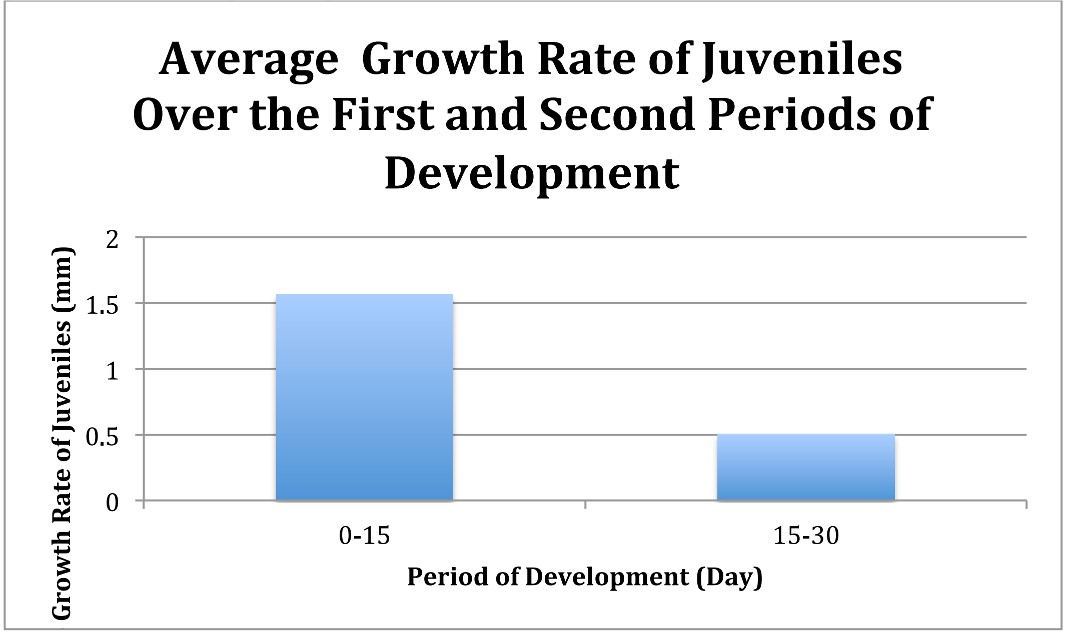


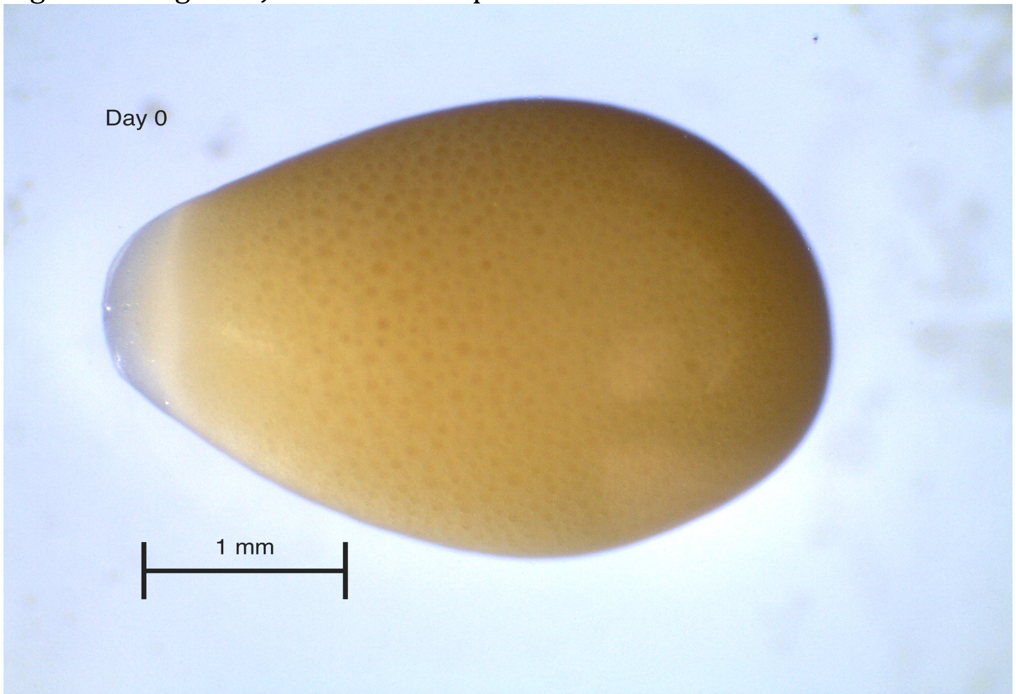
Figure 7: Difference in the average growth rate of juveniles over the first and second periods of development (p-value =<0.05)



