Dissertation for the degree of doctor of philosophy

Ecological modeling of Lake Victoria

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Abstract

Lake Victoria is of immense ecological and socio-economic significance for the riparian communities. However, the lake is faced with human induced pressures such as overfishing, introduction of alien species, increased eutrophication and climate change impacts. Its large spatial extent and complex ecology have also limited the understanding of the system dynamics, major processes, drivers and responses. To address this challenge, Atlantis, the first end-to-end whole ecosystem model for the lake was developed. First, a Regional Oceanographic Model System (ROMS) for the lake was developed to provide hydrodynamic forcing data for the ecosystem model. The ROMS model was based on real bathymetry, river runoff and atmospheric forcing data. Results from this model revealed diverse spatial and temporal water circulation patterns and temperature trends in Lake Victoria. The ROMS output provided water currents and temperature forcing data for the Atlantis model.

The Lake Victoria Atlantis model was spatially resolved into 12 unique dynamic areas based mainly on their biophysical attributes. A total of 38 functional groups constituted the biological model while fishing was implemented by four fleets with different targeting options. The model was validated by fitting simulated output to available observational data sets. Simulations showed elevated nutrients and primary production in inshore areas and gulfs that can be linked to point sources of pollution and limited flushing.

The model also revealed complex inter-specific relationships among the biological groups. For example, the introduced Nile perch (*Lates niloticus*) exhibited a strong negative correlation with haplochromine cichlids (their prey) as well as most of other fish groups. This brings to fore the significance of predator-prey relationships and the impact of introduced species; information that is critical for effective fisheries and ecosystem management.

The model was then used to simulate the impact of different fishing scenarios on the ecosystem. Scenarios tested included varied fishing pressure for Nile perch (the main predator at the top of the food chain), key prey species (haplochromines) and other species. The effects of these scenarios were tested using six common ecosystem-level indicators. Predictions showed that no particular scenario excels in all the six indicators. However, halting harvesting of haplochromines results in the best overall ecosystem performance. This scenario is projected to result in the highest yield of commercially important species and possibly cause minimal disruption to fishing activities. Findings of this study reinforce the need for an ecosystem approach to fisheries management in Lake Victoria.

Ágrip

Viktoríuvatn er mikilvægt strandbyggjum sínum, vistfræðilega, félagslega og efnahagslega. Talsvert álag er á vistkerfið sakir ofveiði, innleiðingar framandi tegunda, mengunar og loftlagsbreytinga. Breytingar af þeim sökum, auk flókinnar vistfræði, hafa takmarkað möguleika á skilning á kerfinu sjálfu, helstu ferlum, áhrifavöldum og viðbrögð kerfisins við breytingum. Til að mæta þessari áskorun hefur heildstætt vistkerfislíkan (Atlantis) verið þróað fyrir vatnið. Sérstakt straumalíkan var þróað fyrir vatnið til að setja upp straumkerfi gögn fyrir vistkerfislíkanið. Straumalíkanið var byggt á upplýsingum um dýpi, rennsli áa ásamt upplýsingum um loftþrýsting og úrkomu. Straumkerfislíkanið sýndi hringrás vatns og þróun hitastigs í vatninu.

Atlantis líkanið fyrir Viktoríuvatn inniheldur 12 svæði, byggt á líf- og eðlisfræðilegum eiginleikum. Notast var við 38 hópa lífvera og fjóra veiðiflota með ólíkt valmynstur. Líkanið var mátað við ýmis fyrirliggjandi gögn. Útreikningar sýna aukið magn næringarefna og frumframleiðslu, bæði á grunnslóð og dýpi, sem tengist þekktum uppsprettum mengunar og takmörkuðu gegnumstreymi. Í líkaninu komu einnig fram flókin tiltekin tengsl milli líffræðilegra hópa. Þannig sýndi Nílarkarfi sterka neikvæða fylgni við bráð (haplochromines) og raunar flesta hópa fiska. Þetta sýnir vel mikilvægi samspils afræningja og bráða auk áhrifa innfluttra tegunda og nauðsyn þess að líta á allt vistkerfið þegar stjórna skal veiðum.

Líkanið var síðan notað til að prófa áhrif mismunandi veiðistjórnunar á lífríkið. Sviðsmyndir voru m.a. breytilegt veiðiálag á Nílarkarfa (ránfiskur og efstur í fæðukeðjunni), lykilbráð (haplochromines) og aðrar tegundir. Áhrif sviðsmyndanna voru metin með sex algengum mælikvörðum. Niðurstöðurnar bentu ekki til þess að nein stjórnunaraðferðanna bæri af í öllum sex mælikvörðunum. Prófanir sýna hins vegar að sú aðferð að stöðva veiðar á helstu bráð gefi bestan almennan árangur. Hér fæst mestur afli úr efnahagslega mikilvægum stofnum og lágmarks röskun á veiðum. Niðurstöður rannsóknarinnar sýna vel þörfina fyrir vistkerfisnálgun við stjórnun fiskveiða í Viktoríuvatni.

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List of Publications

This thesis is based on three papers and references to them will be given by their Roman numbers. These papers are the following:

Paper I: Nyamweya, C., Desjardins, C., Sigurðsson, S., Tómasson, T., Taabu-Munyaho, A., Sitoki, L. & Stefánsson, G. (2016). Simulation of Lake Victoria circulation patterns using the Regional Ocean Modeling System (ROMS). *PLoS ONE*, 3, e0151272.

Paper II: Nyamweya, C., Sturludóttir, E., Tómasson, T., Fulton, E. A.,Taabu-Munyaho, A., Njiru, M. & Stefánsson, G. (2016). Exploring Lake Victoria Ecosystem Functioning using Atlantis Modeling Framework. *Environmental Modelling and Software*, 86, 158-167.

Paper III: Nyamweya, C., Sturludóttir, E., Tómasson, T.,Fulton, E. A.,Taabu-Munyaho, A., Njiru, M. & Stefánsson, G. (Accepted). Prediction of Lake Victoria's response to varied fishing regimes using the Atlantis ecosystem model. *Fisheries Research.*

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Part I

Thesis

1

Introduction

1.1 Background

From ancient times, aquatic ecosystems and humans have been closely associated (Hoffmann, 2010). This is evidenced by human settlements around the world being concentrated adjacent to large water bodies (Halpern et al., 2008). Whether it is for food, transportation, water for domestic and industrial uses, recreation or regulation of climate, aquatic ecosystems have been and will always be an integral part of human survival and wellbeing (Whelan et al., 2008). For a long time, aquatic resources were considered inexhaustible among fishing communities and even by some prominent scientists (Anyanova, 2008; Hauge et al., 2007; Huxley, 1883; IPCC, 2014). However, this view did not last long. Increasing human population heightened the demand for fisheries resources. This, together with improved fishing efficiency that came with the onset of industrial/technological revolutions, resulted in extraction rates that exceeded replenishment. As a consequence, a number of fish stocks collapsed, while a large proportion of them were left overexploited. The reduced fish stocks, apparent ecosystem degradation and the realization that aquatic resources are not infinite, necessitated a dialogue on the need for prudent management. Ultimately this gave rise to the United Nations Convention on the Law of the Sea in 1982 that called for responsible utilization of aquatic resources to benefit both the current and future generations (FAO, 2008). Thereafter, a number of international instruments like the Code of Conduct for Responsible Fisheries were established that advocate for an ecosystem approach to fisheries (EAF) management. This was based on the recognition that fisheries have a direct impact on the ecosystem, which is also impacted by human activities and consequently they need to be managed in an ecosystem context (Mackinson, 2010).

However, ecosystems are ever-changing entities made up of several interactive biotic and abiotic components that determine their production and productivity levels. Equally complex are the ecological processes that govern ecosystem structure and function, the inherent variability in biophysical processes and the interactions between ecological, economic and social processes. Understanding this complexity is a prerequisite for effective management. Nevertheless, this is difficult when the said complexity is compounded with uncontrolled exploitation, the introduction of invasive species, resource use conflicts and climate change. This is especially so in large ecosystems where adequate data collection is expensive and logistically difficult (Petrovskii and Malchow, 2004). Lake Victoria in East Africa (the focus of this study) is a classic example of such ecosystems (Figure 1.1). In the recent past, there have been developments in modeling that have rendered a holistic understanding of ecosystem dynamics and processes possible.

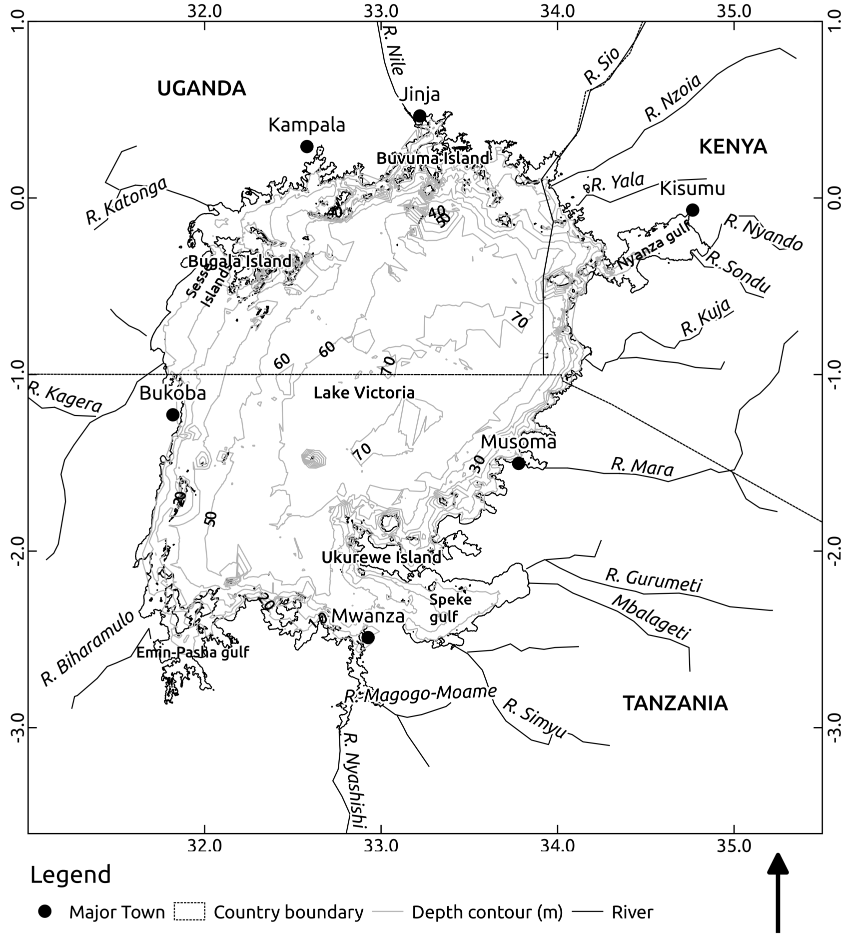


Figure 1.1: Lake Victoria and riparian countries.

1.2 Ecosystem models

Ecological modeling is the use of systems analysis and simulation/estimation to mimic complex ecological processes. It involves the development of conceptual and quantitative models to answer specific research questions (Acosta et al., 2010). An ecosystem model can be described as an abstract (mathematical) representation of an ecological system, which is studied to gain an understanding of the real system (Hall and Day, 1977). In complex ecological systems, models can be used to describe intricate interactions among detailed processes for purposes of prediction, forecasting and system understanding (Acosta et al., 2010; Bennett et al., 2013; Kelly et al., 2013). Intelligibly, ecosystem models make it possible to simulate large-scale experiments that would be economically/logistically expensive and risky to perform on a real ecosystem. Moreover, they allow alternative scenarios to be developed, simulated, analyzed, compared and ranked according to their effect. As a result, these models can be used as tools to support management decision-making (Bennett et al., 2013; Kelly et al., 2013; Punt et al., 2016). Ecosystem models have applications in a wide variety of disciplines, such as natural resource management, ecotoxicology and environmental health, agriculture, wildlife conservation and marine systems.

Currently there exist a number of marine ecosystem/multi-species models that have application to fisheries management. Plagányi (2007) gives a comprehensive review of existing models for an ecosystem approach to fisheries. Broadly they can be categorized as:

1. Extensions of single-species assessment models that expand on current single-species assessment models taking only a few additional interactions into account (e.g. Hollowed

et al. (2000); Livingston and Methot (1998); Tjelmeland and Lindstrøm (2005)).

2. Minimally Realistic Models which only represent a subset of the ecosystem (Begley, 2005; Punt and Butterworth, 1995).

3. Whole ecosystem models that attempt to take into account all trophic levels in the ecosystem. Ecopath with Ecosim (EwE) (Christensen and Pauly, 1992; Christensen and Walters, 2004; Pauly et al., 2000) is one of the widely used and freely available whole ecosystem models.

4. Dynamic system models that attempt to represent both bottom-up (physical) and top-down (biological) forces interacting in an ecosystem. At the apex of this category is Atlantis (Fulton and Smith, 2004).

Atlantis is one of the very few modeling platforms that can handle all processes from sunlight to fish markets (Fulton et al., 2011). It is spatially explicit and incorporates submodules that represent oceanography, biogeochemistry, trophic interactions and fisheries (Morzaria-Luna et al., 2013). Arguably, it is the best whole ecosystem model in the context of fisheries management worldwide (Plagányi, 2007). Atlantis was developed in 2001 by Dr. Elizabeth Fulton of the Commonwealth Scientific and Industrial Research Organization (CSIRO). Currently, there are over 30 applications of the model in Australia, the US, South Africa and Europe. Most of the applications are on temperate marine ecosystems (Fulton et al., 2011). There are also Atlantis models for polar regions, tropical coral reefs, estuaries, lakes (e.g.,this study), as well as models that span temperate-tropical domains (Weijerman et al., 2016). Atlantis is intended as a strategic management tool to evaluate hypotheses about ecosystem response, to understand cumulative impacts of human activities, and to rank broad categories of management options (Fulton et al., 2014).

1.3 Lake Victoria ecosystem

Located in East Africa, Lake Victoria is iconic in both its size and function. With a surface area of approximately 68,0000 km^2, it is the largest freshwater lake in the tropics and second in the world. The lake's fisheries annual catch of close to 1 million tons (LVFO, 2016) accounts for about 1% and 8% of the world's total and inland capture landings respectively (FAO, 2016; World Bank, 2012). The fisheries provide employment, income and export earnings to lakeside communities and regional governments (Geheb et al., 2007). The catchment (approximately 193,000 km^2) extends across five East African Community (EAC) states of Kenya, Uganda, Tanzania, Rwanda and Burundi. Over 70 million people live in the basin most of whom directly depend on its ecosystems services such as water for domestic and industrial use, transport, hydro-power generation and food. Owing to its size the lake plays an important role in modulating regional climate (Crul, 1995; Stager and Johnson, 2008).

1.3.1 Ecological changes in Lake Victoria

Soon after it's discovery by John Speke in 1858, British colonialists began to exploit the Lake Victoria watershed. Surrounding natural vegetation, forests and swamps were reclaimed to give way to cash crop plantations which have continued to grow in size and number over the years (Balirwa et al., 2003). Agricultural chemicals and fertilizer applied on the plantations are washed into rivers during the rainy season and end up in the lake providing nutrients for algal blooms. The plantations attracted migrant workers who settled in the area (Hecky, 1993). As the population grew and with the subsequent introduction of flax gill nets by the British in 1905 to replace the local villagers' papyrus nets and fish traps, fishing pressure on the lake began to intensify (Graham, 1929). Overfishing soon became a problem: catches began to drop and fishermen turned to nets with ever smaller mesh sizes and thus decimated both the breeding adults and young of many native species. By the 1950s, popular species, such as Graham's tilapia (*Oreochromis esculentus*), had diminished severely (Witte et al., 1992a). At that time the lake was however still teeming with small sized bony haplochromine cichlids (Kitchell et al., 1997). To remedy the situation, British officials thought introducing new fish in the lake (Graham, 1929; Lowe-McConnell, 1987; Welcomme, 1967). Nile perch, *Lates niloticus*, was presumed to be a solution to boost stocks as well convert the small sized cichlids into bigger attractive flesh (Witte et al., 1999).

Before 1954, the lake's ecology was characterised by high biodiversity. It was inhabited by over 500 species of fish (Graham, 1929) dominated by cichlids, which accounted for more than 80% of the fish biomass (Kudhongania and Cordone, 1974). During that time, local communities were fishing largely for subsistence. Surplus catch was consumed by internal markets (Pringle, 2005). In the 1950- 1960s, new tilapine species *Oreochromis leucostictus, Tilapia zillii, T. rendalli, O. niloticus O. mossambicus* and the predacious Nile perch were introduced (Balirwa et al., 2003; Coulter et al., 1986).

The introduction of the Nile perch had a major impact on the haplochromine stocks, which it favoured as prey, affecting both their abundance and diversity. The latter's contribution to biomass was reduced to less than 1% (Witte et al., 1992a). Up to 65%

of haplochromine species are thought to have been lost, an event which may well represent the largest species extinction amongst vertebrates in the 20th century (Goldschmidt et al., 1993; Kaufman, 1992; Kitchell et al., 1997). Reduction of haplochromine species eased the competition pressure on the diminutive endemic silver cyprinid *Rastrineobola argentea* (dagaa), which in turn flourished developing into huge shoals (Goudswaard et al., 2011; Pringle, 2005; Witte et al., 1992a). Currently only 3 species (Nile perch, Nile tilapia and dagaa) are exploited on a commercial scale. The introduced species, Nile perch and Nile tilapia, revolutionized the fishery from mere subsistence to highly commercial making it one of the world's most productive inland fishery (Kayanda et al., 2009).

Pollution has been increasing in the Lake Victoria region with population growth. Many riparian towns release raw sewage and municipal waste into the lake. This, together with fertilizer and chemicals from farms in the catchment, contribute to increased pollution and eutrophication. Invasive species such as the water hyacinth *(Eichhornia crassipes)* and Nile perch are thought to have been responsible for the ecological damage of Lake Victoria (Opande et al., 2004; Taabu-Munyaho et al., 2016; Witte et al., 1992a). Water hyacinth reproduces rapidly and covers large areas of the lake forming dense mats of plants that block sunlight needed for survival of life below the surface.

1.3.2 Management of Lake Victoria

The first formal management of Lake Victoria dates back to 1908 following the enactment of the Fish Protection Ordinance (Geheb et al., 2007). This was followed by the first fish stock assessment on the lake in the late 1920s by Graham (Graham, 1929) that recommended the establishment of fisheries management authorities in the three riparian countries as well as regulating the minimum limit of mesh sizes. Subsequently, the Lake Victoria Fisheries Commission was established in 1932 under the East African High Commission. However, detailed record keeping and data collection were not formalized at that time due to the pressures of the Second World War. It was only after the war that more useful records began to be collected. This was after the creation of the Lake Victoria Fisheries Service (LVFS) in 1947 and establishment of the East African Fisheries Research Organization (EAFRO) in 1949. In 1967, the Lake Victoria Research Project (LVRP) was launched with the objective of establishing a lake wide sampling system for the collection of resource, catch and effort data. The next major event as regards to fisheries data system development in the Lake Victoria basin was the establishment of the Lake Victoria Fisheries Commission (LVFC) in 1973. LVFC objectives included the standardization of fishery statistics. Following the collapse of the East African Community in June 1977, EAFFRO was abolished. As a result, Uganda, Kenya and Tanzania formed their own national fisheries research organizations. Management and development of the fisheries of Lake Victoria was taken over by the Committee for the Inland Fisheries of Africa (CIFA) operating under the auspices of FAO (Muyodi, 2009). CIFA was replaced by the Lake Victoria Fisheries Organization (LVFO) in 2001.

1.3.3 Ecosystem modeling in Lake Victoria

Major management programs and research projects that have been undertaken in Lake Victoria are discussed in Muyodi (2009). Also, there have been a number of attempts to model ecosystem structure and functioning of Lake Victoria (Musinguzi et al., ress). For instance, Ecopath model has been used in Lake

Victoria to investigate the role of new species introductions and subsequent changes in ecosystem functioning (Moreau, 1995), the evolution of biological groups (Villanueva and Moreau, 2002) and the effect of possible management strategies (Moreau et al., 2000). The shortcoming of the mentioned models is that they were parameterized for a small section of the lake. A more comprehensive application of EwE was done by Matsuishi et al. (2006) who simulated the ecosystem assuming different exploitation pressures on Nile perch. The authors, however, condensed all the haplochromine trophic groups into one. More recently, Ecopath has been used to investigate the reorganization of the food web and changes of structural properties of the lake (Downing et al., 2012; Natugonza et al., 2016). However, the parameterisation process in Downing et al. (2012) has been questioned (Kolding, 2013). Other modeling approaches to simulate ecosystem change include Kitchell et al. (1997) who used a bioenergetics model of Nile perch predation rates to evaluate the consequences of various exploitation pattern and their ecological implications. In a recent study, van Zwieten et al. (2016) used a size-based predictive model to investigate the mechanism behind the take over of Nile perch and concurrent collapse of the haplochromine stocks in Lake Victoria.

Despite the efforts, little headway has been made in identifying the major drivers of ecosystem changes that have been witnessed in the last six decades. Work done on the lake has usually focused on a few aspects of the system or been limited in time and space. For instance, Ecopath models constructed for Lake Victoria provide only a “snapshot” of the ecosystem, inherit the steady state assumptions, and for the time period of the models, which is normally one year, biomass and energy flows in an ecosystem are calibrated so that no more is used than can be accounted for. In the absence of an end to end whole ecosystem model, it is quite difficult to predict the implications of any management measures instituted on the lake. This is further complicated given that the threats (including overfishing, habitat change, eutrophication, climate variability and change) are intensifying and becoming increasingly interconnected.

2

Aim

This study sought to describe the Lake Victoria ecosystem functioning, trophic cascade mechanisms as well as complex non-linear system responses to different fishing regimes. These tasks are addressed in three papers described in Part II of the thesis whose individual objectives were the following.

Paper I: The aim of the study was to simulate circulation patterns in Lake Victoria with the objective of generating hydrodynamic flows and temperature regimes on a spatial temporal scale.

Paper II: The aim of the study was to develop a virtual Lake Victoria ecosystem detailing linkages in the biological realms and their interaction with the physical-chemical environment. The developed model was to enhance the understanding of the system dynamics, major processes/drivers and responses to human induced pressures such as fishing, introduction of alien species and eutrophication.

Paper III. The aim of the study was to predict the Lake Victoria ecosystem response and varied fishing scenarios with the objective of identifying the best option.

3

Materials and methods

This study used the Atlantis ecosystem model to simulate the Lake Victoria ecosystem as well as test its response to different fishing scenarios. The Atlantis ecosystem model was chosen because of its ability to simulate all parts of an ecosystem (Fulton et al., 2011; Fulton and Smith, 2004). First, a Regional Oceanographic Model System (ROMS) was used to simulate water circulation and temperature spatial and temporal trends. A detailed description of the model configuration and statistical analyses is given in Paper I of this thesis. Output from the ROMS was then used as hydrodynamic input for the Atlantis model. The methods describing the biophysical regime, trophic interactions and impact of fishing fleets are detailed in Paper II. In Paper III, methods and statistical analyses that were used to test the impacts of different fishing scenarios on the ecosystem are described. This chapter presents a summary description of the ROMS and Atlantis models, their configuration, key equations, statistical analyses and assumptions.

3.1 Regional Oceanographic Model System (ROMS)

ROMS is a free-surface, hydrostatic, terrain-following, primitive equations ocean model widely used by the scientific community for a diverse range of applications (Haidvogel et al., 2008). The algorithms that comprise ROMS computational nonlinear kernel are described in detail in Shchepetkin and McWilliams (2005), and the tangent linear and adjoint kernels and platforms are described by Moore et al. (2004). ROMS includes accurate and efficient physical and numerical algorithms and several coupled models. It also includes several vertical mixing schemes (Warner et al., 2005), multiple levels of nesting and composed grids.

3.1.1 Lake Victoria ROMS design

Lake Victoria ROMS model extends from 31.5° - 34.88° E and 3.05° S to 0.55° N. It has a horizontal grid resolution of 1.86 km and 20 terrain-following vertical levels. The ROMS model is based on real bathymetry, forced with wind stress, surface heat fluxes, solar radiation and river inflow/outflow data. The model was initialized with a uniform temperature of 24°C, zero salinity and no momentum on 1st January 2000.

