Dissertation for the degree of doctor of philosophy

A comparative analysis of ecosystem models of Lake Victoria (East Africa)

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Abstract

The advent of ecosystem-based fisheries management (EBFM) in recent years has expanded the scope of fisheries management, where policies are aimed not only at maximizing production (or biological yield) but also maintaining an optimal balance between socio-economic and conservation objectives when utilizing aquatic living resources. Ecosystem models help to assimilate diverse information on the drivers of ecosystem change, thereby providing integrated assessment and advice that is needed for EBFM. Different ecosystem models, however, often provide different predictions, and this uncertainty is one of the major challenges impeding their use in EBFM.

This thesis compares ecosystem models of Lake Victoria (East Africa), focusing on Ecopath with Ecosim (EwE) and Atlantis modelling frameworks, to get insights into sensitivity of fishing policy scenarios to model choice. The thesis is based on six papers. Paper I highlights the history of ecosystem modelling, both in African lakes and globally. Paper II describes temporal changes in food web of Lake Victoria using Ecopath models. Paper III compares a historic Ecopath model of Lake Victoria, fitted to time series data, to recent models that are not fitted to time series data to show how reliable none-fitted models are in terms of evaluating long-term ecosystem impacts of fishing. Paper IV compares EwE and Atlantis models of Lake Victoria to show how ecosystem impacts of fishing may be sensitive to model structure and complexity. Paper V explores socio-ecological trade-offs in Lake Victoria using both EwE and Atlantis models. Paper VI explores spatio-temporal variation in fishing patterns and fishing pressure in Lake Victoria in relation to the balanced harvesting approach (where fishing mortality is distributed across taxa or species in proportion to biological productivity).

Overall, these studies contribute to understanding of how advice from ecosystem models can be affected by model structure, data assumptions and quality. The findings in this thesis suggest that simpler models may also support robust qualitative advice, which is vital for long-term strategic planning, but key ecological mechanisms explaining the differences in fishery responses between models (simple vs. complex, data-rich vs. data-poor) must be identified before hand. In view of this finding, the importance of multi-model simulations as an aid to guarding against the effects uncertainty on strategic management decisions can not be overstated. This further implies that the lack of model diversity observed on most African lakes requires urgent attention.

Ágrip

Notkun vistkerfisnálgunar við stjórn fiskveiða á undanförnum árum hefur breikkað svið fiskveiðistjórnunar með því að ákvarðanir miðast ekki einvörðungu við hámörkun heildarafla eða afraksturs heldur er einnig tekið tillit til félagslegra og hagrænna þátta við nýtingu lifandi auðlinda sjávar. Vistkerfislíkön draga saman fjölbreytt upplýsingasöfn um hvað ræður vistkerfisbreytingum og gefa þannig samræmt heildarmat á ástandi og þá ráðgjöf sem þarf að nota fyrir vistkerfisnálgun við stjórn fiskveiða (ecosystem-based fisheries management, EBFM). Ólík vistkerfislíkön geta hins vegar gefið talsvert ólíkar spár um þróun. Slíka líkan-óvissa er talsverð hindrun við notkun þessara líkana við EBMF. Þær rannsóknir sem hér eru kynntar rýna í áhrif flækjustigs líkana og óvissu í gögnum á ákvarðanir um auðlindanýtingu í ljósi EBFM og eru niðurstöður kynntar í sex greinum.

Í þessari ritgerð eru borin saman vistkerfislíkön fyrir Viktoríuvatn í Austur-Afríku, mest með Ęcopath with Ecosim"(EwE) og Atlantis, til að sýna áhrif líkanavals á ályktanir um afleiðingar stjórnvaldsaðgerða. Ritgerðin byggir á 6 greinum. Í Grein I er gefið yfirlit um notkun vistkerfislínana á vötn í Afríku. Grein II lýsir líkani fyrir fæðuvef Viktoríuvatns stöðulíkani (Ecopath). Grein III ber saman sögulegt EwE líkan fellt að eldri tímaraðargögnum við jafnstöðu líkan lagt að nýrri gögnum. Tilgangurinn er að skilja áreiðanleika jafnstöðulíkana sem ekki nota formlega aðlögun að gögnum þegar þau eru notuð til að spá fyrir um afleiðingar stjórnvaldsákvarðana. Grein IV ber saman EwE og Atlantis líkön til að auka skilning á hvernig líkagerð, flækjustig og forsendur hafa áhrif á mat á stjórnvaldsaðgerðum. Grein V fjallar um mat á félagslegum og efna-

hagslegum áhrifum stjórnunaraðgerða með Atlantis og EwE. Grein VI metur breytileika í veiðimynstri og sókn í tíma og rúmi í samhengi við aðferðar jafnrar sóknar (balanced harvest strategy) þar sem sókn er sett sem hlutfall af framleiðslu tegundar.

Sú heildarmynd fæst úr þessum tilraunum að ráðgjöf byggð á ólíkum líkönum getur orðið talsvert háð innri byggingu hvers líkans, gagnanýtingu og gæðum gagna. En niðurstöður benda líka til þess að einföld líkön geti veitt trausta almenna ráðgjöf, sem er mikilvæg fyrir langtíma áætlanagerð. Lykileiginleika vistkerfis, sem útskýra mun á spá einfaldra og flókinna líkana, þarf hins vegar að auðkenna fyrirfram. Í ljósi þessa er mikilvægi þess að prófa mörg líkön augljóst og nauðsynlegt að beina sjónum að fæð þeirri sem auðkennir breytileika í líkanagerð fyrir vötn í Afríku.

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List of Publications

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

Paper I: Musinguzi L., Natugonza V., & Ogutu-Ohwayo R. (2017). Paradigm shifts required to promote Ecosystem Modelling for Ecosystem-Based Fishery Management for African Inland Lakes. *Journal of Great Lakes Research.* 43, 1-8.

Paper II: Natugonza V., Ogutu-Ohwayo R., Musinguzi L., Kashindye B., Jónsson S., & Valtysson H. (2016). Exploring the structural and functional properties of the Lake Victoria food web, and the role of fisheries, using a mass balance model. *Ecological Modelling*, 342, 161-174.

Paper III: Natugonza, V., Ainsworth, C., Sturludóttir, E., Musinguzi, L., Ogutu-Ohwayo, R., Tomasson, T., Nyamweya, C., & Stefansson, G. (2020). Ecosystem modelling of data-limited fisheries: how reliable are Ecopath with Ecosim models without historical time series fitting? *Journal of Great Lakes Research*, 46, 414-428.

Paper IV: Natugonza, V., Ainsworth, C., Sturludóttir, E., Musinguzi, L., Ogutu-Ohwayo, R., Tomasson, T., Nyamweya, C., & Stefansson, G. (2019). Ecosystem models of Lake Victoria (East Africa): can Ecopath with Ecosim and Atlantis predict similar policy outcomes? *Journal of Great Lakes Research* , 45, 1260-1273.

Paper V: Natugonza, V., Ainsworth, C., Sturludóttir, E., Musinguzi, L., Ogutu-Ohwayo, R., Tomasson, T., Nyamweya, C., & Stefansson, G. (2020). Simulating trade-offs between socio-economic and conservation objectives in Lake Victoria (East Africa) using multispecies, multifleet ecosystem models. *Fisheries Research* 229, 105593. `https://doi.org/10.1016/j.fishres.2020.105593`

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Paper VI: Natugonza, V., Sturludóttir, E., Musinguzi, L., Ogutu-Ohwayo, R., Bassa, S., Tomasson, T., Nyamweya, C., & Stefansson, G. Spatiotemporal variation in fishing patterns and fishing pressure in Lake Victoria (East Africa) in relation to balanced harvest. *Fisheries Research* (under review).

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Part I

Thesis

1

Introduction

1.1 Background

The application of science to fisheries management dates back to the mid-19th century (Smith, 2008). Within the last 100 years, many science-based measures have been proposed and implemented to control both fishery output, for example, limiting catches through the use of quotas, and fishery input, for example, gear limitations and closures of fishing areas (Stefansson and Rosenberg, 2005). Initially, both output and input control measures aimed at maintaining harvested stocks at levels that can produce maximum sustainable yield (MSY), i.e., the highest equilibrium yield that can be continuously harvested from a stock under existing environmental conditions (Tsikliras and Froese, 2018). The MSY-based approach is a single-species approach, focusing on the direct consequences of management actions on targeted stocks and, sometimes, protected non-target species (Tsikliras and Froese, 2018). Whereas MSY is still an essential concept in fisheries management (Mangel et al., 2002), there need to recognize and account for species interactions, feedbacks and trade-offs within fished systems (Fogarty, 2013; Leslie et al., 2015).

Ecosystem-based fisheries management (EBFM) is a management approach that seeks to integrate various interactions within an ecosystem, including non-human components, rather than considering single issues, species, or ecosystem services in isolation (Stefansson et al., 2019). EBFM is part of the Code of Conduct for Responsible Fisheries (CCRF) (FAO, 1995) that was adopted to address the limitations of the single-species MSY approach (FAO, 2003). The CCRF, among other things, provides a framework for integrating objectives of the existing international (legally binding) instruments related to fisheries, particularly the 1982 United Nations Convention on the Law of the Sea (UNCLOS) (United Nations, 1982) and the 1992 Convention on Biological Diversity (CBD) (United Nations, 1992). The UNCLOS aims to prevent overfishing, while CBD aims to maintain ecosystem structure and function.

Several countries, including the USA, Canada, and Australia, are increasingly adopting EBFM (Fulton et al., 2019; Leslie et al., 2015; Pikitch et al., 2012). Some of the positive outcomes registered to date under this approach include protection of critical benthic habitats and habitat restoration (Murawski et al., 2000), reduced by-catch (Dunn et al., 2011; Little et al., 2014; Melvin et al., 2014), protection of forage fishes (Pikitch et al., 2012), and increased participation of stakeholders through community quota development programs (Carothers, 2011). In countries where conventional single-species management is still prevalent, especially in Europe (Hyder et al., 2015), stock assessments are increasingly linking recruitment to environmental conditions, tracking changes in mortality due to predators, or using the information on habitats to better standardize the abundance indices (Essington et al., 2016). Other countries, especially the developed countries, are increasing the number of assessed stocks, and thereby adopting the multispecies management form. Recent studies show that this approach is also beneficial towards achieving EBFM goals, despite being costly (Fulton et al., 2019).

1.2 The role of ecosystem modelling in EBFM

The transition towards EBFM, which accounts for both biophysical, ecological, and socio-economic aspects in management decisions, requires decision support tools (DST) that can provide integrated assessment and advice (Stefansson et al., 2019). The DST required for EBFM are those that consider relationships among the ecology of species under management (for example, habitat requirements and response to environmental change), ecological interactions among species (for example, predation and competition), and technical interactions (for example, discards and by-catch) (Latour et al., 2003). Ecosystem models meet these criteria (Plagányi, 2007). Ecosystem models help in understanding the links between human and environmental pressures, exploring management measures amid conflicting objectives and tracking progress concerning those objectives, and assessing the performance of management options based on their environmental, social, and economic consequences (Canham et al., 2003). The ability of ecosystem models to allow *a priori* testing of policies, through "what-if" management scenarios and their likely consequences, in particular, make them essential DST for EBFM (Stefansson et al., 2019).

Ecosystem models are increasingly being used to support management and policy development in many parts of the world. In the USA, ecosystem models have been used to inform policies for minimizing by-catch, habitat restoration, protection of forage fish, and rebuilding declining stocks (Townsend et al., 2019). In Australia, ecosystem models have also been used in the strategic restructuring of federal fisheries (Fulton and Link, 2014; Fulton et al., 2011a). These case studies show the potential of ecosystem modelling to influence EBFM decisions, especially when the modelling process is transparent and involves a wide range of stakeholders (Essington et al., 2016; Hyder et al., 2015; Townsend et al., 2019).

1.3 Structural and functional forms of ecosystem models

Many different models exist for studying ecosystem processes and dynamics. The conventional model types, however, are conceptual and simulation models. Conceptual models represent the scope of the problems to be addressed and the required assessments (Broszeit et al., 2019; Harvey et al., 2016; Potschin-young et al., 2018). Simulation models include a variety of biophysical, multispecies, food-web, and end-to-end models that are used to predict ecosystem dynamics at different scales (Plagányi, 2007). While both conceptual and simulation models can aid EBFM, more emphasis has been put on simulation models because of their ability to test a wide range of management scenarios before implementation (Fulton and Link, 2014; Fulton et al., 2011a).

Simulation models have been broadly categorized into three forms (Plagányi, 2007). (i) Extended single-species assessment models (ESAMs): single-species models that include information on other species and processes. Examples include the extended surplus production models (Horbowy, 2005). (ii) Minimum realistic models (MRMs): multispecies models that include only enough species/processes to test a hypothesis. An example is Gadget (Begley and Howell, 2005). (iii) Dynamic simulation models: multispecies models that represent bottom-up and top-down forces in an ecosystem at varying levels of complexity. Examples include Ecopath with Ecosim (EwE, Christensen and Walters, 2004a) and Atlantis (Fulton et al., 2011a). The three forms of simulation models differ in the detail of their biological processes and how they are represented, projection length, and time resolution. Each model type also has strength and weaknesses, and the choice of the modelling strategy depends on the questions being answered and the data available to parameterize the model (Christensen and Walters, 2005; Fulton et al., 2011a; Plagányi, 2007).

In ESAMs and MRMs, parameters are estimated through formal statistical procedures, for example, utilizing likelihood functions to obtain parameter estimates and bootstrap techniques to estimate variance and evaluate uncertainty (Elvarsson et al., 2014). However, formal statistical estimation of parameters is not possible for complex multispecies models. Instead, parameters are manually adjusted until reasonable model fits are achieved (Plagányi, 2007). This modelling technique precludes an understanding of the sensitivity of model outputs to input information. Recently, Ecosampler has been incorporated in EwE modelling framework to test the sensitivity of model outputs to input parameters (Steenbeek et al., 2018). However, full-scale sensitivity analysis is still impossible in complex, end-to-end models such as Atlantis, although sensitivity analysis of individual model components have been attempted (Hansen et al., 2019; Mcgregor et al., 2020; Ortega-Cisneros et al., 2017; Sturludottir et al., 2018). Consequently, tracking the impact of imperfect knowledge of model parameters, input data, or relationships among parameters on model results, and how these affect predictions and subsequent management decisions, remains a challenge.

This uncertainty is believed to be the major challenge impeding the use of ecosystem models in EBFM (Collie et al., 2016). Currently, the confidence in outputs from ecosystem models relies on how well the model fits observations through model skill assessment (Olsen et al., 2016; Stow et al., 2009). However, model fitting is often not possible because of the paucity of fisheries data (Heymans et al., 2011). In such cases, modellers tend to rely on default parameters within the modelling packages/software (Ainsworth and Walters, 2015; Colleter et al., 2015; Fulton et al., 2011a). How reliable are multispecies models without historical time series fitting? To understand the reliability of models that cannot be formally tested for their predictive skill, there is a need to determine how fitted models compare with non-fitted models in terms of predicting consequences of alternative management scenarios.

1.4 Ensemble/structured modelling in multispecies models

Model uncertainty has implications for the choice of the modelling strategy to inform management decisions. Fitting a model to time series data may not guarantee that the model captures well the natural processes and is, therefore, the right choice. Similar fits can be obtained with different parameter combinations that do not necessarily reflect the reality (Collie et al., 2016; Heymans et al., 2016), implying that relying on a single ecosystem model to address all the questions under the

EBFM framework may give misleading advice (Espinoza-Tenorio et al., 2012; Plagányi, 2007). One potential strategy that is increasingly being advocated to address this problem is ensemble or structured modelling, where a range of ecosystem models are considered, from simple models with few parameters, whose outputs are scientifically robust but possibly of limited scope within the EBFM, to models that include a large number of ecosystem elements yet at the expense of increased uncertainty (Espinoza-Tenorio et al., 2012).

Indeed, ensemble/structured modelling is increasingly being adopted in fisheries to address limitations in single models through model intercomparisons and/or taking weighted averages (Gårdmark et al., 2013; Lotze et al., 2019; Pope et al., 2019a; Spence et al., 2018). Model intercomparisons are hinged on the notion that if multiple ecosystem models, despite their different structure and assumptions, lead to consistent and converging results, sound management decisions can be supported (Espinoza-Tenorio et al., 2012). Can structurally-distinct ecosystem models give similar policy evaluations? Previous studies have shown that structurally-distinct ecosystem models have potential to give consistent qualitative advice (Bauer et al., 2019; Forrest et al., 2015; Fulton and Smith, 2004; Gårdmark et al., 2013; Pope et al., 2019a; Smith et al., 2015; Travers et al., 2010). These studies show coherence in qualitative results (similar trends) across models, especially for the direct effects of fishing on target species ("single-species effects"). However, considerable variations exist in the indirect effects of fishing target groups on the non-target species ("multispecies effects"). Because model parameters are not estimated, the modelling process tends to be subjective, and the final model depends on the modeller. Therefore, more studies are needed to better understand uncertainty caused by differences in model structure as well as individual considerations and biases during model parameterization.