After analyzing qualitative data associated with juvenile development I found that day zero is the earliest stage of embryonic development, which is when the zygote forms

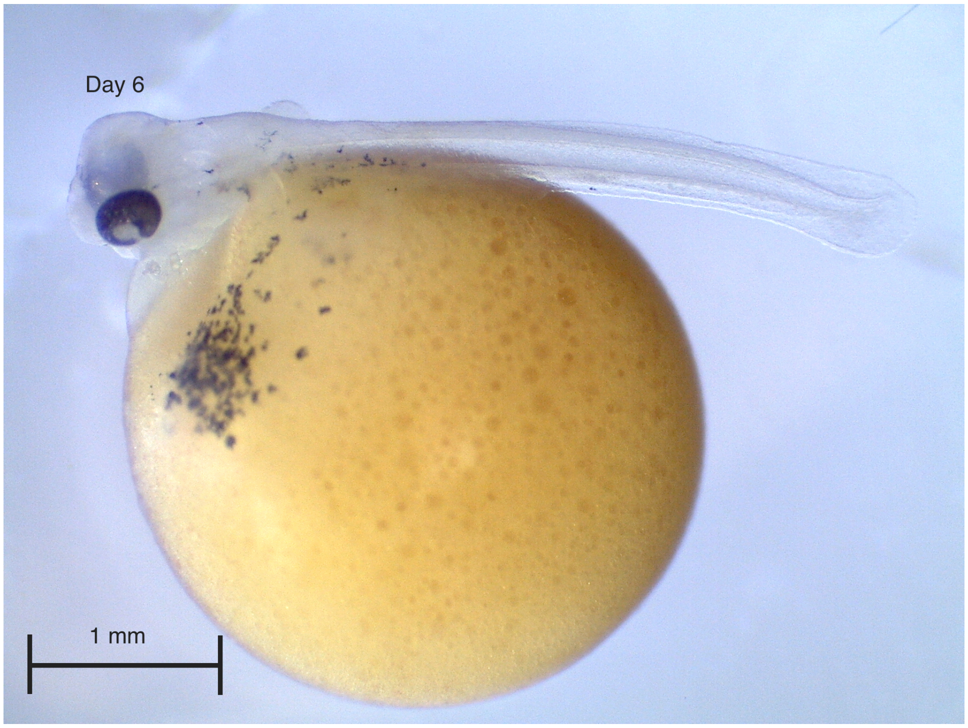
(Fujimura, 2007). I found that day three is the middle stage of embryonic development where the pharyngeal arches (gills) form, while development of the heart, brain, notochord, tail, fins, and optic cup/lens becomes visible (Fujimura, 2007). I found that day six is the last stage of embryonic development where the mouth, melanophores, and iridophores become visible as morphogenesis of the pharyngeal skeleton occurs (plus further development of above aspects) (Fujimura, 2007). I found that days 9-15 were associated with the early stage of larval development where the mouth begins to move and the gills become externally visible (plus further development of above aspects) (Fujimura, 2007). I found that days 18-27 were associated with the late stage of larval development where inflation of the swimbladder occurs (plus further development of above aspects) (Fujimura, 2007). Finally, I found that day thirty is the first stage of “juvenile development” where the yolk sack has been absorbed, but there are no noticeable changes in the external appearance of the individual (see figure 8 for all) (Fujimura, 2007).

