Environmental Modelling & Software 86 (2016) 158–167

Contents lists available at ScienceDirect

Environmental Modelling & Software

journal homepage: www.elsevier.com/locate/envsoft

Exploring Lake Victoria ecosystem functioning using the Atlantis modeling framework

Chrispine Nyamweya [a], [b], [*], Erla Sturludottir [b], Tumi Tomasson [c], Elizabeth A. Fulton [d], Anthony Taabu-Munyaho [e], Murithi Njiru [a], Gunnar Stefansson [b]

[a] Kenya Marine and Fisheries Research Institute, Kenya
[b] University of Iceland, School of Engineering and Natural Sciences, Iceland
[c] United Nations University Fisheries Training Programme, Marine Research Institute, Iceland
[d] CSIRO Oceans and Atmosphere Research, Hobart, Australia
[e] National Fisheries Research Institute, Jinja, Uganda

A R T I C L E I N F O

Article history:
Received 20 May 2016
Received in revised form
20 August 2016
Accepted 28 September 2016

Keywords:
Atlantis
Ecosystem
Invasive species
Lake Victoria
Simulation
Management

A B S T R A C T

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.

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, 2007). 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., 1992). 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., 1992). 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, 2013; Kitchell et al., 1997). Another challenge is the booming fishing industry that evolved around the

---

[*] Corresponding author. Kenya Marine and Fisheries Research Institute, Kenya.
E-mail address: sanychris@yahoo.com (C. Nyamweya).

http://dx.doi.org/10.1016/j.envsoft.2016.09.019
1364-8152/© 2016 Elsevier Ltd. All rights reserved.

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.

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

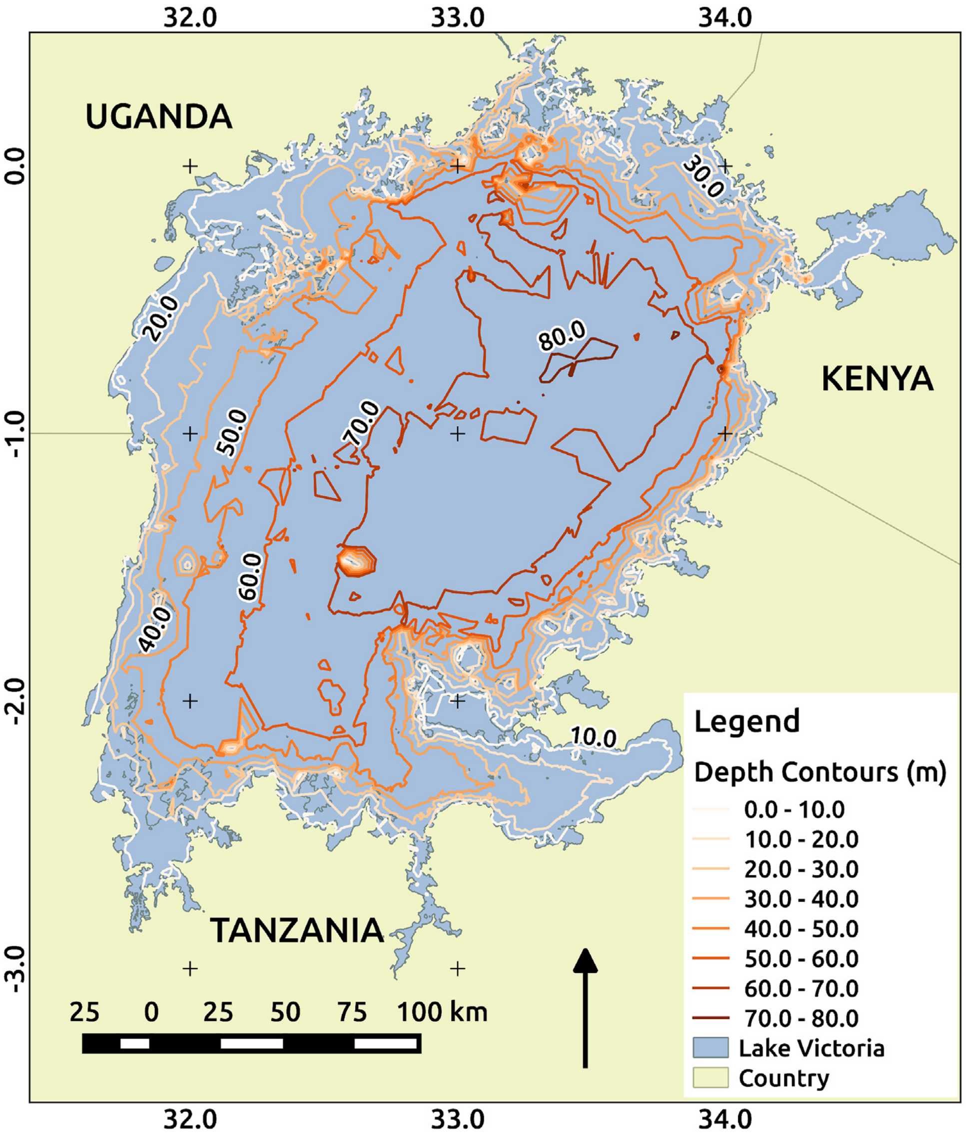


Fig. 1. The topography/bathymetry of Lake Victoria and the three surrounding countries.