1.5 The case of EwE and Atlantis

EwE and Atlantis are the most widely used ecosystem modelling tools globally (Colleter et al., 2015; Fulton et al., 2011a). Both tools represent the food webs, abiotic environment, including climate impacts, and fisheries, but at different scales and varying levels of complexity. EwE is a 0-dimensional biomass model, where predation is regulated by explicit diet parameters, through a fixed diet matrix, and foraging vulnerability (Christensen and Walters, 2004a). Atlantis, on the other hand, is a whole ecosystem, age- and size-structured, 3-dimensional population model; predation is regulated by a diet preference matrix, but the actual resulting diet is subject to mouth-gape limitations and prey availability (Audzijonyte et al., 2017a). Comparing such models, therefore, would help in highlighting scenarios that are robust to model choice, and for which simpler models, such as EwE, could also provide reliable advice.

1.6 Status of ecosystem modelling of the African inland lakes

The African inland fisheries provide livelihoods to about 5 million people (de Graaf and Garibaldi, 2014). Despite the huge contribution in terms of livelihoods to the riparian populations, the fisheries are among the most threatened in the world (Welcomme et al., 2010). The threats include overexploitation, eutrophication, pollution, habitat degradation, invasive species, water extraction, and damming (see Hecky et al., 2010). These threats are intensifying and becoming increasingly interconnected. To design mitigation measures to counter the undesirable consequences, understanding and making predictions about the direction and magnitude of these threats is vital. Elsewhere, the use of ecosystem models to evaluate the consequences of these threats on ecosystems has taken root (Townsend et al., 2019), possibly because of the progressive nature of ecosystem modelling (Christensen and Walters, 2005; Colleter et al., 2015; Fulton et al., 2011a).

Ecosystem models have been developed for the major (in terms of size)

African lakes, such as Victoria (Downing et al., 2012; Matsuishi et al., 2006; Moreau et al., 1993a), Tanganyika (Moreau and Nyakageni, 1988; Moreau et al., 1993b), Malawi (Darwall et al., 2010), Kivu (Villanueva et al., 2007), and Turkana (Kolding, 1993). Christensen and Walters (2005), however, suggest that for ecosystem modelling to be considered active, the trend in the number of primary publications dealing with ecosystem approaches to fisheries and developing or applying ecosystem modelling must be showing a continuous increase in recent years. Indeed, the global trend indicates that ecosystem modelling is an active field of research, which is experiencing rapid growth, with more than 20% growth per year in the number of publications developing, applying, or reviewing ecosystem modelling approaches (Christensen and Walters, 2005; Colleter et al., 2015; Fulton et al., 2011a). The rapid growth in ecosystem modelling, especially using EwE, is attributed to, *inter alia*, the extended support for EwE modelling, with many training courses and workshops offered by the developers and other experts (Christensen and Walters, 2005; Plagányi, 2007). In Africa, these training sessions are not common, while the online courses have only been offered recently (Cameron Ainsworth, pers. com.). Consequently, one would expect ecosystem modelling of the African inland fisheries to be less active. This hypothesis can be tested by examining publication trends of the application of ecosystem modelling approaches on the African inland lakes, using the same approach as Christensen and Walters (2005), but possibly focusing on the most widely used platforms such as EwE and Atlantis.

1.7 The case of Lake Victoria (East Africa)

1.7.1 Ecosystem changes (food web dynamics)

Lake Victoria is the largest, in terms of size and fisheries production, among the African inland lakes (Ogutu-ohwayo et al., 2016). Before 1960, the food web of Lake Victoria was comprised of the endemic tilapiine cichlids (*Oreochromis esculentus* and *O. variabilis*), native predators, mainly catfishes (*Clarias*, *Bagrus*, *Synodontis* spp.) and lungfish (*Protopterus* *aethiopicus*), cyprinids (main genera: *Labeo, Labeobarbus, Enteromius*, and *Rastrineobola*), and the small-bodied haplochromine cichlids (Ogutu-ohwayo, 1990b). Haplochromines were the most abundant, constituting more than 80% of the total demersal fish biomass (Kudhongania and Cordone, 1974) in more than 15 trophic groups (Witte et al., 1992). Despite a rich fishery in terms of diversity, the total annual landings were less than 100,000 tonnes (Goudswaard et al., 2008). Because of the little commercial value of haplochromines, the piscivorous Nile perch (*Lates niloticus*) was introduced in the mid-1950s to convert them into fish flesh of commercial importance (Goudswaard et al., 2008; Pringle, 2005). Also, four other tilapiine cichlids, Nile tilapia (*Oreochromis niloticus*), *O. leucostictus*, *Coptodon zillii*, and *C. rendalli*, were introduced alongside Nile perch to boost the then declining tilapiine fishery, but only Nile tilapia flourished and became abundant (Ogutu-ohwayo, 1990b). Three decades later, the population of Nile perch grew exponentially, with the species' landings increasing from almost nothing in 1980 to 300,000 tonnes in 1990, constituting 66% of the total catch (Ogutu-ohwayo, 1990b). During the same period, haplochromines virtually collapsed, apparently because of predation by Nile perch (Marshall, 2018; Ogutu-ohwayo, 1990b; Witte et al., 1992) and environmental change (van Zwieten et al., 2015). The native tilapia fishery also collapsed because of intensive fishing and competition and hybridization from the introduced *Oreochromis* and *Coptodon* species (Ogutu-ohwayo, 1990b). A complex food web (see Moreau, 1995; Moreau et al., 1993a) was reduced to a four-species dominated fishery, comprising of introduced Nile perch and Nile tilapia and the native silver cyprinid (*Ratsrineobola argentea*) and the freshwater shrimp (*Caridina nilotica*) (Ogutu-ohwayo, 1990b).

During the 1990s, Nile perch abundance declined, possibly because of intensive fishing (Mkumbo and Marshall, 2015). Also, the limnological conditions of the lake improved, as seen from the reduction of deep-water anoxia (Marshall et al., 2013; Sitoki et al., 2010). Subsequently, haplochromines started recovering (Kishe-Machumu et al., 2014; Witte et al., 2000) and by 2014, despite diversity remaining low, the biomass was comparable to the pre-1980 levels (Taabu-Munyaho et al., 2016).

Following the recovery of some trophic groups, a reorganization of the food web was expected (to some extent). Indeed, mass balance models representing the food web near Mwanza Gulf, Tanzania, before (i.e., the 1970s), during (i.e., 1980s), and after (i.e., 2000s) the Nile perch boom showed that the overall trophic structure had recovered, despite biodiversity remaining lower than the pre-Nile perch levels (Downing et al., 2012). This research finding is significant as it paves the way for understanding ecosystem functioning and of changes in the growth of trophic groups. However, the conclusion in Downing et al. (2012) was later questioned on the account that the parameters used in the models were unrealistic (Kolding, 2013). Therefore, understanding the evolution of the Lake Victoria food web, especially following such massive perturbations, requires further investigation.

1.7.2 Fisheries and management

Lake Victoria has the world's largest inland lake fishery, with landings of approximately one million tonnes per year (Taabu-Munyaho et al., 2016). The fishery employs about one million people through fishing and other value-chain related activities and supports livelihoods of about four million people (Mkumbo and Marshall, 2015). The total annual landings are worth the US $600-850 million from the direct sales of fish at the landing sites (LVFO, 2016b). The landings are dominated by silver cyprinid and Nile perch, constituting more than 80% of the total landings (LVFO, 2016b). A similar pattern is reflected in standing stock biomass (Taabu-Munyaho et al., 2016). The main fishing gears are long lines (targeting Nile perch), gill nets (targeting both Nile perch and Nile tilapia and other harvested species), and small seines (targeting the silver cyprinid). The gears are mainly operated by paddled parachute canoes in shallow nearshore areas (less than 20 m depth) and sail/outboard engine-propelled Sesse boats in coastal and deep areas (greater than 20 m depth) (LVFO, 2016c).

The fishery has generally been open access, with limited input and output restrictions. The Lake Victoria Fisheries Organisation (LVFO) is mandated to, among other things, coordinate the management and development of Lake Victoria fisheries. While there are sector-specific objectives within the management plan developed by LVFO (LVFO, 2016a), the overall plan emphasizes multiple objectives, by maximizing revenues from fish exports and maintaining high employment through fishing and value-chain related, while maintaining biodiversity and ecosystem structure. Elsewhere, studies have shown that total ecosystem yield may not be maximized without depleting some stocks, while protecting all exploited species from overfishing may only be possible by reducing fishing effort and potential yield (and hence employment) in every fishing sector/fleet (Andersen et al., 2015; Forrest et al., 2015; Hilborn, 2010; Hilborn et al., 2004; Pascoe et al., 2013; Sparholt and Cook, 2010). Whereas these findings apply to many exploited fisheries globally, trade-offs can also be influenced by local conditions such as productivity of the individual stocks and strength of species interactions (Shelton et al., 2014; Voss et al., 2014) and the socio-economic set-up of the fishing communities (Bene, 2009). How to achieve a balance between fish production, profits from fishing, employment, and conservation objectives at a local scale requires additional investigation. One potential approach to conducting such an investigation is by using the optimal policy search (OPS) procedure in EwE (Christensen and Walters, 2004a). The OPS uses a calibrated EwE model to search for long-term, gear-specific fishing effort ("optimal fishing effort") that can maximize a specified management objective, for example, net economic value (profit), social value (employment), and conservation status (ecosystem structure and biomass diversity). These objectives can be maximized either individually or in combination with other objectives by choosing appropriate weights. The optimal fishing effort can then be used to simulate and compare long-term changes in the ecosystem in response to each management objective.

The sustainability of the Lake Victoria fisheries amid increasing fishing pressure has been a central focus of discussion by scientists and managers, although no consensus has been reached to date. Some authors have suggested that the levels of exploitation are not sustainable and that fisheries are exhibiting signs of overfishing, as seen from the reduction in catch rates (catch per unit effort (CPUE)) and size structure of main commercial fish species (Nile perch and Nile tilapia) (Matsuishi et al., 2006; Mkumbo and Marshall, 2015; Njiru et al., 2006; Pitcher and Bundy, 1995). This conclusion has been strongly opposed by other authors (for example, Kolding et al., 2008; Kolding et al., 2014). These authors argue that the overall landings have not plummeted, despite the continuous increase in fishing effort, and that the reduction in CPUE, biomass, and size structure of primary commercial fish species is a normal response to fishing.

The disagreements among scientists partly emanate from the mixed nature of the fishery, which makes it challenging to assess fishing effort on individual fish species and to estimate catch rates precisely. The CPUE is mainly approximated using indirect methods, for example, from the combined catches and either the total number of fishers or fishing crafts (Kolding et al., 2014). While this approach may help to give a general picture of the fishery, it has shortcomings, arising from lack of separation of catches and fishing effort. Consequently, a different method is needed to assess the status of the fisheries at the functional group level. One potential approach is by examining how fishing pressure is distributed across the broader trophic spectrum in relation to the biological productivity (turn over rate) of an individual group or TL, similar to the one used by Kolding et al. (2016a). This approach draws from the concept of balanced harvesting (BH), an approach to fishing where moderate fishing pressure is applied across the broader range of species, trophic levels (TL), stocks, or sizes in an ecosystem in proportion to natural production (total cumulated new biomass produced from an ecological group during a given period, irrespective of its fate) instead of putting pressure on particular, selected taxa, or sizes (Garcia et al., 2015; Zhou et al., 2019). The new approach would help in identifying species that are over-exploited relative to biological production, where exploitation rate (E, the ratio of yield to production) is consistently above 50% (Alverson and

Pereyra, 2001), and those that are sustainably fished, where E is less than 40% (Patterson, 1992; Pikitch et al., 2012). Because of the current size-selective regulations on the lake, for example, the minimum mesh size policy, and the emphasis by governments on maximizing revenue from high-value fish species (Johnson and Bakaaki, 2016; LVFO, 2016a), one would expect higher-TL species to be exploited harder than lower-TL groups, resulting in a fishing pattern that is inconsistent with the BH strategy. The data required for this analysis are yield and production for all exploited species in an ecosystem, either by TL or size (Kolding et al., 2016a). These data are readily available in standardized formats in Ecopath models by species or functional groups and TL (Christensen and Pauly, 1992).

1.7.3 Ecosystem modelling

Among the African inland fisheries, Lake Victoria has received the greatest attention in terms of research and ecosystem modelling, with over 10 EwE models (Downing et al., 2012; Matsuishi et al., 2006; Moreau et al., 1993a; Moreau and Villanueva, 2002) and one Atlantis model (Nyamweya et al., 2016b). Emphasis has been put on the use of EwE and Atlantis modelling frameworks, possibly because of the popularity of these modelling tools across the globe (Colleter et al., 2015; Fulton et al., 2011a). However, most of the models were Ecopath "snapshots", representing short periods (one year), used to study trophic relationships. Also, the models that applied Ecosim to explore outcomes of management scenarios (for example, Matsuishi et al., 2006; Moreau and Villanueva, 2002) were not fitted to time series data to ensure that parameters were consistent with historical fishery dynamics. Instead, these models relied on default Ecosim parameters and their reliability in terms of predicting effects alternative management strategies can hardly be ascertained.

The prevalence of unfitted EwE models on Lake Victoria likely emanates from the paucity of consistent long-term time series data, especially biomass. Two fishery-independent methods are commonly used to estimate biomass on Lake Victoria: hydroacoustic surveys and bottom trawl surveys. Hydroacoustic surveys started in 1999, but these have not been consistent because of sporadic funding; also, the methodology can only provide biomass estimates for two species: Nile perch and silver cyprinid (Taabu-Munyaho et al., 2016). The bottom trawl surveys started in 1969 (Kudhongania and Cordone, 1974). These surveys have primarily been conducted through donor-funded projects, mainly the Lake Victoria Fisheries Research Project (LVFRP), Implementation of the Fisheries Management Plan (IFMP), and Lake Victoria Environmental Management Project (LVEMP I and II) (Kolding et al., 2014). Consequently, data is missing for most of the years due to lack of funding. Also, the methods were never standardized across different projects until standard operating procedures (SOPs) were developed in 2007 (Kolding et al., 2014). Another limitation is that trawl surveys tend to underestimate biomass grossly, especially in nearshore, nontrawlable areas (Kolding et al., 2008).

The presence of an Atlantis model, however, provides an opportunity to fit and test parameters of a simpler model such as EwE (Sturludottir, 2017; Weijerman et al., 2016). Atlantis is a whole of ecosystem model that is age- and size-structured, and spatially-resolved, accounting for both physical (bathymetry, hydrography) and biological (species life history and distribution) components in a heterogeneous environment (Fulton et al., 2011a). Therefore, Atlantis model can be used as a reference ecosystem, where the simulated biomass data is used to fit and test the performance of the EwE model.

The Atlantis model of Lake Victoria is calibrated against historical time series of CPUE (Nyamweya et al., 2016b). The model simulates distributions of nutrients, primary production, and commercial fish species that match well with available data; also, the temporal trends of biomass and catch resemble community shifts reported in the literature (Nyamweya et al., 2016b). However, these aspects of model validity do not imply that the Atlantis model of Lake Victoria is a true reflection of the absolute biomass or catch amounts. Therefore, when using Atlantis-simulated biomass to calibrate EwE model, more emphasis should be put on fitting the trends rather than absolute values.

2

Aim

This study aims to examine the effect of model complexity and data uncertainty on policy evaluations, which could impact advice for EBFM. The individual objectives, which are addressed in six papers in part II of the thesis, are summarised here as follows.

Paper I examines the application of ecosystem modelling approaches (featuring EwE and Atlantis) to the African Great Lakes (AGL). The aim is to explore the progress of ecosystem modelling of tropical inland fisheries, and the implication for fisheries research and management. This paper is published in the Journal of Great Lakes Research (2017): `http://dx.doi.org/10.1016/j.jglr.2016.11.007`.

Paper II describes the development of an Ecopath model of Lake Victoria, representing present-day conditions (2014), and reparameterisation of two existing historical Ecopath models, representing conditions in the 1970s and 1980s. The aim is to explore the evolution of Lake Victoria food web with respect to perturbations, particularly species introductions. This paper is published in the Journal of Ecological Modelling (2016): `http://dx.doi.org/10.1016/j.ecolmodel.2016.10.002`.

Paper III compares a historical EwE model, fitted to time series data, with a present-day model, assuming equilibrium conditions, using fishing scenarios. The aim is to understand how reliable non-fitted models are compared to fitted ones in terms of predicting consequences of alternative management strategies. This paper is published in the Journal of Great Lakes Research (2020): `https://doi.org/10.1016/j.jglr.2020.01.001`.

Paper IV compares EwE and Atlantis models of Lake Victoria using fishing scenarios. The aim is to understand how model structure, complexity, and assumptions affect policy evaluations. This paper is published in the Journal of Great Lakes Research (2019): `https://doi.org/10.1016/j.jglr.2019.09.018`.

Paper V examines socio-ecological trade-offs between management objectives using EwE and Atlantis modelling frameworks. The aim is to understand the relative risks and benefits of different management objectives in a fishery with limited livelihood options. This paper is published in Fisheries Research (2020): `https://doi.org/10.1016/j.fishres.2020.105593`

Paper VI examines spatial and temporal variation in fishing patterns and fishing pressure in relation to the biological productivity of individual harvested fish species/groups. The aim is to understand the focus of fisheries (harvest strategy), and its effect on species composition and size structure. This paper is under review (Fisheries Research).