The primitive equations of motion in Cartesian coordinates are given hereafter (adapted from Nurujjaman et al. (2013)). The momentum balance in the x- and y-directions are:

$$\frac{\partial u}{\partial t} + \mathbf{v} \cdot \nabla u - fv = -\frac{\partial \phi}{\partial x} - \frac{\partial}{\partial z}\left(\overline{u'w'} - v\frac{\partial u}{\partial z}\right) + \mathcal{F}u + \mathcal{D}u \quad (3.1)$$

$$\frac{\partial u}{\partial t} + \mathbf{v} \cdot \nabla v + fu = -\frac{\partial \phi}{\partial y} - \frac{\partial}{\partial z}\left(\overline{v'w'} - v\frac{\partial v}{\partial z}\right) + \mathcal{F}v + \mathcal{D}v \quad (3.2)$$

Evolution of a S, T and nutrients (C(x, y, z, t)) is governed by the advective-diffusive equation:

$$\frac{\partial C}{\partial t} + \mathbf{v} \cdot \nabla C = -\frac{\partial}{\partial z}\left(\overline{C'w'} - v_\theta \frac{\partial C}{\partial z}\right) + \mathcal{F}_C + \mathcal{D}_C \tag{3.3}$$

The equation of state is given by:

$$\rho = \rho(T, S, P) \tag{3.4}$$

Boussinesq approximation: density variations are neglected in the momentum equations except in their contribution to the buoyancy force in the vertical momentum equation. Hydrostatic approximation: vertical pressure gradient balances the buoyancy force:

$$\frac{\partial \phi}{\partial z} = -\frac{\rho g}{\rho_o} \tag{3.5}$$

Equation 6 expresses the continuity equation for an incompressible fluid:

$$\frac{\partial u}{\partial x} + \frac{\partial u}{\partial y} + \frac{\partial w}{\partial z} = 0 \tag{3.6}$$

where

- $\mathcal{D}_u, \mathcal{D}_v, \mathcal{D}_C$ are diffusive terms
- $\mathcal{F}_u, \mathcal{F}_v, \mathcal{F}_C$ are forcing terms
- $f(x, y)$ is the Coriolis parameter
- g is acceleration of gravity
- $h(x, y)$ is bottom depth
- v, v_θ is molecular viscosity and diffusivity
- P is total pressure ($P \approx -\rho_o g z$)

- $\phi(x, y, z, t)$ is dynamic pressure $\phi = (P/\rho_o)$
- $\rho_o + \rho(x, y, z, t)$ is total *in situ* density
- $S(x, y, z, t)$ is salinity
- t is time
- $T(x, y, z, t)$ is potential temperature
- u, v, w are the (x, y, z) components of vector velocity $\mathbf{v}$.
- x, y is horizontal coordinates
- z is vertical coordinate
- $\zeta(x, y, t)$ is the elevation.

Model validation was done by comparing simulated $(\hat{y})$ and observed (y) temperature profiles using the Root Mean Squared Error (RMSE).

3.1.2 ROMS model data sources

In the present study, the three dimensional (3D) lake geometry is based on bathymetry data collected from a lake wide hydro-acoustic survey (LVFO, 2010). Water circulation in the model is driven by the bottom terrain as well as meteorological conditions at the lake's surface boundary. Meteorological fields used to force the model include: cloud cover, net longwave radiation flux, surface air pressure, surface air relative humidity, rain fall, surface air temperature, surface v- and u-wind components 10 meters above the water surface. These data were obtained from the European Centre for Medium- Range Weather Forecasts (ECMWF) ERA Interim, daily data set (Dee et al., 2011). The were extracted at 3 hour time steps with 0.125° horizontal resolution from 1st January 2000 to 31st December 2014. River discharge estimates were obtained from on Awange and Ong'ang'a (2006). Observational spatio-temporal temperature profiles used to validate the ROMS output were obtained from bi-annual hydro-acoustic surveys conducted in 2008 (LVFO, 2008).

3.2 The Atlantis ecosystem model

Atlantis is an end-to-end model, that when fully developed, considers all aspects (parts) of an ecosystem i.e. biophysical, economic and social (Fulton et al., 2011; Smith et al., 2015). The model tracks changes in three dimensional space consisting of horizontal polygons and vertical layers. This 3D structure represents the physical environment and is matched to the major geographical and bioregional features of the simulated ecosystem. Using this box-based representation facilitates tracking of flows of limiting nutrients i.e. nitrogen and silica through the main biological groups via a system of differential equations (typically solved in 6, 12 or 24 hour time steps) using a simple forward difference integration algorithm (Fulton et al., 2011). The primary ecological processes modeled are consumption, production, waste production, migration, predation, recruitment, habitat dependency and mortality. The trophic resolution is typically at the functional group level, with primary producers and invertebrates represented as biomass pools and vertebrates represented using an explicit age-structured formulation. Biological model components are replicated in each depth layer of each polygon. Movement between the polygons is by advective transfer or by directed movements depending on the variable in question.

3.2.1 Atlantis equations

Nutrients

The rate of change of nutrients takes place according to formulations depicted in equations 3.7 and 3.8.

$$\frac{d(NH_w)}{dt} = -\sum_{i=PX_w} P_{NH_w,i} - P_{NH_w,MB_w} - P_{NH_w,MA} - P_{NH_w,PFB} + \sum_{i=CX_w,BF} E_i + \sum_{i=FX} E_i + \sum_{i=pelagicbacteria} E_i - S_{NIT,PAB} + R_{NET,w} \tag{3.7}$$

$$\frac{d(NO_w)}{dt} = -\sum_{i=PX_w} P_{NO_w,i} - P_{NO_w,MB_w} - P_{NO_w,MA} + S_{NIT,PAB} \tag{3.8}$$

where $P_{N,XX}$ is the uptake of NH or NO by the autotrophs (either generic, microphytobenthos MB, or macroalgae MA) , E_{CX} is the production of NH by the consumer CX, $S_{NIT,XB}$ is the amount of NH converted to NO during nitrification by the bacteria XB, R_{NET} is the amount of NH produced by denitrification.

Primary producers

The rate of change and growth of primary producers in the model follow equations 3.9 and 3.10 respectively.

$$\frac{d(PX_w)}{dt} = G_{PXw} - M_{lys,PX} - M_{lin} - M_{quad} - \sum_{i=predatorgroups} P_{PXw,i} \tag{3.9}$$

$$G_{PX} = \mu_{PX} \cdot \delta_{irr} \cdot \delta_N \cdot \delta_{space} \cdot PX \tag{3.10}$$

Where G_{PX} is growth of PX, $M_{lys,PX}$ is the loss of PX due to lysis, M_{lin} and M_{quad} are loss due to linear and quadratic mortality,

$P_{PX,I}$ are the losses of PX due to predation by i species, μ_{PX} is the maximum growth rate, δ_{irr} is light limitation, δ_N is nutrient limitation , and δ_{space} is space limitation.

Invertebrates

The rate of change and growth of invertebrates are modeled as depicted in equations 3.11 and 3.12 respectively.

$$\frac{d(CX)}{dt} = G_{CX} - M_{linCX} - M_{quadCX} - \sum_{i=predatorgroups} P_{CX,i} - F_{CX} \tag{3.11}$$

$$G_{CX} = \left(\varepsilon_{CX} \cdot \sum_{i=livingprey} P_{i,CX} + \sum_{j=DL,DR} (P_{j,CX} \cdot \varepsilon_{CX,j})\right) \cdot \delta_{space} \cdot \delta_{O^2} \tag{3.12}$$

where G_{CX} is growth, M_{linCX} and M_{quadCX} are linear and quadratic mortality, $P_{i,j}$ is predation by group j and group i, and F_{CX} is fishing on this group (this is set to zero for the unfished scenario here). ε_{CX} is the growth efficiency of CX when feeding on live prey, $\varepsilon_{CX,j}$ the efficiency when feeding on detritus (DL treated separately to DR), δ_{space} is space limitation, and δ_{O^2} is oxygen limitation.

Vertebrates

The rate of change and growth of vertebrates are modeled following equations 3.13 - 3.15.

$$\frac{d(FX_{i,s})}{dt} = G_{FX_{i,s}} \tag{3.13}$$

$$\frac{d(FX_{i,r})}{dt} = G_{FX_{i,r}} \tag{3.14}$$

$$\frac{d(FX_{i,d})}{dt} = T_{IMM,FX_i} - T_{EMM,FX_i} - M_{lin,i} - M_{quad,i} - \sum_{j=predatorgroups} P_{FX,j} - F_{FXi} \tag{3.15}$$

where i = age group i , s = structural weight, r = reserve weight , and d = density. The T terms represent the movement of fish in to ($T_{IMM,Fxi}$) and out of ($T_{EM,Fxi}$) the cell. In addition there are short-term spawning and recruitment events which affect the various FX pools. The growth for each fish group is calculated by equations of the same form as (6), but per age group of each fish. The result is then apportioned to structural and reserve weight, favoring replenishment of reserves when the animal is underweight.

Predation

Predation in the Lake Victoria Atlantis model was implemented using the Holling type II formulation as depicted in equation 3.16

$$P_{ij} = \frac{B_i \cdot \alpha_{ij} \cdot B_j \cdot C_j}{1+\frac{C_j}{g_j}\left(E_j^l \cdot \sum_{k=1}^{l} B_k \cdot \alpha_{k,j} + E_j^f \cdot \sum_{h=1}^{f} B_h \cdot \alpha h,j + E_j^d \cdot \sum_{x=1}^{d} B_x \cdot \alpha x,j + E_j^r \cdot \sum_{y=1}^{r} B_y \cdot \alpha y,j\right)} \tag{3.16}$$

where P_{ij} = consumption of prey i by predator j, B_i = biomass of prey i and B_j = biomass of predator j; a_{ij} = availability of prey i to predator j; C_j = maximum ingestion rate of predator j; g_j = maximum growth rate of predator j; E_j^l = efficiency of predator j on live food (the l superscript), E_j^l is the efficiency of predator j on seagrass, macroalgae or phytoplankton, E_j^d is the efficiency of predator j on labile detritus, and E_j^r is the efficiency of predator j on refractory detritus.

Spawning and Recruitment

Recruitment of fish followed a Beverton-Holt formulation as shown in equation 3.17

$$R = \alpha * S/(\beta + S) \tag{3.17}$$

where α = maximum number of recruits produced (number of indivuals), and β = spawning stock biomass at which recruitment is 1/2 maximum (measured in mg N).

For birds and crocodiles, reproduction was based on fixed offspring/adult.

3.2.2 Lake Victoria Atlantis model setup

Lake Victoria Atlantis model is spatially resolved into areas based on their unique depth, species composition, physical-chemical parameters, and anthropogenic influences (Taabu-Munyaho et al., 2014). The lake is categorized into inshore (boxes 1:4), coastal (boxes 5:8) and deep (box 9) areas (Figure 3.1). Nyanza, Speke and Emin Pasha Gulfs (i.e. boxes 10, 11 and 12) are categorized as unique strata. The boxes have up to three layers (layer 1 = 0 - 20 m, layer 2 = 20 - 40 m, layer 3 = 40 - 80 m). Boxes 1 - 12 serve as dynamic boxes. Five major river mouths (boundary boxes) serve as regions of fluxes into and out of the model domain (Boxes 0, 13-16). Hydrodynamic input providing current flows for dispersion and temperature trends are derived from the ROMS model described in section 3.1 and Paper I of this thesis. The Lake Victoria Atlantis model runs from 1958 to 2015 and has 34 functional groups constituting the biological component. These include 17 fish, 1 bird, 1 reptile, 9 invertebrate and 6 primary producer groups. Additionally there are 2 groups which represent labile and refractory detritus. Biomass data on the model groups

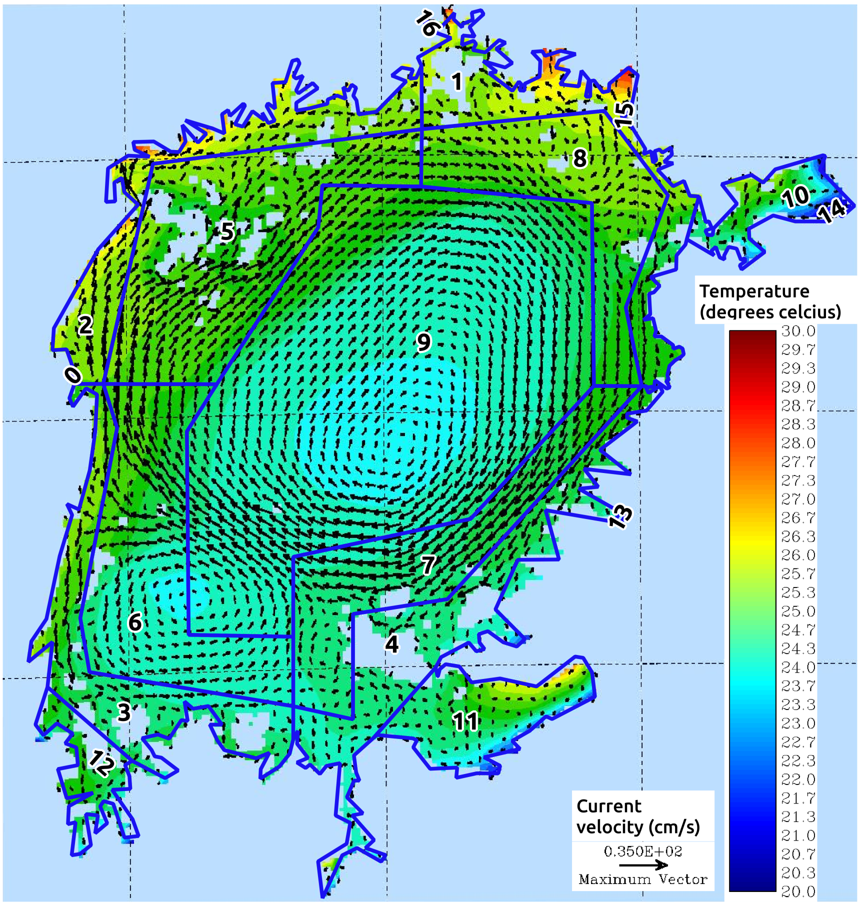


Figure 3.1: Spatial areas used for creating the box geometry for the Lake Victoria Atlantis model. Surface temperature and currents for 22$^{\text{nd}}$ January 2009 are also depicted (as an example of the physical regime).

are scarce and consequently initial numbers were based on inference from existing literature (e.g Kudhongania and Cordone (1974); Pringle (2005)) for fish groups and expert judgment for the rest. Expert judgment involved discussions with scientist specializing on the various aspects of Lake Victoria. For this reason, a 10 year burn in period was allowed for system stabilization based on model parameterization. Fishing was implemented using four fleets (gill-net, long-line, small-seine and inshore) with different targeting options.

3.2.3 Model parameterization and data sources

The Lake Victoria Atlantis was developed in phases. The first phase involved parameterizing the biophysical model with the objective of producing an ecosystem with stable biomasses of all the biological groups in the model. Hydrodynamic flows were derived from the outputs of a ROMS model (see Paper I). Parameterization was iteratively performed simultaneously across multiple functional groups with the ultimate goal of optimizing the ability of the model to reproduce observed system responses. Atlantis has a large number of parameters and as such, its is not practical to perform a comprehensive statistical estimation of their values. Rather, ad hoc tuning is performed where model output is compared with expected values. In case of large deviations, the parameters are adjusted for multiple groups simultaneously before rerunning the model. Atlantis model simulations usually have high run-times making individual tuning of single parameters impractical. Furthermore, Atlantis simulates many low-level processes such as respiration and nutrient assimilation in detail, and hence does not explicitly use many of the commonly reported species parameters (such as von-Bertalanffy growth parameters) (Smith et al., 2015). The main objectives of calibration are: to prevent any species going extinct; to get vertebrate growth rates reasonable (within 20% of the expected von Bertalanffy curve); to get overall biomass levels and diet interactions to reflect available data; and to capture expected spatial distributions. The parameters that generally receive the most attention are growth rates, consumption rates, linear and quadratic mortality, and reproduction parameters.

The initial parameterization of reproduction, growth and diet was conducted based on estimates of the relevant biological components from survey data (LVFO, unpublished data) and Fishbase (Froese and Pauly, 2016). Diet matrix parameters were adjusted to produce predation patterns similar to available diet data. In Atlantis, predation is represented by a diet preference matrix, but the realised predation in the model is mediated through gape limitations, potential clearance rates of the predator, refuge habitat modifiers (where appropriate) and spatio-temporal co-occurrence.

The movement of planktonic groups is entirely advective and is governed by hydrodynamic fluxes between model regions. Post-larval animals move within the model guided by food availability and population density. The average swimming of each functional group is defined in the model and the extent of movement is constrained by the minimum and maximum depth parameters. Vertebrate recruitment is spatially directed to known recruitment areas, and does not necessarily occur at the location of the adults. Fishing was implemented using four fleets with different targeting options and gear characteristics (see Paper III).

3.2.4 Model validation

After preventing functional groups from going extinct as well as achieving stable growth for vertebrates, tuning was then geared to matching simulated biomass and catch to observed catch per unit effort (CPUE) and officially reported landings respectively of the main commercial fish species. Data on catch and effort are presently only available in aggregated format (Kolding et al., 2008), which means that the catches and CPUE used for comparison with Atlantis output were based on these aggregated data. The fit between the model output and observational data were tested using Pearson's correlation, coefficient of variation (CV) (equation 9.1) and modeling efficiency (E). This was done to check whether the model output preserves trends and magnitude of observational data. Given that in Lake Victoria data collection is weak or inadequate and lacks quantitative measures of abundance or age structure (Cowx et al., 2003), priority was given to reproducing trends rather than magnitude.

3.2.5 Fishing strategy evaluation

The validated model was used to test the impact of different fishing scenarios on the ecosystem 20 years into the future. Variation of fishing pressure was mainly on key prey species (haplochromines) and the top predator (Nile perch). The different scenarios simulated included: 1. maintaining current fishing mortalities of all fish groups ($F_{current}$), 2. no fishing of haplochromines ($F0_{haplochromines}$), 3. no fishing of Nile perch ($F0_{Nileperch}$), 4. reducing fishing pressure on Nile perch by 40% ($F0.6_{Nileperch}$), 5. increasing fishing pressure on Nile perch by 40% ($F1.4_{Nileperch}$) and 6. reducing fishing pressure on other fish groups by 40% ($F0.6_{others}$).

The impact of these scenarios was assessed using six ecosystem indicators i.e. Biomass-weighted average weight of fish ($\overline{W}_b$), Biomass-weighted average age of fish ($\overline{A}_b$), Number-weighted average weight of fish ($\overline{W}_n$), Mean trophic level in catch (Tl_{catch}), reorganization index (BI) and proportion of predatory fish (Smith et al., 2015). Details of these indicators and their hypothesized effects are detailed in Paper III of this thesis.

4

Results

This chapter presents the main results on Lake Victoria hydrographic dynamics, ecosystem functioning and fishing scenario evaluation based on Papers I, II and III respectively that form Part II of this thesis.

4.1 Hydrographic patterns

Results from the ROMS simulations show that water temperature exhibits seasonal oscillations over the model domain with periods of clear differences between surface and bottom layers intercepted with spells of near isothermal conditions (Fig. 4.1). Isothermal conditions generally appear to start in either May or June and extend to July or August in different years of the model domain. Surface water temperatures are highest during the months of May and June.

In January, surface temperatures are generally uniform throughout the lake while water movement sustains a northward flow in most of the open lake (Fig. 4.2a). In April, surface temperatures are higher in the northern near-shore areas relative

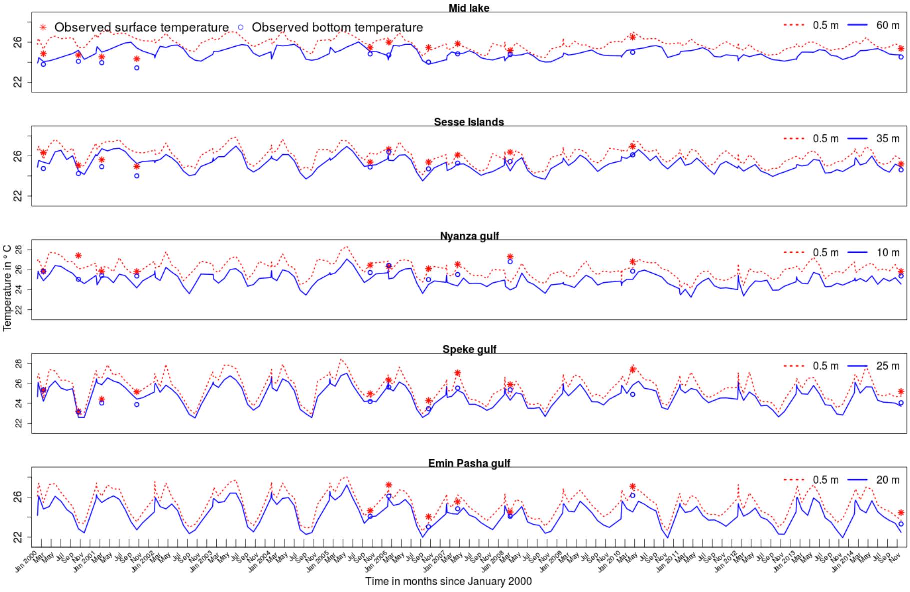


Figure 4.1: Simulated and observed temperature trends at selected sites in Lake Victoria.

to the rest of the lake. During this period, surface currents flow in a gyre formation whose center is drawn towards the warmer regions in the north (Fig. 4.2b). Surface temperatures are generally lowest in July and August. As the surface temperature decreases, the gyre circulation disappears and the currents flow northwards (Fig. 4.2c). The temperatures are highest in the month of October, with the western and northern shorelines being relatively warmer than the rest of the lake. A gyre circulation pattern is also evident during this period, and like in April, its center is drawn towards the warmer region (Fig. 4.2d). Current velocities are higher in the middle of the lake. However relatively slow flow rates are observed within the three major gulfs of Lake Victoria.

Vertical water velocities are higher during the isothermal period as compared to the stratified period (Fig. 4.3). In the stratified period, when vertical velocities are lower, there is minimal exchange

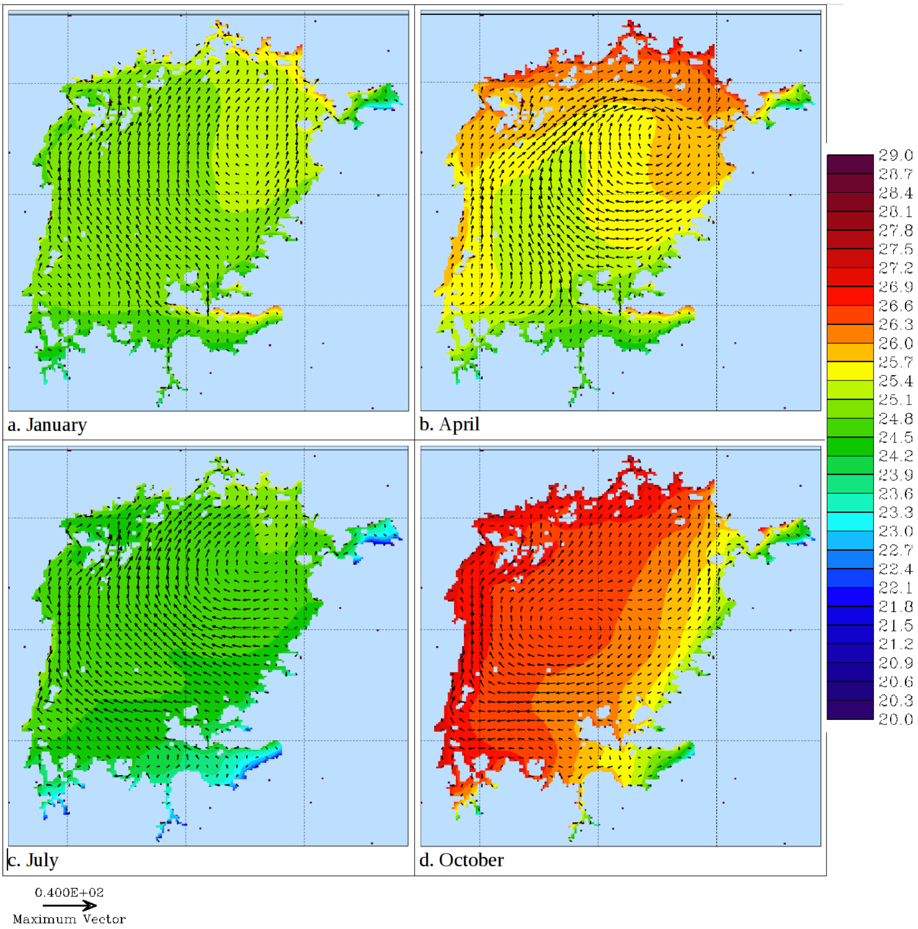
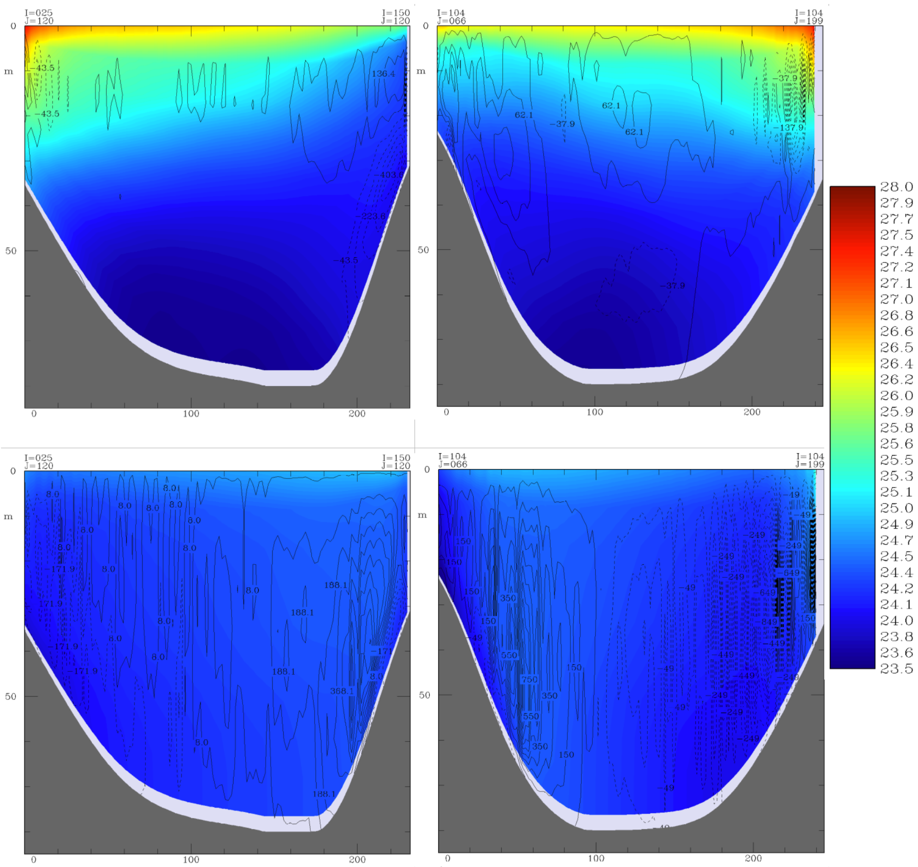


Figure 4.2: Simulated 20 day averaged surface temperature (shaded) and currents (vectors) in Lake Victoria in different seasons of 2008.



a. West-East b. South-North

Figure 4.3: Simulated daily averaged water temperature (shaded, in °C) and vertical velocity (contour, in cm/day and positive upward) during stratified (upper row) and isothermal (lower row) seasons of 2008.

of water across the thermocline. During the stratified period downwelling occurs at the western and eastern ends of the lake. Generally there is net upward water circulation in the south and some downwelling in the north. During the mixed (isothermal) period, there is upward and downward movement of water in the east and west respectively (Fig. 4.3a). Similarly there is upwelling in the south and downwelling in the north (Fig. 4.3b).