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 h 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.

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 (Figs. 1 and 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).

2.2. Model structure

Given the heterogeneity, the Lake Victoria Atlantis model is partitioned into areas that would represent unique habitats based on depth (Fig. 1), species composition, physical-chemical parameters, fisheries management zones 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 (Fig. 2). Each of the inshore and coastal areas are divided into four regions,

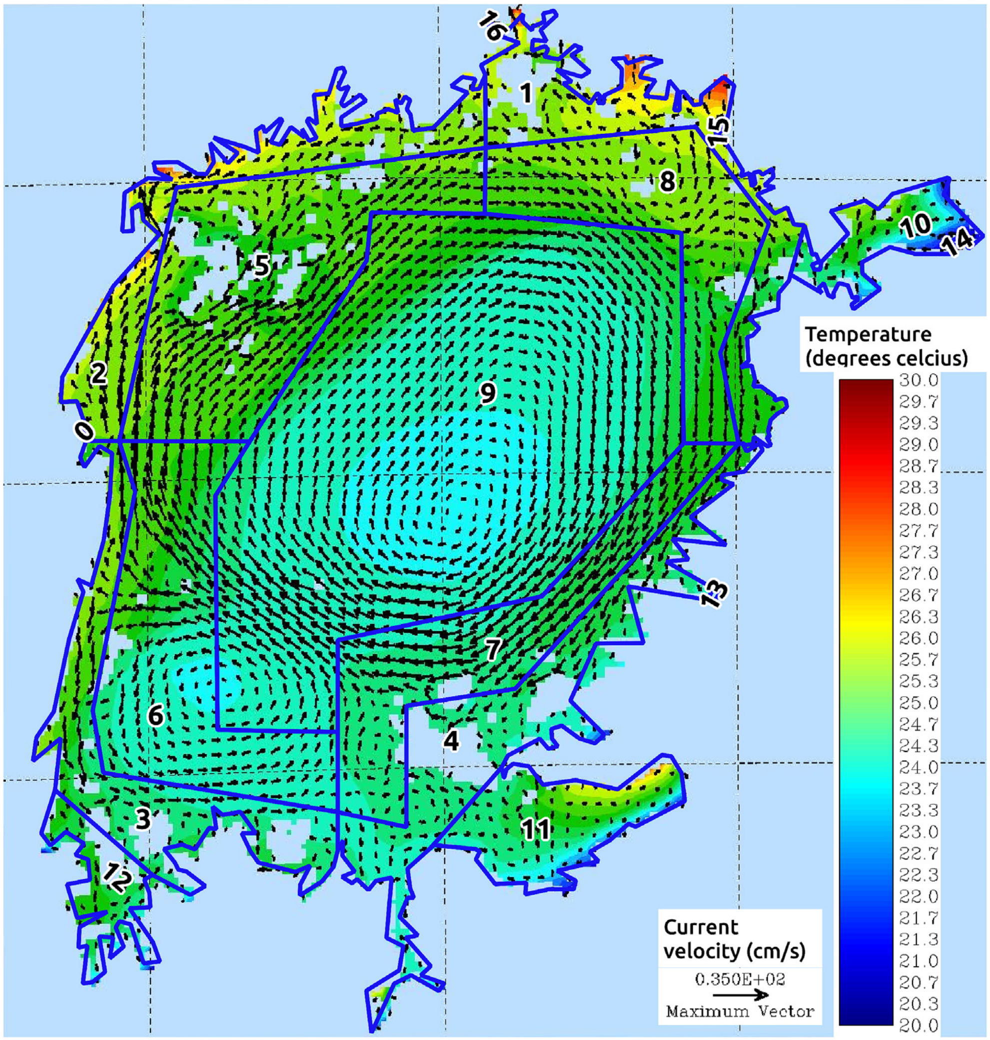


Fig. 2. Spatial areas, dynamic (1–12) and boundary (0, 13–16) boxes used for creating the box geometry for the Lake Victoria Atlantis model. Surface temperature and currents for 22nd January 2009 are also depicted (as an example of the physical regime).

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 south-eastern corner of the lake and is up to 30 m 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 Fig. 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., 2016). 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 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. Fig. 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., 2012). The interactions are based on stomach content analysis survey data supplemented by information obtained from FishBase (Froese and Pauly, 2015). 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 (1)) and modeling efficiency (E) as proposed by Olsen et al. (2016).

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

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

Modeling efficiency is computed as described by Nash and Sutcliffe (1970) (equation (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.