3

Material and methods

3.1 Modelling frameworks

EwE and Atlantis were the main modelling frameworks (tools) used in this study. These tools are described in detail elsewhere, for example, in Christensen and Walters (2004a) for EwE and Audzijonyte et al. (2017a,b) for Atlantis; a summary is included in this section.

3.1.1 EwE

EwE is a biomass model that is widely used in modelling food web dynamics, with over 400 models (Colleter et al., 2015). Using the trophic mass balance routine (Ecopath), the system is partitioned into groups comprising species having a common physical habitat, similar diet, or life history characteristics (Christensen and Pauly, 1992). The functional groups are regulated by gains (consumption, production, and immigration) and losses (mortality and emigration), and they are linked to each other by predatory relationships (Christensen and Walters, 2004a). Parameterization is based on an assumption of mass balance over a defined period, usually one year. The residual of mass balances (the difference between gains and losses) is equivalent to the instantaneous rate of biomass change, represented by the biomass accumulation (BA) parameter. If biomass at the beginning and end of the modelled period is known, the rate of biomass increase or depletion is accounted for, thereby mitigating the risk associated with steady-state assumption (equilibrium conditions).

Input data are needed for three of the four key parameters: biomass per unit of habitat area (B), production rate per unit of biomass (P/B), consumption rate per unit of the biomass of predator j (Q/B), and ecotrophic efficiency (EE, the proportion of production that is utilized in the system). Ecopath sets up a system with as many linear equations (Equation 3.1) as there are functional groups in a system, and solves the set for one of the four key parameters. In addition to these input parameters, mandatory data, for every functional group i, are required for exports (usually catches, Y), net migration rate (E), BA, and diet composition (DC). Ecopath estimates, iteratively, as many missing parameters as possible before setting up the set of linear equations (Christensen and Walters, 2004a). The values of EE vary between 0 and 1, and usually approach 1 for groups with considerable predation mortality or fishing pressure (Darwall et al., 2010; Heymans et al., 2016). Therefore, the model is mass-balanced when EE is $\leq$1 for every group. The term $P \cdot (1 - EE)$ represents everything that cannot be explained by the model (i.e., other mortality, MO). The mass balance equation is as follows:

$$B_i \cdot (\frac{P}{B})_i = \sum_{j=1}^{n} B_j \cdot (\frac{Q}{B})_j \cdot DC_{ji} + B_i \cdot (\frac{P}{B})_i \cdot (1 - EE_i) + Y_i + E_i + BA_i \quad (3.1)$$

Some outputs are generated for each functional group during the mass balancing, particularly trophic level (TL, the biomass-weighted average TL of all prey $+1$) and net growth efficiency (g, production/consumption). The TL of each functional group is calculated based on the average annual predation by aggregating diet data. Primary producers and detritus are assigned a TL of 1. EE is never estimated experimentally; when all other parameters are given, Ecopath uses the input data to estimate EE as shown in Equation 3.2.

$$EE = \frac{E_i + Y_i + BA_i + B_i + M2_i}{P_i} \tag{3.2}$$

where, M2 is predation mortality, estimated as $M2_i = \sum_{j=1}^{n} \frac{Q_j \cdot DC_{ji}}{B_i}$.

Ecosim derives its initial parameters from the balanced Ecopath model to produce dynamic estimates of biomass and catch rates over time. These biomass dynamics are expressed through a series of coupled differential equations of the form below.

$$\frac{dB_i}{dt} = g_i \cdot \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - B_i \cdot (MO_i + F_i + e_i) \tag{3.3}$$

where, dB/dt is the rate of change of biomass, Q_{ji} is the consumption rate on group j, Q_{ij} is the predation mortality rate by group j, F is fishing mortality rate, e is emigration rate, and I is the immigration rate.

The model provides biomass predictions of each group in the system as affected directly by fishing and predation, change in food availability (through changes in environmental factors), and indirectly by fishing or predation on other groups in the system. Predation is governed by foraging arena theory (Ahrens et al., 2012). Here, functional groups are divided into vulnerable and non-vulnerable components, such that the overall feeding rate is somehow limited by prey density. Consumption is computed as shown in Equation 3.4.

$$Q_{ij} = \frac{v_{ij} \cdot a_{ij} \cdot B_i \cdot B_j \cdot T_i \cdot T_j \cdot S_{ij} \cdot \frac{M_{ij}}{D_j}}{v_{ij} + v_{ij} \cdot T_i \cdot M_{ij} + a_{ij} \cdot M_{ij} \cdot B_j \cdot S_{ij} \cdot \frac{T_j}{D_j}} \tag{3.4}$$

where, v_{ij} is the vulnerability of prey i to predator j, a_{ij} is the rate of effective search of i by j, T_i is the relative feeding time of i, T_j is the relative feeding time of j, S_{ij} is the representation of seasonal or long-term forcing effects, and D_j is the impact of handling time as the limit of consumption.

Calibration is performed using fishery drivers (for example, catch, effort, fishing mortality) by adjusting foraging arena parameters (v_{ij}) to ensure that predation mortality rates are within the tolerable limits, given the prescribed groups' productivity (production per unit biomass). This step is implemented in Ecosim, where v_{ij} are iteratively adjusted until the sum of squared deviations (SS) between predictions and observations (mainly biomass and landings) is lowest. The physical or other environmental parameters (abiotic factors) that may influence trophic interactions can be represented in the model through forcing functions (Christensen et al., 2008). The forcing functions can be used directly to control primary production or to modify consumption of the consumer groups in the model, but these are not used in this study.

3.1.2 Atlantis

Atlantis, on the other hand, is a deterministic, spatially resolved tool that is based on dynamically coupled biophysical and fisheries sub-models. These sub-models include production, consumption and predation, waste production and cycling, migration, reproduction and recruitment, habitat dependency, and mortality (Audzijonyte et al., 2017a,b; Fulton et al., 2011).

Hydrodynamics model

At the core of Atlantis is a deterministic hydrodynamics model, which is spatially-resolved, where physical processes are modelled. The spatial domain is 3-dimensional, consisting of user-defined boxes (polygons) and slab-like depth layers that represent biogeographic features (hydrography, bathymetry, and species distribution). The hydrodynamics model simulates water fluxes, which control advection of nutrients and plankton, temperature, and salinity, although these can also be included by observational data or calculated within Atlantis (Audzijonyte et al., 2017a). The most widely used hydrodynamics model in Atlantis models is the Regional Oceanographic Model (ROMS) (Audzijonyte et al., 2017a).

Biological model

The biological model consists of functional groups that are defined based on niche similarity (ecological roles, ontogenetic behaviour, and feeding interactions). Exchange of biomass occurs between regions according to seasonal migration and foraging behaviour. The flow of energy is tracked as nitrogen, which in all vertebrate groups is partitioned into structural and reserve nitrogen. Structural nitrogen determines growth, while reserve nitrogen, the amount of which varies depending on the food intake, is used for reproduction.

In most Atlantis models, predation is based on a modified Holling type II response, as shown in Equation 3.5.

$$P_{ij} = \frac{C_j \cdot a_{ij} \cdot B_i}{1 + \frac{C_j}{mum_j} \sum_{k=1}^{n} a_{kj} \cdot B_k \cdot E_{kj}} \tag{3.5}$$

where, P_{ij} is the consumption rate of prey i by predator j, mum_j is the maximum growth rate, C_j is the clearance rate of predator j, B_i is the biomass of prey i, a_{ij} is the availability of prey i to predator j, and E_{kj} is the assimilation rate of prey k for predator j. The ratio between C and mum determines the steepness of the consumption curve.

Recruitment in most Atlantis models is based on Beverton-Holt function as shown in Equation 3.6.

$$R = \frac{\alpha \cdot SSB}{\beta + SSB} \tag{3.6}$$

where, R is the number of recruits, α is the maximum number of recruits, β is the size of the spawning stock that gives half the maximum recruitment, and SSB is spawning stock biomass. The spawning stock biomass depends on individual weight and the proportion spawning in each age-class across the model domain, while for non-fish groups that are vertebrates, reproduction can be based on fixed offspring/adult (Audzijonyte et al., 2017a).

The TL of each group is also computed based on the average annual predation by aggregating diet data supplied through a preferential diet matrix.

Fisheries/harvest model

The fisheries model simulates user-defined fishing fleets that are assigned to harvested groups with selectivity curve set by the user. Fishing mortality can be applied in different ways, either through imposed landings forced through time-series data, user-defined mortality that sets a proportion of biomass to be harvested, or dynamic fishing by setting the effort for each fishery in days. However, most Atlantis models use imposed catch data to define fishing mortality, given that the main question in models developed for management strategy evaluation is to understand the ecosystem dynamics given the specified catch biomass that the fisheries may want to take (Audzijonyte et al., 2017b).

Model calibration and validation

Atlantis models are calibrated through manual adjustment of parameters; as a result, the final model tends to depend on the modeller. However, the model is considered a reasonable representation of the true ecosystem when the following five conditions are met, usually, in the order listed (Audzijonyte et al., 2017a). (i) Species present in the model do not go extinct unless they do so in the time series being fit to the model. (ii) Size-at-age is within 20% of von Bertalanffy curve expected from the literature. (iii) The model recreates observations of abundance from surveys or assessments, especially for species with historical data. Skill assessment (Olsen et al., 2016) is increasingly being used to test this condition (Nyamweya et al., 2016b; Ortega-Cisneros et al., 2017; Sturludottir et al., 2018). (iv) For species with no historical data, the model yields a reasonable time-series of abundance. (v) The model captures observed spatial distributions.

3.2 Exploring the progress of ecosystem modelling of the AGL

The analysis focused on the AGL (within the AGL region) as representatives of other African inland lakes. The lakes include Victoria, Tanganyika, Malawi, Turkana, Albert, Kivu, and Edward. The AGL region, therefore, consists of any country that borders any of these lakes, i.e., Democratic Republic of the Congo (DRC), Burundi, Rwanda, Uganda, Kenya, Tanzania, Zambia, Malawi, Mozambique, and Ethiopia.

To determine how active the field of ecosystem modelling related to fisheries management is, trends were examined on the number of primary publications applying ecosystem modelling using two leading ecosystem modelling platforms, EwE and Atlantis. The criteria for equating trends in publications numbers with activity levels followed Christensen and Walters (2005), where, for ecosystem modelling to be considered active, the number of publications appearing must be showing a continuous increase in recent years. Scientific publications applying EwE and Atlantis on the AGL were searched from web-based libraries and databases, including EcoBase (`http://sirs.agrocampus-ouest.fr/EcoBase/`), which archives published EwE models, and compared with those of the North American Great Lakes. From these publications/models, the variables of interest were the publication year, authorship affiliation, location (country), model area, model period, main assumptions, data uncertainty, and other features, for example, whether the model included all the tree main routines (Ecopath, Ecosim, and Ecospace). The data on the publishing trends was then used to examine the progress of ecosystem modelling of the AGL, implications for ecosystem models and modelling, fisheries research and management, and to identify the strategies required to promote the application of ecosystem modelling.

3.3 Development of models

After assessing the status of ecosystem modelling on the African inland fisheries, subsequent analysis (model development and comparisons) focused on Lake Victoria, East Africa, which is the largest among the AGL in terms of size, fisheries, and economic value (Ogutu-ohwayo et al., 2016).

3.3.1 EwE

The development of the EwE models for Lake Victoria was done in three phases. In most cases, model considerations changed at each phase, depending on the question being answered.

In the first phase, an Ecopath model was constructed for the whole lake, representing ecosystem conditions in 2014 (“new model”, Paper II). Two other existing models for the Nyanza Gulf, initially developed by Moreau et al. (1993a), representing ecosystem conditions in the 1970s and 1980s, were reparameterized and compared with the new model. The main question was to understand the evolution of the food web following the perturbations in the 1980s. Biomasses of fish groups, which were initially estimated by Ecopath in the existing models, were entered based on trawl survey data, especially from Kudhongania and Cordone (1974), and the models rebalanced. The number of functional groups was different in the three models (18 for the new model, 14 for the model of the 1980s, and 16 groups for the model of the 1970s). The difference arose from the treatment of haplochromines and Nile perch. Haplochromines had almost collapsed in the 1980s, and these were combined into one group for the model of the 1980s. Nile perch was separated into the juvenile and adult stages in the 2014 model to account for the ontogenetic diet shifts between life stages (Kishe-machumu et al., 2012b). The three models were compared using outputs from Ecopath alone, and no attempt was made to fit the models to time series data in Ecosim. Assessment of data uncertainty was only based on indirect methods, for example, using PREBAL diagnostics (Link, 2010) and other physiological constraints (Darwall et al., 2010; Heymans et al., 2016).

In the second phase, a historical Ecopath model was constructed, representing ecosystem conditions of the entire lake in 1980 (“historical model”, paper III). The main question was to understand the ecosystem dynamics given the historical levels of fishing, and potential ecosystem changes given the future fishing levels. The historical model was fitted to time series biomass and catch data in Ecosim using fishing mortality (F) as a driver. Time series of F were generated from annual landings and Atlantis-simulated biomasses (F = catch/biomass). Model validity was assessed through skill assessment using multiple metrics, including modelling efficiency (MEF), reliability index (RI), and Pearson correlation (r) (Olsen et al., 2016; Stow et al., 2009). Also, the simulated diet composition and other ecosystem metrics, such as TL of catch (TLC, the mean TL of all landed fish, weighted by the biomass of catch), total biomass, and total landings, were compared with those estimated directly from recent data to supplement skill assessment metrics.

In the third phase, the new model was modified and reparametrized with data representing average conditions for the period 2010-2105 ("present-day model", paper III). The main question was to understand how the present-day model (assuming equilibrium conditions) compares with the historical model (where key Ecosim parameters, especially biomass accumulation and vulnerability, are estimated by fitting model to time series data) in predicting consequences of alternative management scenarios. The following changes were made to the functional groups in the new model to standardize the functional groups and trophic interactions. Catfishes were separated into three groups, i.e., North African catfish (*Clarias gariepinus*), Semutundu (*Bagrus docmak*), and silver catfish (*Schilbe intermedius*). Squeakers (*Synodontis* spp.) and snout fishes (Mormyridae) were separated into two groups. Other tilapias (all tilapiine cichlids apart from Nile tilapia) and cyprinids were separated into five groups, i.e., Ningu (*Labeo victorianus*), Rippon barbell (*Labeobarbus altianalis*), small barbs (*Enteromius* spp.), 'robbers' (*Brycinus* spp.), and other tilapias. Haplochromines were merged into one group due to the lack of species-specific data for consideration in the historical model. Juvenile and adult Nile perch were also merged into one group. When all the functional groups were defined, data pedigree criteria (Christensen and Walters, 2004a) was used to assess the data uncertainty. Also, PREBAL diagnostics (Link, 2010) and other mass balance criteria (Darwall et al., 2010; Heymans et al., 2016) were used to ensure that the models were consistent with physiological rules.

3.3.2 Atlantis

The Atlantis model of Lake Victoria was developed by Nyamweya et al. (2016b). The model is freely accessible at `https://doi.org/10.6084/m9.figshare.4036077.v1`. Due to the recent updates in the Atlantis source code, the Atlantis model of Lake Victoria was recalibrated by retuning biological parameters, especially those related to growth and recruitment, until the simulated biomass and landings were comparable to those in Nyamweya et al. (2016b). The new biology.prm file used in this study can be found at `https://www.dropbox.com/s/ch70yzgzw0ernnp/LV_biol_r2019.prm?dl=0`.

The Atlantis model of Lake Victoria is spatially resolved into 12 active and five boundary layers, each with up to three depth layers, depending on the depth of the water column, and a total of 36 functional groups (19 age-structured vertebrate groups and 17 lower TL biomass pools). The physical processes are forced through a coupled Regional Oceanographic Model (ROMS, Nyamweya et al., 2016a). Consumption is based on a modified Holling type II response (Equation 3.5), while recruitment is modelled using Beverton-Holt function (Equation 3.6). The fisheries model simulates four fishing fleets: gillnet and inshore fleet, using the normal selection pattern, and longline and small seines, using logistic length-based selectivity curve (Nyamweya et al., 2017). The model covers a period of 1958-2015. The validity of the model is judged from its ability to simulate distributions of nutrients, primary production, and the main commercial fish species, and temporal trends of biomass and catch that match well with observed data and community shifts reported in the literature (Nyamweya et al., 2016b).

3.4 Model comparisons

In paper III, two EwE model types were compared: the 2015 end-state of the historical model (A) and the present-day model representing average conditions for the period 2010-2015 (B). Preliminary work involved comparing the simulated biomasses, diet composition, TLC, and total catches of model A with those of model B to ensure the models were comparable, and that any of the differences in their projections were attributable to model calibration (fitting the model to time series data). Forward simulations were conducted using models A and B under different assumptions of vulnerability and BA. In model A, projections were run using fitted vulnerabilities (A1) and default vulnerabilities (A2). In model B, projections were run using default Ecopath BA rates (B1) and empirically-derived BA rates (B2). BA rates in model B2 were derived as $(B_{2015} - B_{2010})/n$, where B_{2010} and B_{2015} are biomass estimates in 2010 and 2015, respectively; n is the number of years covered by the present-day model. In both B1 and B2, vulnerabilities were maintained at default values. In all simulations, i.e., involving models A1, A2, B1, and B2, all other parameters in Ecosim, for example, feeding time adjustment rate, predator effect on feeding time, and switching power, were maintained at their default values. Each model was projected forward for 20 years, starting from 2015 (the baseline), under different fishing scenarios, but mainly focusing on the most ecologically important groups: Nile perch (the top predator) and haplochromines (key prey species). The fishing scenarios were defined as: halting haplochromine fishing (*HP:0.0F*), increasing fishing mortality of haplochromines by 200% from basline (*HP:3.0F*), reducing and increasing Nile perch fishing mortality by 60% from the baseline, respectively (*NP: 0.4F* and *NP:1.6F*), and maintaining fishing mortality for all functional groups at the baseline level (status quo, SQ).