4.2 Biophysical system

Simulated nitrate distributions from the Atlantis model generally matches the patterns described by Hecky et al. (2010). Inshore areas including the major gulfs have relatively high Chlorophyll *a* concentrations (i.e primary producers). Inshore areas also have high densities of fish biomass for most species. Most fish species exhibit close correlation between predicted biomass and CPUE (Figure 4.4). Modeled catch fits well to officially reported catch with strong correlation for most of the species. CV shows minimal deviation between simulated and actual catch (Table 4.1).

Simulations show that prey species biomass declines with increase in the predator biomass and vice versa. Competition is observed between the indigenous tilapines and the introduced Nile tilapia. The two groups of species occupy the same niche but the latter is a faster grower and more fecund (Njiru et al., 2006); a reason why it out competes the former driving them to near collapse. Introduced species (Nile perch and Nile tilapia) show negative correlation with the native species (Figure 4.5). This is especially so for Nile perch that exhibits the strongest negative correlation with predatory haplochromines; on the other hand, it shows a strong positive correlation with Nile tilapia and dagaa.

4.3 Fishing scenario testing

The response of the Lake Victoria ecosystem to various fishing scenarios is described based on Atlantis model simulations. Predictions based on mantaining the current fishing mortality show that the biomass of Nile perch and its main prey (haplochromines and *Caridina*) will remain stable around their current levels over the next 20 years (Figure 4.6). However other fish species including

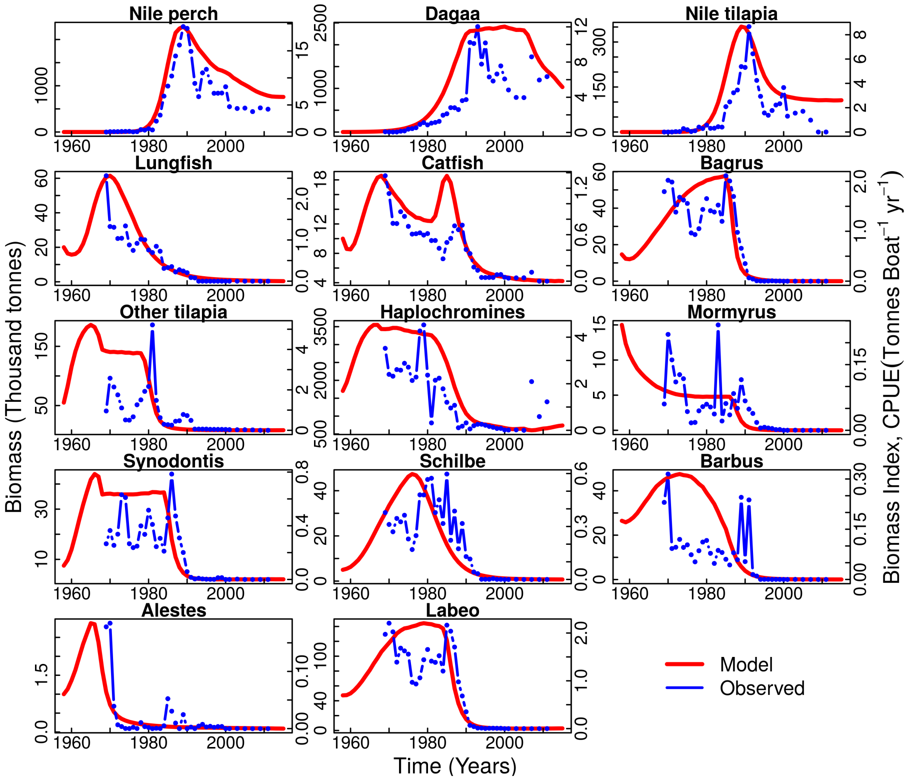


Figure 4.4: Simulated biomass and observed CPUE trends of exploited fishes of Lake Victoria from 1958 - 2015.

Table 4.1: Perfomance indicators (Coefficient of variation (CV), Model efficiency (E) and Pearson's correlation (r_{catch}) and ($r_{biomass}$)) of the Lake Victoria Atlantis model.

Fish Species	**CV**	**E**	r_{catch}	$r_{biomass}$
Nile perch	0.39	0.76	0.95	0.94
Dagaa	0.30	0.92	0.97	0.85
Nile tilapia	0.73	0.62	0.87	0.86
Other tilapia	0.69	0.63	0.81	0.54
Catfish	0.31	0.68	0.86	0.85
Lungfish	0.51	0.09	0.78	0.90
Haplochromines	0.95	0.54	0.81	0.82
Mormyrus	0.82	0.17	0.60	0.60
Synodontis	0.69	0.52	0.76	0.72
Schilbe	0.69	0.37	0.84	0.73
Barbus	0.99	0.11	0.46	0.54
Bagrus	0.52	0.63	0.81	0.88
Alestes	1.13	0.52	0.72	0.85
Labeo	0.46	0.64	0.84	0.86

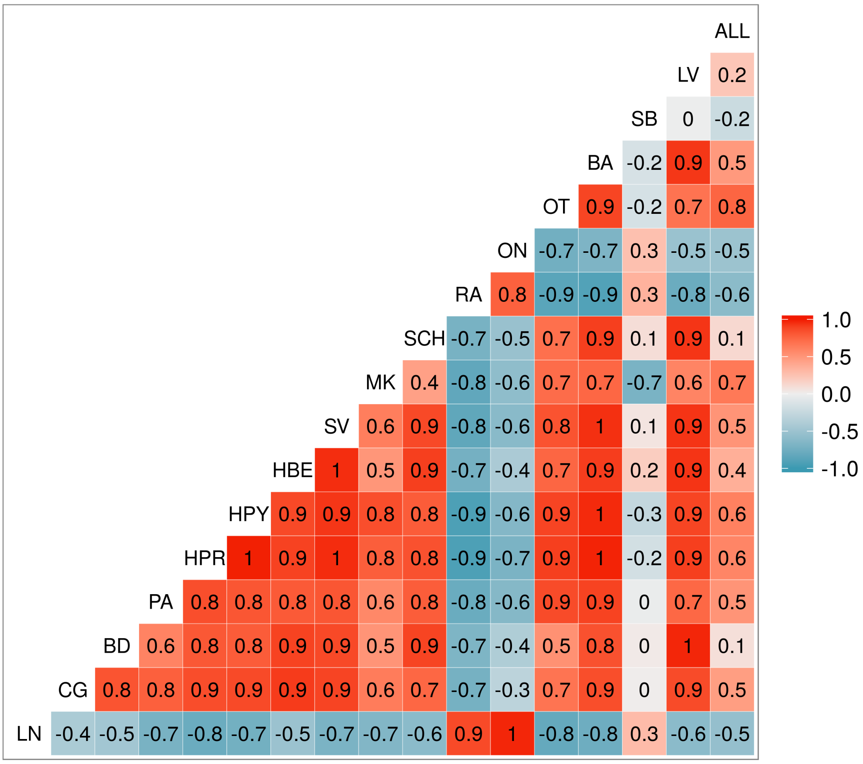


Figure 4.5: Relationship between biomass trends of the fish groups in the Lake Victoria Atlantis model.(for Fish group code - see Table 1 for Functional group name).

dagaa will exhibit a decline, below their current levels. Landings of Nile perch, haplochromines and *Synodontis* remain stable under the current fishing level. For the rest of the species, landings decline in the long run (Figure 4.7).

If fishing is halted on the Nile perch, initially its biomass increases to about double the current biomass in about five years and then declines drastically to below the current level. This scenario has the worst effect on haplochromines whose biomass dives to the lowest level in the prediction period. With the exception of dagaa, other fish species also exhibit their greatest decline in this scenario. Notable decline is also seen in *Caridina*, another key prey for juvenile Nile perch.

Reducing fishing pressure on Nile perch by 40% increases its biomass to about 1.4 times there current level in about a decade. Thereafter, there biomass declines slightly and stabilizes at about their current level. On the other hand haplochromines and *Caridina* show a steady decline with the increasing perch biomass; a trend that is observed in the rest of the fish groups. In the long term, Nile perch and haplochromines have their lowest catch.

Increasing fishing pressure on Nile perch by 40% drastically decreases its biomass whereas haplochromines and other species exhibit their highest increase in the simulation. This shows a negative correlation of these species with Nile perch. However it exhibits a positive correlation with Nile tilapia and dagaa. The increased fishing pressure results in the second highest long term catch of Nile perch as depicted in Figure 4.7. Dagaa records the lowest catch among all the scenarios. Just like in biomass, haplochromines long term catch is highest in this scenario. Increasing fishing pressure on Nile perch by 40% results in increased catch of the other species.

Stopping fishing of haplochromines results in the highest biomass

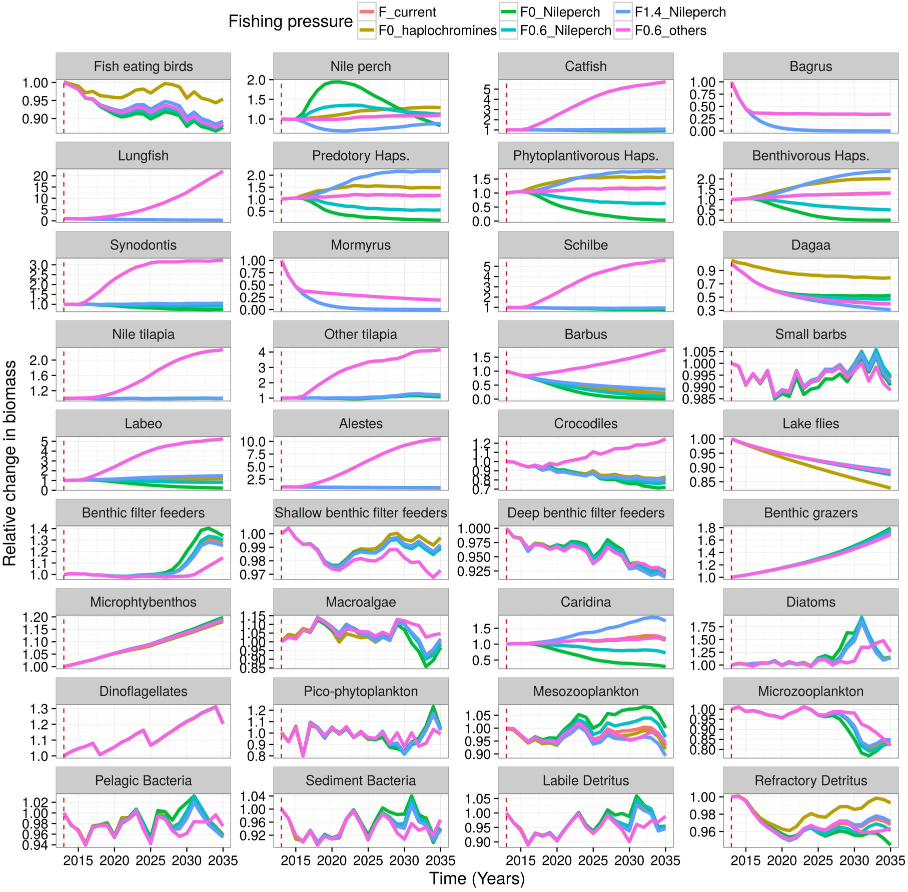


Figure 4.6: Evolution of biomass of biological groups in the Lake Victoria Atlantis model under different fishing scenarios.

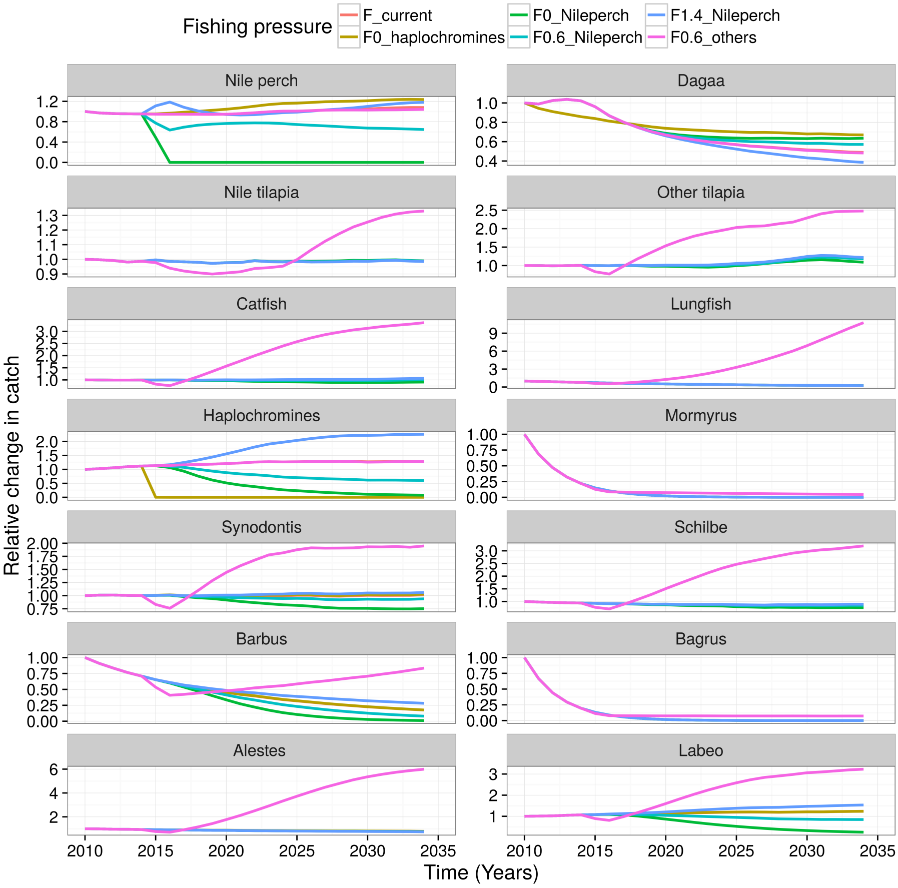


Figure 4.7: Catch predictions of the Lake Victoria Atlantis model under different fishing scenarios.

levels of Nile perch and dagaa (the main commercial species) in the long run. The described trends are also reflected in the predicted catch with Nile perch and dagaa catches being highest in this scenario.

Decreasing fishing pressure on other fish groups increases their biomass and catch. In this scenario, the ‘others’ group exhibit high recovery probably indicating their sensitivity to fishing pressure.

4.3.1 Ecosystem performance indicators

Simulations show that the average weight of individuals is highest when fishing on either Nile perch or other species is reduced by 40%, followed by when haplochromines are not harvested and when fishing on Nile perch is increased by 40% respectively (Table 4.2). The average weight of individuals is lowest when Nile perch fishing is halted. A similar pattern is witnessed on the average weight normalized by abundance. The average age is highest when there is no fishing of Nile perch and lowest when haplochromines are not harvested. The average trophic level of catch is highest when haplochromines are not fished and lowest when Nile perch are not fished. The proportion of predatory fish is highest when there is no/or reduced fishing of Nile perch. The greatest change in ecosystem structure occurs when fishing on Nile perch is halted followed by when there is increased harvesting of the species (i.e. extreme changes in fishing pressure on Nile perch affects the ecosystem organization structure most). The ecosystem organization structure is least disturbed in the scenario where haplochromines are not harvested.

Table 4.2: Indicators of perfomance metrices for ecosystem function and structure under the simulated fishing scenarios

Indicator	$F0_{haplochromines}$	$F0_{Nileperch}$	$F0.6_{Nileperch}$	$F1.4_{Nileperch}$	$F0.6_{others}$	$F_{current}$
$\overline{W}_{b(g)} \times 10^3$	1.55	1.06	1.64	1.53	1.65	1.20
$\overline{A}_{b(yrs)}$	1.31	1.68	1.39	1.56	1.45	1.39
$\overline{W}_{n(g)}$	1.50	1.21	1.45	2.06	1.87	1.50
Tl_{catch}	3.86	3.21	3.65	3.82	3.73	3.80
Proportion of predatory fish	0.30	0.44	0.43	0.25	0.33	0.37
Reorganization index (BI)	0.067	0.105	0.080	0.089	0.075	0.06

5

Discussion

Like any other, models used in this study have their limitations and assumptions. The ROMS model used to simulate the hydrodynamics and temperature regimes for Lake Victoria assumes the Boussinesq (water density is nearly constant) and hydrostatic (neglect of inertial accelerations in the vertical momentum) assumptions when solving the primitive equations (Shchepetkin and McWilliams, 2003). Despite the resultant simplification of the equation of motion and vertical component of velocity, the model output compared well with available spatial and temporal temperature profiles. Besides that, ROMS is a state-of-the-art ocean model capable of high resolution descriptions of coastal and basin-wide flows that has been widely used (Haidvogel et al., 2008; Shchepetkin and McWilliams, 2005). Consequently, the developed model was considered reliable.

On the other hand, Atlantis being an end to end whole ecosystem model, the most obvious challenge was its high data requirements and large number of input parameters whose uncertainty is difficult to determine. Additionally, the model does not capture activities outside the model domain that could be influencing the Lake

Victoria ecosystem functioning. For example, fish groups like *Labeo* and *Barbus* depend on rivers for spawning. However, activities like damming of rivers, habitat degradation and use of destructive gears in rivers that irreversibly interfere with their reproductive cycle are not explicitly modeled. These could lead to a mismatch between predicted and observed trends for such groups. Due to these challenges and limitations, end-to-end models like the one developed for this study are best suited for strategic advice. For this reason, model tuning was geared more to capturing trends than magnitude of observations. That notwithstanding, the good comparison of simulations output with available datasets, as attested by various performance indicators, injected confidence in the model.

There have been several earlier attempts to model the Lake Victoria ecosystem. For instance Natugonza et al. (2016) used the Ecopath component of Ecopath with Ecosim modeling software (Christensen and Walters, 2004) to simulate the structural and functional properties of the lake's food web and the role of fisheries on the ecosystem. Downing et al. (2012) also used Ecopath to simulate the ecosystem functioning and trophic dynamics of Mwanza Gulf of Lake Victoria. Although their work was limited to a small part of the lake, relative biomass proportions of functional groups in the years of 1977, 1987 and 2005 was reminiscent to findings of this study. In 1977, the system was dominated by haplochromines and the mean trophic level of catch was low due to high contribution of detritivores. The trophic level of catch was high in 1987 due to the large contribution by the piscivorous Nile perch which experienced a biomass boom in the 1980s. In 2005, the mean trophic level catch had dropped slightly due to the increased presence of juvenile Nile perch and dagaa in landings. Results of this study also concur with Matsuishi et al. (2006), who simulated the evolution of biomass of different fish groups in Lake Victoria under increased (120%) and reduced (90%) fishing pressure on Nile perch. In both studies, the biomass of Nile perch declined increased fishing pressure whereas those of haplochromines and Nile tilapia increased. An opposite trend was observed under reduced fishing pressure on Nile perch

Kitchell et al. (1997) used a bioenergetics model of Nile perch predation rates to evaluate the consequences of previous, current and future exploitation patterns and their ecological implications. In another study, Downing et al. (2014) developed a socio-ecological model of the lake. They concluded that environmental factors: eutrophication, hypoxia, and anoxia and fishing drive the development of fish stocks in Lake Victoria which is partly in concurrence with findings of the present study. The shortcoming of these and other previous studies include the failure to capture all components of the ecosystem the models were not spatially nor temporally explicit and they did not make use of age disaggregation of vertebrates groups. The contributions of this study include consideration of the three stated dimensions to the modeling approach of Lake Victoria ecosystem.

The spatially explicit structure used in this study avoids the over generalization of the ecosystem state that typifies most scientific literature on Lake Victoria (Graham, 1929; Taabu-Munyaho et al., 2014). The lake is highly heterogeneous such that Taabu-Munyaho et al. (2014) alluded to it being composed of ‘many small lakes’. The hydrographic model explained the different limnological conditions in different parts of the lake; attributing the same to circulation patterns. Gulfs were observed to have limited exchange with the open lake. This, together, with having most of the river inlets results in the gulfs being more turbid. Being direct recipients of nutrients from the catchment and municipal waste, these areas are relatively more eutrophic than the rest of the lake. This information is corroborated by the developed Atlantis model that shows higher nitrate and Chlorophyll-a levels in gulfs and inshore areas. In addition these areas had different bio-attributes especially in fish distribution patterns. It is therefore recommended that management measures should take into account unique attributes that are apparent on a spatial scale. Better land use practices and waste management in the catchment could also reduce eutrophication and pollution of gulfs/inshore areas and ultimately the entire lake.

Age disaggregation of the vertebrate groups is another significant contribution to the Lake Victoria ecosystem modeling. This is because different age groups of the same species are known to occupy different habitats and niches. In Lake Victoria, ontogenic diet shifts have been observed. For instance, young Nile perch feed on zooplankton and then shift to *Caridina*. Adults of the same species consume fish, haplochromines being their most preferred prey (Mkumbo and Ligtvoet, 1992). The two dimensions, in addition to capturing to all parts of the ecosystem, contribute to the improved understanding of the system functioning and responses to various changes.

The ecological modeling of Lake Victoria was done in three stages. First, a hydro-graphic model (ROMS) was developed to simulate the physical processes (currents and temperature) of the lake. The model brought to fore information on underlying physical processes and consequently formed the basis for developing a whole ecosystem model for the lake. Besides its contribution to this study, the ROMS model can be used to predict the fate of pollutants which are a major concern in Lake Victoria. The model can also be used to predict suitable sites, with good circulation, for cage culture. Fish farming in cages in Lake Victoria has been rapidly increasing following the decline of catch rates of wild stocks. However, of recent, massive fish kills have been witnessed in some cage sites. Preliminary studies have attributed the fish mortalities to localized upwelling events that lead to depletion of dissolved oxygen due to release of decomposing matter into the water column (KMFRI, unpublished data). The developed ROMS model can be used to predict such events and ultimately play a critical role in cage culture site selection.

The second task involved developing an Atlantis model to describe the Lake Victoria ecosystem functioning. The model highlights the significance of predator-prey relationships and the impact of introduced species, information that is critical for instituting sustainable measures for managing the fisheries and ecosystem. Such a model comes in handy in understanding system dynamics, major processes and responses to change of large systems like Lake Victoria where adequate data collection is expensive and logistically difficult. The model provides a platform to test the impact of different fishing scenarios on the ecosystem.

Decline in fish catches in Lake Victoria has coincided with increase in human population in the region. A significant proportion of the people depend on the lake's fisheries for food and livelihood. It has been a challenge for fisheries managers to effect measures that would reduce harvesting pressure on commercial species. Against this backdrop, this study is a significant contribution to the management of the Lake Victoria fisheries by providing a framework for management strategy evaluation before actual implementation. Management alternatives are numerous but the third task of this study used the model to simulate the Lake Victoria ecosystem 20 years into the future under selected fishing scenarios. The impact of alternative scenarios on the system function and structure was evaluated using ecosystem performance indicators. It was observed that considering the evolution of biomass and catch of fish groups simultaneously with the ecosystem performance indicators, a fishing strategy that stops harvesting of haplochromines while maintaining the current harvest levels for the rest of the fish groups is most favorable. Predictions indicate that this strategy would result in increased production of commercially important species, enhanced ecosystem function and would cause minimal interruption to fishing activities. Going forward, it is envisaged that the model could be used to explore and test additional ecological theories as well as for broader management strategy evaluation.

6

Conclusion and future perspectives

The importance of Lake Victoria to local communities and states for providing food, income, transport and other ecosystem services cannot be overstated. However, the resource is under duress courtesy of human induced changes. To help understand the lake's functioning, dynamics, major processes and response to change, a whole ecosystem model for the lake was developed for the first time. Hydro-dynamic input was derived from ROMS model for the lake, also developed as part of this study. Despite underlying assumptions and limitations, validation routines showed that both models were reliable in predicting the functioning of the lake.

Unlike previous works, this study considered all parts of the ecosystem and was resolved on all the four dimensions of space-time. This helped avoid generalizations of the whole lake given its heterogeneity. Findings from hydrographic modeling showed circulation patterns and temperature profiles that vary on spatial and temporal scales. Apart from showing the monomictic nature of the lake, the model predicted regions and timing of upwelling events. Such information could be vital in informing site selection and placement of cages for aquaculture; an enterprise that is rapidly expanding in Lake Victoria. Additionally, the model can be used to track pollutants and simulate primary productivity, among other process that are circulation driven in the lake.