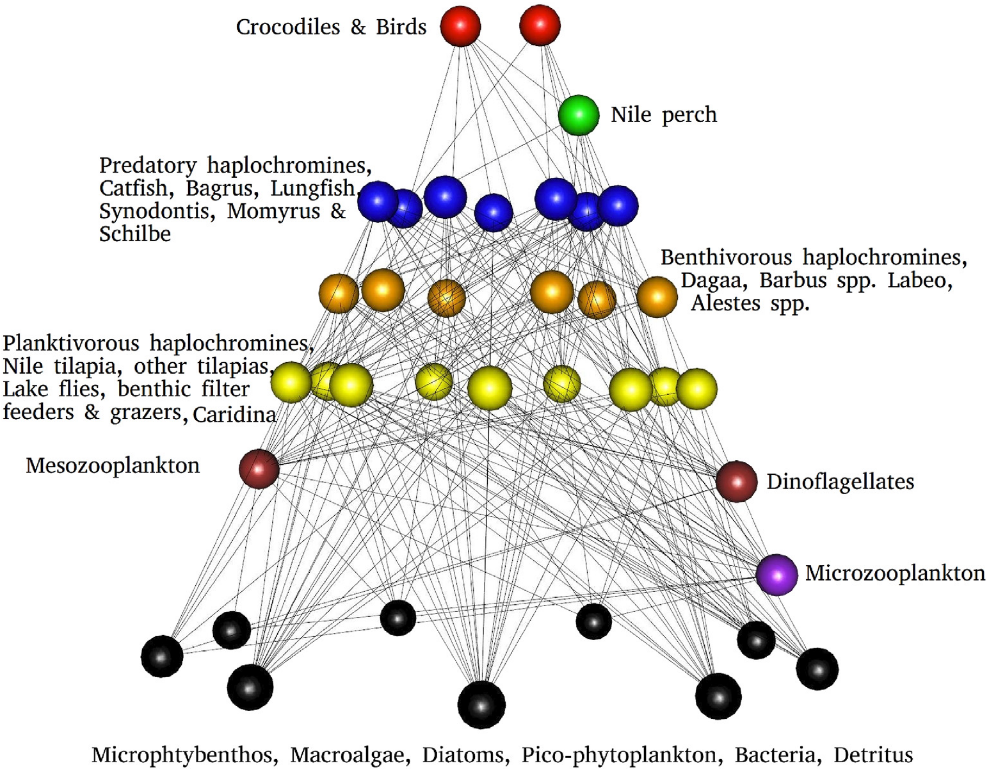


Fig. 3. Food web illustrating trophic interactions in the Lake Victoria Atlantis model.

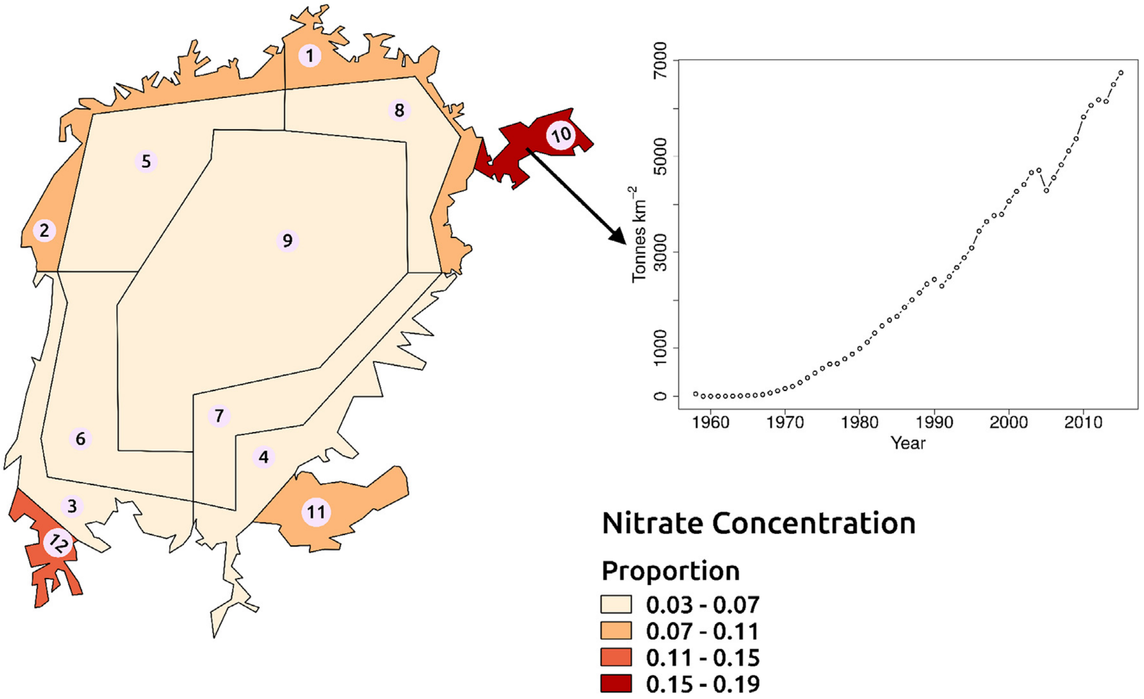


Fig. 4. Simulated spatial and temporal trends of nitrate concentrations in Lake Victoria. The graph shows changes of nitrate concentration in box 10 (Nyanza gulf) over time.

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

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.