In paper IV, the historical EwE model was compared with the Atlantis model, also using fishing scenarios. Fishing scenarios were defined as: status quo (SQ), no fishing for haplochromines (*HP: 0.0F*), Nile perch fishing mortality reduced by 40% from baseline (*NP: 0.6F*), Nile perch fishing mortality increased by 40% from baseline (*NP: 1.4F*). As in Paper

III, 2015 was used as the baseline. The two models were compared at the ecosystem level, using globally-tested “robust” ecosystem indicators (Fulton et al., 2005), and also at the level of functional groups. At the functional group level, the analysis focused on changes in the biomass of targeted groups and the consequent effects of changes in target groups on non-target groups. The comparison was not intended to lead to the recommendation of one model over another. Instead, the objective was to understand how model outputs are sensitive to the model structure. Because outputs from Atlantis models are massive, comparisons of the two models were based on biomass and catch predictions aggregated into annual trends without spatial and size- and age-structure considerations.

In paper V, the historical EwE model was compared with the Atlantis model using fishing effort levels that would potentially maximize social, economic, and conservation objectives (optimal fishing effort). The OPS procedure in EwE (Christensen and Walters, 2004a) was used to search for the long-term, gear-specific fishing effort that can maximize these objectives. Atlantis does not have a similar computationally-flexible procedure. For purposes of comparing the two models in this study, a simpler approach, similar to the one used in Forrest et al. (2015), was used. The OPS procedure was applied EwE, where different weightings and objectives could be easily defined, and the resulting optimal fishing effort levels were applied to both EwE and Atlantis to evaluate long-term changes in species abundance (biomass).

In Paper VI, eight Ecopath models published from 1970 through 2015 were compared to assess the focus of fisheries in relation to balanced harvest (BH). Two complementary methods were used: the logarithmic Y/P plots, showing if all the exploited fishes have the same E, hence BH (Kolding et al., 2016a), and fishing indicators, trophic balance index (TBI) and exploitation index (EI), showing the variability of exploitation across ecosystem-specific TLs (Bundy et al., 2005). Both methods rely on data on yield and production for all exploited species in an ecosystem by species or TL. These data were extracted from Ecopath models by species/functional groups as follows. Production (P) for each functional group i, P_i, was derived from two Ecopath input parameters: production per unit of biomass (P/B = total mortality, Z (/year)) and biomass per unit of habitat area (B, ton/year), i.e., $P_i = \frac{P_i}{B_i} \cdot B_i$. Catch, which is an input parameter in Ecopath, was used to represent total yield (Y) for each functional group i. A full exposition of equations and the rationale for interpretation of the results can be found in Paper VI. Briefly, for the graphical method of Kolding et al. (2016a), exploitation is consistent with BH strategy if all exploited groups have the same E and groups lie on a straight line, with a slope $b = 1$, in a plot of yield against production. The magnitude of the difference from the slope of 1 indicates how unbalanced fishing is, and the higher the deviation around the slope, the more unbalanced is the exploitation pattern. Concerning fishing indicators, interpretation of data follows that when E is the even across all TL groups (i.e., BH), TBI is zero. Exploitation is unbalanced if TBI is further away from zero (Bundy et al., 2005).

4

Results

The main goal of this study was to understand (through multimodel comparisons) the effect of model structure and data assumptions on simulated policy outcomes, which could impact management advice for EBFM (Papers III-VI). Paper I gives an overview of the status of ecosystem modelling of the African inland fisheries. Paper II develops one of the models that is used in the subsequent analyses (model comparisons). This chapter summarises the findings on which the thesis is based, while detailed results can be found in the respective papers in part II of the thesis. The sections are arranged by the aims of the thesis.

4.1 Publication trends applying EwE and Atlantis on the AGL

The main question in paper I was to understand the progress of ecosystem modelling of the African inland fisheries, and whether this has impacted on management strategies. The examination of publication trends featuring EwE and Atlantis indicated ecosystem modelling to be limited on the AGL compared to other similar systems, especially the North American Great Lakes. Also, the use of data from other systems and periods other than those modelled was prevalent. Only 14 publications applying EwE, published during the period of 1988-2016, were retrieved for all the lakes (Table 4.1), equivalent to a publication rate of 0.5 per year. The number of publications applying EwE on the AGL decreased over time, with almost every year of publication followed by a reduction or no growth in the number of publications in the following year (Figure 4.1). Two of the AGL, Lakes Edward and Albert, which are shared by Uganda and DRC, did not have a single study applying EwE or Atlantis.

All the EwE models assumed stable equilibrium conditions ("steady-state" models), mainly describing the trophic structure of the modelled system. Only 4 models applied the time dynamic routine (Ecosim) to explore different management options, despite not being fitted to historical time series data. No model utilized the Ecospace routine of the EwE modelling package, indicating that EwE has not been utilized to inform decisions related to spatial aspects, for example, closed fishing areas, which is one of the fisheries management measure promoted by EBFM. On the authorship, except for one thesis, the first authors for all the publications applying EwE were affiliated to institutions outside the AGL region (Table 4.2).

As of August 2016, only one Atlantis model was under development on Lake Victoria.

In comparison to the American Great Lakes, the search revealed 17 publications, published within 24 years since 1993. While this number may also indicate dismal publication rate, 65% of the publications retrieved were for the most recent five years (2012-2016), indicating that the application of EwE is increasing and ecosystem modelling is becoming more active (*sensu* Christensen and Walters, 2005), compared to 7% for the AGL over the same period. Also, Atlantis models have been developed for the American Great Lakes to understand invasive species, climate, and acidification (CSIRO, 2016).

Table 4.1: A list of studies in literature in which Ecopath with Ecosim (EwE) modeling approach has been applied on the African Great Lakes.

Lake	Model area (country of location)	Modelled year/period	Main feature	Reference
Malawi	Southern and western shelves (Malawi)	1998-1999	Steady-state	Darwall et al. (2010)
Kivu	Southern part of Lake Kivu (DRC)	2002-2003	Steady-state	Villanueva et al. (2007)
Victoria	Kenyan part of Lake Victoria	1971-1972 and 1985-1986	Steady-state	Moreau et al. (1993a)
Malawi	Pelagic zone of central Lake Malawi	1979-1981	Steady-state	Degnbol (1993)
Tanganyika	Pelagic zone (Burundi)	1974-1976 and 1980-1983	Steady-state	Moreau et al. (1993b)
Tanganyika	Pelagic zone	1974-1975 and 1983-1984	Steady-state	Moreau and Nyakageni (1988)
Turkana	Pelagic	1987 and 1973	Steady-state	Kolding (1993)
Victoria	Kenyan sector of Lake Victoria	1985-1986 to 1995-1996	Steady-state and Ecosim	Moreau and Villanueva (2002)
Victoria	Nyanza Gulf in the Kenyan sector of Lake Victoria	1985-1986 to 1995-1996	Steady-state and Ecosim	Villanueva and Moreau (2002)
Victoria	Mwanza Gulf in Tanzanian sector of Lake Victoria	1977, 1987, 2005	Steady-state and Ecosim	Downing et al. (2012)
Victoria	Parts of Lake Victoria (Kenya, Uganda, and Tanzania), and whole lake	2000	Steady-state and Ecosim	Matsuishi et al. (2006)
Malawi	Lake Malawi	1976-1996	Steady-state and Ecosim	Nsiku (1999)
Malawi	Pelagic zone		Steady-state	Allison et al. (1995)
Victoria	Kenya	1971-1972	Steady-state	Moreau (1995)

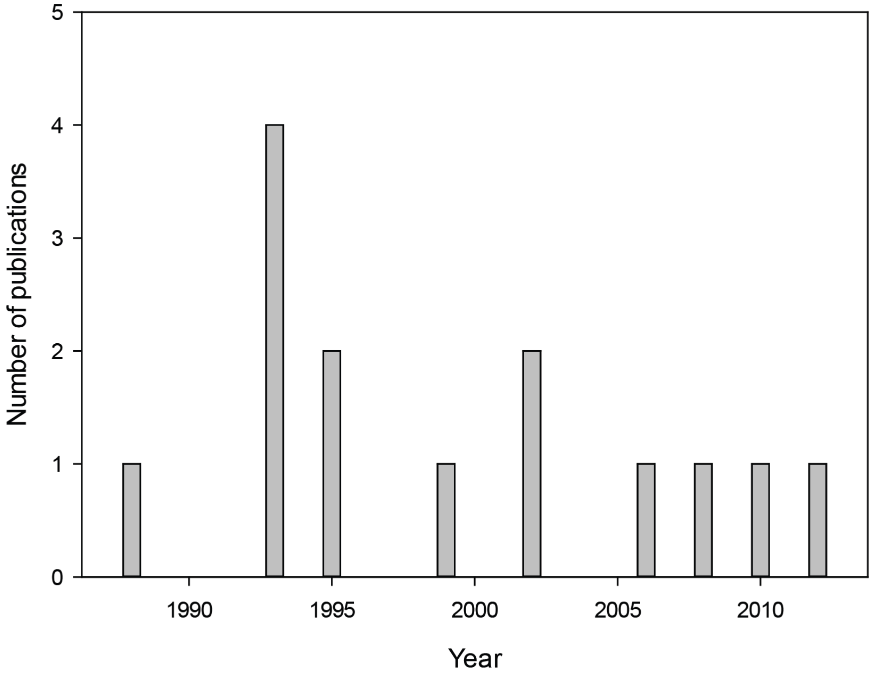

Figure 4.1: Number of publications since 1988 in which the Ecopath with Ecosim (EwE) modeling approach was applied on the African Great Lakes (AGL).

Table 4.2: Affiliation of first and co-authors, where applicable, of publications (excluding thesis) applying Ecopath with Ecosim (EwE) modelling approach on the African Great Lakes. The affiliation stated is that at the time of publication.

Reference	First author affiliation	Country of affiliation	Number of native co-authors	Number of native institutions	Country(ies) of native institutions
Darwall et al. (2010)	Non-native	United Kingdom	0	0	-
Villanueva et al. (2007)	Non-native	France	2	1	DRC
Moreau et al. (1993a)	Non-native	France	0	0	-
Degnbol (1993)	Non-native	Denmark	N/A	N/A	N/A
Moreau et al. (1993b)	Non-native	France	2	2	Burundi and Zambia
Moreau and Nyakageni (1988)	Non-native	France	1	1	Burundi
Kolding (1993)	Non-native	Norway	N/A	N/A	N/A
Moreau and Villanueva (2002)	Non-native	France	0	0	-
Villanueva and Moreau (2002)	Non-native	France	0	0	-
Downing et al. (2012)	Non-native	Netherlands	0	0	-
Matsuishi et al. (2006)	Non-native	Japan	6	3	Uganda, Tanzania and Kenya
Allison et al. (1995)	Non-native		0	0	-
Moreau (1995)	Non-native	France	N/A	N/A	-

4.2 Evolution of the food web in Lake Victoria

Paper II aimed at examining the changes in Lake Victoria's trophic structure amid perturbations, especially species introductions. Three Ecopath models representing periods before, during, and after the collapse of the original food web (1971-1972, 1985-1986, and 2014, respectively) showed a decrease, over time, in productivity (in relation to biomass and respiration) and food web connectivity, and an increase in biomass cycling. The total system throughput (TST, the measure of the size of the entire system in terms of the summation of biomass flows from total consumption, respiration, export and flows, to detritus) decreased fivefold between 1971-1972 and 1985-1986 and remained relatively the same through 2014, with a moderate shift from herbivory to detritivory. The connectance index (CI), showing the ratio of the number of actual connections to the number of possible connections in the food web, of 0.32 in 2014 was 22% lower than CI in 1971-1972. The system omnivory index (SOI), showing the average omnivory index of all consumers weighted by the logarithm of each consumer's food intake, of 0.12 in 2014 was 30% lower than the SOI in 1971-1972. The Finn's cycling index increased from 4.33 during the 1970s to 5.84 during the 1980s but decreased again to 4.75 by 2014.

The TLC increased between 1971-1972 and 1985-1986, following the establishment of the introduced piscivorous Nile perch, but decreased afterwards. The decrease in TLC between 1985-1986 and 2014 can be attributed to an expansion of the silver cyprinid (low TL species) fishery, especially after 2005, i.e., fishing through the food web (Essington et al., 2006), rather than to a decline in high TL stocks.

4.3 Historical time series fitting of EwE models and the effect on policy evaluations

The main question in paper III was: how reliable are EwE models without historical time series fitting? Comparison of the present-day EwE model (B1 and B2) with a historical EwE model (A1) using fishing scenarios showed different predictions, but the differences were slightly lower when the BA rates in the present-day EwE model were adjusted to reflect recent biomass trends as estimated from short-term empirical data (Figure 4.2). Biomass projections were consistent across models (in terms of the direction of change) for the direct fishing-induced effects on target species. However, the cascading effects of changes in target groups on their respective prey/predators groups ("indirect trophic effects") were different, especially in the present-day model assuming equilibrium conditions (BA=0, B1, Figure 4.2). When short-term empirically-derived BA rates were applied to the present-day EwE model (B2), qualitative similarities in model predictions (A1 versus B2) were observed for most of the functional groups (Figure 4.2). In terms of quantitative results, however, the fitted EwE model (A1) predicted higher biomass change compared to the unfitted models (B1 and B2), even after incorporating short-term empirically-derived BA rates (Figure 4.2). The discrepancy in quantitative results is associated with different BA rates, because BA rates for most groups in the fitted model were negative and higher by several orders of magnitude compared to the unfitted models B1 and B2 (see paper III for detailed explanation of fishing scenarios tested).

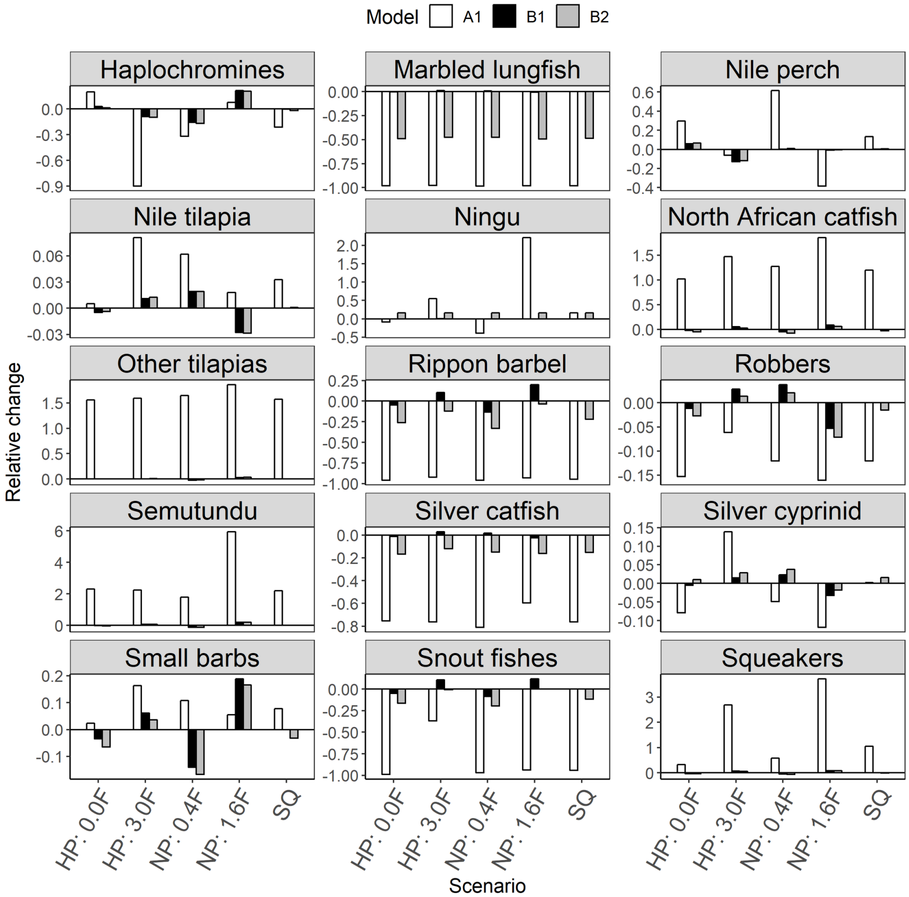

Figure 4.2: Percentage change (2035 relative to 2015) in biomass of functional groups as predicted by the historical model end-state (A1) and present-day models: B1 (using default biomass accumulation) and B2 (using empirically-derived biomass accumulation rates). Bars on the same side of zero line (positive or negative) indicate qualitative agreements between models.