The Atlantis model for Lake Victoria brought to fore information on interaction of the physical, chemical, biological and fishing processes. The simulation period included key human induced changes (species introductions, increased eutrophication and overfishing) whose impacts has been difficult to assess. For example, predator-prey interactions were observed to be a key driver in the evolution of biomass of fish species – a factor that has been overlooked in the current single species approach to fisheries management of the lake. Introduced species, Nile perch and Nile tilapia, were found to have a negative impact on native species especially those they prey on or compete with respectively. As a way forward, species introductions are discouraged without proper ecological impact and longterm sustainability assessments that can be done with ecosystem models like the one used in this study.

The validated ecosystem model presents an opportunity for management strategy evaluation. Considering the whole ecosystem, areas and magnitude of interventions are numerous. For this study, ecosystem state was predicted assuming various levels of fishing pressure. It was apparent that increase in fisheries yield and enhancement of ecosystem function without adversely affecting fisher folk are possible. These could be achieved by halting harvesting of haplochromines, an option that has not been considered before.

In future, the model can be re-parameterized depending on emerging information to explore research questions of interest as well as for further management strategy evaluation. Similarly it can be used to investigate the effect of management strategies that have been suggested by various authors. For instance, it provides a unique opportunity to test the impact of the balanced harvest approach advocated by Kolding et al. (2014). Other management strategies on priority to be tested by the model include closed seasons and areas that are proposed in the current Nile perch management plan (LVFO, 2015). Further, the model can be used to disentangle the impacts of climate change from those of anthropogenic activities on the Lake Victoria ecosystem.

Part II

Papers

7

Paper I

Simulation of Lake Victoria circulation patterns using Regional Ocean Modeling System (ROMS)

Chrispine Nyamweya, Christopher David Desjardins, Sven Þ Sigurðsson, Tumi Tómasson, Anthony Taabu-Munyaho, Gunnar Stefánsson

Abstract

Lake Victoria provides important ecosystem services including transport, water for domestic and industrial uses and fisheries to about 33 million inhabitants in three East African countries. The lake plays an important role in modulating regional climate. Its thermodynamics and hydrodynamics are also influenced by prevailing climatic and weather conditions on diel, seasonal and annual scales. However, information on water temperature and circulation in the lake is limited in space and time. We use a Regional Oceanographic Model System (ROMS) to simulate these processes from 1^{st} January 2000 to 31^{st} December 2014. The model is based on real bathymetry, river runoff and atmospheric forcing data using the bulk flux algorithm. Simulations show that the water column exhibits annual cycles of thermo-stratification (September - May) and mixing (June - August). Surface water currents take different patterns ranging from a lake-wide northward flow to gyres that vary in size and number. An under flow exists that leads to the formation of upwelling and downwelling regions. Current velocities are highest at the center of the lake and on the western inshore waters indicating enhanced water circulation in those areas. However, there is little exchange of water between the major gulfs (especially Nyanza) and the open lake, a factor that could be responsible for the different water quality reported in those regions. Findings of the present study enhance understanding of the physical processes (temperature and currents) that have an effect on diel, seasonal, and annual variations in stratification, vertical mixing, inshore – offshore exchanges and fluxes of nutrients that ultimately influence the biotic distribution and trophic structure. For instance information on areas/timing of upwelling and vertical mixing obtained from this study will help predict locations/seasons of high primary production and ultimately fisheries productivity in Lake Victoria.

Key words: Lake Victoria, Currents, ROMS, Thermo-stratification

7.1 Introduction

Lake Victoria is thought to have formed about 400,000 years ago by down-warping of land between the two arms of the Great Rift Valley. Westward-flowing rivers were dammed by an upthrown crustal block, reversing their flow into the down warped land. During its geological history the lake topography went through changes ranging from its present shallow depression, to what may have been a series of much smaller swampy lakes that gradually became interconnected, lost their outlet to the west and were drained northwards by the Nile (Temple, 1969). Geological cores taken from bottom sediments show that Lake Victoria has dried up completely at least three times since it formed (Kendall, 1969). Measured by surface area (68,000 km^2), it is the largest fresh water lake in the tropics and second in the world. However, due to its shallowness, it is the 17$^{\text{th}}$ largest among the world lakes by volume (Kendall, 1969). The lake is shared among Kenya (6%), Uganda (43%) and Tanzania (51%). The catchment is about 193,000 km^2 extending to Rwanda and Burundi. About 33 million inhabitants in the basin within the three East African countries depend on the lake for transport, water for domestic and industrial uses and fisheries (Crul, 1995).

The lake plays an important role in modulating regional climate. Its thermodynamics and hydrodynamics are also influenced by climatic factors such as the Intertropical Convergence Zone (ITCZ), El Nino/Southern Oscillation (ENSO), complex orographic forcing, and the Indian Ocean zonal temperature gradient anomalies (Anyah and Semazzi, 2009; Sun et al., 2014) on diel, seasonal and annual scales (Macintyre et al., 2014). The ITCZ that separates the northeast and southeast monsoons, crosses East Africa twice every year, once during March-April-May and again during October-

November-December. This incursion and retreat of the ITCZ is responsible for the two main rainfall and dry seasons of the region. The rainy season from March through to May is commonly known as the ‘long rains’; the second rainy season of October through to December is called the ‘short rains’ (Song et al., 2004).The water budget is controlled mainly through precipitation over the lake surface, catchment inflow, controlled outflow at a hydroelectric dam on River Nile and evaporation (Kendall, 1969; Swenson and Wahr, 2009; Tate et al., 2004). The lake does have a season of deep vertical mixing when the lake becomes isothermal. During June and July the established thermocline breaks down under the seasonal onset of the south-east trade winds and for a brief period at the end of July the main body of the lake becomes isothermal with respect to depth. The thermocline most often occurs at 30-40 m depth. Complete mixing occurs once a year (Talling, 1966).

Lake Victoria is not physico-chemically homogenous. Much of the shoreline in the north and south is highly irregular. The northern shallow waters are intercepted by numerous islands. East and west of the lake, the basin rises over a thousand meters to highlands bordering the respective rift valleys, but to the north and south the watershed is less than 25 m above lake level (Kendall, 1969). Water quality varies spatially in Lake Victoria. Gulfs, near-shore areas adjacent to big human settlements and river mouth areas are relatively turbid and eutrophic (Okely et al., 2010). The diverse topography/terrain, prevailing weather/climatic conditions as well as river inflows and outflows influence water circulation patterns. This in turn determines the temporal-spatial water quality which can be linked to the distribution of biota in the lake (Okely et al., 2010).

Previous hydrographic studies have explored water movements on a small scale either in space or time. Anyah and Semazzi (2009) developed an idealized simulation of hydrodynamic characteristics of Lake Victoria. The authors relied on idealized (and real) bathymetry and uniform surface wind stress over a period of sixty days. Macintyre et al. (2014) studied thermo-stratification and factors affecting horizontal exchange while Okely et al. (2010) evaluated processes affecting horizontal mixing and dispersion in the Nyanza Gulf of Lake Victoria.

To better understand annual and seasonal water circulation (currents) in Lake Victoria, a Regional Oceanographic Model System (ROMS) is developed. The model is based on real bathymetry, wind stress, surface heat fluxes, solar radiation and river inflow/outflow forcing. The ROMS includes accurate and efficient physical and numerical algorithms and several coupled models. It also includes several vertical mixing schemes (Warner et al., 2005), multiple levels of nesting and composed grids.

7.2 Materials and Methods

The Lake Victoria ROMS model extends from 31.5° - 34.88° E and 3.05° S to 0.55° N (Fig. 7.1). It has a horizontal grid resolution of 1.9 km. The total number of grid points is 209 and 216 in the longitudinal and latitudinal directions respectively. The fine grid resolution is chosen to adequately resolve processes within narrow gulfs, bays and indented coastlines. The model has 20 terrain-following vertical levels with a minimum depth set to 5 m. Preliminary model runs with fewer vertical levels did not realistically mimic observed temperature profiles failing to accurately predict the thermocline depth as result of averaging values over wide depth ranges. The model has surface stretching factor θ_s=3 to maintain high resolution throughout surface layers of the model domain. θ_b is set to 1 to allow the influence of bathymetry on overlying layers.

Table 7.1: Basic model configuration

Parmeter	Value	Description
Lm	209	number of points in longitude direction
Mm	216	number of points in latitude direction
N	20	number of vertical (sigma) levels
h_{max}	80 m	maximum depth of the domain
h_{min}	5 m	minimum depth of the domain
θ_s	3	sigma coordinate surface stretching factor
θ_b	1	sigma coordinate bottom stretching factor
Δ_t	60 s	baroclinic time-step
Δ_{tf}	20 s	barotropic time step
r	$3.0\ 10^{-4}\ \mathrm{m}^2\mathrm{s}^{-1}$	linear bottom drag coefficient
$Tcoef$	$2.4725\ 10^{-4}$	Thermal expansion coefficient
ρ	$997\ \mathrm{kgm}^{-3}$	Background density value

Here, θ is a refinement parameter that determines the magnitude of stretching of the vertical grid in either the surface (θ_s) or bottom layers (θ_b). The thermal expansion coefficient and background density values are estimated for fresh water at 24°C. A typical linear bottom drag coefficient (Rocha et al., 2013; Taylor and Sarkar, 2008) is applied for the entire computation domain given the small depth range of the lake. Other model parameters are described in Table 9.1

The bathymetry/topography (Fig. 7.1) is derived from lake wide hydro-acoustic survey data. Meteorological surface forcing data are obtained from the European Centre for Medium-Range Weather Forecasts (ECMWF) ERA Interim, daily data set extracted at 3 hour time steps with 0.125° horizontal resolution from 1st January 2000 to 31st December 2014. Cloud cover, net longwave radiation flux, surface air pressure, surface air relative humidity, rain fall, surface air temperature, Surface v- and u-wind components 10

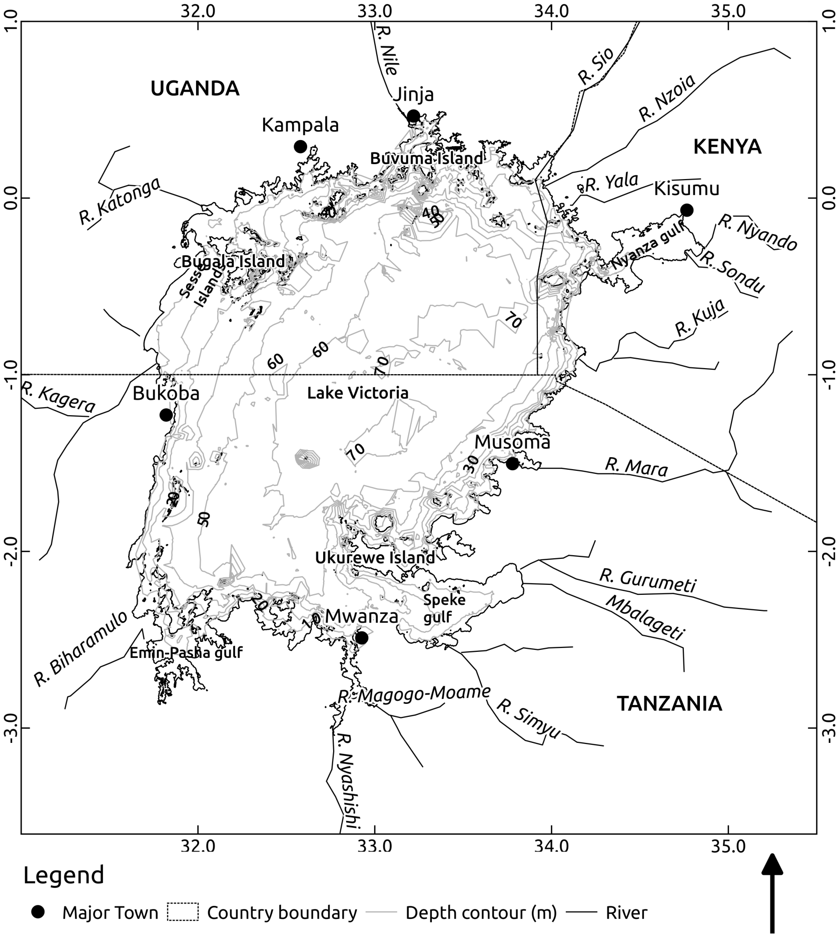


Figure 7.1: Map of Lake Victoria, its major rivers and bathymetry.

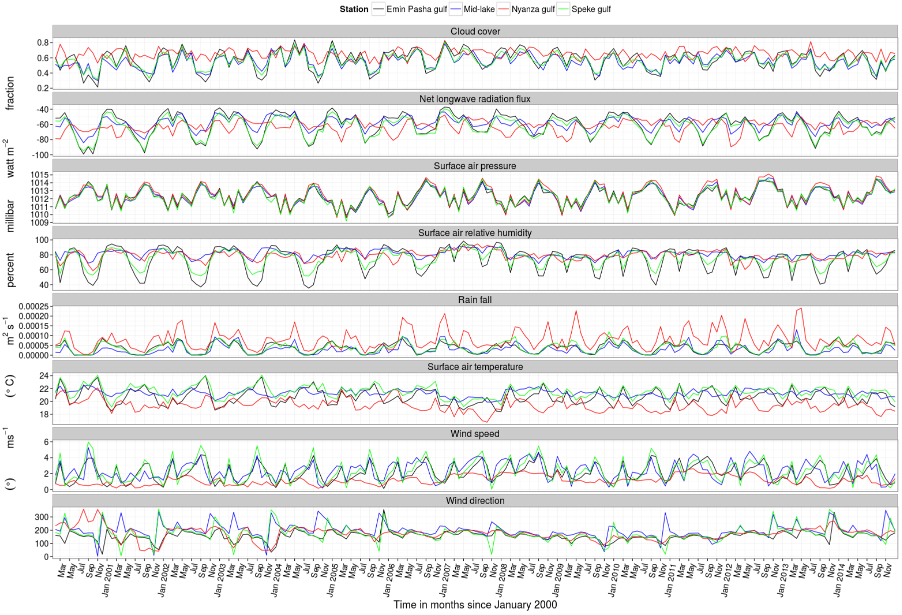


Figure 7.2: Evolution of different model forcing variables: cloud cover, net longwave radiation, surface air pressure, surface air relative humidity, rainfall, surface air temperature, wind speed and direction at selected locations in Lake Victoria from the year 2000 - 2014.

meters above the water surface and river runoff forcing fields (Fig. 7.2) are implemented using the bulk flux algorithm (Fairall et al., 2003). The model is initialized with a uniform temperature of 24°C and no momentum on 1$^{\text{st}}$ January 2000. Salinity is set to zero. Simulated spatial-temporal temperature trends are fitted to observation data collected during the 2000-2001 and 2005-2014 lake wide hydro-acoustic surveys. Modeled ($\hat{y}$) and observed (y) vertical temperature profiles are compared using the Root Mean Squared Error (RMSE).

$$RMSE = \sqrt{\frac{1}{n}\sum_{i=1}^{n}(y_i - \hat{y}_i)^2} \tag{7.1}$$

Table 7.2: Temperature (°C) variations at selected sites in Lake Victoria

Station	Mean± sd	Maximum	Minimum
Emin Pasha gulf	24.79±1.26	28.18	21.93
Mid lake	25.26±0.63	27.45	23.75
Nyanza Gulf	25.24±0.79	28.33	23.25
Sesse islands	25.53±0.79	28.00	23.41
Speke Gulf	25.16±1.16	28.50	21.89

7.3 Results

Results from the Lake Victoria ROMS model show spatial and temporal variations in water temperature. Modeled temperatures largely agree with observations (Fig. 7.3) except at the beginning of the model run in the deeper stations. Table 9.2 shows simulated temperature statistics at 5 selected sites. Mean temperatures are similar in all the stations. However, fluctuations are more pronounced in Emin Pasha and Speke gulfs located on the southern shores of the lake. In the middle of the lake which is relatively deeper, there is less variability in temperature (Fig. 7.3).

Water temperature exhibits seasonal oscillations over the model domain with periods of clear differences between surface and bottom layers intercepted with spells of near isothermal conditions (Fig. 7.3). Isothermal conditions generally appear to start in either May or June and extend to July or August in different years of the model domain. Surface water temperatures are highest during the months of May and June. Temperatures then decline to an annual low in the months of August and October in the surface and bottom layers respectively. Thereafter the temperature steadily rises before taking a downward turn in March and May for the surface and bottom layers respectively. The two month

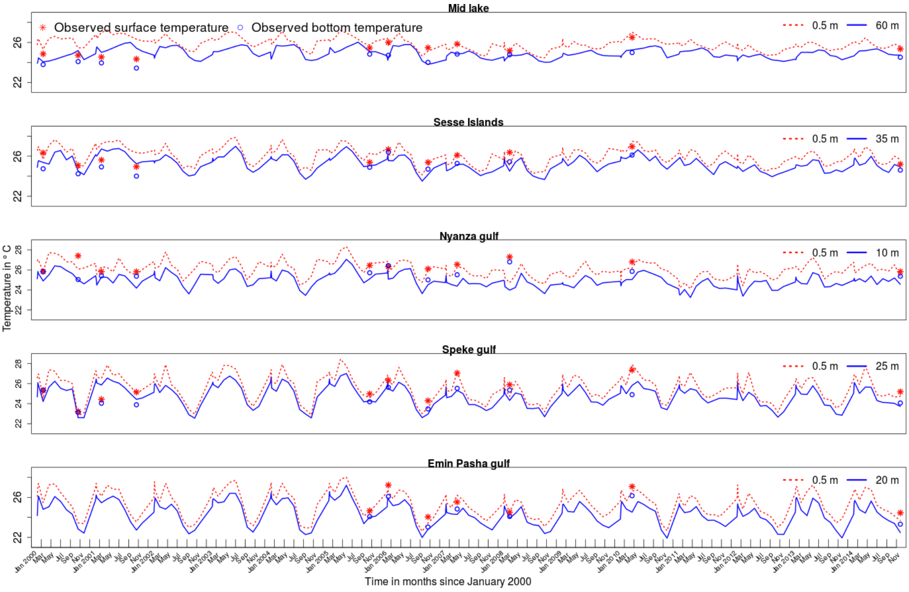


Figure 7.3: Modeled and observed surface and bottom temperature trends at selected sites in Lake Victoria.

lag in either warming or cooling of the bottom layers leads to stratification when the two processes are out of sync. Fig. 7.4 shows modeled and observed vertical temperature profiles in the middle of the lake during the months of February (stratified) and August (isothermal) 2008. Differences in RMSE values between modeled and observed temperature profiles are 0.73 and 0.22 in February and August respectively, and generally the modeled temperature closely matches the observed profile.

Figures 7.5 & 7.6 show temperature and water circulation patterns (currents) at 0.5 m and 35 m depths respectively in different months of 2008. The modeled circulation at the surface follows the general pattern of the wind curl depicted in Fig. 7.7. In January, 20 day average surface temperatures are generally uniform throughout the lake with the exception of Nyanza Gulf. Surface currents

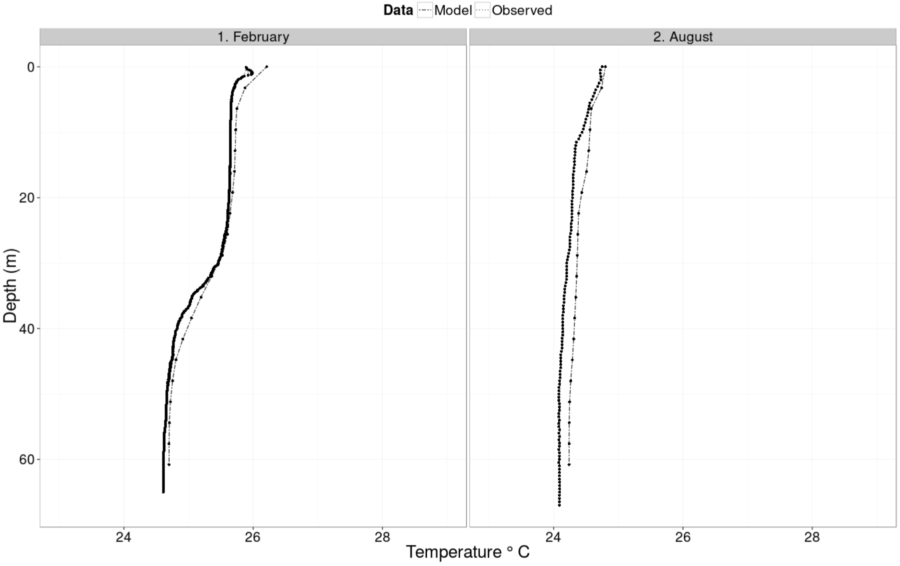


Figure 7.4: Observed and modeled vertical temperature profiles in Lake Victoria during the months of February and August 2008.

generally flow northwards in most of the open lake (Fig. 7.5a). In April, surface temperatures are higher in the northern near-shore areas relative to the rest of the lake. During this period, surface currents flow in a gyre formation whose center is drawn towards the warmer regions in the north (Fig. 7.5b). Surface temperatures are generally lowest in July and August. This is especially so in the south. As the surface temperature decreases, the gyre circulation disappears and the currents flow northwards (Fig. 7.5c). The temperatures are highest in the month of October, with the western and northern shorelines being relatively warmer than the rest of the lake. A gyre circulation pattern is also evident during this period, and like in April, its center is drawn towards the warmer region (Fig. 7.5d).

At 35 meters depth, the trend is similar to the surface except that the temperatures are a bit lower and they hit their lowest levels

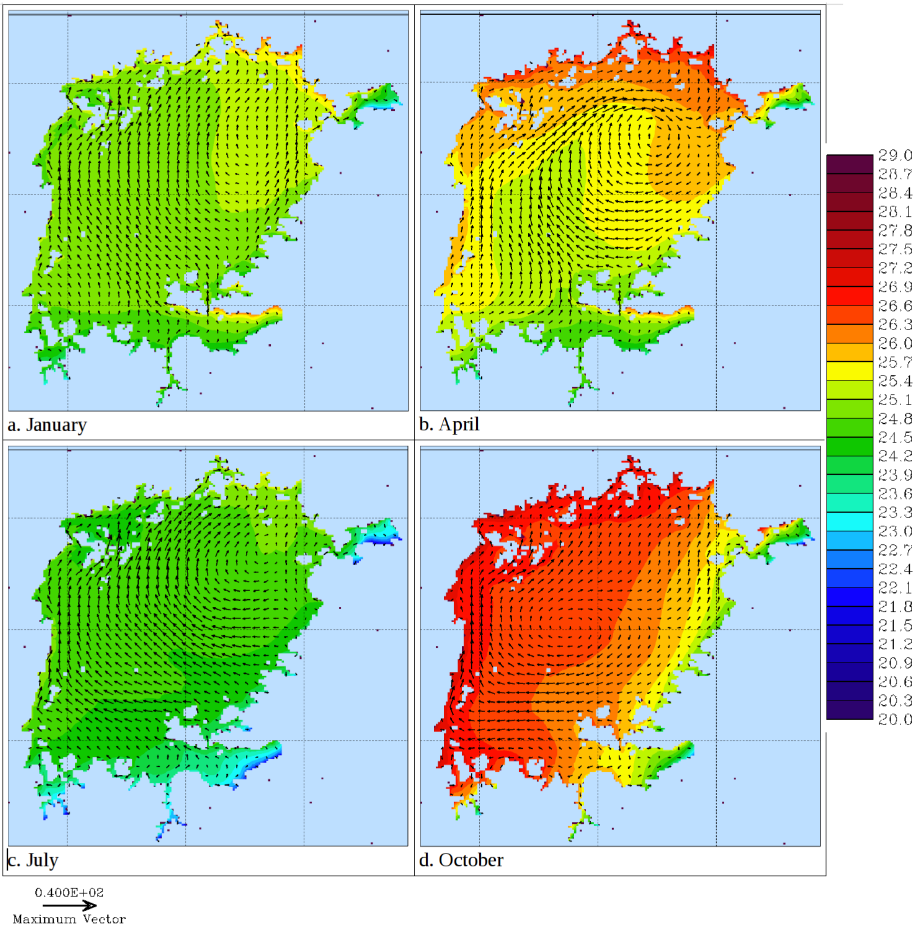


Figure 7.5: Modeled 20 day averaged near surface (5 m) temperature (shaded) and currents (vectors) in Lake Victoria in different seasons of 2008.