Figure 8: Stages of Juvenile Development



Start of embryonic development- zygote period (Fujimura, 2007)

Mid embryonic development- pharyngula period-formation of pharyngeal arches (gills), development of heart, brain, notochord, tail, fins, and optic cup and lens (Fujimura, 2007)



Late embryonic development- hatching period-morphogenesis of pharyngeal skeleton, mouth visible, melanophores begin to appear on body, iridophores appear in eyes, plus further development of above aspects (Fujimura, 2007)

Early Larval development- movement of mouth, gills become external, plus further development of above characteristics (Fujimura, 2007)

Early larval development- further development of above characteristics (Fujimura, 2007)

Early larval development- further development of above characteristics (Fujimura, 2007)

Late larval development- inflation of swim bladder, plus further development of above characteristics (Fujimura, 2007)

Late larval development- further development of above characteristics (Fujimura, 2007)

Late larval development- further development of above characteristics (Fujimura, 2007)

Late larval development- inflation of swim bladder (Fujimura, 2007)

Early juvenile development- absorption of yolk sack, no significant change in external appearance (Fujimura, 2007)

After analyzing qualitative data associated with trends in juvenile rearing I found that brooding is an energy intensive and time-consuming process for females where they would often change behaviors drastically. For example, I noticed that brooding females would often hide in sheltered secluded areas of the tank such as under water filters, rocks, or flowerpots that were not easily visible from the outside of the tank and protected by the rest of the community. I also noticed that the brooding females were not receptive to feeding as they would remain in their hideout as food was added to the tank when normally all the individuals, male, female, adult, or juveniles, rush to the surface to get their share of the food.

These qualitative findings associated with juvenile rearing were consistent with trends identified in a literature review of Malawian cichlid reproduction as it was evident that parental care of juveniles and eggs is an energy intensive process that is most closely associated with female care (Duponchelle, 2008; Genner, 2005; Kocher, 2000; Stiassny, 1999; Sturmbauer, 2011). For example, after spawning has occurred the male plays no further role in parental care while the female hides away for a 20-30 day period, often not eating, while her brood develops into free-swimming juveniles (Genner, 2005.) Once the brood has developed, female Malawian cichlid species often stand guard over their offspring allowing them to seek refuge in her mouth if threated by predators or aggressive males (Genner, 2005). Moreover, it is evident that community structure also plays a large roll in the success of rearing juveniles as the high density populations and territoriality associated with the Malawian cichlid flock help to deter predators or other intruders that would threaten the brooding female or her offspring (Genner, 2005; Kocher, 2000; Sturmbauer, 2011).

While I found no literature on Malawian cichlid juvenile development, my qualitative findings are consistent with trends identified in cichlid species in general as the early stages of development contribute to the growth and development of the more vital biological and physiological anatomical features, while the later stages of development contribute to the structural and aesthetic anatomical features. However, my quantitative findings in juvenile development are unique to my research, but they can be explained by my qualitative findings as the increased growth rate is occurring in the early stages of development when the growth and development of the vital biological and physiological anatomical features is occurring.

Part III – Implications of Ecosystem Degradation in Lake Malawi On Malawian Cichlid Reproduction

Part III of the project consists of an extensive analysis comparing the results from Part's I and II in order to describe how deteriorating ecosystem conditions in Lake Malawi could impact the fitness of Malawian cichlids by negatively influencing their reproductive success.

Discussion

Potential Impact of Ecosystem Degradation on Malawian Cichlids

From the information gathered in Part I of the project it is evident that deteriorating ecosystem conditions in Lake Malawi can lead to a number of biological, physiological, and behavioral impacts on fish that negatively impact their fitness. Moreover, from information gathered in Part II of the project it is evident that historical ecosystem conditions played a major role in shaping the similar biological, and behavioral characteristics of Malawian cichlid reproduction, most notably of which are aspects of sexual section, courtship, spawning, and juvenile development and rearing (Chafota, 2005; Duponchelle, 2008; Kocher, 2000; Sturmbauer, 2011). With that being said, based on these trends it is clear that deteriorating ecosystem conditions in Lake Malawi could negatively impact Malawian cichlid reproductive traits by disrupting biological, physiological, and behavioral aspects of their evolutionary history because they were shaped by historical ecosystem conditions. As a result, this could negatively impact their fitness due to the central role that these reproductive traits played in their evolutionary success (Duponchelle, 2008; Kocher, 2000; Sturmbauer, 2011).