4.4 Model structure/complexity and the effect on policy evaluations

Paper IV aimed at testing the sensitivity of model output to model structure, by changing fishing mortality of individual model groups (Nile perch and haplochromines). At the functional group level, the models showed qualitative agreements (similar trends) in the historical reconstruction simulation (hindcast) for most functional groups (Table 4.3). However, not all the agreements in the hindcast translated into agreements in the forward projections (forecast) (Table 4.4), although qualitative agreements between models were observed for the dominant fisheries such as Nile perch and silver cyprinid (Figure 4.3). For other groups such as haplochromines, the models generally showed similar trends in the hindcast, but the forecast showed different prediction in most of the scenarios. At the ecosystem level (see Paper III for detailed description of ecosystem-level indicators and functional groups aggregated for each indicator), three main observations were made. (i) Ecosystem indicators were less responsive (low magnitude of change in the order of 1-5%) in both models compared to species-level indicators. (ii) Ecosystem indicators were more coherent across models compared to species-level indicators. (iii) Atlantis was generally more sensitive to changes in fishing mortality than EwE (Figure 4.4).

Table 4.3: Correlation of EwE versus Atlantis-simulated biomass and catch trends in the historical simulations (1980-2015).

Group	Biomass	Landings
Nile perch	0.90	0.85
North African catfish	0.89	0.86
Semutundu	0.83	0.77
Marbled lungfish	0.98	0.96
Squeakers	0.92	0.88
Snout fishes	0.98	0.88
Silver catfish	0.98	0.97
Rippon barbell	0.98	0.61
Robbers	-0.44	0.18
Ningu	0.87	0.86
Haplochromines	0.74	0.95
Silver cyprinid	0.64	0.95
Nile tilapia	0.70	0.81
Other tilapias	0.47	0.31

Table 4.4: Correlation of EwE versus Atlantis-simulated biomass trends in the forward simulations (2015-2035).

Species/scenario	SQ	HP:0.0F	NP:0.6F	NP:1.4F
Nile perch	-0.96	0.39	0.44	-0.44
African catfish	0.78	0.803	-0.13	0.95
Semutundu	1.0	0.44	1.0	1.0
Marbled lungfish	1.0	1.0	1.0	1.0
Squeakers	0.30	0.54	-0.86	0.91
Silver catfish	0.66	0.62	0.80	0.54
Rippon barbell	1.0	1.0	1.0	1.0
Small barbs	0.65	0.49	0.63	0.52
Ningu	-0.97	-0.97	0.99	-1.0
Haplochromines	-0.95	-0.14	0.99	-0.99
Silver cyprinid	1.0	0.99	0.99	1.0
Nile tilapia	-0.63	-0.64	-0.72	-0.45
Other tilapias	0.88	-0.17	0.83	0.90

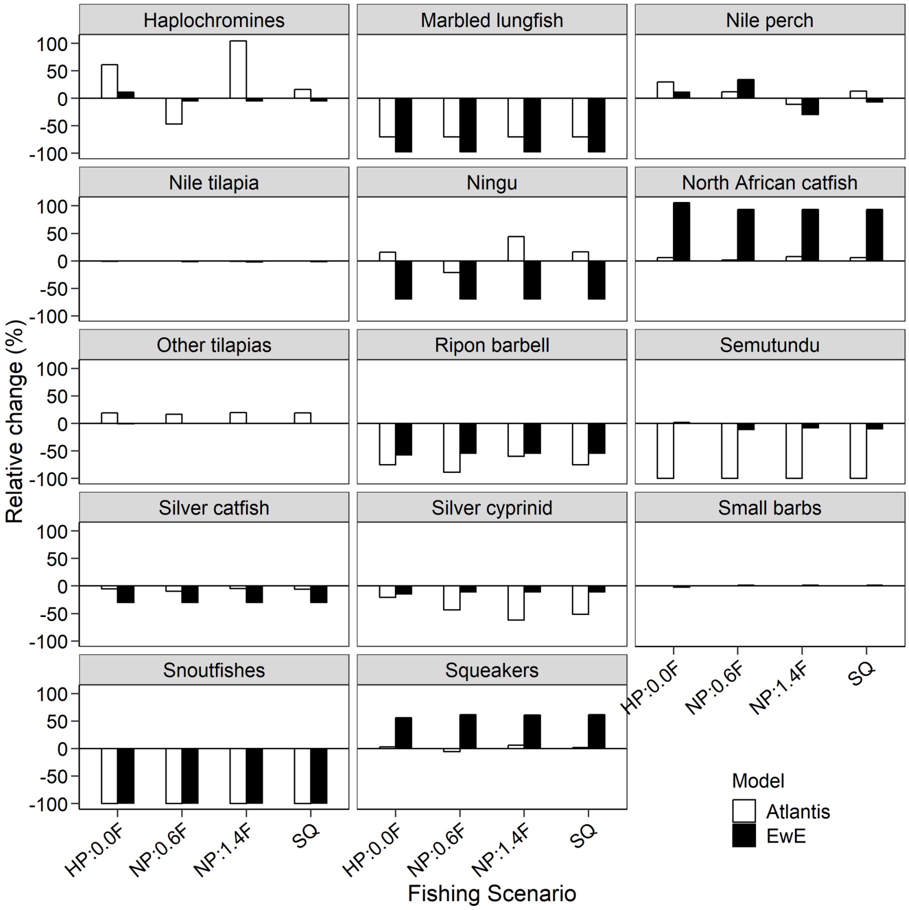

Figure 4.3: Percentage change (2035 relative to 2015) in biomass of functional groups as predicted by Atlantis and EwE models. Zero indicates no change. Bars on the same side of zero line (positive or negative) indicate qualitative agreements between models.

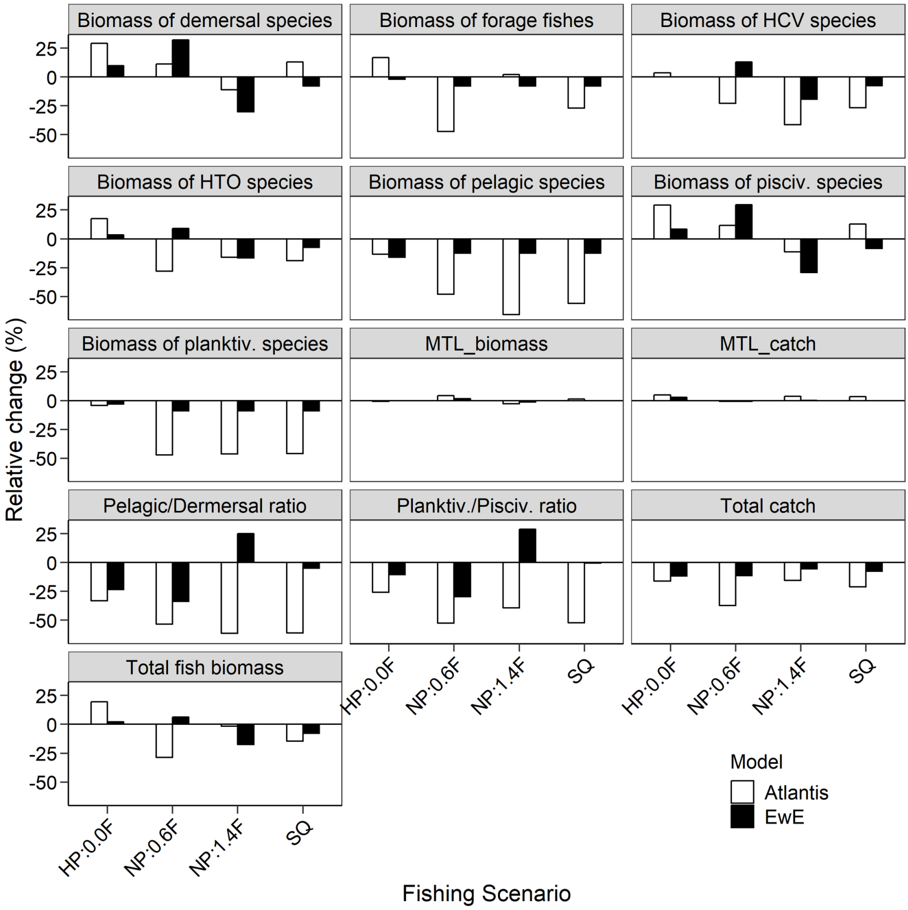

Figure 4.4: Indicators based on biomass and catch of fish groups as predicted by EwE and Atlantis. Values represent 2035 value of indicator under each fishing scenario relative to 2015 baseline value. Zero indicates no change. Abbreviations stand for piscivorous (pisciv.), planktivorous (planktiv.), high commercial value (HCV), high turnover species (HTO), mean trophic level of catch (MTL_catch), and mean trophic level of biomass ($MTL_biomass$).

4.5 Trade-offs between socio-economic and conservation objectives

Paper V aimed at comparing trade-offs between socio-economic and conservation objectives across EwE and Atlantis models. The OPS in EwE showed profit maximization to be more compatible with conservation objectives than is the maximization of yield (or employment) (Table 4.5; also, see paper V). When a penalty was applied to illegal gears (i.e., by increasing fishing costs until the gears were unprofitable), economic benefits and biomass of major commercial fisheries were highest, but not when the objective was set to maximize ecosystem structure exclusively (see paper V). Also, the OPS showed that economic or conservation objectives could be achieved simultaneously, but this would require a reduction in fishing effort (and potential yield) in almost every fishing sector/fleet (Figure 4.5).

When the optimal fishing effort was applied to both EwE and Atlantis to simulate long-term changes in the ecosystem, the two models generally gave contrasting biomass predictions, especially when no penalty was applied to the illegal gears (Figure 4.6). Exceptions were the species/groups with strong diet interactions (for example, Nile perch and haplochromines) and other demersal and benthopelagic groups (for example, North African catfish, semutundu, Ningu, other tilapias, Rippon barbel, silver catfish, and squeakers), where biomass trends were relatively consistent, despite the differences in the magnitude of predictions. For these demersal and benthopelagic groups, biomass decreased in most optimizations, but the decrease was more pronounced in EwE than in Atlantis (Figure 4.6).

When a penalty was applied to the illegal gears, both models showed that maximizing economic value would result in approximately 50% increase in the biomass of Nile perch relative to the baseline, which is two times higher compared to the no-penalty scenario, and a decrease in the biomass of haplochromines. However, the magnitude of change in haplochromines was two times higher in EwE than Atlantis (Figure 4.7). Optimization for social benefits gave variable results, but generally, biomass decreased for most fish groups. Optimization for ecosystem structure caused the most significant change in the main commercial fish species, resulting in a collapse of Nile perch and silver cyprinid in both EwE and Atlantis. This objective was associated with the recovery of most demersal and benthopelagic groups (marbled lungfish, North African catfish, semutundu, Rippon barbell, silver catfish, Robbers, squeakers, and snout fishes), especially in EwE, majority of which were in a collapsed state at the start of the simulation. Optimization for biomass diversity also resulted in a consistent increase and decrease in the biomass of Nile perch and haplochromines, respectively, in both models. The trends for other major fisheries, such as silver cyprinid and Nile tilapia, however, were different, with biomass generally increasing in EwE and decreasing in Atlantis. Mixed objective optimization, especially those emphasizing economic value and ecosystem structure, resulted in biomass changes comparable to those from single-objective optimization for economic value (Figure 4.7).

Table 4.5: Changes in metrics used to measure benefits from economic, social, and conservation objectives relative to the Ecopath baseline values. Arrows show direction of change: increase (upward/north-east arrow) and decrease (downward/south-east arrow). An arrow is slanting (north-east or south-east) when the magnitude of change is at least two-times lower in one scenario compared to the other scenario. Long dash shows no change in objective metrics relative to the baseline. NPV stands for net present value, while B/P is biomass to production ratio. Objectives are arranged as NPV:catch value:B/P:Q90.

Objective/metric (weighting)	B/P ratio	Catch value	NPV	Q90 index
Scenario: no penalty applied to illegal gears				
Economic value (1:0:0:0)	↑	↘	↗	—
Social value (0:1:0:0)	—	—	↗	—
Ecosystem structure (0:0:1:0)	↗	↘	↑	—
Biomass diversity (0:0:0:1)	↑	↓	—	—
Economic value and ecosystem structure (1:0:1:0)	↑	↓	↓	—
Mixed objectives (equal weights, i.e., 1:1:1:1)	↑	↓	↗	—
Mixed objective (10·B/P+10·Q90, i,e., 1:1:10:10)	↗	↘	↑	—
Mixed objective (100·B/P+100·Q90, i,e., 1:1:100:100)	↗	↘	↑	—
Mixed objective (10·catch value, i,e., 1:1:10:1)	↑	—	↗	—
Mixed objective (100·catch value, i,e., 1:1:100:1)	↑	—	↗	—
Scenario: penalty applied to illegal gears				
Economic value	↑	↓	↑	—
Social value	—	—	↑	—
Ecosystem structure	↑	↓	↓	↓
Biomass diversity	↑	↓	↑	—
Economic value and ecosystem structure (1:0:1:0)	↑	↓	↑	—
Mixed objectives (equal weights, i.e., 1:1:1:1)	↑	↓	↑	—
Mixed objective (10·B/P+10·Q90, i,e., 1:1:10:10)	↑	↓	↑	—
Mixed objective (100·B/P+100·Q90, i,e., 1:1:100:100)	↑	↓	↑	—
Mixed objective (10·catch value, i,e., 1:1:10:1)	↑	—	↑	—
Mixed objective (100·catch value, i,e., 1:1:100:1)	↑	—	↑	—

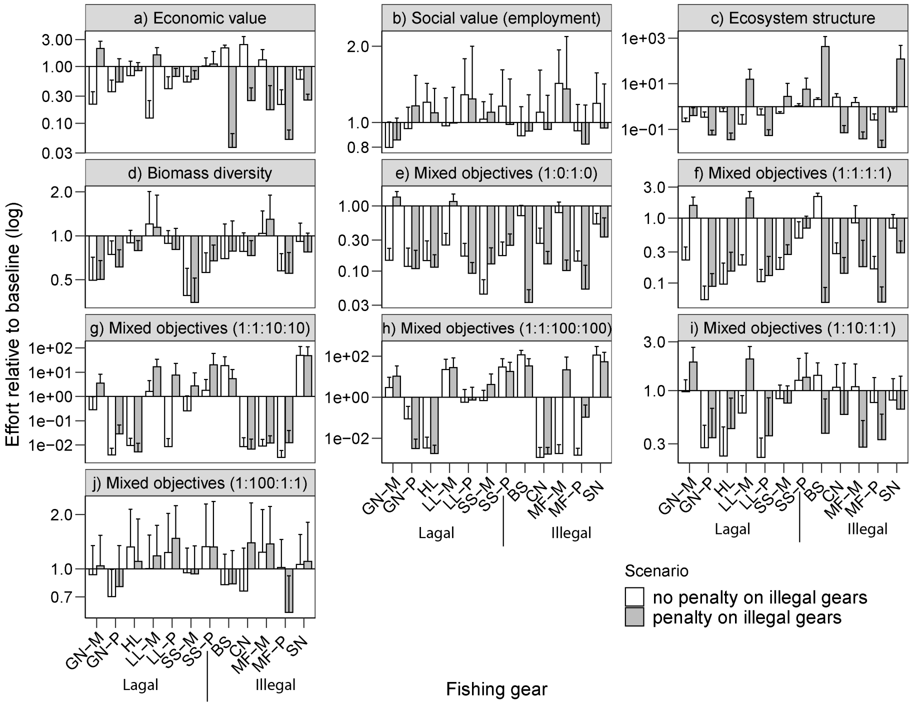

Figure 4.5: Gear effort configurations required to maximize economic, social and conservation benefits. All values are expressed relative to the Ecopath baseline run; values below and above 1 show decrease and increase in effort from the baseline, respectively. Error bars indicate the range of values obtained from 10 runs for each criterion.

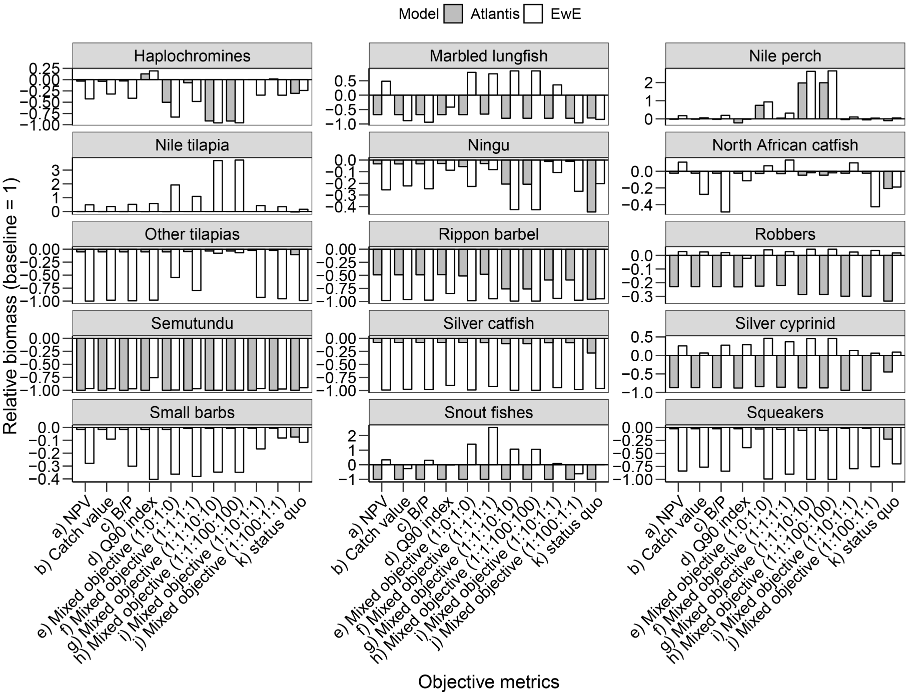

Figure 4.6: Biomass change (2034 relative to 2014 baseline) for the different functional groups as predicted by EwE and Atlantis when no penalty is applied to the illegal gears during the optimal fishing policy search. Bars below and above the zero lines indicate a decrease and increase in biomass from the baseline, respectively. Bars on the same side of the zero lines (either positive or negative) indicate consistent qualitative results across models. Results of the 2015 status quo scenario are included for comparison because the ecosystem would be expected to change under any level of fishing, including the baseline fishing rates.