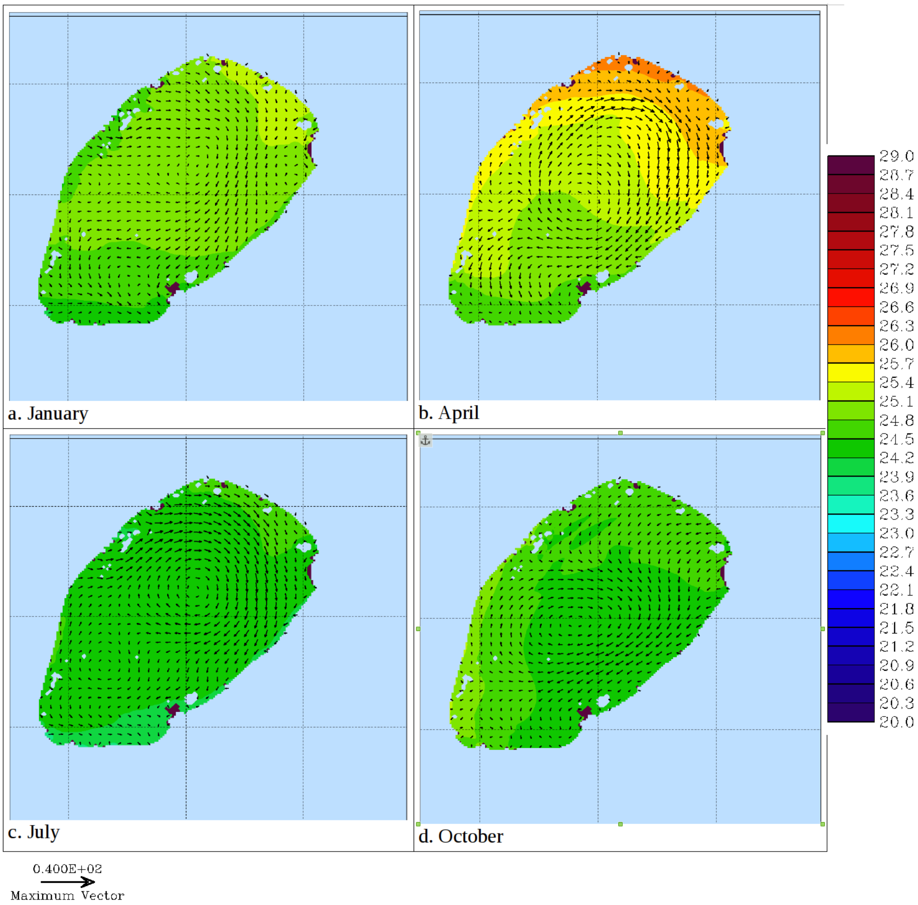
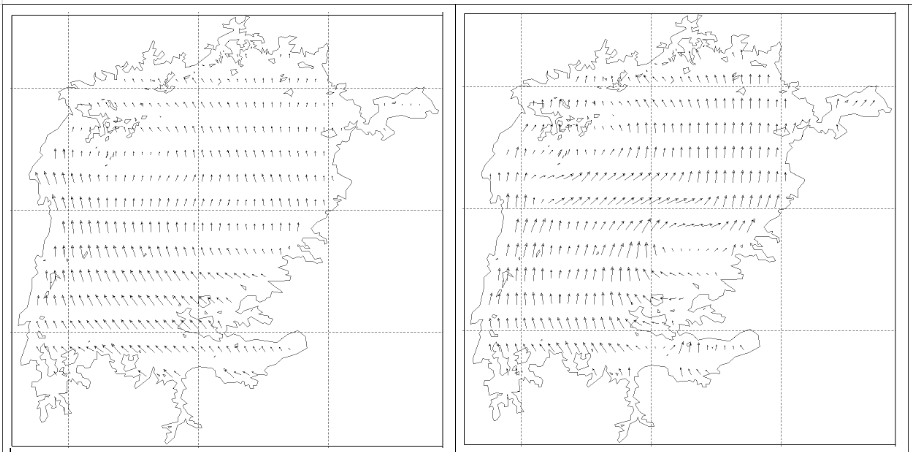
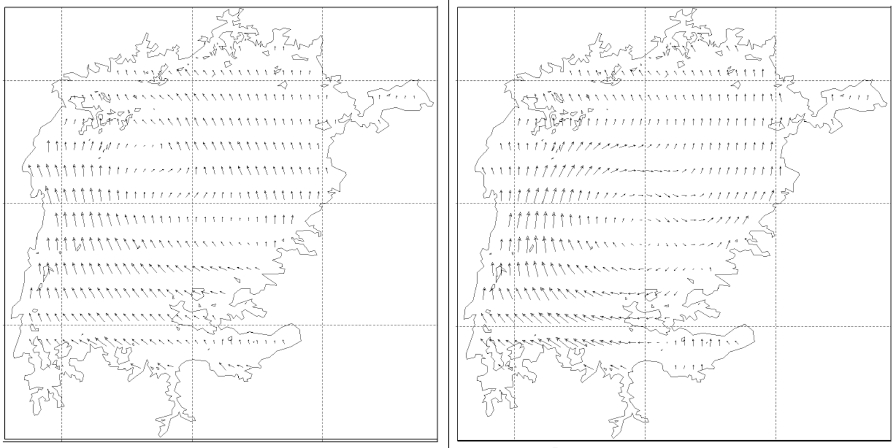


Figure 7.6: Modeled 20 day averaged temperature (shaded) and currents (vectors) at 35 m in Lake Victoria in different seasons of 2008.



a. January

b. April



c. July

d. October

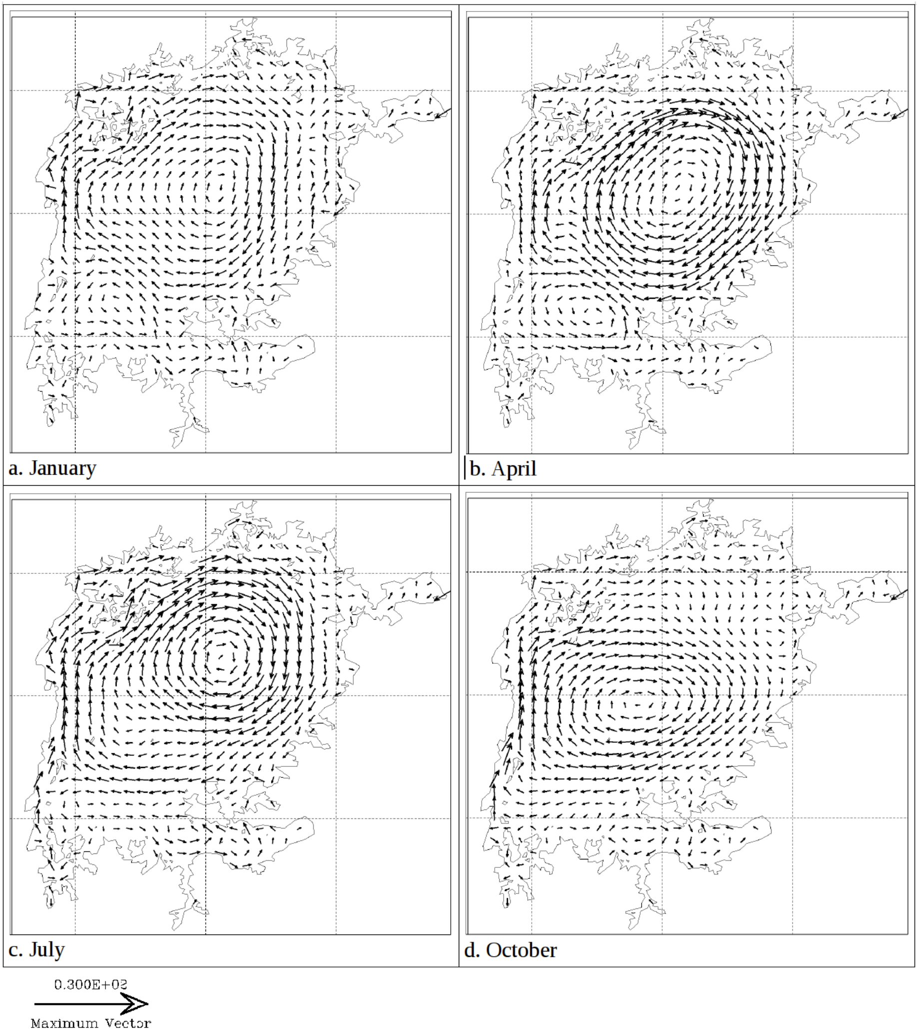
Figure 7.7: Modeled 20 day averaged wind curl (vectors) in Lake Victoria in different seasons of 2008.

two months later than at the surface. Water circulation takes on various patterns at different times of the year (results not shown). Largely it is a one gyre pattern but two or more gyres are manifest at different times of the year. Figure 6c shows two gyre currents at a depth of 35 meters. Gyres are more pronounced in two dimensional (depth averaged) currents (Fig. 7.8). Current velocities are higher in April and July around the gyre formation, especially so in the northern part near Sesse Islands (Fig. 7.9). High current velocities also prevail in the middle of the Lake. However relatively slow flow rates are observed within the three major gulfs of Lake Victoria.

As expected, model results indicate that vertical water velocities are higher during the isothermal period as compared to the stratified period (Fig. 7.10) in both west-east and south-north cross sections. In the stratified period, when vertical velocities are lower, there seems to be minimal exchange of water across the thermocline. On the other hand there is water circulation throughout the water column in the mixed season. During the stratified period there appears to be downwelling at the western and eastern ends of the lake with minimal upwelling above the thermocline at the center of the lake. Generally there is net upward water circulation in the south and some downwelling in the north. During the mixed (isothermal) period, there is upward and downward movement of water in the east and west respectively (Fig. 7.10a). Similarly there is upwelling in the south and downwelling in the north (Fig. 7.10b).

7.4 Discussion

The present study used ROMS to simulate water temperature and circulation patterns in Lake Victoria. Model results are compared to available spatial-temporal temperature data collected during the 2000-2001 and 2005-2014 lake-wide hydro-acoustic surveys.



a. January

b. April

c. July

d. October

Figure 7.8: Modeled 20 day verically averaged currents (vectors) in Lake Victoria in different seasons of 2008.

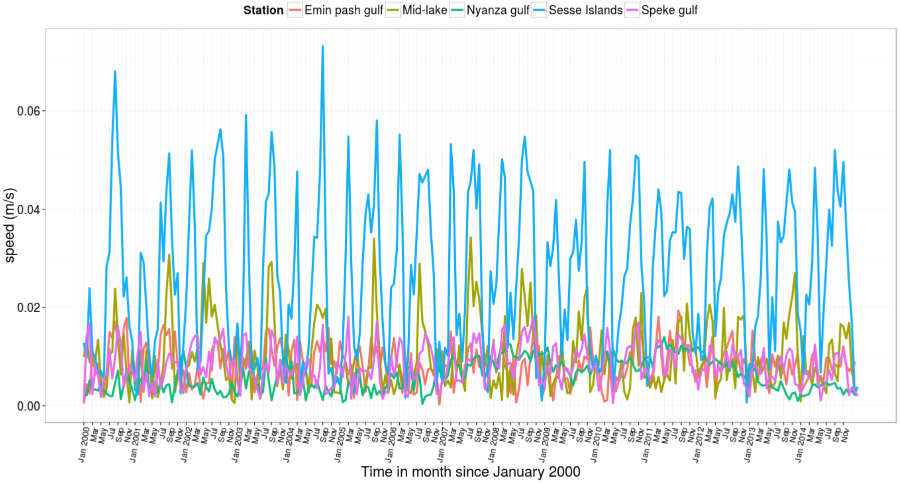
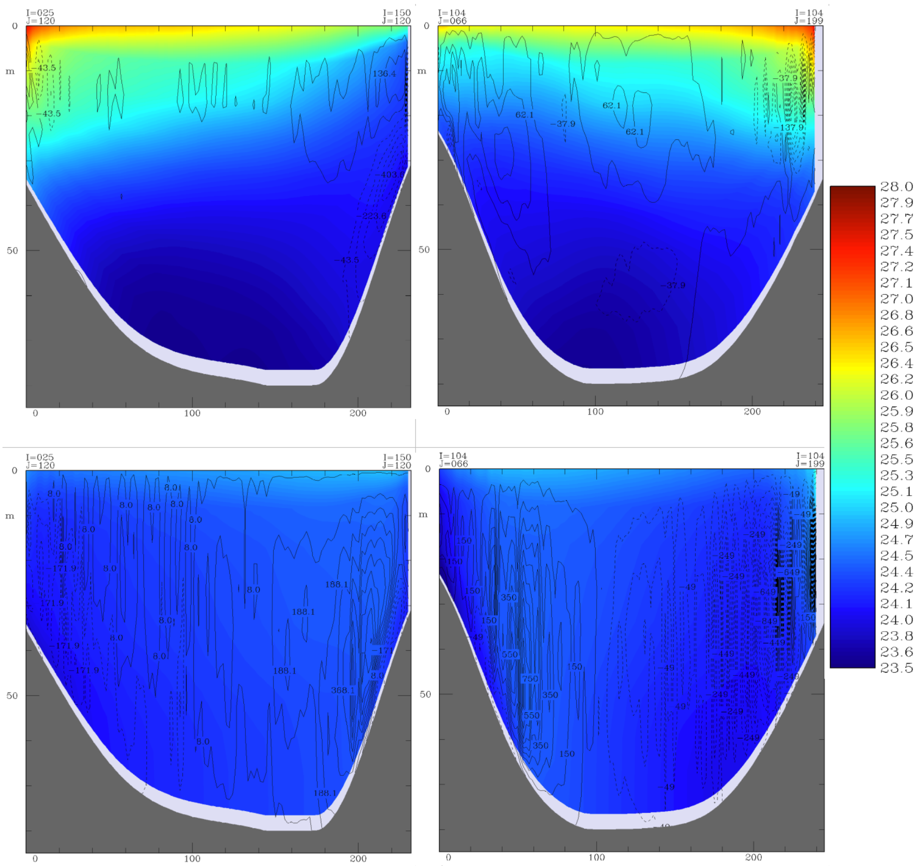


Figure 7.9: Modeled 20 day currents velocities from the year 2000 - 2014 at selected sites in Lake Victoria.

Modeled temperature trends both at the surface and the bottom fit well to observation data. This is especially so for data collected during the 2005-2014 surveys. At the beginning of the simulation (2000-2001), predictions deviate from data points because of the spin-up time the model requires to reach a state of equilibrium under the applied forcing. This is more pronounced in the deeper regions that require a longer spin-up time. Comparison of simulated and observed vertical temperature profiles in the middle of the lake are also presented with RMSE showing minimal inconsistencies between the two profiles. Additional model validation is derived from the general conformity of surface water currents and wind curl fields. Results show that the water column is thermally stratified most of the time, only experiencing complete vertical mixing once a year during the months of June to July. Isothermal conditions last up to August in some years. The seasonal changes in water column temperature profiles coincide with those observed in other studies conducted in Lake Victoria (Macintyre et al., 2014;



a. West-East

b. South-North

Figure 7.10: The modeled daily averaged water temperature (shaded, in °C) and vertical velocity (contour, in cm/day and positive upward) in Lake Victoria in stratified (upper row) and isothermal (lower row) conditions in 2008. The west−east section (left) is along 1.0°S while the south−north section (right) is along 33.2°E.

Sitoki et al., 2010; Taabu-Munyaho et al., 2013; Talling, 1965). The ability of ROMS to mimic seasonal changes in surface and vertical water temperature profiles confirm the reliability of the simulations. It therefore presents a unique opportunity of exploring other physical processes, mainly water circulation patterns, in Lake Victoria. Water circulation is important in influencing water quality, distribution of nutrients, movement of plankton biota and ultimately influences other ecosystem dynamics (Sun et al., 2014).

Thermal stratification occurrs when surface waters warm up faster than the underlying layers. This leads to the formation of a thermocline across which there is little exchange of water. Breakdown of the thermocline can be attributed to a number of factors. As the surface waters start to cool down, the lake becomes isothermal and stratification breaks down. Changes in surface temperatures correspond well with fluctuations in solar radiation implying that the latter plays a crucial role in stratification and mixing of the water column of Lake Victoria. The long rains of March through May could also play a role in reducing surface temperature given that precipitation accounts for up to 80 percent of the lake's water inputs. Currents resulting from increased wind stress accelerate the process of vertical mixing and the eventual breakdown of the thermocline, an observation also made by Macintyre et al. (2014).

Currents take several forms throughout the year. When water temperatures at the surface are nearly uniform spatially, a general northward flow is sustained in the open lake. This pattern has also been reported in Lake Victoria by Macintyre et al. (2014). However, when surface waters in some regions are warmer, gyres prevail. Gyres range from a single one, that engulfs most of the lake and generally flows clockwise at the surface, to two that spin in opposite directions. Sometimes several short-lived small gyres drive water circulation in the lake. Anyah and Semazzi (2009) also reported gyre formation in Lake Victoria. Deeper water masses exhibit a counter flow to surface water layers. Counter currents occur at the fringes of gyres. A consequence of this, is the formation of upwelling and downwelling regions that shift spatially due to the changing of circulation patterns. Upwelling causes a motion of dense, cooler, nutrient-rich water towards the surface, replacing the warmer, nutrient-depleted surface water. The nutrient-rich upwelled water stimulates the growth and reproduction of primary producers (phytoplankton). Knowledge of the location and timing of upwelling obtained from this study will help predict presence of high levels of primary productivity and thus fishery production in Lake Victoria. Macintyre et al. (2014) observed that upwelling occurs on the basin scale in response to increased southerly winds over Lake Victoria. Vertical velocities in both the west-east and south-north cross-sections depict the influence of stratification on water circulation. The velocities are minimal during the stratified period and water movements are limited to either side of the thermocline. Lack of exchange of water between surface and bottom layers explain the development of anoxic conditions in the latter that are prevalent during the stratified period (Macintyre et al., 2014; Talling, 1966).

Water circulation patterns in the three gulfs (Nyanza, Speke, and Emin Pasha) are localized. They are characterized by relatively slow water current velocities, probably because they are sheltered and shallow (especially Nyanza which is connected to the main lake via a narrow channel). This could inhibit water exchange between the gulfs and the open lake. The gulfs coincidentally host major river mouths and large urban settlements through which nutrients, sediments and pollutants enter the lake. Due to the little flushing with water from the lake, these regions are limnologically different from the open lake and are particularly more turbid and eutrophic.

Circulation in Lake Victoria is mainly driven by differential heat fluxes, wind stress and bottom terrain. Spatial variability in latent heat fluxes creates conditions conducive for horizontal convective circulation (Talling, 1966,6). The difference in water density as a result of temperature variations causes gravity currents at the surface (Ochumba, 1996).

7.5 Conclusion

Information on water temperature and circulation patterns in Lake Victoria has been limited prior to this study. Reliability of the generated model is reinforced by its ability to fit to observational spatial-temporal temperatures trends as well as replicating vertical temperature profiles in the lake during both mixed and stratified periods. Simulated data show that the water column exhibits annual cycles of thermal stratification (September - May) and mixing (June - August). Vertical velocities are low during the stratified period and are localized to either side of the thermocline. This explains the low oxygen levels that occur in deep waters during the stratified period.

Surface water currents in Lake Victoria take on different patterns ranging from a lake-wide northward flow to gyres that vary in size and number. An underflow is a constituent of the circulation leading to the formation of upwelling regions that shift in time and space. Current velocities are highest at the center of the lake and also in the western inshore waters indicating enhanced water circulation in those areas. On the contrary, there seems to be little exchange of water between the major gulfs (especially Nyanza) and the open lake, a factor that could be responsible for the different water quality reported in those regions Macintyre et al. (2014). Information on the location and timing of upwelling and vertical mixing obtained from this study will help predict presence and location of high levels of primary productivity and thus fishery production in Lake Victoria.

Temporal and spatial differences in both water temperature and circulation (currents), are attributable to a range of atmospheric forcing effects and lake terrain. Findings of the present study enhance our understanding of the physical processes of the Lake Victoria and consequently form a basis for future comprehensive ecosystem studies that quite often require physical hydrodynamic components. The developed model also forms a basis for which future observations could be made to refute or corroborate findings of this study.

7.6 Acknowledgement

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8

Paper II

Exploring Lake Victoria Ecosystem Functioning using the Atlantis Modeling Framework

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Abstract

Lake Victoria has experienced human induced pressures such as overfishing, introduction of alien species, increased eutrophication and climate change impacts. However, there is limited understanding of the system dynamics, major processes, drivers and responses to the changes. To address this challenge, we developed the first end-to-end whole ecosystem model (Atlantis) for the lake. The model is spatially resolved into 12 unique dynamic areas based on depth, species composition, physical-chemical characteristics and fisheries management zones. A total of 38 functional groups constitute the biological model. Four fishing fleets with different targeting options are simulated. Reliability of the model is confirmed by the good fit of simulations output to observational data sets. Herein, we describe the evolution of the biophysical system, illustrating how it responded to the aforementioned induced perturbations since 1958. The constructed virtual Lake Victoria ecosystem model provides a platform for exploring the impact of management interventions before actual implementation.

Keywords: Atlantis, Ecosystem, Invasive species, Lake Victoria, Simulation, Management

8.1 Introduction

Lake Victoria, with a surface area of 68,800 km^2, is the largest tropical and second largest freshwater lake on the planet. The lake's waters straddles three countries (Kenya, Uganda and Tanzania) and supports Africa's largest inland fishery (Geheb et al., 2007). The lake is large enough to create its own weather system as well as influence regional climate (Crul, 1995; Stager and Johnson, 2008). The lake provides ecosystem services such as water for domestic and industrial use, transport, hydro-power generation and food to about 40 million people. Its fisheries provide employment, income and export earnings to the lake-edge communities. Lake Victoria is home to diverse flora and fauna which are intricately connected ecologically.

The lake's ecological health is in jeopardy, and had been for decades, mainly due to a myriad of anthropogenic activities (Hecky et al., 2010). Many riparian towns release raw sewage and municipal waste into the lake on a daily basis. This, together with fertilizer and chemicals from agricultural farms in the catchment, contribute to increased pollution and eutrophication. Invasive species such as water hyacinth (*Eichhornia crassipes*) and Nile perch (*Lates niloticus*) are thought to have been responsible for the manifest of ecological damage in Lake Victoria (Opande et al., 2004; Taabu-Munyaho et al., 2016; Witte et al., 1992b). Water hyacinth reproduces rapidly and covers large areas of the lake forming dense mats of plants that block sunlight needed for survival of life below the surface. The introduction of the Nile perch had a major impact on haplochromine cichlids stocks which remain favorite prey, affecting both their abundance and diversity (Witte et al., 1992b). Several haplochromine species had gone extinct and their abundance was reduced to less than 1% of their original biomass barely two decades after the introduction of Nile perch. The number of species in demise has only continued to grow and now up to 65% of haplochromine species are thought to have been lost, an event which may well represent the largest species extinction amongst vertebrates in the 20th century (Goldschmidt et al., 1993; Kaufman, 1992; Kaufman and Cohen, 1993; Kitchell et al., 1997). Another challenge is the booming fishing industry that evolved around the explosion in biomass of the Nile perch. The lake region is among the most densely populated areas in Africa (Ewald et al., 2004) and demand for fish locally has been increasing rapidly with population growth. This has lead to overexploitation of fish populations, reducing them to dangerously low levels (Taabu-Munyaho et al., 2016).

The complex ecology mixed with adverse human actions on the lake and its catchment (often without prior research of potential impacts) have limited the understanding of the system dynamics, major processes, drivers and responses with no scientific consensus on the subject (Cornelissen et al., 2015; Downing et al., 2014; Odada et al., 2009). Little headway has been made in identifying the major drivers of ecosystem changes that have been witnessed in the last six decades. Work done on the lake usually focuses on one or a few aspects of the system and often falls short of giving “the big picture". With such a scenario in place, it is quite difficult to predict the implications, both for the ecosystem and the local communities, of any management measures instituted on the lake. In the recent past it has been acknowledged that an ecosystem approach to management is necessary if the lake is to offer ecosystem services in a sustainable way (Cornelissen et al., 2015; Downing et al., 2014; Njiru et al., 2014). This study seeks to describe the Lake Victoria ecosystem functioning, trophic cascade mechanisms as well as complex non-linear system responses. A coupled component modeling approach is employed aiming to describe complex interactions among detailed processes for the purposes of prediction, forecasting and system understanding (Bennett et al., 2013; Kelly et al., 2013). We implement these by developing the first end-to-end (whole of ecosystem) model for Lake Victoria. It is envisaged that the developed model (Atlantis) will be used to predict how the lake might respond to different management measures.

8.2 Materials and methods

We used the Atlantis ecosystem modelling framework to develop the model. Atlantis provides an opportunity to build a virtual ecosystem which can be used to road test different management regimes before actual implementation (Fulton et al., 2011; Smith et al., 2015). In its fullest form it considers all aspects (parts) of an ecosystem i.e. biophysical, economic and social. The model tracks changes in three dimensional space consisting of horizontal polygons and vertical layers. This 3D structure represents the physical environment and is matched to the major geographical and bioregional features of the simulated ecosystem. Using this box-based representation facilitates tracking of flows of limiting nutrients i.e. nitrogen and silica through the main biological groups via a system of differential equations (typically solved in 6, 12 or 24 hour time steps) using a simple forward difference integration algorithm (Fulton et al., 2011). The primary ecological processes modeled are consumption, production, waste production, migration, predation, recruitment, habitat dependency and mortality. The trophic resolution is typically at the functional group level, with primary producers and invertebrates represented as biomass pools and vertebrates represented using an explicit age-structured formulation.

Biological model components are replicated in each depth layer of each polygon. Movement between the polygons is by advective transfer or by directed movements depending on the variable in question.

8.2.1 Study area

Owing to its large spatial extent (3.05°S to 0.55°N and 31.5° to 34.88°E), Lake Victoria is subject to different climatic, topography and drainage regimes. The western shoreline is largely monotonous, whereas the rest of the shoreline is heavily indented with shallow bays fringed with macrophytes. The vegetated wetlands serve as breeding, feeding and refugia grounds for many aquatic organisms (Balirwa et al., 2003). The northern part of the lake has numerous islands which act as wind breaks, making the area calm compared to the southern regions, which experience strong waves and currents (Figures 9.1 and 9.2). Most rivers flow in from the eastern side of the lake. Inshore areas are characterized by high biodiversity, high nutrient levels and high turbidity (Balirwa et al., 2003). They are also the worst impacted by point sources of pollution and other anthropogenic activities. The north and north-eastern shorelines are the most affected by coastal development and industrial waste. Furthermore, artisanal fishing is quite intense in these areas (Balirwa et al., 2003; Taabu-Munyaho et al., 2016).