Impacts of Ecosystem Degradation on Sexual Selection

Increases in the occurrence of hypoxia, sedimentation, turbidity, and warm, nutrient poor waters in Lake Malawi could have a significant impact on Malawian cichlid sexual selection by disrupting male and female recognition of fitness level in potential mates. For example, because the size and shape of sand-castle bowers and the body size and color intensity of individuals are major indicators of mate fitness in sand and rock dwelling species of Malawian cichlids, a reduction in their size (body size, bower size) due to lack of energy availability could significantly decrease the degree to which fitness is observably different in individuals. As a result, this could lead to mating with lower fitness individuals if they seem fitter than those mates subjected to deteriorating ecosystem conditions, even if they might not be genetically. If this misidentification of fitness occurred frequently enough, it could significantly reduce the fitness of the Malawian flock by leading to decreased rates of survival and reproduction in the next generation as less viable offspring would likely be produced.

Additionally, increases in turbidity in Lake Malawi could have a significant impact on sexual selection by leading to the deterioration of selective forces driving mate choice. For example, because mate choice in Malawian cichlid populations is highly contingent on selective forces associated with visual cues in body size, color intensity/pattern, and the intricacy of sand-bower construction, a reduction in water clarity could significantly reduce the effectiveness of these visual cues. As a result, this could lead to a reduction in species diversity in Lake Malawi as these selective forces served as reproductive barriers that ensured assertive mating among specific Malawian cichlid populations. A reduction in species diversity could significantly impact the fitness of the Malawian cichlid flock by decreasing the degree of community structure and genetic variability within the population. For example, because Malawian cichlid populations are highly specialized in terms of niche partitioning behaviors, a reduction in the degree of community structure would likely reduce the level of species coexistence in a particular niche by reducing the abundance of specialized species while increasing the prevalence of generalist species. As a result, this would likely reduce the carrying capacity of a particular niche, as species would be competing for the same resources. Moreover, a loss in genetic diversity could impact the fitness of Malawian cichlids by reducing phenotypic variation as a reduction in the number of functional traits decreases the populations ability to respond to selective pressures, while increasing the chances that a harmful allele becomes fixated. As a result, these changes could significantly reduce survival and reproductive rates in the Malawian cichlid population both in the parental generation and offspring.

Impacts of Ecosystem Degradation on Courtship

Increases in the occurrence of hypoxia, sedimentation, turbidity, and warm, nutrient poor waters in Lake Malawi could have a negative impact on Malawian cichlid courtship by reducing the number of attempted displays. For example, because the courtship process is highly energy intensive, a reduction in the amount of available energy for cichlids could significantly decreases the number of attempts at courting an individual in order to conserve the little energy they have access to. Moreover, because visual cues are highly important in the courtship process, a reduction in water clarity due to turbidity could inhibit the effectiveness of these visual cues, which could lead to a reduction in the number of attempts at courting an individual as mates would likely not be as receptive to displays. As the courtship process is highly important in the initiation of Malawian cichlid spawning, a reduction in the number of courtship attempts could significantly impact the fitness of Malawian cichlids by reducing the number of spawning events, and thus the offspring born.