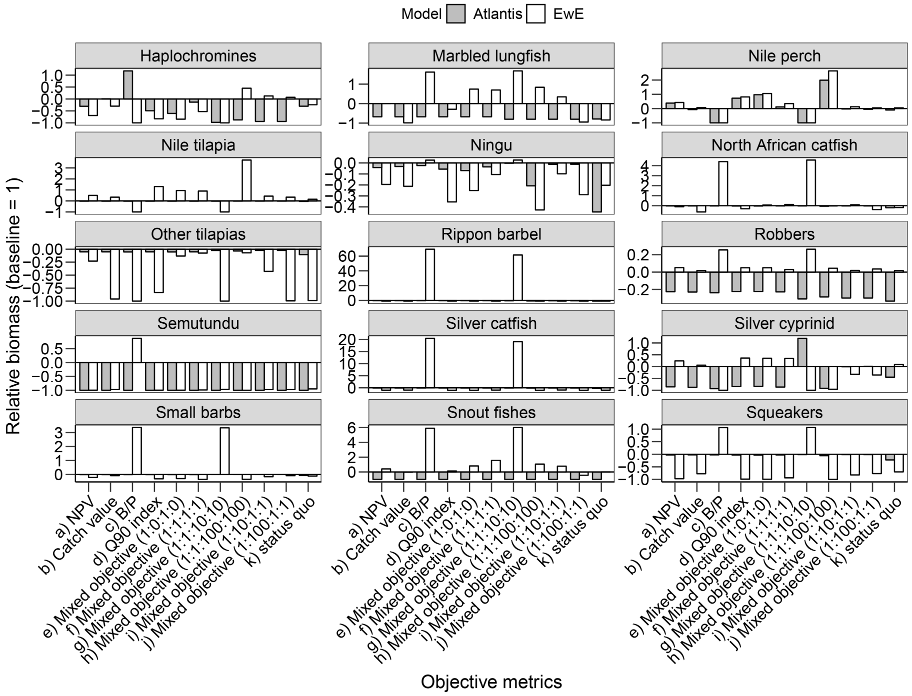

Figure 4.7: As for Figure 4.6, but a penalty is applied to the illegal gears during the optimal fishing policy search.

4.6 Focus of fisheries

Paper VI compared eight Ecopath models published from 1970 through 2015 to understand the focus of fisheries in relation to BH. Higher TL groups with lower production were exploited harder than low TL groups with higher production, and the overall fishing pattern was inconsistent with BH strategy (Figure 4.8). Exploitation was concentrated on the large demersal fishes. For example, adult Nile perch, catfishes, mormyrids and squeakers, and marbled lungfish, had E that exceeded 50% of the group's annual production, except during the 1980s and 1990s. The small pelagic groups (for example, juvenile Nile perch, silver cyprinid, and haplochromines) were less exploited, considering their production, except in 2000, when E for silver cyprinid approached 50% in Kenyan and Tanzanian waters. However, by 2014, E for silver cyprinid, averaged for the whole lake, was less than 10% of total production (Figure 4.8). A similar trend was observed in fishing indicators (Table 4.6). The TBI was much higher than zero for all the areas and periods covered in the analysis, indicating an exploitation pattern that was inconsistent with BH. The EI ranged between 4 and 60%; both the highest and lowest values were recorded in Kenyan waters, but this index has generally been declining since the 1990s.

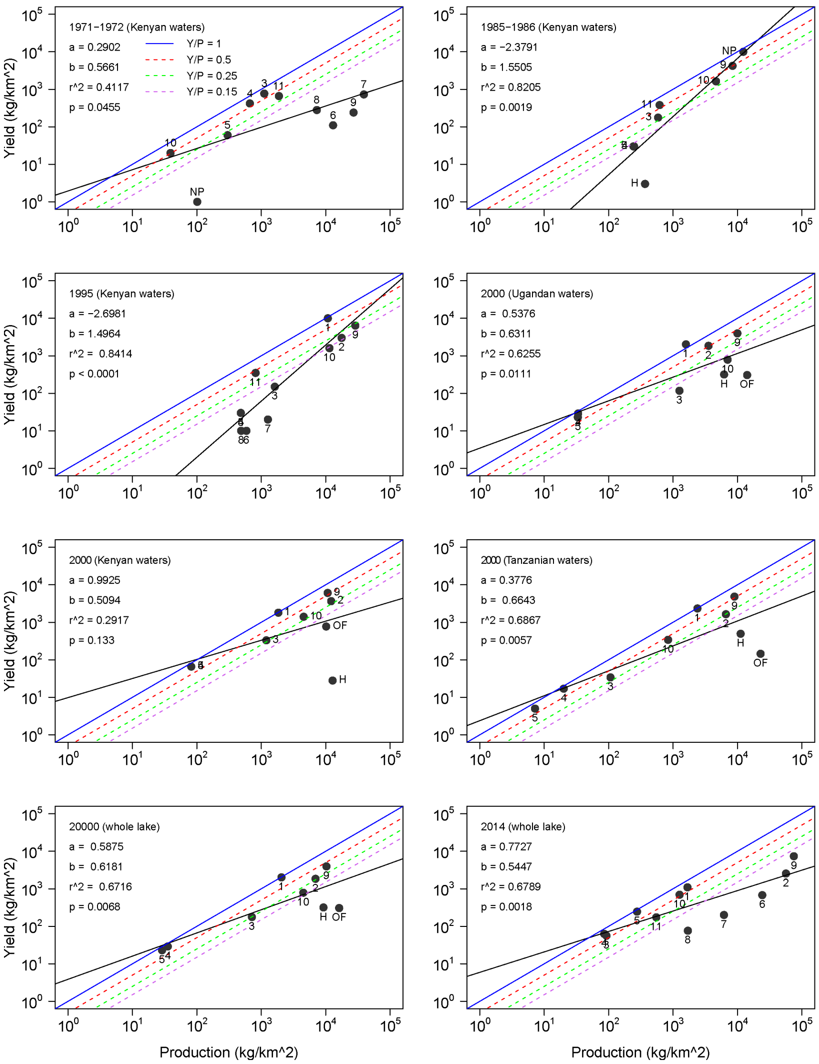

Figure 4.8: Harvest relative to production (on logarithm scales) for species harvested in Lake Victoria over time. The more the slope deviates from the 1:1 line between yield and production (i.e., F/Z = Y/P = 1), the more "unbalanced" (*sensu* Garcia et al., 2012) exploitation is. Exploitation rates equivalent to 15, 25, and 50% of production are given as dotted parallel lines. p-values give the test of slope ≠ 1. Numbers/letters represent species/functional groups: adult Nile perch (1), juvenile Nile perch (2), catfishes (3), marbled lungfish (4), squeakers and snout fishes (5), zooplanktivorous haplochromines (6), Detritivorous haplochromines (7), other haplochromines (8), dagaa (9), Nile tilapia (10), other tilapias (11), other fishes (OF), unseparated haplochromines (H), unseparated Nile perch.

Table 4.6: Fishing indicators from eight ecopath models representing Lake Victoria ecosystem for the period 1971-2014. TBI = Trophic Balance Index, and EI = Exploitation Index.

Model period/location	TBI	EI
1971-1972 (Kenyan waters)	1.03	0.03
1985-1986 (Kenyan waters)	0.77	0.60
1995 (Kenyan waters)	1.38	0.28
2000 (Ugandan waters)	0.96	0.21
2000 (Kenyan waters)	0.75	0.26
2000 (Tanzanian waters)	0.75	0.18
2000 (whole lake)	0.97	0.18
2014 (whole lake)	0.99	0.07

5

Discussion

This study provides insight into the status of ecosystem modelling on the African inland fisheries, in relation to global trends, and the implication for management. The study further shows how Lake Victoria's trophic structure and ecosystem functioning have evolved following major disturbances in the 1980s, the effect of model complexity and data assumptions on policy evaluations, and the effect of fishing pattern on species composition and size structure.

5.1 Status of ecosystem modelling on the African inland fisheries

The African inland lakes are threatened by multiple stressors, including overexploitation, habitat degradation, species introductions, nutrient enrichment, and damming of inflowing rivers (Welcomme et al., 2010). Because of these various threats, which are also increasingly becoming interconnected, ecosystem modelling is key to understanding how the threats interact as a basis for providing integrated assessment and advice for management. This study sought to analyze how dynamic ecosystem modelling is on African inland lakes and the implication for EBFM. Because ecosystem modelling is growing globally partly as a result of support offered by experts and developers through short training courses (Christensen and Walters, 2005; Plagányi, 2007), ecosystem modelling of the African inland lakes, where these training programs are absent, was expected to be limited. This assumption is consistent with the study findings, including a decline in the number of publications applying ecosystem models in the recent years, all existing models (excluding Atlantis model that was under development) being led by scientists affiliated to institutions outside the AGL region, and some of the major lakes, such as Albert and Edward, having no single study applying EwE or Atlantis. These findings suggest that management of African inland lake fisheries predominantly relies on single-species approaches. On some of the major lakes, particularly Lake Victoria, these approaches have not been successful, although other factors such as weak enforcement of fishery regulations as well as lack of compliance by fishers may have played a role (Njiru et al., 2006).

Many factors may contribute to limited or total lack of application of ecosystem modelling to fisheries problems. The paucity of data available to parameterize and validate the model is the primary challenge limiting the development or use of ecosystem models (Heymans et al., 2011). Even when the data are available to construct an ecosystem model, the quality varies, leading to uncertainty in model outputs (Rose, 2012). However, a review of the ecosystem models available on the African inland fisheries suggests that insufficient data may not be the primary cause of limited ecosystem modelling, but the insufficient capacity to use most of the available ecosystem modelling tools. All the existing models being led by researchers affiliated to institutions outside Africa may be related to the extended support for EwE modelling offered by developers and other experts (Christensen and Walters, 2005; Plagányi, 2007). Although most ecosystem modelling tools come with manuals, many do not cover all aspects comprehensively and training workshop sessions, such as those featuring EwE, are useful in starting-off new users (Christensen and Walters, 2005; Colleter et al., 2015; Plagányi, 2007).

The level of research attention given to ecosystem modelling seems to influence the use of models in fisheries management. For example, the increasing use of ecosystem models in fisheries management in the USA and Australia may be attributed to the active field of ecosystem modelling and the presence of model diversity, both of which aid understanding of appropriate model structure (Christensen and Walters, 2005; Collie et al., 2016; Fulton et al., 2011a). Model diversity also increases confidence in policy recommendations, especially for the scenarios that are less sensitive to model choice (Stefansson et al., 2019). For the African inland fisheries, limited ecosystem modelling, coupled with the prevalence of models with high data uncertainty, may explain the limited use of ecosystem models in actual management decision making and EBFM.

Based on the observations presented here, the strategies that are needed to improve ecosystem modelling on the African inland lakes include increasing local and regional capacity for ecosystem modelling and strengthening monitoring programs on the lakes to improve the availability of data for ecosystem modelling. Christensen and Walters (2005) showed that by 2005, more than 600 scientists had been trained in applying different modules of EwE to answer questions related to species invasions, acidification, climate change, habitat restoration, and marine protected areas. This number has more than doubled in recent years (Steenbeek et al., 2014). Such training sessions provide practical skills for ecosystem modelling platforms, and these will be necessary to increase capacity and activate ecosystem modelling on the African inland fisheries. Also, targeted data collection surveys should be conducted to fill data gaps in the existing models. Data gaps that need to be urgently filled to improve exiting models and stimulate the development of new models include abundance per age class, growth rates of organisms, habitat preferences, migratory characteristics, biogenic habitats, stomach content analyses (especially for non-commercial species), import and export roles of other organisms, such as non-predatory birds that are frequent in freshwater aquatic systems, and describing unknown species of fish and invertebrates and their roles in the ecosystems.

5.2 Evolution of the Lake Victoria food web

Lake Victoria's food web was transformed in the 1980s, following the disappearance of 300+ *Haplochromis* spp (Witte et al., 1992) and the collapse of most native non-haplochromine fisheries (catfishes, *Oreochomis* spp.) (Goudswaard and Hecky, 1997; Ogutu-ohwayo, 1990b). The primary food pathways changed, and the complex food web changed to a linear system, with the apex predators (Nile perch) feeding on invertebrates (freshwater shrimp) (Moreau et al., 1993a). During the 1990s, some haplochromine trophic groups started reappearing, especially detritivores and zooplanktivores (Witte et al., 2000). This study sought to examine whether the trophic structure has recovered following the resurgence of some trophic groups and if there is potential for the reorganization of the food web. The study relied on Ecopath models representing the three periods: before, during, and after the collapse of the original food web. Results showed a system that is still simple, with low connectivity (low CI and SOI) and high biomass cycling (high Finns cycling index). Values of both CI and SOI indicate a relatively simple food web, with most functional groups exhibiting some degree of diet specialization. Because trophic connections are expected to evolve from linear to web-like as the system matures (Odum, 1969), the values obtained for CI and SOI denote a system that is not mature. Also, the results suggest that the trophic structure has not recovered after the disruptions during the 1980s, especially at the functional group level, which is in agreement with Downing et al. (2012).

The recovery of haplochromine biomass after its nearly complete collapse is remarkable, but its species diversity is only a fraction of what it was before the collapse (Witte et al., 2007). Before 1980, detritivorous haplochromines formed about 60% of total haplochromine biomass, while zooplanktivorous haplochromines constituted approximately 30% (Witte et al., 1992). After the collapse of both groups in the mid-1980s, zooplanktivorous haplochromines recovered first, starting in 1991, and by 2006, this trophic group constituted 70% of the biomass in open waters despite low species diversity (Witte et al., 2007). More recently, however, detritivores have again become dominant (Kishe-Machumu et al., 2015). This instability in the abundance of trophic groups may not allow the trophic structure to recover because the two groups influence the feeding relationship and abundance of other groups, especially the silver cyprinid, freshwater shrimp, and other macro-invertebrates due to competition (Downing et al., 2012).

The resurging haplochromine cichlids exhibit both morphological and ecological modifications, reflecting an adaptation to the changing environment (Kishe-Machumu et al., 2017; Rijssel et al., 2014). The zooplanktivores, in addition to extending their distribution from deeper (8-14m) (Witte et al., 1992) to shallow waters, have diversified the diet to insects and other larger prey (Kishe-Machumu et al., 2017; van Rijssel et al., 2017). The small benthivores have shifted from a diet dominated by detritus and phytoplankton, supplemented with small quantities of midge larvae and zooplankton, to a carnivorous diet of invertebrate prey of larger sizes (zooplankton, midge larvae, shrimps and molluscs) (Wanink et al., 2008). Also, the diet of the typical detritivores is similar to that of the zooplanktivores (Wanink et al., 2008). These changes have mainly been attributed to the changing availability of food types and a decline of the nutritional quality of detritus and phytoplankton due to a strong increase of cyanobacteria in the lake, reduction of the former trophic specialists, and reduced water clarity (Kishe-Machumu et al., 2015; Wanink et al., 2008). Cyanobacteria is still the dominant algae in the lake (Witte et al., 2012). Also, the observed morphological changes, including a decrease in both the ratio of intestine length to the standard length of the benthivores by 30% and stomach fullness (Wanink et al., 2008) and the changes in the structure of the oral jaw (Rijssel et al., 2014), may not easily be reversed unless another big evolutionary event occurs with the same magnitude as in the 1980s (Nile perch boom and eutrophication). Otherwise, the recovery of the trophic structure to the pre-1980 system is unlikely.

5.3 Effect of data assumptions on policy evaluations in EwE models

In paper I, results showed that all the existing EwE models on the AGL were steady-state (present-day) models, possibly because of insufficient time series fisheries data. The trend is almost comparable to the global situation, where less than 15% of all the EwE models are fitted to time series data (Heymans et al., 2014). With this global reality (prevalence of unfitted EwE models), it was unclear how much confidence can be attached to policy evaluations from EwE models without time series fitting. A present-day model (assuming default parameters: BA = 0; vulnerability=2) was compared with a historical model (BA and vulnerability parameters estimated by fitting the model to time series data). The differences in model outputs were remarkable, often involving predictions in the opposite direction. However, the differences were comparatively lower, especially for the less productive demersal groups (see Table 10.1), when BA terms in present-day model were set to reflect recent biomass trends (i.e., near the model's initialisation year) as observed from short-term empirical data. This finding is significant, suggesting that the reliability of present-day EwE models can be improved even when time-series data are not available. The results also indicate that it is not appropriate to use the default assumption regarding BA (equilibrium conditions), especially for the less productive groups and other groups that suffer substantial mortality, either due to predation or fisheries. When the stocks are suspected to be in decline, a negative BA may be used as a first draft assumption. This assumption may be more realistic than assuming stable, equilibrium conditions (Ainsworth and Walters, 2015) as seen in all existing Ecopath models for the African inland lakes (Table 7.2).