8.2.2 Model structure

Given the heterogeneity, the Lake Victoria Atlantis model is partitioned into areas that would represent unique habitats based on depth (Figure 9.1), species composition, physical-chemical parameters, fisheries management zones and anthropogenic influences (Taabu-Munyaho et al., 2014). The lake is categorized

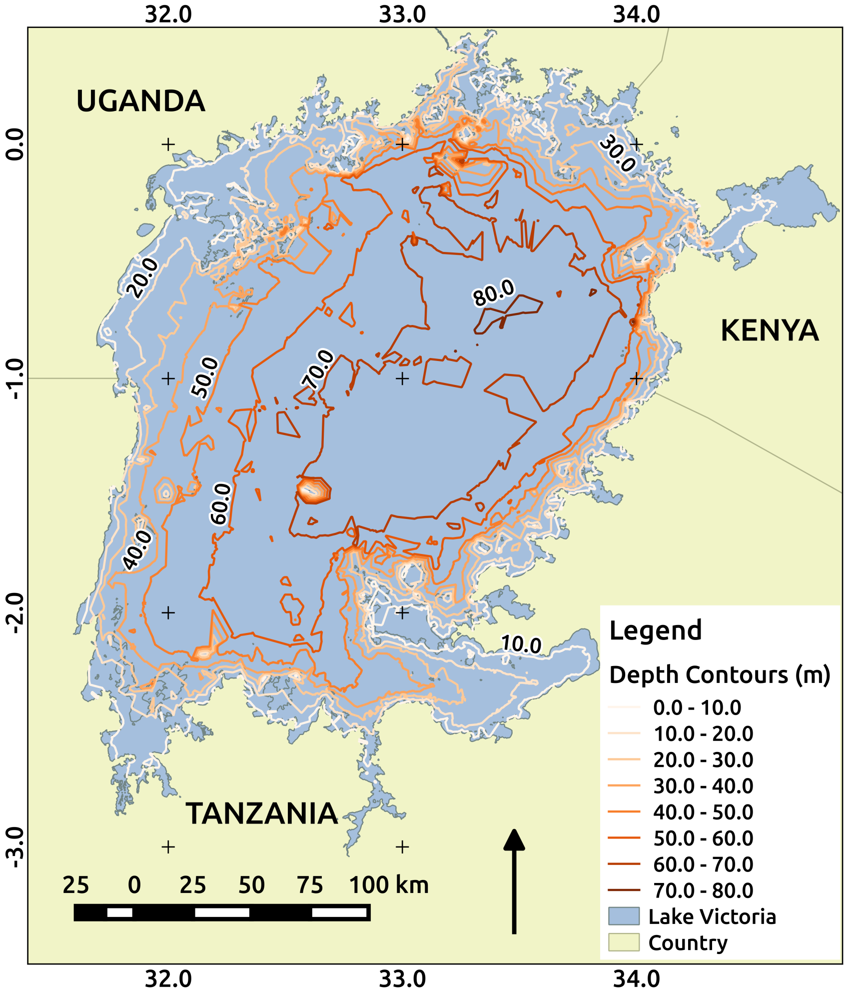


Figure 8.1: The topography/bathymetry of Lake Victoria and the three surrounding countries.

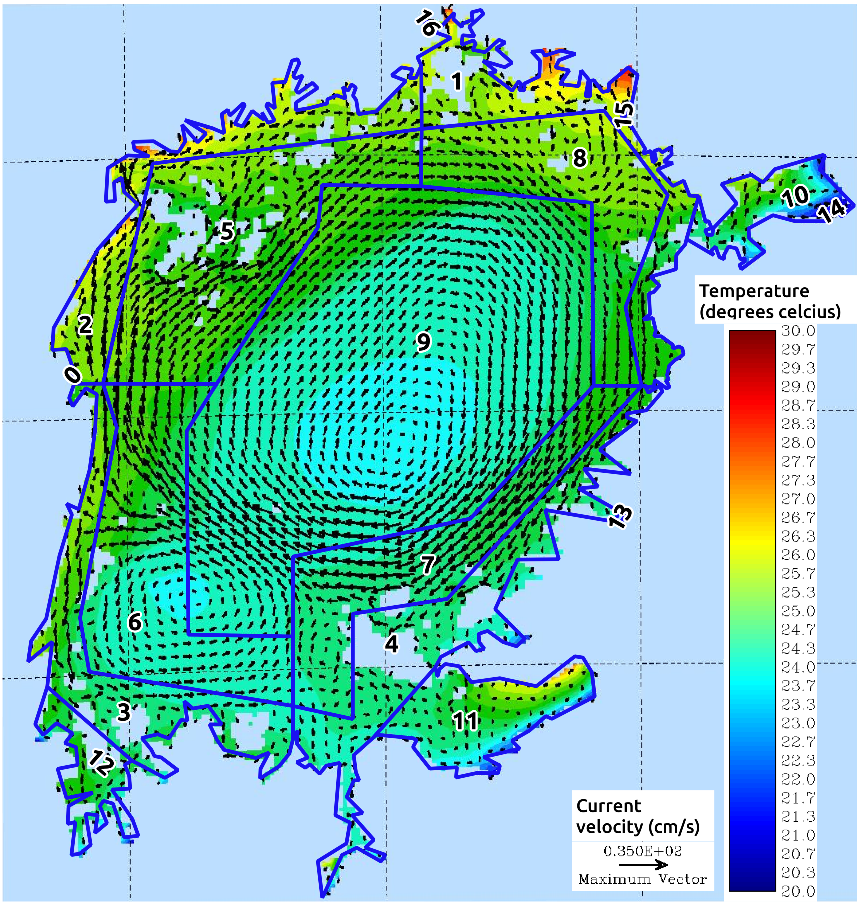


Figure 8.2: Spatial areas, dynamic (1-12) and boundary (0, 13-16) boxes used for creating the box geometry for the Lake Victoria Atlantis model. Surface temperature and currents for 22nd January 2009 are also depicted (as an example of the physical regime).

into inshore (boxes 1:4), coastal (boxes 5:8) and deep (box 9) areas (Figure 9.2). Each of the inshore and coastal areas are divided into four regions, namely the north west (NW), south west (SW), south east (SE) and north west (NW). Nyanza, Speke and Emin Pasha Gulfs (i.e. boxes 10, 11 and 12) are categorized as unique strata (appendages to the main lake). Nyanza Gulf is a significant extension of northeastern Lake Victoria into western Kenya. It is the shallowest stratum with only one water column layer. The gulf is connected to the main lake by the Rusinga Channel, which is partly masked from the main body of the lake by islands. It has an average width of 16 miles (25 km) and extends for 40 miles (64 km) from Kisumu to the channel with a maximum depth of 10 m. Nyanza Gulf has greater fish biodiversity with relatively high abundance of catfishes *Clarias gariepinus* and *Synodontis victoriae* and lungfish *Protopterus aethiopicus*. Water in this stratum is highly turbid and eutrophic relative to other strata. The high level of turbidity is attributed to siltation and nutrients brought in by rivers with high effluent concentrations from the agricultural uplands. It is also a recipient of municipal waste from Kisumu and Homa Bay towns. Persistent algal blooms that deplete oxygen from the water column are common in this part of the lake. The Speke Gulf is at the southeastern corner of the lake and is up to 30 meters deep. Emin Pasha Gulf is situated at the southwestern end and harbors diverse species of haplochromine cichlids (Taabu-Munyaho et al., 2014). Water circulation within the three gulfs is relatively slow as depicted in Figure 9.2.

Each of the areas can have up to three model depth layers (layer 1 = 0 - 20 m, layer 2 = 20 - 40 m, layer 3 = 40 - 80 m). Boxes 1 - 12 serve as dynamic boxes for the Lake Victoria Atlantis model. Five major river mouths are designated as boundary boxes serving as regions of fluxes into and out of the model domain.

The Kagera River (box 0), the largest and most important of the lake tributaries, enters the western side of Lake Victoria just north of latitude 1° S. Other major rivers draining into the lake include Mara (box 13), Sondu (box 14) and Nzoia (box 15), all of which are on the eastern side. Lake Victoria has only one outlet, the River Nile (box 16). The Nile flows out to the north and is dammed at Jinja for hydro-power generation. Hydrodynamic input providing current flows for dispersion and temperature trends are derived from a Regional Oceanographic Model System (ROMS) of the lake (Nyamweya et al., 2016a). The ROMS model is based on real bathymetry, forced with wind stress, surface heat fluxes, solar radiation and river inflow/outflow data.

The Lake Victoria Atlantis model runs from 1958 to 2015. A total of 34 functional groups constitute the biological components of this model (Table 9.1). These include 17 fish, 1 bird, 1 reptile, 9 invertebrate and 6 primary producer groups. Additionally there are 2 groups which represent labile and refractory detritus. Figure 9.3 shows trophic levels and interactions of the functional groups in the Lake Victoria Atlantis model. It is produced using the "foodweb R package" (Perdomo et al., 2016). The interactions are based on stomach content analysis survey data supplemented by information obtained from FishBase (Froese and Pauly, 2016). Four fishing fleets (gill-net, long-line, small-seine and inshore) with different targeting options are simulated in the present model run. The gillnet fishery targets most of the species with the exception of small bodied fish like the silver cyprinid *Rastrineobola argentea*, locally known as dagaa, and some *Barbus* species. The long-line fleet mainly targets Nile perch (*L. niloticus*). Other species targeted by the long-liners are catfish (*C. gariepinus*), *Bagrus docmak*, *Synodontis spp* and to a small extent lungfish (*P. aethiopicus*). Small-seines mainly target dagaa and haplochromines. The inshore fleet, an aggregation of several gears operating in shallow near-shore waters, targets all species that inhabit such areas. In the model, fishing mortality is varied with multiplication factors reflecting changes in fishing effort in the simulation period. Initial model tuning is done simultaneously across several parameters to prevent the functional groups from going extinct. Once this is achieved, tuning is then geared to modeled biomass and catch; by matching the general trends of observed catch per unit effort (CPUE) and officially reported landings respectively of the main commercial fish species. CPUE is chosen as index of abundance due to the lack of time series fish biomass data in Lake Victoria. It is calculated as annual landings per fishing craft for each of the commercial species. Multiple model performance evaluation metrics are used to counteract the weaknesses of individual metrics (Bennett et al., 2013). The used metrics were chosen based on availability of observational data sets for corresponding model outputs of interest and their ability to check whether the model output preserves trends and magnitude of observational data (Bennett et al., 2013). Generated catch ($\hat{y}$) is compared to actual landing statistics and the fit of the two is tested using Pearson's correlation, coefficient of variation (CV) (equation 9.1) and modeling efficiency (E) as proposed by Olsen et al. (2016).

$$CV = \frac{1}{\bar{y}}\sqrt{\frac{1}{n}\sum_{i=1}^{n}(y_i - \hat{y}_i)^2} \tag{8.1}$$

Modeling efficiency is computed as described by Nash and Sutcliffe (1970) (equation 9.2). In this case, it is defined as one minus the sum of the squared differences between the predicted (P) and observed (O) catch normalized by the sum of squares of the observed catch.

Table 8.1: Biological groups in the Lake Victoria Atlantis model, with initial biomass in tonnes and model representation.

Code	Model Group	Initial Biomass (t)	Modeled as
LN	Nile perch (*Lates niloticus*)	0.4	Age-structured
CG	African catfish (*Clarias gariepinus*)	1.0 x 10^4	
BD	*Bagrus* (*Bagrus docmak*)	1.4 x 10^4	
PA	Lungfish (*Protopterus aethiopicus*)	2.0 x 10^4	
HPR	Predatory haplochromines	1.0 x 10^6	
HPY	Phytoplantivorous haplochromines	5.4 x 10^5	
HBE	Benthivorous haplochromines	1.5 x 10^5	
SV	*Synodontis* (*Synodontis Victoriae*)	7.5 x 10^3	
MK	*Mormyrus* (*Mormyrus kanume*)	1.5 x 10^4	
SCH	*Schilbe* (*Schilbe intermedius*) *sp.*	5.0 x 10^3	
RA	Dagaa (*Rastrineobala argentea*)	1.0 x 10^3	
ON	Nile tilapia (*Oreochromis niloticus*)	2.2 x 10^{-2}	
OT	Other tilapia	5.5 x 10^4	
BA	*Barbus* (*Barbus altinialis*)	2.6 x 10^4	
SB	Small *Barbus*	1.5 x 10^3	
LV	*Labeo* (*Labeo victorianus*)	4.7 x 10^4	
ALL	*Alestes*	1.0 x 10^3	
REP	Reptiles	5.0 x 10^3	
BFE	Birds	5.0 x 10^2	
MIN	Macroinvertebrates	1.3 x 10^6	Biomass pool
BFF	Benthic filter feeder	1.5 x 10^5	
BFS	Shallow filter feeder	2.6 x 10^3	
BFD	Deep filter feeder	4.0 x 10^4	
BG	Benthic grazer	5.2 x 10^3	
MB	Microphtybenthos	8.8 x 10^5	
MA	Macroalgae	7.9 x 10^5	
ZL	*Caridina nilotica*	6.7 x 10^5	
PL	Large phytoplankton	1.0 x 10^6	
DF	Dinoflagellates	4.3 x 10^5	
PS	Pico-phytoplankton	1.1 x 10^5	
ZM	Mesozooplankton	4.1 x 10^7	
ZS	Microzooplankton	2.9 x 10^7	
PB	Pelagic Bacteria	4.3 x 10^4	
BB	Sediment Bacteria	7.9 x 10^5	
DL	Labile detritus	3.9 x 10^6	
DR	Refractory detritus	1.6 x 10^7	

$$E = 1 - \frac{\sum_{i=1}^{n}(O_i - P_i)^2}{\sum_{i=1}^{n}(O_i - \bar{O})^2} \tag{8.2}$$

Data analyses and the production of spatial maps were undertaken using R version 3.2.2 (R Core Team, 2015) and QGIS version 2.8 (QGIS Development Team, 2015) respectively.

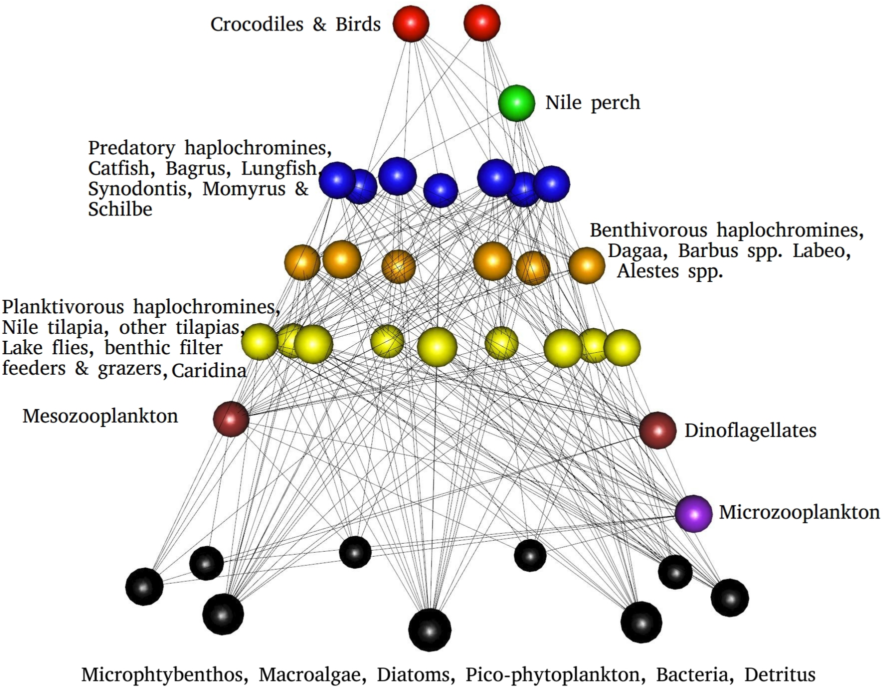


Figure 8.3: Food web illustrating trophic interactions in the Lake Victoria Atlantis model.

8.3 Results

The developed Atlantis model simulates the Lake Victoria ecosystem functioning from 1958 to 2015. The model runs for 57 years including 10 years burn-in for the system to stabilize. The model's performance is assessed by comparing the general patterns of primary production (Chlorophyll a), fish biomass and time series catch trends with observational data. Figure 9.4 shows the spatial distribution of nitrates in the model which is required for the growth of primary producers. Higher concentrations are observed in the Nyanza Gulf in the north-east of the lake. Offshore areas exhibit lower nitrate concentrations. The distribution of nitrates in the model generally matches the patterns described by Hecky et al. (2010), albeit their study describing trends derived from sediment cores. A steady increase in nitrates commences in the late 1970s and is sustained for the rest of the model period. Figure 9.5 shows the distribution of Chlorophyll a. Inshore areas including the major gulfs have relatively high Chlorophyll a concentrations (i.e primary producers). Inshore areas also have high densities of fish biomass for most species (Figure 9.6). Biomass trends of commercial species are compared with CPUE as an index of abundance (Figure 8.7). For most species there is close correlation between predicted biomass and CPUE. The explosion of biomass of the introduced species (Nile perch and Nile tilapia), coincides with observed data. Modeled catch fits well to officially reported catch (Figure 8.8) with strong correlation for most of the species. CV shows minimal deviation between simulated and actual catch (Table 9.2). All E values are greater than zero indicating that model performance is within acceptable limits (Krause and Boyle, 2005; Moriasi et al., 2007).

The biomass of biological functional groups in the model exhibits changes over time. A complete output of the model and an illustration of the evolution of biomass of all biological groups can be found at `https://figshare.com/articles/Lake_Victoria_Atlantis_model_output/3364717`. The prey species biomass declines with increase in the predator biomass and vice versa. For instance, at the start of the model run, the biomass of Nile perch, a top predator, is quite low. This is about the time the species was introduced in to Lake Victoria (only 380 specimens were officially introduced into the lake in 1962 at Entebbe and another 8 specimens in Kisumu in 1963 (Pringle, 2005)). During this period, biomass of haplochromine cichlids, the main prey for Nile perch is relatively high. However, as the perch establishes and its biomass grows rapidly (over about two decades), a sudden decline of the prey species is observed. A resurgence of the haplochromines is observed only as the biomass of Nile perch declines towards the end of the model run. This happens because of the reduced predation on them by the declining Nile perch stock. Another inter-stock relationship is observed between the indigenous tilapines and the introduced Nile tilapia. The two groups of species occupy the same niche but the latter is a faster grower and more fecund (Njiru et al., 2006). Consequently, after the establishment of the Nile tilapia, a steady decline of the indigenous tilapia species is observed to a point of near collapse. The biomass of dagaa, which faces minimal predation pressure because it occupies a different location in the water column from the predators, seems to be regulated by the zooplankton biomass (the major and almost exclusive food item for the species) and fishing mortality. Other fish species generally decline in biomass over the model period. The introduced species Nile perch and Nile tilapia show negative correlation with the native species (Figure 8.9). Nile perch show the strongest negative correlation with predatory haplochromines; on the other hand, it shows a strong positive correlation with Nile tilapia and dagaa.

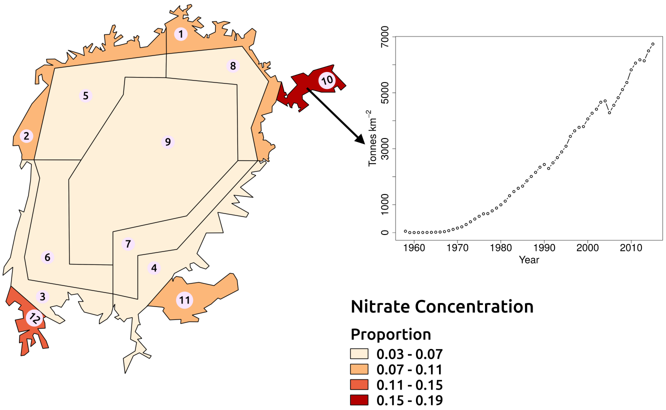


Figure 8.4: Simulated spatial and temporal trends of nitrate concentrations in Lake Victoria. The graph shows changes of nitrate concentration in box 10 (Nyanza Gulf) over time.

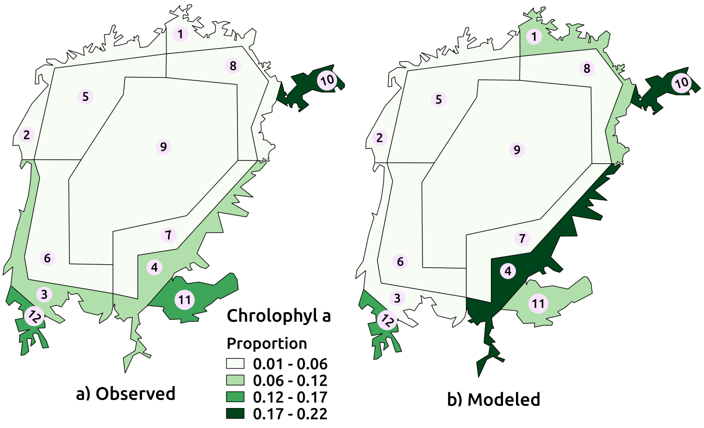


Figure 8.5: Observed and modeled Chlorophyll *a* distribution in Lake Victoria.

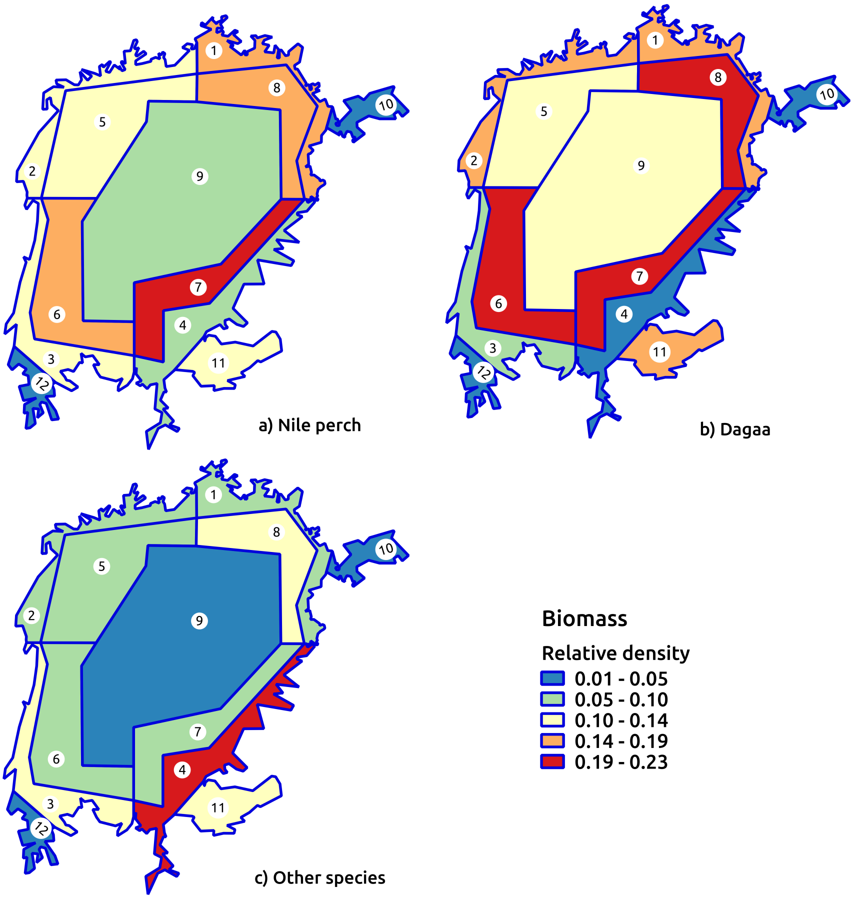


Figure 8.6: Prescribed spatial distribution of fish groups in the Lake Victoria Atlantis Model.

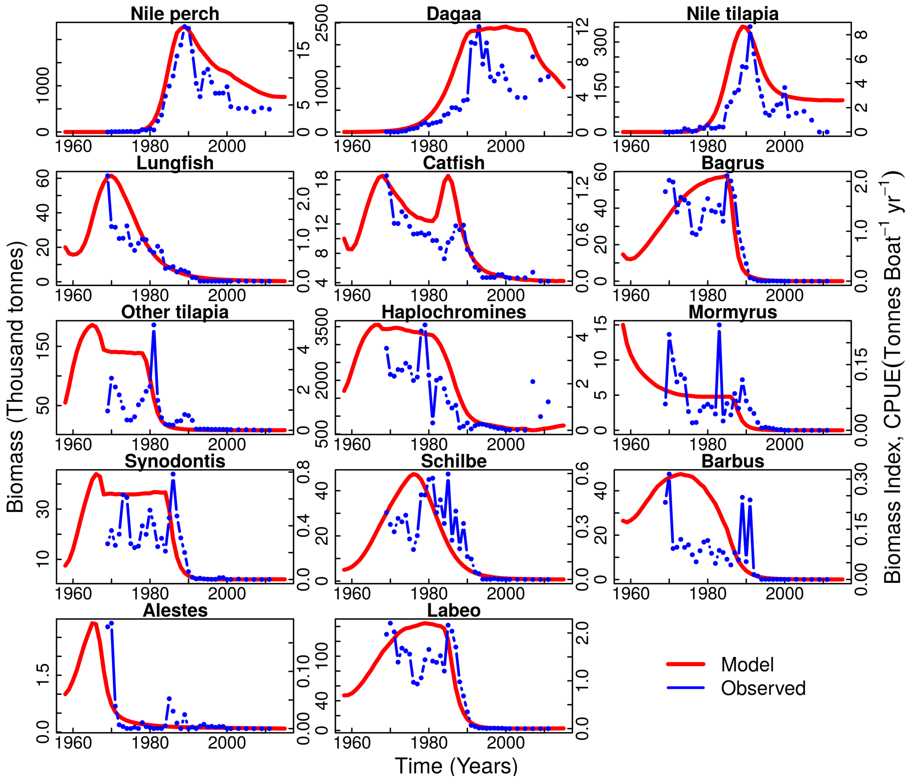


Figure 8.7: Modeled biomass and observed CPUE trends of the main fish reported in commercial landings of Lake Victoria from 1958 - 2015.