3. Results

The developed Atlantis model simulates the Lake Victoria

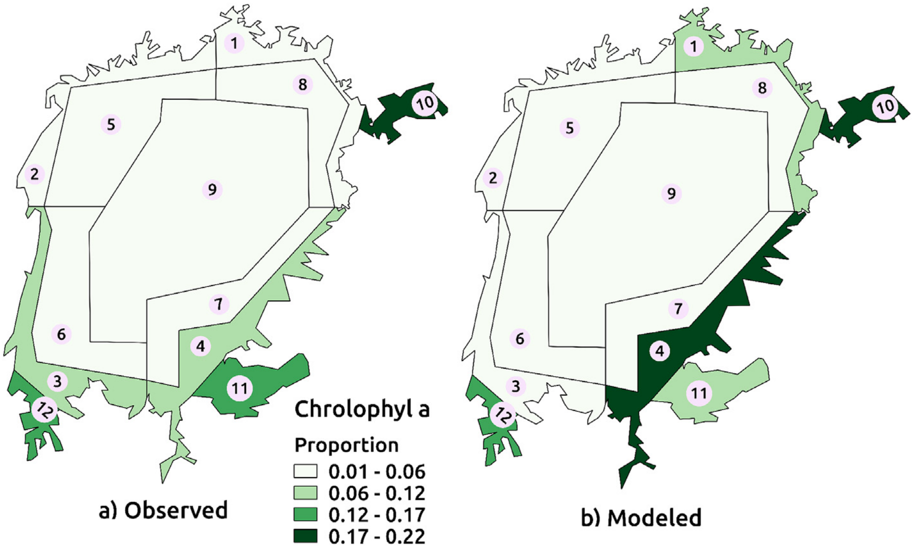


Fig. 5. Observed and modeled Chlorophyl *a* distribution in Lake Victoria.

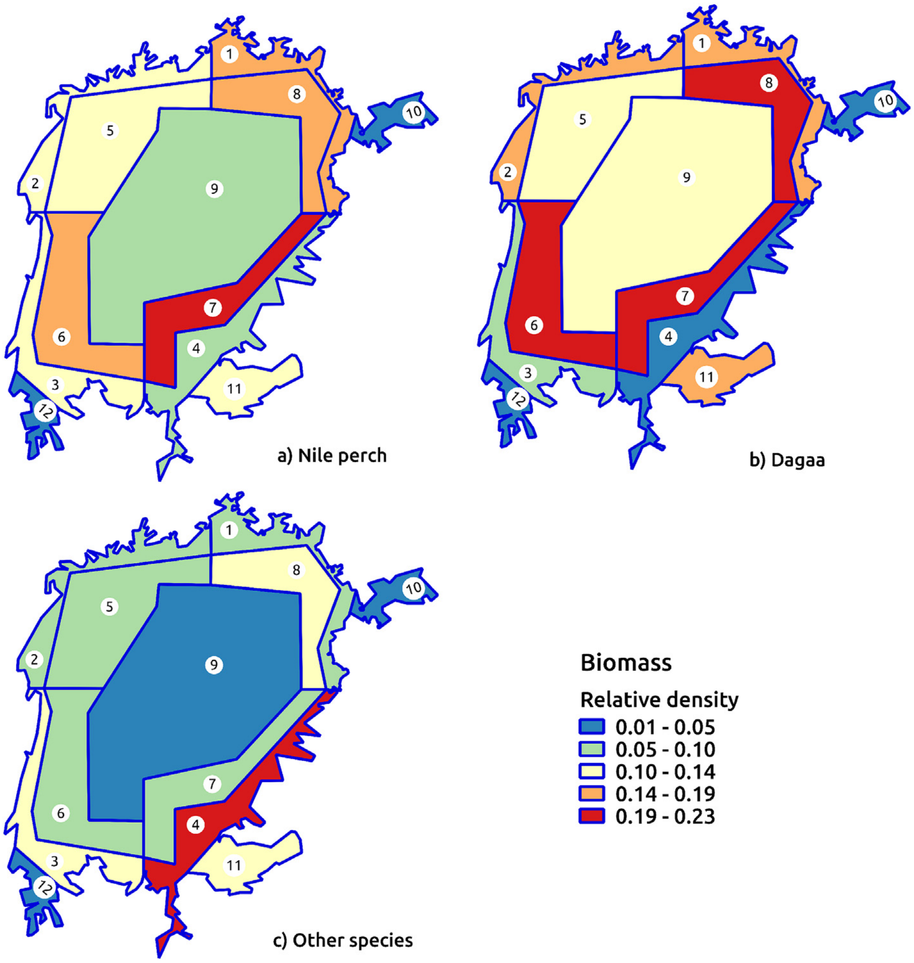


Fig. 6. Prescribed spatial distribution of fish groups in the Lake Victoria Atlantis Model.