5.4 Sensitivity of model outputs (policy evaluations) to model choice

Both fitting the model to time series data and skill assessment (Olsen et al., 2016; Stow et al., 2009) may not guarantee that the model captures ecosystem processes well and is, therefore, the right choice (Collie et al., 2016). Ensemble or structure modelling is being widely used as an "insurance" against uncertainty inherent in complex ecosystem models (Gårdmark et al., 2013; Lotze et al., 2019; Pope et al., 2019a; Spence et al., 2018). Other advantages of ensemble/structured modelling include identifying fundamental ecological mechanisms that cause the differences in simulated fishery responses between models, separating uncertainty caused by differences in ecological model assumptions from that caused by individual considerations and biases by the modeller, and identifying scenarios that are robust to model choice and from which sound management decisions can be supported (Gårdmark et al., 2013). Paper IV, which compared structurally-distinct models, EwE and Atlantis, is an example of such application. While large differences were observed in model predictions at the functional group level, the models gave similar qualitative results. The ability of these structurally-distinct models to provide comparable qualitative results highlights the capacity of simpler ecosystem models such as EwE to support sound qualitative advice, which is needed for EBFM, even when quantitative results differ.

Various factors have been identified as contributing to the discrepancies in policy evaluations across different models, especially EwE and Atlantis. These are related both to model structure (for example, treatment of biological processes such as predation and fishing), complexity (for example, representation of environmental and biophysical attributes and spatial considerations), and individual model considerations (for example representation of functional groups and trophic interactions) (Forrest et al., 2015). Many previous studies have found EwE to be more responsive to fishing than Atlantis, and this has been attributed to the “delaying” features (age- and size-structure, life history stages and reproductive behaviour) incorporated in the Atlantis modelling framework, with an effect of delaying the reproductive response of a population (Forrest et al., 2015; Kaplan et al., 2013; Smith et al., 2011). The present study, instead, showed Atlantis to be more responsive than EwE, especially at high fishing pressure, even when the Atlantis model of Lake Victoria also incorporated age- and size-structure and other life-history stages (Nyamweya et al., 2016b), an observation that is also consistent with Smith et al. (2015). The findings of both the present and previous studies suggest that there may not be a single key ecological mechanism explaining the differences in simulated fishery responses between structurally-distinct models. Forrest et al. (2015), for example, indicated that the variation in qualitative responses between EwE and Atlantis models emanated from differences in the representation of functional groups and trophic interaction feedbacks. For the EwE and Atlantis models of Lake Victoria, the description of functional groups differs for the lower TLs, i.e., biomass pools, but the vertebrate groups are comparable, except haplochromines, which are modelled as one group in EwE and three groups in Atlantis. This consistency in the representation of groups may explain the observed qualitative similarities in model responses to fishing scenarios.

Forrest et al. (2015) further showed that the differences in the representation of biophysical processes contributed to major deviations between model predictions. The dynamics of several functional groups in Atlantis were more influenced by bottom-up processes (fluctuations in primary production, driven by the physical components in the hydrodynamics model) than in EwE, where there were no explicit primary productivity drivers. Similarly, the Atlantis model used in this study shows seasonal variation in lakes' physical processes and heterogeneity in nutrient concentrations, which are all positively correlated with fish species abundance (Nyamweya et al., 2016b). Yet, the EwE model is used in this study in its simplest form, with no explicit environmental and spatial considerations. These discrepancies in functional processes considered in the models could have contributed to the differences in quantitative differences observed in this study.

Despite the vast differences in model structure, complexity, and assumptions, the study showed that it is possible to identify scenarios with predictions that are less sensitive to model choice for which simpler models, such as EwE, could also provide reliable advice. The study further suggests that minimizing the differences in the trophic linkages between the models, for example, by using similar functional groupings and feeding interactions, may help to minimize variations in fishery responses due to model structure. This particular aspects highlights the need to improve the accuracy of diet data through rigorous stomach content analyses, especially for the non-commercial groups that are always ignored during surveys.

5.5 The focus of fisheries

Lake Victoria has been a subject of debate for many years on whether the fishing is sustainable or not (Kolding et al., 2008, 2014; Mkumbo and Marshall, 2015). The catch rates (CPUE) of main commercial fish species, especially Nile perch and Nile tilapia, have plummeted over the years (LVFO, 2016b), concomitant with the continuous increase in fishing effort (LVFO, 2016c). At the same time, the average individual sizes in these fisheries, including the silver cyprinid, have shrunk (Mangeni-Sande et al., 2018; Mkumbo and Marshall, 2015; Njiru et al., 2008). What complicates the discussion of overfishing, though, is that overall landings for some species, such as Nile perch, have remained stable for more than two decades (Kolding et al., 2014), while others, such as silver cyprinid, have increased more than threefold during the same period (Mangeni-Sande et al., 2018). In this study, the status of Lake Victoria exploited fisheries was investigated using a different approach, focusing on the productivity of individual species/groups rather than the changes in catch rates. Because of the influence of markets on fishing patterns (Sethi et al., 2010), the minimum mesh size regulations on Lake Victoria (LVFO, 2016a), and emphasis on fishery revenues through exports (Johnson and Bakaaki, 2016; Nunan, 2014b), exploitation was expected to be skewed to less productive, large commercial fish species at the top of the food chain, and hence inconsistent with BH. The results were in agreement with the expectation; E above 50% were observed for large Nile perch, Nile tilapia, and other demersal fisheries (for example, catfishes, including squeakers, and marbled lungfish), while E less than 15% were observed for the more productive groups such as silver cyprinid, small-sized Nile perch, and haplochromines. These findings suggest that generalising on the exploitation status of the whole lake may not be appropriate and that each ecological group may need to be analysed separately. Here, overexploitation seems evident for large Nile perch (the adult sizes), Nile tilapia, and other demersal groups, but not for small-sized Nile perch, silver cyprinid, and haplochromines.

Selective fishing is associated with inefficient utilization of food energy value of aquatic systems (Kolding et al., 2016a). This fishing pattern can cause changes in species composition and size structure and contribute to lower yields compared to BH strategy (Jacobsen et al., 2013; Kolding et al., 2016c; Law et al., 2013,1; Zhou et al., 2015), making it a barrier to achieving EBFM goals (Garcia et al., 2015; Zhou et al., 2010). The fishing pattern observed on Lake Victoria, which is inconsistent with BH, may, therefore, explain why the demersal fisheries, particularly of catfishes, have collapsed and never recovered, although habitat degradation may also have played a role (Goudswaard and Hecky, 1997). The fishing pattern may also explain why Nile perch yield has remained stagnant for more than two decades, despite the increasing effort, and the size structure of high-valued commercial fisheries (Nile perch and Nile tilapia) has contracted.

The observed fishing pattern on Lake Victoria, however, does not suggest that the fishing effort on less productive groups be shifted to the more productive species without a detailed study. Some groups such as haplochromines are primary prey for other fishes, where fishing, even in direct proportion to productivity (BH), may endanger the higher TLs, particularly Nile perch (see, for example, Nyamweya et al., 2017). Elsewhere, Nilsen (2018) used an Atlantis model of the Barents Seas to test the effect of BH on yield and found a marginal increase in yield compared to the conventional selective fishing. However, when low TL groups were included in the fished taxa, following the BH strategy, stock collapses were observed in the ecosystem. This stock collapse is possible because lower TL groups generally have higher natural mortality than commercially harvested species, implying that BH can also be unsustainable, except where additional fishing on these groups helps to reduce competition among forage fishes that depend on the same prey (Law et al., 2013). Nilsen (2018) concluded that the marginal increase in yield was because the Barents Seas fisheries were already balanced, as earlier noted by Kolding et al. (2016a). This conclusion is interesting and will need to be explored in future on Lake Victoria, where fishing is clearly inconsistent with the BH strategy.

6

Conclusion and future perspectives

This thesis reports on the status of ecosystem modelling on African inland fisheries, the evolution of Lake Victoria's food web following major perturbations, the effect of model structure and data assumptions on policy evaluations, and the focus of Lake Victoria's fisheries concerning the recently proposed BH strategy. The results fall into six thematic highlights as follows. (i) Ecosystem modelling is less used on the African inland fisheries compared with the global trends, which correlates with the insufficient local and regional capacity for ecosystem modelling, with existing models predominantly led by researchers outside the AGL region. Consequently, management on the African inland fisheries mostly relies on single-species approaches, and could, therefore, be missing on the benefits of EBFM (Townsend et al., 2019). (ii) The present Lake Victoria's food web is simple, with low connectivity and high biomass cycling, implying that the original trophic structure has not recovered after the disruptions during the 1980s. The results suggest that the original trophic structure may never recover, especially at the functional group level, considering the new energy pathways and trophic groups associated with the species that have undergone ecological and morphological changes to fit in the new environment. (iii) Fitted and non-fitted EwE give contrasting predictions, but those differences can be lessened by adjusting rates of biomass change in the present-day model to reflect biomass trends near the model's initialization year. Therefore, unfitted EwE models should be used cautiously in practical management. In particular, the default EwE assumption regarding the rates of biomass change (equilibrium conditions, BA = 0) should not be used, especially for the less productive groups and other groups that suffer massive mortality, either due to predation or fisheries. (iv) EwE and Atlantis can give consistent qualitative results, especially for the direct fishery-induced effects on target groups, although quantitative results are different. These models can, therefore, give reliable qualitative advice that is needed for EBFM. (v) Socio-ecological trade-offs exist in multiple fisheries management objectives. Profit maximization is more compatible with conservation objectives than is the maximization of catch (or employment). However, maximizing both economic and conservation benefits would require a reduction in fishing effort (and hence employment) in every fishing fleet/sector. These results underscore the importance of identifying fishery objectives and preparing for the associated trade-offs, considering that achieving multiple goals is unlikely. (vi) Fishing on Lake Victoria is skewed to low productive groups at high TL, and hence inconsistent with the BH strategy. This particular fishing pattern may have contributed to the changes species in composition and contraction of individual sizes of the main commercial fish species, for example, Nile perch and Nile tilapia. However, the transition to a balanced harvest (BH) strategy, where fishing pressure is proportional to the biological productivity of species, will require additional investigations.

For ecosystem models to be trusted and used in management, ecosystem modelling needs to be an active field of research, with model diversity that can account for uncertainty about the most appropriate model structure (Hyder et al., 2015). Involvement of key stakeholders at every stage of the management strategy evaluation is also key to making ecosystem models count in policy planning (Hyder et al., 2015; Townsend et al., 2019). Participation of key stakeholders assures not only transparency during model development, but also easy sharing of information, which are all crucial under the EBFM framework (Townsend et al., 2019).

Ecosystem models may not precisely depict the structures and dynamics in real ecosystems, but they are built to be the best possible representation of the basic features and dynamics of the ecosystems. For African inland fisheries, limited ecosystem modelling and prevalence of models that are not validated against time series of historical dynamics is a concern, which could be contributing to the low confidence in the models for fisheries management. Indeed, comparison of fitted and unfitted EwE models gave conflicting predictions, suggesting that unfitted EwE models ought to be used cautiously. However, the study does not suggest that unfitted EwE models are useless. Unfitted Ewe models can be improved by incorporating information on short-term biomass trends near the model's initialization year in the biomass accumulation parameter, especially for the less productive groups and groups that suffer heavy mortality. For such groups, if no empirical biomass data are available near the model's initialisation year, negative rates of biomass change may be used as a first draft assumption rather than assuming stable, equilibrium conditions.

Whereas the prevalence of models that are not validated against observations is a concern (Heymans et al., 2016), insufficient data does not make ecosystem modelling attempts useless (Heymans et al., 2011; Rose, 2012). EBFM is adaptive (FAO, 2003), and so is ecosystem modelling. One approach that may help to stimulate data collection and ultimately advance ecosystem modelling on African inland fisheries is to create the models, and then use the models to identify critical data gaps (Christensen and Walters, 2004a; Rose, 2012). The data gaps can be used to inform data collection priorities, which can later be used to improve the models.

This thesis contributes the first EwE model on Lake Victoria that is calibrated to emulate historical fishery dynamics. The model provides an opportunity to test a range of hypotheses, including the effect of parameter uncertainty on safe removal rates and trade-offs among alternative management goals. However, several data gaps need to be filled, including improving the reporting of diet composition and landings of non-commercial fisheries. Also, while the model's reliability has been tested using multiple skill assessment metrics, the sensitivity of model results to input parameters remains unknown. Because similar fits may be produced using different parameter combinations, the parameters in the developed historical EwE model may not necessarily be the overall best Ecosim parameters. Consequently, the model is open to further improvements. Specifically, the sensitivity of model outputs to input parameters needs to be tested, and one can use Ecosampler (Steenbeek et al., 2018) in EwE to complete this task. Other approaches that can be applied to the Ecopath model to increase the confidence of results include linear inverse modelling (Bentley et al., 2019a) as well as co-creation by combining scientific and fishers knowledge in the modelling process (Bentley et al., 2019b). The present contribution, therefore, should be viewed, interpreted, and used as the best working hypothesis rather than a definitive representation of the Lake Victoria ecosystem.

Real ecosystems are never known, but only data from the system. Even when a model is fitted to the best time-series data, it may not be free from the uncertainty that is associated with complex ecosystem-level processes. Comparison of structurally-distinct models showed qualitative similarities in predictions across models, although variations occurred in quantitative results. The findings in this thesis suggest that simpler models may also support robust qualitative advice, which is vital for long-term strategic planning, but key ecological mechanisms explaining the differences in fishery responses between models (simple vs. complex, data-rich vs. data-poor) must be identified before hand. In view of this finding, the importance of multi-model simulations as an aid to guarding against the effects uncertainty on strategic management decisions can not be overstated. This further implies that the lack of model diversity observed on most African lakes requires urgent attention. The present work, however, focused on scenarios concerning well-documented species, especially Nile perch and haplochromines. Based on the study findings, it will also be useful to compare model behaviour under a range of fishing pressure scenarios on other functional groups, either individually or in combination with other groups in the ecosystem. Also, the EwE model was used in its simplest, non-spatial form. Yet, non-fishing, anthropogenic changes, such as limnological and other physical attributes, especially nutrient inputs, have been reported to affect Lake Victoria's ecosystem functioning (Hecky et al., 2010; Kolding et al., 2008; van Zwieten et al., 2015). The Atlantis model also shows seasonal variation in lakes' physical processes and heterogeneity in nutrient concentrations, which are all positively correlated with fish species abundance (Nyamweya et al., 2016b). Future studies may need to compare the models that are standardised as much as possible. For example, environmental and non-fishing anthropogenic factors may be incorporated in the EwE model using appropriate forcing functions (Christensen et al., 2008), while spatial effects may be considered using the Ecospace routine of EwE (Christensen and Walters, 2004a). Also, because of the influence of spatial heterogeneity on fish distributions (Nyamweya et al., 2016b), it may be appropriate to compare the two models using fishing scenarios at habitat level: inshore versus coastal versus deep open waters.

Part II

Papers

7

Paper I

Paradigm shifts required to promote ecosystem modelling for ecosystem-based fishery management of African inland lakes

Laban Musinguzi, Vianny Natugonza, Richard Ogutu-Ohwayo

Abstract

Ecosystem-based fishery management (EBFM) is the best option where other fishery management options have failed to achieve sustainable fisheries. EBFM is, therefore, important for the African inland lakes and fisheries resources, which are among the most threatened fisheries in the world despite the existing management interventions. Ecosystem modelling provides information that guides EBFM. This paper proposes strategies required to promote ecosystem modelling, and hence EBFM of the African inland lakes and fisheries. The strategies are based on an examination, presented herein, of (i) publication trends in literature applying two leading aquatic ecosystem modelling platforms, Ecopath with Ecosim (EwE) and Atlantis, on the African Great Lakes (AGL) as representatives of African inland lakes and (ii) deficiencies in data eminent in ecosystem models existing on these lakes. Results indicate that ecosystem modelling is not an active field of research on the AGL, which correlates with the limited local and regional capacity for ecosystem modelling, with existing models predominantly led by foreign researchers and marred by data deficiencies. The implications of these observations for ecosystem modelling and EBFM of the African inland fisheries are discussed. The strategies required to promote ecosystem modelling include supporting short-term training programs to equip local scientists with basic skills for ecosystem modelling, mainstreaming ecosystem modelling in the fisheries training curriculum of local universities, and conducting data collection surveys to fill data deficiencies. These strategies are envisaged to increase local and regional capacity, activate ecosystem modelling, and, consequently, promote EBFM.