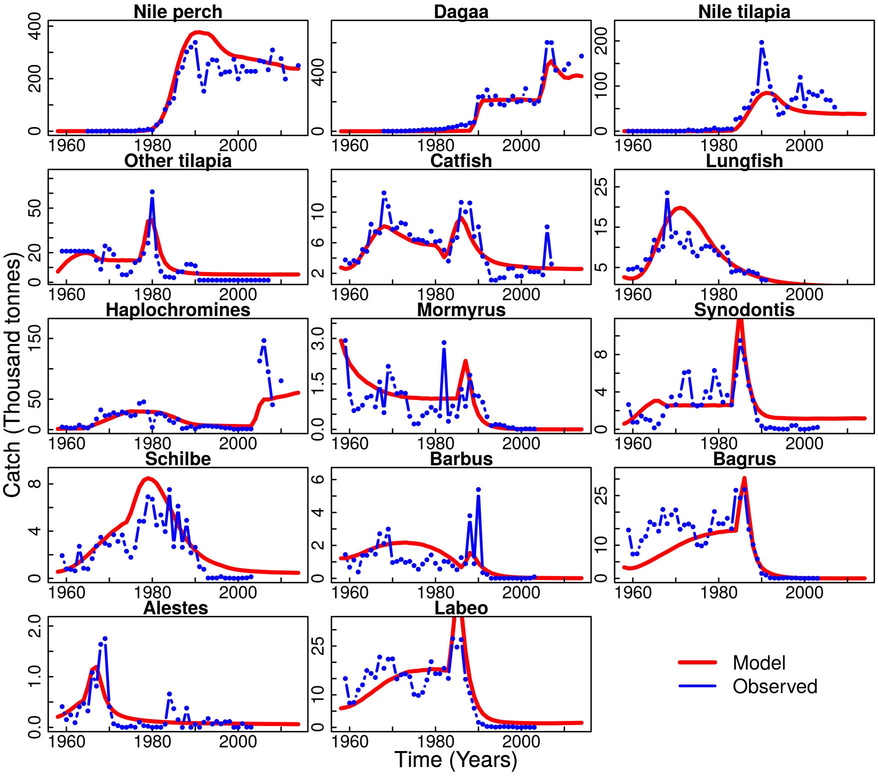
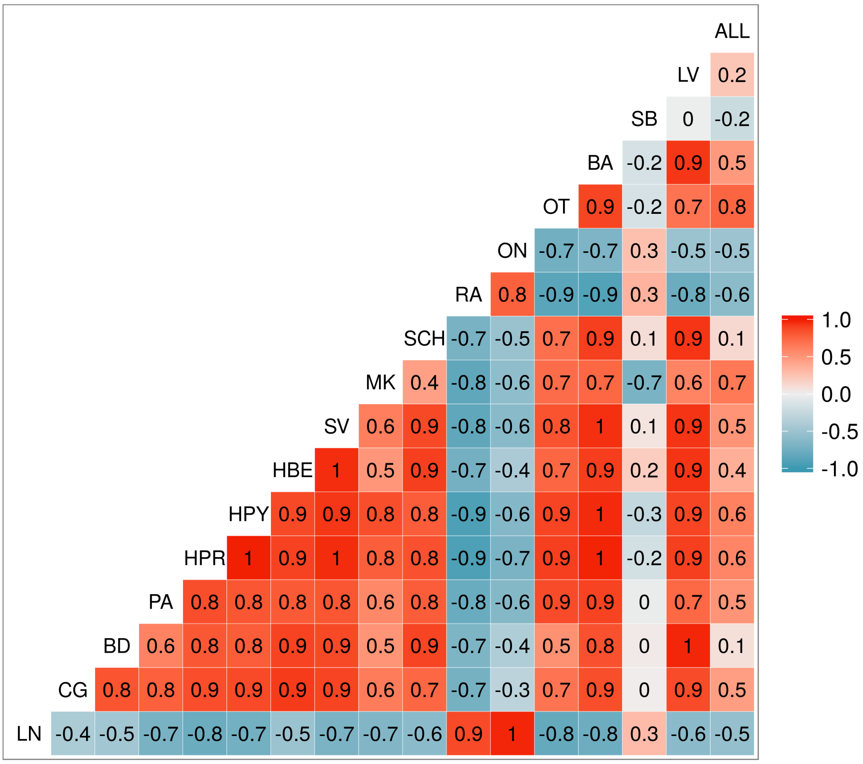


Figure 8.8: Modeled and observed catch trends of fish species reported in commercial landings of Lake Victoria from 1958 - 2015.

Table 8.2: Perfomance indicators (Coefficient of variation (CV), Model efficiency (E) and Pearson's correlation (r_{catch}) and ($r_{biomass}$)) in the Lake Victoria Atlantis model for the main commercial stocks. CV and E are only calculated for catch.

Fish Species	**CV**	**E**	r_{catch}	$r_{biomass}$
Nile perch	0.39	0.76	0.95	0.94
Dagaa	0.30	0.92	0.97	0.85
Nile tilapia	0.73	0.62	0.87	0.86
Other tilapia	0.69	0.63	0.81	0.54
Catfish	0.31	0.68	0.86	0.85
Lungfish	0.51	0.09	0.78	0.90
Haplochromines	0.95	0.54	0.81	0.82
Mormyrus	0.82	0.17	0.60	0.60
Synodontis	0.69	0.52	0.76	0.72
Schilbe	0.69	0.37	0.84	0.73
Barbus	0.99	0.11	0.46	0.54
Bagrus	0.52	0.63	0.81	0.88
Alestes	1.13	0.52	0.72	0.85
Labeo	0.46	0.64	0.84	0.86



ALL																
LV																0.2
SB															0	-0.2
BA														-0.2	0.9	0.5
OT													0.9	-0.2	0.7	0.8
ON												-0.7	-0.7	0.3	-0.5	-0.5
RA											0.8	-0.9	-0.9	0.3	-0.8	-0.6
SCH										-0.7	-0.5	0.7	0.9	0.1	0.9	0.1
MK									0.4	-0.8	-0.6	0.7	0.7	-0.7	0.6	0.7
SV								0.6	0.9	-0.8	-0.6	0.8	1	0.1	0.9	0.5
HBE							1	0.5	0.9	-0.7	-0.4	0.7	0.9	0.2	0.9	0.4
HPY						0.9	0.9	0.8	0.8	-0.9	-0.6	0.9	1	-0.3	0.9	0.6
HPR					1	0.9	1	0.8	0.8	-0.9	-0.7	0.9	1	-0.2	0.9	0.6
PA				0.8	0.8	0.8	0.8	0.6	0.8	-0.8	-0.6	0.9	0.9	0	0.7	0.5
BD			0.6	0.8	0.8	0.9	0.9	0.5	0.9	-0.7	-0.4	0.5	0.8	0	1	0.1
CG		0.8	0.8	0.9	0.9	0.9	0.9	0.6	0.7	-0.7	-0.3	0.7	0.9	0	0.9	0.5
LN	-0.4	-0.5	-0.7	-0.8	-0.7	-0.5	-0.7	-0.7	-0.6	0.9	1	-0.8	-0.8	0.3	-0.6	-0.5

Figure 8.9: Relationship between biomass trends of the fish groups in the Lake Victoria Atlantis model.(for Fish group code - see Table 1 for Functional group name).

8.4 Discussion

This study presents the first end-to-end ecosystem model ever for Lake Victoria. Physical-chemical processes, interaction of biological groups with the environment and impact of fishing fleets are simulated. Model validity is affirmed by its ability to produce distributions of nutrients, primary production and major fish species that generally match with observed data and those reported in the literature. The temporal trends of biomass of fish species match well with the variation of reported CPUE overtime. CPUE is used as an index of abundance as there exists no long term estimates of fish biomass in Lake Victoria. Biomass estimation from acoustic surveys in the lake only started in the year 1999 with gaps in-between due to erratic funding (Taabu-Munyaho et al., 2014). Even so, only two fish species (Nile perch and dagaa) are distinguished from the biomass pool and the surveys do not adequately cover shallow waters, hence the choice of CPUE as an index of abundance. Additional validation is provided by the good fit of modeled catch to observational time series data of fish species that are reported in landings. The performance indicators (CV and Pearson's correlation) indicate that the model compares well with available observational data.

The model run starts in 1958 thereby giving an opportunity to assess the impact of the introduced species (Nile perch and Nile tilapia) on the ecosystem. Other notable ecosystem perturbations that are simulated include the increase of nutrients (especially in inshore waters and gulfs) and increased fishing mortality. The steady increase of the nitrates is mainly attributed to point sources that bring in nutrients from the agricultural uplands, municipal waste that has increased several fold due to urbanization and human population growth (Hecky, 1993; Mugidde et al., 2005). Industrial waste water also forms a significant proportion of point sources of nutrients. A direct consequence of the elevated levels of nutrients is increased eutrophication that is usually manifested in excessive algal blooms that have characterized the lake in recent times. These can lead to depletion of oxygen in the water, which may cause death to aquatic animals (Ochumba, 1990; Okely et al., 2010; Talling, 1966). The water column effects of eutrophication is exacerbated by the decline of haplochromine cichlids that would otherwise feed on plankton, keeping their biomass at lower levels than the current status (Taabu-Munyaho et al., 2016).

Nile perch prefers haplochromine cichlids as primary prey (Goldschmidt et al., 1993). With the explosion of Nile perch, decimation of haplochromines was inevitable. This is especially so because haplochromines in Lake Victoria evolved without intense predation pressure and thus could not cope with the predation from the introduced perch. Fish that evolve under heavy predation pressure reproduce quickly (Lévêque, 1997), which is not the case for the haplochromines of Lake Victoria. The upsurge of Nile perch biomass has also profound implications for other species such as the piscivorous fish like *B. docmak* which preys on the haplochromines.

The biomass of most groups stays relatively steady until the 1980s. Thereafter a decline in many groups is witnessed with the exception of Nile perch which have a contrary trend. This scenario is driven by the predation of Nile perch on most fish species. This observation brings to the fore the importance of predator prey interactions in Lake Victoria. Several studies have attributed the decline of other species to the Nile perch (Goldschmidt et al., 1993; Kaufman, 1992; Kaufman and Cohen, 1993; Kitchell et al., 1997). The present study supports this with Nile perch biomass growth exhibiting negative correlation with other species. Inherently this is an ecological disaster that could possibly have been averted if the fisheries managers of the time had had prior knowledge of the “adverse" impacts of introducing the perch to Lake Victoria. It took slightly over two decades for the Nile perch to get established and completely dominate a system that had taken over 750,000 years to evolve (Greenwood, 1974; Witte et al., 1992b). Even so, the sustainability of the Nile perch stock is threatened by the danger of exhausting its food, as demonstrated in the model. That notwithstanding, the species interaction information availed in this study can be used as guide to come up with management interventions that improve the ecosystem’s resilience and services.

Landings data show that catch of the most important commercial species (Nile perch, Nile tilapia and dagaa) steadily increased in the 1980s and stabilized since the early 1990s. However model results indicate that the biomass of these species has been on the decline, information that is corroborated with the observed catch rates (CPUE). The apparent steady catch despite the dwindling stocks is maintained by increasing fishing effort (mortality). It is therefore important for management to institute measures that would that will decease fishing mortality if maintaining healthy and sustainable stocks is to be achieved. However reducing fishing effort on the commercial species should not be the only goal, especially for the predatory Nile perch. This is because, as demonstrated by the simulations, Nile perch is highly dependent on the haplochromine stock, for survival. In the coming years it is likely that there will be oscillations of Nile perch and haplochromine biomass. The model gives that indication with the haplochromine stock showing recovery with the decline of Nile perch. Given the complex interactions and responses exhibited in Lake Victoria, an ecosystem based approach to management is required and the herein reported Atlantis model provides a vantage point for a broader view of the effects of any interventions on an ecosystem-wide scale. This will mean a paradigm shift from the current regulation measures that are geared to controlling fishery inputs and are species specific (Downing et al., 2014).

8.5 Conclusion

Lake Victoria is vast and of immense ecological and socio-economic significance for the riparian communities. However, sustainable management of the lake has been a challenge because of inadequate information about the resource dynamics. This study developed an Atlantis ecosystem model to simulate the physical, chemical and biological processes and how the ecosystem responds to anthropogenic activities. Reliability of the model is supported by the ability of the simulations to match well with available observational data sets. Over the model period, key perturbations to the system include elevated eutrophication/pollution, introduction of invasive species and increased fishing pressure. Model results show elevated nutrients and primary production in inshore areas and gulfs that can be linked to point sources of pollution and limited flushing (especially Nyanza gulf). The introduced Nile perch has a strong negative correlation with haplochromine species whose biomass declines sharply as the former's abundance increases. This implies that we may expect oscillations of Nile perch and haplochromine biomass going forward. The same is true for other species with the exception of dagaa which flourishes as Nile perch decimates haplochromines that compete with them. The model highlights the significance of predator-prey relationships and the impact of introduced species, information that is critical for instituting sustainable measures for managing the fisheries and ecosystem of Lake Victoria. The model provides a platform where such measures can be “road tested" before actual implementation.

8.6 Acknowledgement

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9

Paper III

Prediction of Lake Victoria's response to varied fishing regimes using the Atlantis ecosystem model

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Abstract

Fisheries management of Lake Victoria has evolved from traditional belief systems of local fishing communities to one with formal national and regional institutions. The impact of management interventions utilized so far is difficult to assess. With the advent of whole ecosystem models, management strategy evaluation has taken root elsewhere. The first such model for Lake Victoria ecosystem has been developed to simulate the chemical, biophysical as well fishing processes. We use the Lake Victoria Atlantis model to simulate the ecosystem under alternative fishing scenarios as compared with the current harvest levels. The effects of the different scenarios are tested using six common ecosystem-level indicators. Predictions show that no particular scenario excels in all the six indicators. However, looking at all the indicators simultaneously, the scenario where halting harvesting of the main prey species (haplochromines) results in the best ecosystem performance, highest yield of commercially important species and possibly has minimal 'socio-economic cost' implication. Findings of this study reinforce the need for an ecosystem approach to fisheries management in Lake Victoria.

Keywords: Atlantis, Ecosystem-based fisheries management, Lake Victoria, Ecosystem indicators

9.1 Introduction

Lake Victoria supports the largest inland fishery and accounts for about 1% of the world's capture production (Awange and Ong'ang'a, 2006; World Bank, 2012). In the last century, it changed from a multi-species fishery to one that is dominated by the introduced Nile perch (*Lates niloticus*), Nile tilapia (*Oreochromis niloticus*) and the native silver cyprinid (*Rastrineobola argentea*). Although, the introduction of alien species was responsible for the destruction of the indigenous multi-species fishery, it transformed it from subsistence to a commercial enterprise giving riparian countries over USD 250 million annually in export earnings (Downing et al., 2014; Manyala and Ojuok, 2007). The apparent lucrative industry attracted new entrants and increased investment in the fishery. Fishing effort has continually increased since the Nile perch boom in the 1980s resulting in decline of the fish stocks as corroborated by decreasing catch rates (Mkumbo and Mlaponi, 2007; Muhoozi, 2002; Njiru et al., 2014).

Fisheries management in Lake Victoria has undergone different phases utilizing a range of strategies. Before the colonial administration, it was a small scale fishery, managed by traditional belief systems of the fishing communities (Graham, 1929). Afterwards formal institutions (research and management) established in the riparian countries took over the management of the lake (Jackson, 2000). In the more recent times, it was recognized that the trans-boundary resource required a common management policy and hence the establishment of the Lake Victoria Fisheries Organization (LVFO) in 1994 to coordinate and manage fisheries resources of the lake (LVFO, 2007). Over the years several management measures have been introduced in the fishery aimed at sustainable utilization of the resource. Existing measures include mesh sizes limits, ban of beach seining and slot size regulation for the Nile perch (Njiru et al., 2014). Almost all of the measures are aimed at regulating the fishing inputs and much less outputs (Downing et al., 2014). However, stocks have continued to decline bringing into question the effectiveness of the instituted management measures.

Elsewhere management strategy evaluation (MSE) has taken root (Punt et al., 2016). MSE involves assessing the direct and indirect effects of a different management options to assist determine the most appropriate alternative to meet the operational objectives of the fishery (Bunnefeld et al., 2011; Fletcher and Bianchi, 2014; Fulton et al., 2014; Punt et al., 2001; Smith et al., 2007). MSE requires an operating model representing the underlying dynamics of the fishery resource with which different management scenarios can be simulated. The first such model (Atlantis) has been developed to simulate the chemical, biophysical and fishing process of the Lake Victoria ecosystem (Nyamweya et al., 2016b). Atlantis is an end to end model that considers all aspects (biophysical, economic and social) of an ecosystem (Fulton et al., 2011). We use the Atlantis model for Lake Victoria to test the effect of different fishing scenarios on the ecosystem function and fisheries production. The scenarios tested include varied fishing pressure for Nile perch (the main predator at the top of the food chain), key prey species (haplochromines) and other species. The effect of fishing pressure on Nile perch is explored because of its commercial significance and concerns of it being over fished as evidenced in the decline of observed biomass and catch rates (Njiru et al., 2014). Fishing pressure on haplochromines is varied to test their impact on the abundance of Nile perch and other predatory fish. For other species whose contribution to catch has been dwindling, a simulation is done with reduced harvest pressure to help decipher the impact of intense fishing on them. The aim is to identify a fishing strategy that: 1. optimizes yield of commercially important species, 2. is easy to implement with minimal alienation of fishing communities and 3. enhances ecosystem function.

9.2 Materials and methods

The Lake Victoria ecosystem is simulated 20 years into the future assuming different fishing scenarios using the Atlantis modeling framework. The biophysical components and ecosystem functioning of the developed model are described in Nyamweya et al. (2016b). Complete model set up, data and output files used in the simulations are available at `https://figshare.com/articles/Lake_Victoria_Atlantis_model_files/4036077`. The Lake Victoria Atlantis model has 12 unique spatial areas (Figure 9.1) and a total of 34 of biological groups (i.e 17 fish, 1 bird, 1 reptile, 9 invertebrate and 6 primary producer groups) (Table 9.1).

Distribution of nutrients, plankton and temperature are driven by an underlying hydrodynamic flow derived from a Regional Oceanographic Model System (ROMS) of the lake (Nyamweya et al., 2016a). Fishing is done with gill nets, long lines, small seines and inshore fleets. Gill nets target most species but the bulk of the catch is Nile perch. Long lines primarily target Nile perch but other fish like the catfishes *Clarias gariepinus, Bagrus docmak, and Synodontis victoriae* are landed by this fleet. Small seines mainly target dagaa when deployed at night using light attraction. When they are deployed without the aggregation lighting or during the day, haplochromines form a significant proportion of the catch. The inshore fleet is an assortment of several gear operating near shore and usually targets all species in such areas. Gill nets and inshore fleets exhibit a normal selection pattern (Equation 9.1) (Millar and Fryer, 1999) whereas long lines and small seine fleets have a size

Table 9.1: Biological groups in the Lake Victoria Atlantis model.

Code	Model Group	Group type	Modeled as
LN	Nile perch (*Lates niloticus*)	Fish	Age-structured
CG	African catfish (*Clarias gariepinus*)		
BD	*Bagrus* (*Bagrus docmak*)		
PA	Lungfish (*Protopterus aethiopicus*)		
HPR	Predatory haplochromines		
HPY	Phytoplantivorous haplochromines		
HBE	Benthivorous haplochromines		
SV	*Synodontis* (*Synodontis Victoriae*)		
MK	*Mormyrus* (*Mormyrus kanume*)		
SCH	*Schilbe* (*Schilbe intermedius*) *sp.*		
RA	Dagaa (*Rastrineobala argentea*)		
ON	Nile tilapia (*Oreochromis niloticus*)		
OT	Other tilapia		
BA	*Barbus* (*Barbus altinialis*)		
SB	Small *Barbus*		
LV	*Labeo* (*Labeo victorianus*)		
ALL	*Alestes*		
REP	Reptiles	Reptile	
BFE	Birds	Bird	
MIN	Macroinvertebrates	Invertebrate	Biomass pool
BFF	Benthic filter feeder		
BFS	Shallow filter feeder		
BFD	Deep filter feeder		
BG	Benthic grazer		
ZL	*Caridina nilotica*		
DF	Dinoflagellates		
ZM	Mesozooplankton		
ZS	Microzooplankton		
MB	Microphtybenthos	Primary producer	
MA	Macroalgae		
PL	Large phytoplankton		
PS	Pico-phytoplankton		
PB	Pelagic Bacteria		
BB	Sediment Bacteria		
DL	Labile detritus	Detritus	
DR	Refractory detritus		

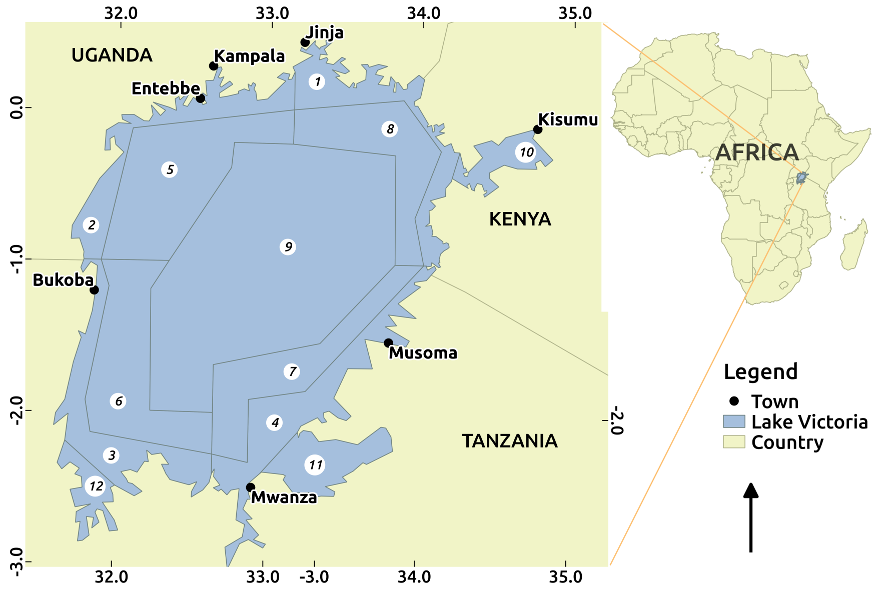

Figure 9.1: Lake Victoria in Africa. The numbers indicate the dynamic spatial areas of the Lake Victoria Atlantis model.

based logistic selectivity (Equation 9.2). In both equations q_{FX_i} is the selectivity of gear with regard cohort i of vertebrate group FX and $l_{i,FX}$ is the length of vertebrate from cohort i.

$$q_{FX_i(gillnet,inshore)} = \exp\left(-\frac{(l_{i,FX} - \mu_i)^2}{2 \cdot (\sigma_i)^2}\right) \tag{9.1}$$

where μ_i is the optimum length for being caught by a fishery of the ith age class of vertebrate group FX, σ_i is the selectivity coefficient (spread of the curve) for the fishery on the ith age class of vertebrate group FX,

$$q_{FX_i(longline,smallseine)} = \big(1 + exp\big(- \beta_i \cdot \big(l_{i,FX} - \alpha_i\big)\big)\big)^{-1} \tag{9.2}$$

where α_i is the inflection point or the length at which 50% of the population is selected for the fishery of the ith age class of vertebrate group FX, β is the shape parameter (steepness) of the logistic curve

The impact of increasing or decreasing fishing mortality for different groups was tested. Considering all the fish groups, changing mortality options are numerous. In this paper we varied fishing mortality of the key prey species (haplochromines), the top predator (Nile perch) and other species. The other species group include: Nile tilapia, other tilapia, catfish, lungfish, *Mormyrus, Synodontis, Schilbe, Barbus, Bagrus, Alestes* and *Labeo.* Simulations were done assuming different fishing scenarios i.e.

1. maintaining current fishing mortalities of all fish groups ($F_{current}$),
2. no fishing of haplochromines ($F0_{haplochromines}$),
3. no fishing of Nile perch ($F0_{Nileperch}$),
4. reducing fishing pressure on Nile perch by 40% ($F0.6_{Nileperch}$),

5. increasing fishing pressure on Nile perch by 40% ($F_{1.4_{Nileperch}}$) and
6. reducing fishing pressure on other fish groups by 40% ($F_{0.6_{others}}$).