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. Fig. 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

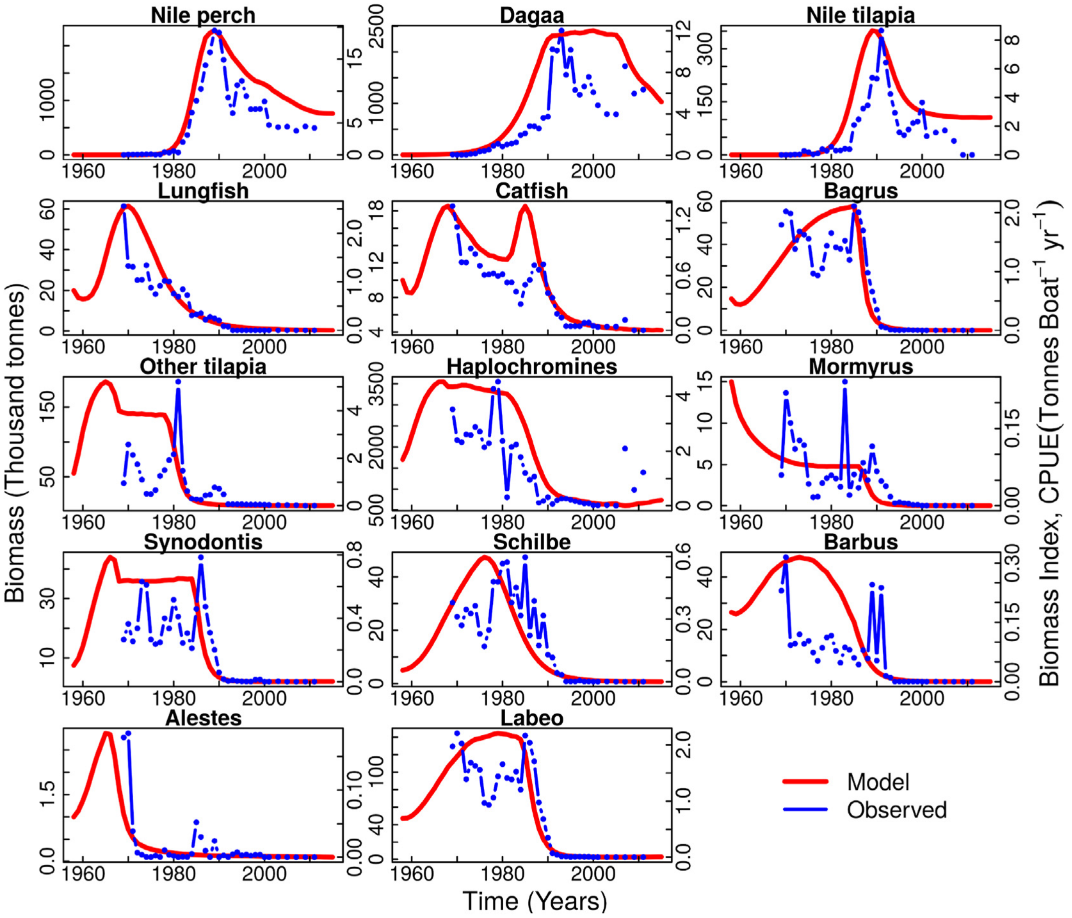


Fig. 7. Modeled biomass and observed CPUE trends of the main fish reported in commercial landings of Lake Victoria from 1958 to 2015.

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. Fig. 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 (Fig. 6). Biomass trends of commercial species are compared with CPUE as an index of abundance (Fig. 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 (Fig. 8) with strong correlation for most of the species. *CV* shows minimal deviation between simulated and actual catch (Table 2). All *E* values are greater than zero indicating that model performance is within acceptable limits (Krause et al., 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 into 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 interstock 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., 2008). 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 (Fig. 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.