Impacts of Ecosystem Degradation on Spawning

Increases in the occurrence of hypoxia, sedimentation, turbidity, and warm, nutrient poor waters in Lake Malawi could have a significant impact on Malawian cichlid spawning by reducing the number of eggs brooded, and the number of spawning attempts. For example, because fecundity in Malawian cichlids is dependent upon female size, a reduction in body size due to losses in available energy could significantly reduce the number of eggs brooded by females. Moreover, because the spawning process is highly energy intensive, a reduction in available energy for cichlids could significantly reduce the number of spawning attempts in order to conserve energy. Additionally, sedimentation can lead to the destruction of preferred spawning grounds, which could reduce the number of spawning attempts due to lack of available resources. Furthermore, turbidity and hypoxia could also reduce the fertilization successes between mates. Turbidity could reduce the fertilization success because female and male egg spots are important visual stimuli in the fertilization process, so a reduction in water clarity could disrupt the effectiveness of visual cues associated with egg spots. Moreover, hypoxia acts as an endocrine disrupter, which could significantly impact fertilization success by leading to the deterioration of physiological and biological mechanisms responsible for sexual hormone production in male and females. With that being said, as female Malawian cichlids already reproduce few times and produce few eggs when they do, a reduction in fertilization success, the number of spawning attempts, and fecundity could negatively influence the population's reproductive capacity. As a result, this could impact the fitness of Malawian cichlids by leading to unsustainable populations through a reduction in the number of offspring born.

Impacts of Ecosystem Degradation on Juvenile development

Increases in the occurrence of hypoxia, sedimentation, turbidity, and warm, nutrient poor waters in Lake Malawi could have a significant impact on Malawian cichlid juvenile rearing successes by limiting energy expenditure in parental care and degrading community structure. For example, because the rearing of juveniles requires an incredible amount of energy due to the high degree of parental care utilized, a reduction in the amount of available energy could limit energy expenditure in parental care, which could reduce the survival rates of juveniles. Moreover, because community structure is highly important in the rearing of juveniles, its deterioration could significantly decrease the success of juvenile rearing as females and their offspring would be more susceptible to predation and influences from other intruders. Additionally, increases in hypoxia could significantly reduce the viability of offspring while also increasing egg mortality by interfering with the stages of juvenile development. Because the yolk contributes to the growth and development of different biological and physiological components of the juvenile in each stage of development, a reduction of oxygen at any stage could significantly impact future stages of development. For example, because the growth and development of the vital biological and physiological anatomical features of a juvenile occur in the early stages of development, a reduction of growth and development in the early stages (due to hypoxia) could significantly increase egg mortality by preventing the establishment of features such as the brain, heart, veins, nerves, and vital organs. Moreover, if hypoxia were to occur in the later stages of development when growth and development of structural and aesthetic anatomical features of a juvenile occur, this could inhibit the formation of features like the fins and skeletal system, which would likely result in deformed or smaller individuals. As a result, increases in egg mortality, and a reduction in the rearing success and viability of juveniles could significantly impact the fitness of the Malawian flock by decreasing juvenile survivorship in the brooding period while also increasing the number of low fitness individuals produced.

Conclusion

As it is evident that ecosystem degradation in Lake Malawi could negatively impact the fitness of Malawian cichlids by reducing their reproductive capacity it is important we try and develop a framework for their management and conservation so as not to lose these unique fish and the amazing evolutionary history that comes with their existence. In order to do so we must focus on the root causes of ecosystem degradation in Lake Malawi such as climate change and increased agricultural activity so that we can try and find ways to limit their harmful impacts. This can be done three ways. Firstly, we must work with the local governments to try and console issues of poverty and inequality so as to reduce the degree to which natural resources are exploited by locals due to their abundance and ease of access as economic commodities. To do so their must be increased intuitional management in the development of these countries public polices and economies so as to enable the growth and diversification of different micro and macro economic sectors. As a result, this would help to reduce poverty and inequality while also diminishing the role of natural resource development in the economy, which would decrease the instance of the exploitation of agricultural lands. Moreover, as that will prove to be a daunting task, we must also work to educate local governments on the benefits of sustainable agricultural and land conversion practices so as to try and reduce the harmful impacts of agricultural activity. To do so we must highlight the economic, societal, and environmental benefits of sustainable agriculture in comparison to the many costs of unsustainable agricultural practices. Based on these benefits we must then suggest public outreach to local citizens in order to educate them on sustainable agricultural practices while also suggesting the implementation of agricultural policies that ensure that these practices are adhered by the local people. Finally, we must work with the global community to continue to try and reduce greenhouse gas emissions so as to try and reduce both the indirect and direct impact of increased temperature on the degradation of the lake's ecosystem associated with increased agricultural activity and increased water temperature in the lake, respectively.

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