To assess the impact of the different simulated fishing regimes we use six ecosystem indicators i.e. Biomass-weighted average weight of fish ($\overline{W}_b$), Biomass-weighted average age of fish ($\overline{A}_b$), Number-weighted average weight of fish ($\overline{W}_n$), Mean trophic level in catch (Tl_{catch}), reorganization index (BI) and proportion of predatory fish (Smith et al., 2015). Apart from the BI, all ecosystem indicators are calculated for the year 2035 to show the longterm effects of the alternative fishing scenarios tested. $\overline{W}_b$ is hypothesized to be lower in high fishing pressure scenario due to the preferential removal of larger fish from the ecosystem. This indicator detects changes in the ecosystem structure due to fishing (Smith et al., 2015) and is calculated as the average size of each species weighted by the biomass contribution of that species (Equation 9.3).

$$\overline{W}_{b,2035} = \sum_i \left(\overline{W}_i \cdot \frac{B_i}{B} \right)_{2035} \tag{9.3}$$

where $\overline{W}_i$ and B_i are the average weight of an individual in functional group i and the total biomass of i respectively whereas B is the total biomass of all fish groups in 2035. The average weight of fish $\overline{W}_n$ is also calculated using numbers instead of biomass since the average weight of a fish in the system may be affected by changes in average size within each species or changes in species composition.

$\overline{A}_b$ is the mean life-span of fish in the system and can be an indicator of turnover rate (Smith et al., 2015). This index can be used to measure system stability and resilience to perturbations as it reflects the relative abundance of long and short-lived species and is calculated as shown in Equation 9.4. It is hypothesized that $\overline{A}_b$ will decrease with increasing fishing pressure long-lived species (Anderson et al., 2008).

$$\overline{A}_{b,2035} = \sum_i \left(\overline{A}_i \cdot \frac{B_i}{B} \right)_{2035} \tag{9.4}$$

where $\overline{A}_i$ is the average age of an individual fish in group i. B_i and B are the same as in Equation 9.3

Tl_{catch} represents the average trophic level of landed fish. It is calculated by the average trophic level of landed functional groups weighted by their biomass contribution to total catch in the final year of simulation (Equation 9.5). Trophic level values are derived from Froese and Pauly (2016). It is hypothesized that the value of this indicator will decrease with increasing fishing of higher trophic level species.

$$Tl_{catch,2035} = \frac{\sum_i (Tl_i \times B_{i,2035})}{\sum_i B_{i,2035}} \tag{9.5}$$

Proportion of predatory fish can be used as an indicator of system stability and biodiversity as a decline of this group can lead to increased variability of prey species (Smith et al., 2015). Increased fishing on this group is hypothesized to reduce their proportion in the ecosystem.

The reorganization index (BI) calculated as the sum, across all functional groups, of the absolute difference in the relative biomass (B_i/B_{Total}) of each functional group i at the end of the first year (2015) and at end of the simulation (2035) is used to identify fishing scenarios with the biggest impact on system organization (Equation 9.6, adapted from Morzaria-Luna et al. (2013)). (BI) is hypothesized to increase with increasing proportion of predatory fish i.e. with reduced fishing pressure on the group.

$$BI = \sum \left| \left(\frac{B_i}{B_{Total}} \right)_{2015} - \left(\frac{B_i}{B_{Total}} \right)_{2035} \right| \tag{9.6}$$

Principal component analysis (PCA) was used to visualize the relationship between fishing scenarios and change in ecosystem indicators.

9.3 Results

The response of Lake Victoria ecosystem to various fishing scenarios is described based on Atlantis model simulations.

9.3.1 Biomass and catch trends

Maintaining status quo ($F_{current}$): Predictions based on the status quo (mantaining the current fishing mortality) show that the biomass of Nile perch and its main prey (haplochromines and *Caridina*) will remain stable around their current levels over the next 20 years (Figure 9.2). However other fish species including dagaa will decline below their current levels. Landings of Nile perch, haplochromines and *Synodontis* remain stable under the current fishing level. The rest of the species landings decline in the long run (Figure 9.3).

No fishing of Nile perch ($F0_{Nileperch}$): If fishing is halted on the Nile perch, initially its biomass increases to about double the current biomass in about five years and then declines drastically to below the current level. This scenario has the worst effect on haplochromines whose biomass dives to the lowest level in the prediction period. With the exception of dagaa, other fish species also exhibit their greatest decline in this scenario. Notable decline is also seen in *Caridina*, another key prey for juvenile Nile perch.

Reducing fishing pressure on Nile perch by 40% ($F0.6_{Nileperch}$): Like in the previous scenario, the biomass of Nile perch increases steadily to about 1.4 times there current level in about a decade. Thereafter, biomass declines slightly and stabilizes at about the current level. On the other hand haplochromines and *Caridina* show a steady decline with the increasing perch biomass; a trend that is also observed in the rest of the fish groups. In the long term, Nile perch and haplochromines have their lowest catch with the except for the scenarios where the two groups are not fished. The rest of the fish groups also witness their lowest catch in this scenario.

Increasing fishing pressure on Nile perch by 40% ($F1.4_{Nileperch}$): Increasing fish mortality on Nile perch by 40% drastically decreases its biomass whereas the biomass of haplochromines and other species exhibit their highest increase in the simulation. This shows a negative correlation between these species and Nile perch abundance. However, Nile perch exhibits a positive correlation with Nile tilapia and dagaa. The increased fishing pressure results in the second highest long term catch of Nile perch as depicted in Figure 9.3. Dagaa records the lowest catch among all the scenarios. Just like in biomass, haplochromines long term catch is highest in this scenario. Increasing fishing pressure on Nile perch by 40% results in increased catch of the other species.

No fishing of haplochromines ($F0_{haplochromines}$): Stopping fishing of haplochromines results in the highest biomass levels of Nile perch and dagaa (the main commercial species) in the long run. The described trends are also reflected in the predicted catch (Figure 9.3) with Nile perch and dagaa catches being highest in this scenario where haplochromines. This represents the most desirable scenario because haplochromines are of low value.

Reducing fishing pressure on other fish groups by 40%

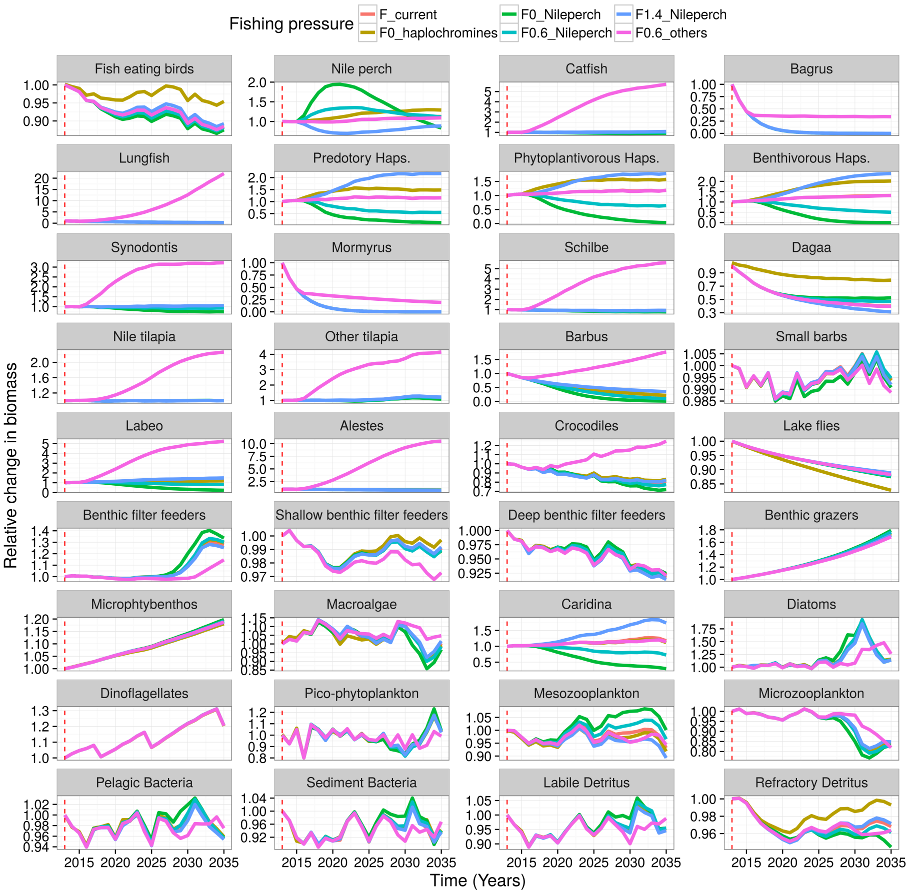

Figure 9.2: Evolution of biomass of biological groups in the Lake Victoria Atlantis model under different fishing scenarios.

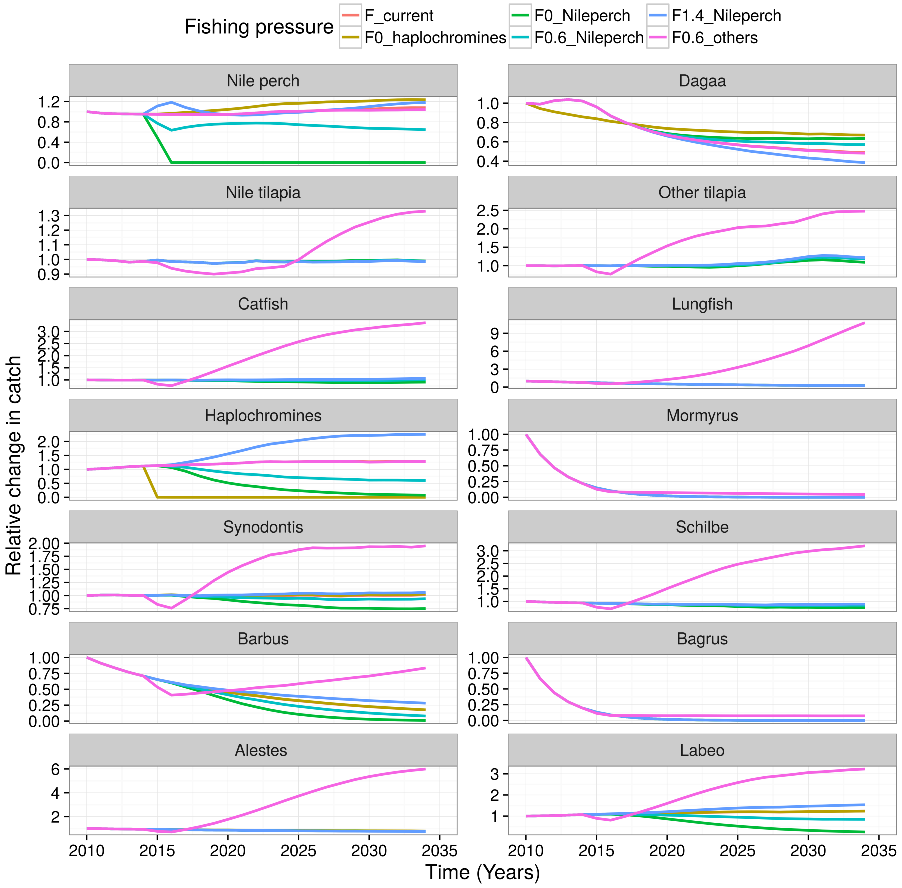

Figure 9.3: Catch predictions of the Lake Victoria Atlantis model under different fishing scenarios.

($F_{0.6_{others}}$): Reduced fishing pressure on other fish groups results in their increased biomass and catch. This is especially so for catfish, lungfish, *Synodontis, Schilbe*, Nile tilapia, other tilapia, *Labeo* and *Alestes* whose biomass increases several times. This is the scenario where the 'others' group exhibit high recovery indicating their sensitivity to fishing pressure.

Ecosystem performance indicators

The relative change in average weight and age of individual fish in each functional group under different fishing scenarios is depicted in Figures 9.4 and 9.5 respectively. There is a relative gain in both average weight and age of individual Nile perch when either their fishing pressure is increased by 40% or when fishing of haplochromines is halted. This is so because the two scenarios result in increased abundance of haplochromines and consequently Nile perch have plenty of food which enhances their growth. However the contrary is true when there is a reduction/halting of fishing on Nile perch. Haplochromines average weight increases with reduction of fishing on them or when harvesting of Nile perch is intensified. These however reduce in average age. With reduced harvesting of Nile perch, a drop in average weight of individual haplochromines is observed. In all the scenarios, the average weight of dagaa falls below the current levels. Overall, the system average weight of individuals is highest when fishing on either Nile perch or other species is reduced by 40%, followed by when haplochromines are not harvested and when fishing on Nile perch is increased by 40% respectively (Table 9.2). The average weight of individuals is lowest when Nile perch fishing is halted. A similar pattern is witnessed on the average weight normalized by abundance. The average age is highest when there is no fishing of Nile perch and lowest when

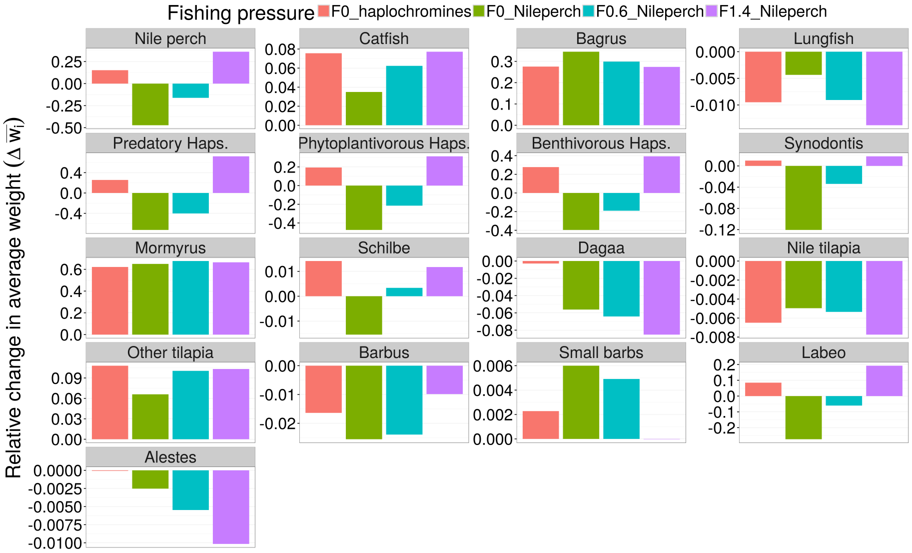

Figure 9.4: Relative change in the average weight of individuals in each fish group under different fishing scenarios.

haplochromines are not harvested. The average trophic level of catch is highest when haplochromines are not fished and lowest when Nile perch are not fished. The proportion of predatory fish is highest when there is no/or reduced fishing of Nile perch. The greatest change in ecosystem structure occurs when fishing on Nile perch is halted followed by when there is increased harvesting of the species (i.e. extreme changes in fishing pressure on Nile perch affects the ecosystem organization structure most). The ecosystem organization structure is least disturbed in the scenario where haplochromines are not harvested.

PCA results indicate that ecosystem indicators change variedly in the different fishing scenarios (Figure 9.6). PC1 and PC2 account for 70% and 24% respectively of the total variation with each of the indicators having similar contribution (as depicted by the length of the red arrows). This implies that no particular indicator is superior

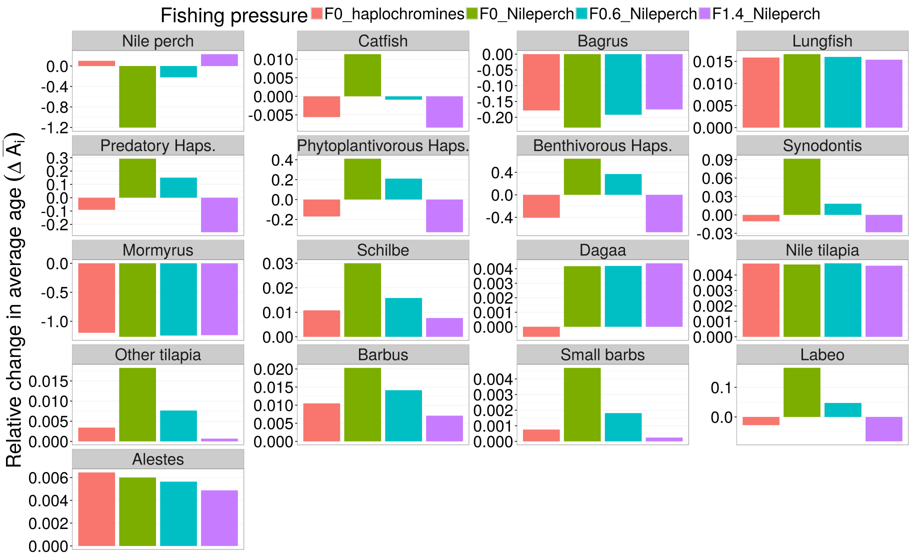

Figure 9.5: Relative change in the average age of individuals in each fish group under different fishing scenarios.

Table 9.2: Indicators of performance metrices for ecosystem function and structure under different simulated fishing scenarios

Indicator	$F0_{haplochromines}$	$F0_{Nileperch}$	$F0.6_{Nileperch}$	$F1.4_{Nileperch}$	$F0.6_{others}$	$F_{current}$
$\overline{W}_{b(g)} \times 10^3$	1.55	1.06	1.64	1.53	1.65	1.20
$\overline{A}_{b(yrs)}$	1.31	1.68	1.39	1.56	1.45	1.39
$\overline{W}_{n(g)}$	1.50	1.21	1.45	2.06	1.87	1.50
Tl_{catch}	3.86	3.21	3.65	3.82	3.73	3.80
Proportion of predatory fish	0.30	0.44	0.43	0.25	0.33	0.37
Reorganization index (BI)	0.067	0.105	0.080	0.089	0.075	0.06

and hence the need to employ a number of them in evaluating effects of different fishing scenarios on the ecosystem. The figure shows that scenarios where haplochromines are not harvested or fishing pressure is reduced on other species result in higher average weight of individuals in the ecosystem and mean trophic level of catch. The reverse is true when Nile perch is not harvested, a scenario that also results in relatively higher proportion of predatory fish in the population, increased average age of individuals and the greatest change in ecosystem structure.

9.4 Discussion

It has been a challenge to implement fisheries management interventions in Lake Victoria because of the real implications of threatening livelihoods of small scale fishers and communities that almost entirely depend on fishing for food and income. The same fear is also true for fish processors who over-invested in the factories who would almost certainly close shop if production was to be scaled down. For the managers, it has been daunting coming with a management strategy that optimizes conservation of fish stocks and ecosystem function without jeopardizing livelihoods of the fishing communities at least in the near term (Geheb et al., 2007). Previous efforts to manage the fisheries have been species specific with the assumption that fishing pressure is the most important driver of stock abundance (Kolding et al., 2008). Consequently these measures have been advocating for cutting down the harvesting capacity of the commercial species of which, Nile perch (the most important commercially), is a top predator. This is evidenced with the current LVFO Nile perch management plan that recommends no further increase in fishing pressure (LVFO, 2015). The shortcoming of this approach is that it does not envisage the effect increased

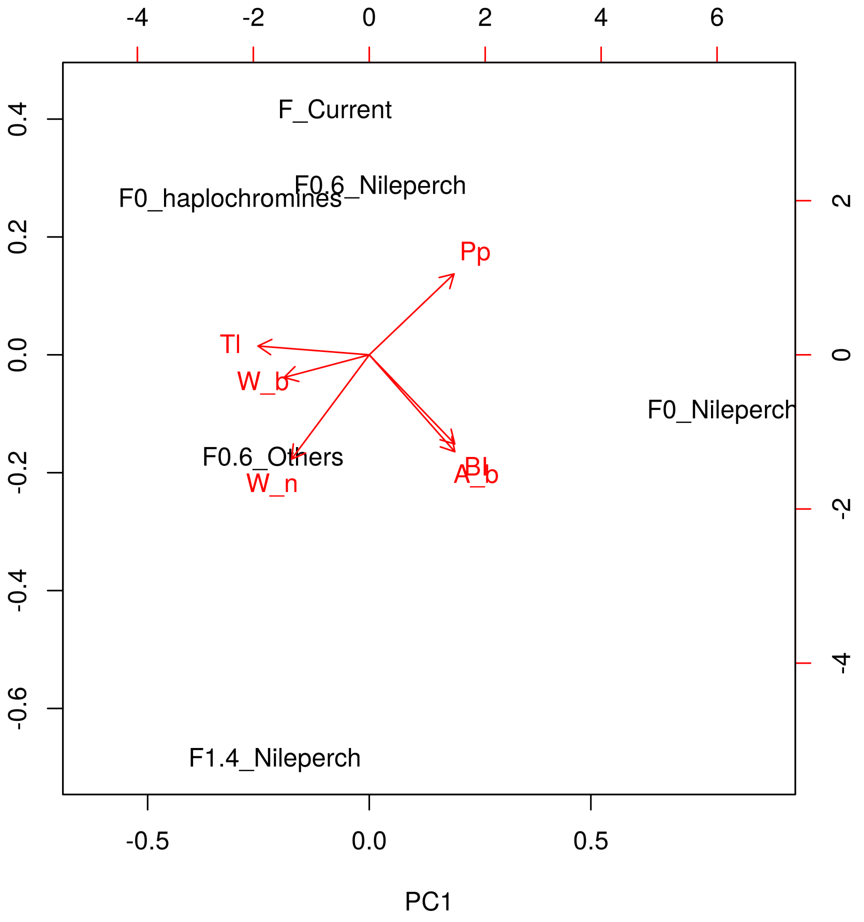

Figure 9.6: Principal component analysis (PCA) biplot of the different ecosystem change indicators under different fishing scenarios. The indicators are Biomass-weighted average weight of fish (W_b), Number-weighted average weight of fish (W_n), Biomass-weighted average of fish (A_b), Mean trophic level in catch (Tl), proportion of predatory fish (Pp) and reorganization index (BI).

Nile perch abundance has on other species. In this study we rely on the first end to end ecosystem model (Atlantis) for Lake Victoria to project a holistic view of the impact of the current fishing as compared with alternative fishing scenarios with the aim of identifying the most appropriate strategy that maximizes fisheries production without adversely disturbing the socio-economic status quo.

Forecasts predict that if the current fishing mortality level for the all fish groups were to be maintained, the biomass of Nile perch and its main prey (haplochromines) will not decline further, but will remain stable, registering some slight gain. This observation is in contrast with other studies (Mkumbo and Marshall, 2015) but is rather expected given the resurgence of the prey species that had declined to very low levels with the increase of Nile perch biomass in the 1980s and 1990s. The resurgence of the haplochromines and decline of Nile perch gives an important clue that predator-prey relationship is significant and should be taken into consideration when formulating management interventions. The implication thereof is that ecosystem approach to fisheries management in Lake Victoria should be given prominence if overall and long term sustainability of the resource is to be achieved.

A simulation with a 40% reduction of fishing mortality on Nile perch increases its biomass in the near term but declines thereafter. The landings with this scenario are much less than if the current fishing pressure is maintained. Furthermore, the biomass of the haplochromines greatly declines and hence this is not a desirable scenario. These findings give caution to the Lake Victoria fisheries management that is currently pursuing the option of reducing harvesting pressure on Nile perch whose decision seems to be informed by single species steady state models (LVFO, 2015). On the other hand, increasing fishing mortality by the same margin will only slightly increase landings above the current harvest levels. Although it seems counterintuitive, increasing fishing mortality will relief haplochromines of predation pressure, consequently increasing their intrinsic growth rates and abundance. In turn Nile perch will get abundant food enhancing their growth and reproduction. Halting fishing of haplochromines is the best alternative given that it has the most positive impact of the more valuable Nile perch in both the standing stock and landings. This scenario also increases the abundance of dagaa, the second most important commercial species. The reason for this is that Nile perch predation on dagaa is reduced when their preferred prey (haplochromines) are plentiful.

The effect of the explored fishing scenarios on the ecosystem is evaluated by a suite of indicators. No fishing scenario had the greatest score across all indicators meaning that there are trade-offs in opting for any of the management scenarios. It is observed that some fishing scenarios enhance ecosystem function but will not necessary translate into increased yield of high commercial value species. For instance, a reduction of fishing pressure on other species (other than Nile perch, haplochromines and dagaa) by 40% results in the highest average weight of individuals in the ecosystem but not the overall landings of commercial species. Other fishing scenarios score variously on the indicators used. This means that the use of a single indicator on choosing the best fishing scenario may be misleading and can lead to undesirable outcomes. In light of this, we find that when considering all ecosystem performance indicators simultaneously, the scenario of not harvesting haplochromines results in the best ecosystem function (lowest reorganization index, highest trophic level in catch, high average weight of individual fish and low turn-over rate) and highest yield of the commercially important species. Additionally, haplochromines are low value species and generally not targeted by many fishers. Most of their landings are by-catch of the dagaa fishery when appropriate lighting (fish aggregation device) is not incorporated in the fishing gear. Use of appropriate fishing methods that minimize by-catch of haplochromines could be the best strategy for management because the cost (trade-off) of effecting such a measure on the fishers is quite low. Apparently, it is the cheapest, most effective and least socio-economically disruptive harvest control for Lake Victoria.

9.5 Conclusion

Local communities around Lake Victoria depend on the fisheries for their survival. Consequently, the impact of management interventions on the resource and the people needs to be well evaluated before implementation. We use a whole ecosystem model (Atlantis) to predict the effect of different fishing scenarios on production. The impact of these alternative scenarios on the system function and structure is evaluated using ecosystem performance indicators. Considering the evolution of biomass and catch of fish groups simultaneously with the ecosystem performance indicators, a fishing strategy that stops harvesting of haplochromines while maintaining the current harvest levels for the rest of the fish groups is recommended. The model predicts that this strategy will lead to increased production of commercially important species, enhanced ecosystem function and have only a minimal 'socio-economic cost'.

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