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

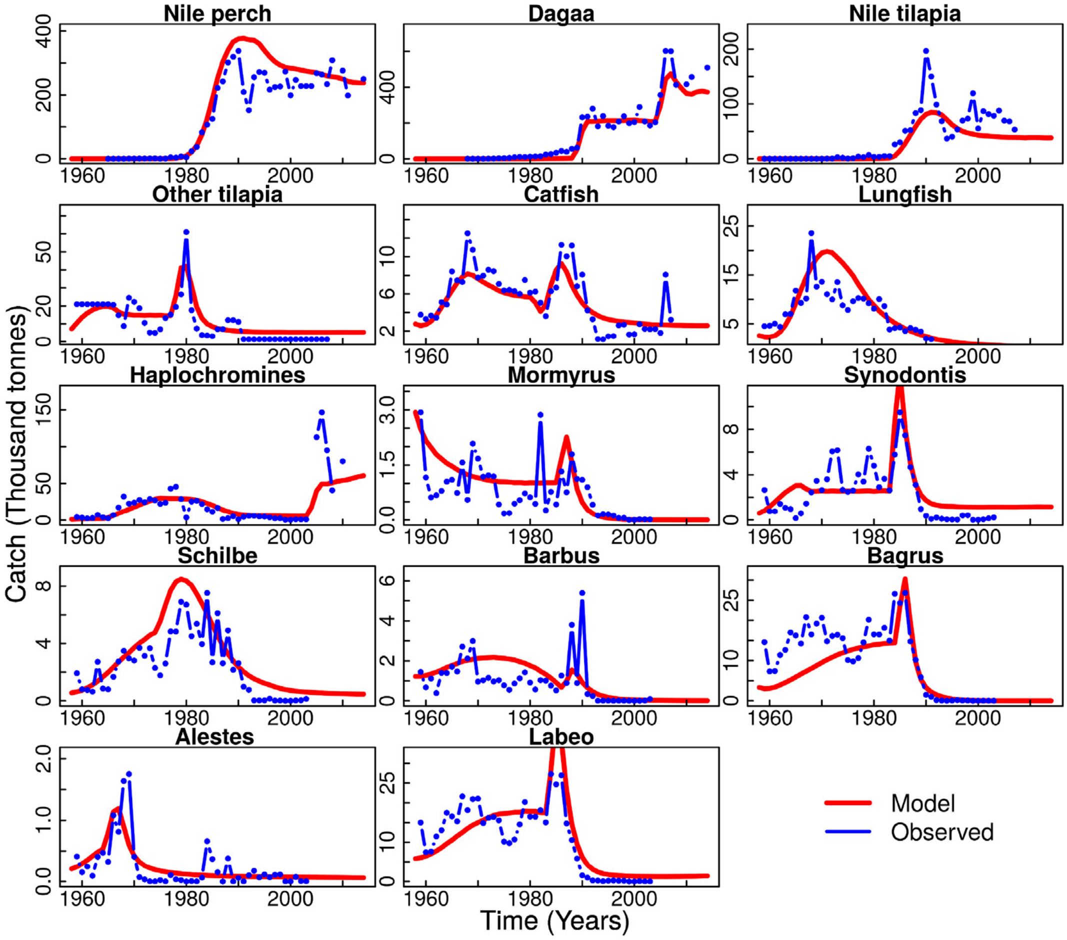


Fig. 8. Modeled and observed catch trends of fish species reported in commercial landings of Lake Victoria from 1958 to 2015.

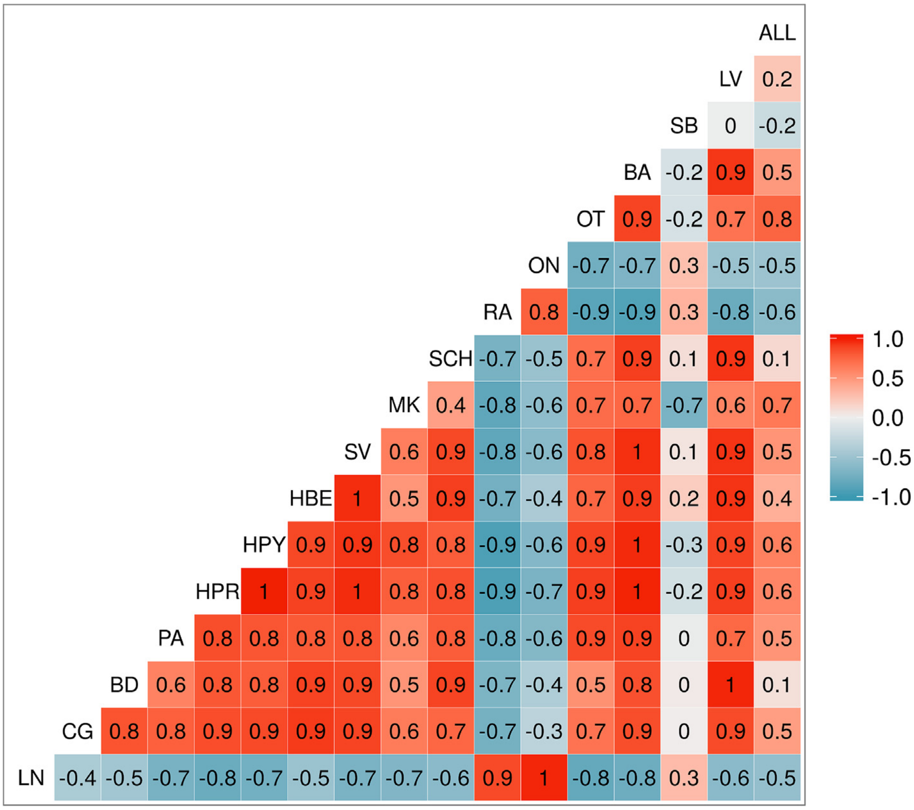
Table 2
Performance indicators (Coefficient of variation (CV), Model Efficiency (E) and Pearson's correlation (r_{catch}) and ($r_{biomass}$)) in the Lake Victoria Atlantis Model for the main commercial stocks. CV and E are only calculated for catch.

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

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



	CG	BD	PA	HPR	HPY	HBE	SV	MK	SCH	RA	ON	OT	BA	SB	LV	ALL
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

Fig. 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).

(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, 2013; 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., 1992). 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).

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.

Software availability

Atlantis: Model documentation found on https://confluence.csiro.au/display/Atlantis/Atlantis+Ecosystem+Model+Home+Page, Author: Elizabeth A. Fulton CSIRO Wealth from Oceans Flagship, Division of Marine and Atmospheric Research, GPO Box 1538, Hobart, Tas. 7001, Australia Tel.: +61 3 62325018 E-mail: beth.fulton@csiro.au, Available under a royalty free licence, Year first available:2004. Relevant model output is available at https://figshare.com/articles/Lake_Victoria_Atlantis_model_output/3364717.

Acknowledgement

Funding for this work was provided by the United Nations University - Fisheries Training Program (UNU-FTP). The authors are greatly indebted to Rebecca Gorton of CSIRO for her expertise and support.

References

Balirwa, J.S., Chapman, C.A., Chapman, L.J., 2003. Biodiversity and fishery sustainability in the Lake Victoria basin: an unexpected marriage? Bioscience 53 (8), 703–716.

Bennett, N.D., Croke, B.F.W., Guariso, G., Guillaume, J.H.A., Hamilton, S.H., Jakeman, A.J., Marsili-Libelli, S., Newham, L.T.H., Norton, J.P., Perrin, C., Pierce, S.A., Robson, B., Seppelt, R., Voinov, A.A., Fath, B.D., Andreassian, V., 2013. Characterising performance of environmental models. Environ. Model. Softw. 40, 1–20.

Cornelissen, I.J.M., van Zwieten, P.A.M., Peter, H.K., Nagelkerke, L.A.J., 2015. Nile perch distribution in south-east Lake Victoria is more strongly driven by abiotic factors, than by prey densities. Hydrobiologia 755 (1), 239–255.

Crul, R., 1995. Monographs of African Great Lakes; Limnology and Hydrology of Lake Victoria. Part 1.UNESCO/IHV-iv Project Comprehensive and Comparative Study of Great Lakes. A project of the fourth phase of the international hydrological programme of the Division of wat. Technical report, UNESCO/IHV-IV project M-5–1.

Downing, A.S., Van Nes, E.H., Balirwa, J.S., Beuving, J., Bwathondi, P., Chapman, L.J., Cornelissen, I.J.M., Cowx, I.G., Goudswaard, K.P.C., Hecky, R.E., Janse, J.H., Janssen, A.B.G., Kaufman, L., Kishe-Machumu, M.A., Kolding, J., Ligtvoet, W., Mbabazi, D., Medard, M., Mkumbo, O.C., Mlaponi, E., Munyaho, A.T., Nagelkerke, L.A.J., Ogutu-Ohwayo, R., Ojwang, W.O., Peter, H.K., Schindler, D.E., Seehausen, O., Sharpe, D., Silsbe, G.M., Sitoki, L., Tumwebaze, R., Tweddle, D., Van De Wolfshaar, K.E., Van Dijk, H., Van Donk, E., Van Rijssel, J.C., Van Zwieten, P.A.M., Wanink, J., Witte, F., Mooij, W.M., 2014. Coupled human and natural system dynamics as key to the sustainability of Lake Victoria???s Ecosystem services. Ecol. Soc. 19 (4) art31.

Ewald, J., Nilsson, A., Stalgren, P., 2004. A Strategic Conflict Analysis for the Great Lakes Region (Technical report, SIDA).

Froese, R., Pauly, D., 2015. Fishbase. World Wide Web electronic publication. www.fishbase.org. version 04/2015.

Fulton, E.A., Link, J.S., Kaplan, I.C., Savina-Rolland, M., Johnson, P., Ainsworth, C., Horne, P., Gorton, R., Gamble, R.J., Smith, A.D.M., Smith, D.C., 2011. Lessons in modelling and management of marine ecosystems: the Atlantis experience. Fish Fish. 12 (2), 171–188.

Geheb, K., Medard, M., Kyangwa, M., Lwenya, C., 2007. The future of change: roles, dynamics and functions for fishing communities in the management of Lake Victoria's fisheries. Aquatic Ecosyst. Health & Manag. 10 (4), 467–480.

Goldschmidt, T., Witte, F., Wanink, J., 1993. Cascading effects of the introduced Nile Perch on the detritivorous/phytoplanktivorous species in the sublittoral areas of Lake Victoria. Conserv. Biol. 7 (3), 686–700.

Greenwood, P., 1974. The cichlid fishes of Lake Victoria, East Africa; the biology and evolution of a species flock. William Rudolf Sabbott.

Hecky, R.E., 1993. The eutrophication of Lake Victoria. Verhandlungen der Internationalen Vereinigung fur Theoretische und Angewandte. Limnologie 25, 39–48.

Hecky, R.E., Mugidde, R., Ramlal, P.S., Talbot, M.R., Kling, G.W., 2010. Multiple stressors cause rapid ecosystem change in Lake Victoria. Freshw. Biol. 55, 19–42.

Kaufman, L., 1992. Catastrophic change in species rich freshwater ecosystems: lessons of Lake Victoria. BioScience 42 (11), 846–858.

Kaufman, L.E.S., Cohen, A.S., 2013. Comment the great Lakes of Africa. Conserv. Biol. 7 (3), 632–633.

Kelly, R.B., Jakeman, A., Barreteau, O., Borsuk, M., ElSawah, S., Hamilton, S., Henriksen, H., Kuikka, S., Maier, H., Rizzoli, A., van Delden, H.I., Voinov, A., 2013. Selecting among five common modelling approaches for integrated environmental assessment and management. Environ. Model. Softw. 47, 159–181.

Kitchell, J.F., Schindler, D.E., Ogutu-Ohwayo, R., Reinthal, P.N., 1997. The Nile perch in Lake Victoria: interactions between predation and fisheries. Ecol. Appl. 7 (2), 653–664.

Krause, P., Boyle, D.P., Base, F., 2005. Comparison of different efficiency criteria for hydrological model assessment. Adv. Geosci. 5, 89–97.

Lévêque, C., 1997. Introductions de nouvelles espèces de poissons dans les eaux douces tropicales: objetifs et conséquences. Bull. Français de la Pêche de la Piscic. 79–91.

Moriasi, D.N., Arnold, J.G., Liew, M.W.V., Bingner, R.L., Harmel, R.D., Veith, T.L., 2007. Model evaluation guidelines for systematic qualification of accuracy in watershed simulations. Trans. ASABE 50 (3), 885–900, 2007.

Mugidde, R., Gichuki, J., Rutagemwa, D., Ndawula, L.M., Matovu, 2005. Status of water quality an its implication on the fishery production. In: The State of the Fisheries Resources of Lake Victoria and Their Management. Proceedings of the Regional Stakeholders' Conference. LVFO, Jinja, Uganda, pp. 106–112.

Nash, J.E., Sutcliffe, J.V., 1970. River flow forecasting through conceptual models part I - A discussion of principles. J. Hydrol. 10 (3), 282–290.

Njiru, M., Knaap, M.V.D., Nyamweya, C.S., Kayanda, R.J., Marshall, B.E., 2014. Management of Lake Victoria fishery: are we looking for easy solutions? Aquatic Ecosyst. Health Manag. 17 (1), 70–79.

Njiru, M., Ojuok, J., Getabu, A., Jembe, T., Owili, M., Ngugi, C., 2008. Increasing dominance of Nile tilapia, Oreochromis niloticus (L) in Lake Victoria, Kenya: consequences for the Nile perch Lates niloticus (L) fishery. Aquatic Ecosyst. Health & Manag. 11 (1), 42–49.

Nyamweya, C., Desjardins, C., Sigurdsson, S., Tomasson, T., Taabu-Munyaho, A., Sitoki, L., Stefansson, G., 2016. Simulation of Lake Victoria circulation patterns using the Regional Ocean modeling system (ROMS). PLoS ONE 11 (3), e0151272.

Ochumba, P., 1990. Massive fish kills within Nyanza gulf of Lake Victoria, Kenya. Hydrobiologia 208, 93–99.

Odada, E.O., Ochola, W.O., Olago, D.O., 2009. Understanding future ecosystem changes in Lake Victoria basin using participatory local scenarios. Afr. J. Ecol. 47 (Suppl. 1), 147–153.

Okely, P., Imberger, J., Antenucci, J.P., 2010. Processes affecting horizontal mixing and dispersion in winam gulf, Lake Victoria. Limnol. Oceanogr. 55 (5), 1865–1880.

Olsen, E., Fay, G., Gaichas, S., Gamble, R., Lucey, S., Link, J.S., 2016. Ecosystem model skill assessment. Yes We Can! PLoS ONE 11 (1), e0146467.

Opande, G.O., Onyango, J.C., Wagai, S.O., 2004. Lake Victoria: the water hyacinth (Eichhornia crassipes [Mart.] Solms), its socio-economic effects, control measures and resurgence in the Winam gulf. Limnologica - Ecol. Manag. Inland Waters 34 (1–2), 105–109.

Perdomo, G., Thompson, R., Sunnucks, P., 2012. Food Web: an Open-source Program for the Visualisation and Analysis of Compilations of Complex Food Webs.

Pringle, R.M., 2005. The origins of the Nile perch in Lake Victoria. BioScience 55 (9), 780.

QGIS Development Team, 2015. QGIS geographic information system.

R Core Team, 2015. R: a Language and Environment for Statistical Computing.

Smith, M.D., Fulton, E.A., Day, R.W., 2015. Using an Atlantis model of the southern Benguela to explore the response of ecosystem indicators for fisheries management. Environ. Model. Softw. 69, 23–41.

Stager, J.C., Johnson, T.C., 2007. The late Pleistocene desiccation of Lake Victoria and the origin of its endemic biota. Hydrobiologia 596 (1), 5–16.

Taabu-Munyaho, A., Marshall, B., Tomasson, T., Marteinsdottir, G., 2016. Nile perch and the transformation of Lake Victoria. Afr. J. Aquatic Sci. 41 (2), 127–142.

Taabu-Munyaho, A., Nyamweya, C.S., Sitoki, L., Kayanda, R., Everson, I., Marteinsdóttir, G., 2014. Spatial and temporal variation in the distribution and density of pelagic fish species in Lake Victoria, East Africa. Aquatic Ecosyst. Health & Manag. 17 (1), 52–61.

Talling, J.F., 1966. The annual cycle of stratification and phytoplankton growth in Lake Victoria (East Africa). Int. Rev. Ges.hydrobiol. 51, 545–621.

Witte, F., Goldschmidt, T., Wanink, J., van Oijen, M., Goudswaard, K., Witte-Maas, E., Bouton, N., 1992. The destruction of an endemic species flock: quantitative data on the decline of the haplochromine cichlids of Lake Victoria. Environ. Biol. Fishes 34 (1), 1–28.