Keywords: Ecosystem-based fishery management, Ecosystem modelling, Africa Great Lakes, Inland lakes

7.1 Introduction

Fish production from African inland fisheries is estimated at 2.7 million tonnes, a third of total fisheries production on the continent (FAO, 2014). The fisheries are important for food and income for riparian populations, national foreign exchange and revenue, employment for about 5 million people, 26.7% of them being women, and contributes 0.33% to GDP of African countries (de Graaf and Garibaldi, 2014). However, inland fisheries resources in Africa are more threatened than anywhere in the world, apart from Asia (Welcomme et al., 2010), probably because of weaker fisheries governance and management institutions compared to developed countries (Sumaila et al., 2011). The fishery resources are faced with many socio-economic and environmental pressures, including overexploitation, eutrophication, pollution, habitat degradation, biodiversity loss, invasive species, water extraction, and damming (Hecky et al., 2010; Ogutu-ohwayo et al., 2016). These threats have modified aquatic ecosystem functioning and services (Ogutu-ohwayo et al., 2016; Welcomme et al., 2010). Also, African fisheries are expected to be hit the hardest by climate change, with associated challenges such as reductions in fish catch, which will intensify livelihood problems of millions of vulnerable people and lead to economic hardships and loss of development opportunities (Allison et al., 2009; Ogutu-ohwayo et al., 2016).

To sustain the benefits from fisheries resources, and particularly prevent or reverse the economic hardships and loss of development opportunities expected under the changing climate, strong fishery management interventions are required to increase production and promote sustainable exploitation. Indeed, management efforts exist for African inland fisheries, spearheaded by national and regional governments, and international development agencies, such as World Wildlife Fund (WWF, `https://www.worldwildlife.org/`) and The Nature Conservancy (TNC, `https://www.nature.org/en-us/`), which have made the management of some of the lakes that support fisheries and biodiversity a priority. A highlight of the fishery management approaches on the African inland lakes is co-management, where resource users, such as fishers, have a recognized role in management (Jul-Larsen et al., 2003). Although this approach has been demonstrated to successfully solve problems in small scale fisheries (Castilla and Defeo, 2001), it has not been completely successful in Africa as lakes remain among the most overexploited in the world, and faced with multiple stressors (Hecky et al., 2010; Jul-Larsen et al., 2003; Njiru et al., 2006; Welcomme et al., 2010). For sustainable development, business-as-usual is not an option. Accordingly, immediate paradigm shifts to improve fishery management are required if the benefits and biodiversity supported by the African inland lakes are to be sustained to contribute to the sustenance of the African population projected to be over 2.4 billion by 2050 (United Nations, 2015).

7.1.1 The role of ecosystem-based fishery management (EBFM)

Ecosystem-based fishery management (EBFM) approach considers the ecosystem in totality to maintain its resilience rather than advancing single-species management measures (Pikitch et al., 2004). The approach facilitates trade-offs between different fisheries and other aquatic resource stakeholders and their needs, improves access to information for management decisions, improves the ability to predict management outcomes, and translates into better management plans (FAO, 2003). The approach, together with its sister approach in aquaculture, Ecosystem Approach to Aquaculture (EAA), has been envisaged to aid the implementation of the FAO Code of Conduct for Responsible Fisheries, which was unanimously adopted by member states at the FAO Conference in October 1995 (FAO, 1995). Consequently, EBFM has been adopted by several developed countries, such as the United States of America (USA), where it currently underlies interventions for the National Oceanic and Atmospheric Administration (NOAA), which is responsible for the management of fisheries resources in the country (National Marine Fisheries Service, 1999). Countries that have complied with the FAO code of conduct, and therefore implementing EBFM, to some extent, such as USA, Norway, Canada, Australia, Iceland, Denmark, Ireland, Norway, United Kingdom, and Japan (Pitcher et al., 2008), have good scores for health coupled human-ocean system, basing on the diverse ecosystem health indicators (Halpern et al., 2012). Because these examples are not just anecdotes, EBFM can transform fisheries management to achieve fisheries management objectives where other approaches have failed. Thus, EBFM seems to be most appropriate for inland water bodies in Africa, where, despite the existing management efforts, manageable challenges have persisted (Jul-Larsen et al., 2003).

However, for EBFM to effectively counter threats of environmental change, as it is designed to (Pauly et al., 1998; Worm et al., 2006), understanding and making predictions about the direction, magnitude, and consequences of the changes, and designing the best mitigation options to counter their undesirable consequences, have increasingly become important, given that the threats are intensifying and becoming increasingly interconnected. This understanding can be best facilitated by ecosystem modelling (Canham et al., 2003; Evans, 2012), which makes it (ecosystem modelling) important for promoting EBFM (Christensen and Walters, 2005).

To recommend evidence-based strategies for promoting ecosystem modelling of the African inland lakes, and ultimately implementation of EBFM, the progress of ecosystem modelling on the African inland lakes was examined by (i) analyzing publishing trends of literature applying leading ecosystem modelling platforms on the lakes, and (ii) assessing data deficiencies on the lakes for ecosystem modelling. The results of the publication trends and data assessment are used to discuss implications for ecosystem models and modelling, fisheries research, and management, and to recommend the strategies required to promote the application of ecosystem modelling.

7.1.2 Publication trends in literature applying leading aquatic ecosystem modelling platforms

Analysis of publication trends in literature applying ecosystem models focused on African Great Lakes (AGL), in the AGL region, as representative of other African inland lakes, and two leading ecosystem modelling platforms, Ecopath with Ecosim(EwE) and Atlantis. The African Great Lakes (AGL), for this paper, are Lakes Victoria, Tanganyika, Malawi, Turkana, Albert, Kivu, and Edward. Consequently, the AGL Region includes any country that borders any of these lakes, i.e., Democratic Republic of the Congo (DRC), Burundi, Rwanda, Uganda, Kenya, Tanzania, Zambia, Malawi, Mozambique, and Ethiopia (source: United States Department of State, Diplomacy in action. About the Great Lakes Region, `http://www.state.gov/s/greatlakes_drc/191417.html`, accessed on 27 April 2016). The AGL (Figure 7.1) were considered for their exceptional attributes that make them outstanding, not only in the AGL region or Africa but globally (Table 7.1).

EwE (Christensen and Pauly, 1992; Christensen et al., 2008; Pauly et al., 2000; Polovina, 1984), which has been described as one of the top ten breakthroughs of NOAA in the last 200 years (`http://celebrating200years.noaa.gov/breakthroughs/ecopath/welcome.html`), is a precursor of EBFM, and the most widely used aquatic ecosystem modelling platform in the world (Aydin et al., 2007; Christensen and Walters, 2005; Colleter et al., 2015). Recently, with only a decade of application, Atlantis (`http://atlantis.cmar.csiro.au/`) has shown potential to support EBFM through fostering the understanding of coupled social and natural dynamics of aquatic ecosystems to guide appropriate and model-tested management decisions (Fulton et al., 2011a).

Scientific publications applying EwE and Atlantis on the AGL were searched using relevant search terms, such as ecosystem modelling for Lake Victoria (or any other AGL), from web-based libraries such as Google Scholar, the Online Access to Research in the Environment (OARE, `http://www.fao.org/agora/en/`), and the Access to Global Online Research in Agriculture (AGORA, `http://www.fao.org/agora/en/`). Models that apply EwE are always archived in a publicly available database, EcoBase (`http://sirs.agrocampus-ouest.fr/EcoBase/`). This database was also searched for the prevalence of models on the AGL. The publication year, authorship, and affiliation were recorded for each publication applying EwE or Atlantis. Additional information was recorded on model

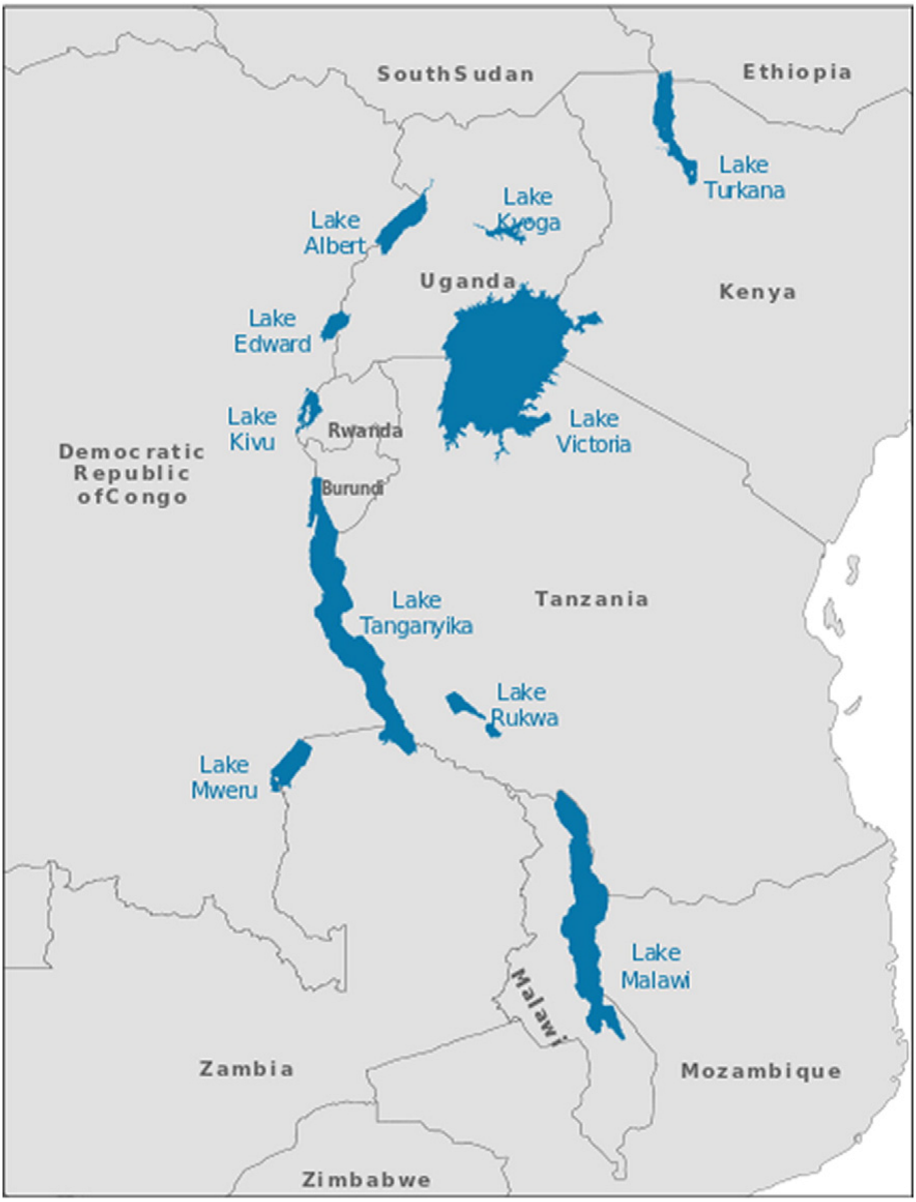

Figure 7.1: The African Great Lakes system made up of Lakes Victoria, Tanganyika, Malawi, Turkana, Albert, Kivu, and Edward. Source: `https://en.wikipedia.org/wiki/File:African_Great_Lakes.svg`. Accessed 16^{th} April, 2016.

Table 7.1: Selected key features of the African Great Lakes that make them unique not only in Africa but in the whole world. The features also justify why ecosystem-based fishery management (EBFM) is the best approach to achieve management objectives on the lakes.

Category	Key feature
Size matters	The African Great Lakes (AGL) cover a total surface of about 147,300 km^2, which is about 70% of surface area covered by inland lakes in Africa. Lake Victoria is the second-largest freshwater lake in the world by surface area. Lake Tanganyika is the second-largest freshwater lake by volume and depth in the world. Lakes Victoria, Tanganyika, and Malawi hold a quarter of the planet's freshwater supply. The AGL are the headwaters of the three longest rivers in Africa: the Nile, the Congo, and the Zambezi.
The expanse of catchment areas	The lakes' catchments altogether cover about 683,553 km^2 and is shared by 10 countries.
Gridlocks in exploitation and management	Each of the lakes is shared by at least two countries, with the catchments of some such as Lake Victoria spanning up to 5 countries. These attributes make exploitation and management a challenge.
Fisheries	The lakes support biggest fish supply from in inland water bodies in Africa. Lake Victoria alone supports the largest freshwater fishery in the world. The lakes contribute to livelihoods of millions of people in the riparian countries, and to the national GDP .
Biodiversity	10% of the world's fish species are found in the AGL. The AGL have rich biodiversity, with at least 2000 cichlid fish species, mostly endemic, as well as other fish taxa, invertebrates, birds, and mammals. The cichlids in the AGL have the greatest array of large, diverse fishes than anywhere in the world developed through adaptive radiation (phenotypic and molecular plasticity driven by ecological factors such as changes in habitats, population sizes, and hybridization) (Brawand et al., 2014; Meyer, 1990; Wagner et al., 2012).

location (country), lake, model area, and model period. The information was analyzed based on the criteria in Christensen and Walters (2005): ecosystem modelling is considered to be an active field of research if the number of publications applying ecosystem models shows an increasing trend in recent years.

As of August 2016, there was no single published Atlantis model on the AGL; only one model was indicated to be under development on Lake Victoria (`http://atlantis.cmar.csiro.au/www/en/atlantis.html`). Developing an Atlantis model takes, on average, 2-3 years (Beth Fulton, pers. com.). The absence of publications applying Atlantis modelling framework on the AGL is surprising given that Atlantis has been in place for more than 10 years, which is a long time for a modelling framework with moderate data requirements to be adopted by fisheries scientists. Indeed, Atlantis has been applied in about 30 systems throughout the world, including the North American Great Lakes, for management and for understanding invasive species, climate change, and acidification (CSIRO, 2016). Because the AGL are among the most stressed inland lakes in the world (Welcomme et al., 2010), thus requiring EBFM, the absence of Atlantis model publications indicates limited ecosystem modelling research activities in the region. This state (limited ecosystem modelling) demonstrates that fisheries management in the AGL region predominantly relies on singles species management solutions. In many of the AGLs, notably Lake Victoria, these solutions have not been successful, although implementation challenges may have contributed to their limited success (Njiru et al., 2006).

The search for publications applying EwE on the AGL revealed 14 publications, including one thesis, published between 1988 and 2012, a period spanning 25 years (Table 7.2). This publication frequency, in about the same period the EwE framework has been in existence (Steenbeek et al., 2014), implies a publication rate of 0.6 papers per year, which is a dismal publication rate compared to the global trends (Christensen and Walters, 2005). The publication rate further drops to 0.5 papers per year if the analysis is extended to cover up to 2015. Over the publication period (1988-2012), 16 years (64%) had no publications, while 6 years (24%) had one publication each. The year 1993 had the highest number of publications (4) in a single year (Figure 7.2), but all the publications were EwE conference proceedings (see Table 7.2). Additional examination of the publications indicated that 50% of the 14 publications were published within the first decade of EwE existence (1988-1997). The subsequent decade (1998-2007) had 28.6% of the publications. Only three publications (21.4%), involving two lakes (Victoria and Malawi), were retrieved for the period after 2008, with the most recent publication (Downing et al., 2012) published in 2012. The number of publications applying EwE on the AGL was found to be decreasing over time, with almost every year of publication followed by a decrease or no growth in the number of publications in the following year (Figure 7.2). This publication trend suggests that ecosystem modelling is not an active field or research on the African inland fisheries compared to global trends (Christensen and Walters, 2005; Colleter et al., 2015).

Table 7.2: Studies in literature in which Ecopath with Ecosim (EwE) modelling approach has been applied on the African Great Lakes.

Lake	Model area (country of location)	Model year/period	Main feature	Reference
Malawi	Southern and western shelves (Malawi)	1998–1999	Steady-state	Darwall et al. (2010)
Kivu	Southern part of Lake Kivu (DRC)	2002-2003	Steady-state	Villanueva et al. (2007)
Victoria	Kenyan part of Lake Victoria	1971-1972 and 1985-1986	Steady-state	Moreau et al. (1993a)
Malawi	Pelagic zone of central Lake Malawi	1979-1981	Steady-state	Degnbol (1993)
Tanganyika	Pelagic zone (Burundi)	1974-1976 and 1980-1983	Steady-state	Moreau et al. (1993b)
Tanganyika	Pelagic zone	1974-1975 and 1983-1984	Steady-state	Moreau and Nyakageni (1988)
Turkana	Pelagic	1987 and 1973	Steady-state	Kolding (1993)
Victoria	Kenyan sector of Lake Victoria	1985-1986 to 1995-1996	Steady-state and Ecosim	Moreau and Villanueva (2002)
Victoria	Winam Gulf in the Kenyan sector of Lake Victoria	1985-1986 to 1995-1996	Steady-state and Ecosim	Villanueva and Moreau (2002)
Victoria	Mwanza gulf in Tanzanian sector of Lake Victoria	1977, 1987, 2005	Steady-state and Ecosim	Downing et al. (2012)
Victoria	Parts of Lake Victoria (Kenya, Uganda, and Tanzania), and whole lake	2000	Steady-state and Ecosim	Matsuishi et al. (2006)
Malawi	Lake Malawi	1976-1996	Steady-state and Ecosim	Nsiku (1999)
Malawi	Pelagic zone		Steady-state	Allison et al. (1995)
Victoria	Kenya	1971-1972	Steady-state	Moreau (1995)

In comparison to the American Great Lakes, a search of publications applying EwE found 17 publications, published within 24 years since 1993 (Figure 7.3). Whereas the search probably underestimates the number of publications, the trend suggests that the application of EwE is also underdeveloped on the American Great Lakes. However, unlike the AGL, 65% of the publications retrieved were for the most recent five years (2012-2016). This trend suggests that the application of EwE is increasing, and that ecosystem modelling is becoming more active on the American Great Lakes compared to the AGL, which have more challenges that have persisted, despite their economic importance to the AGL region.

The publications on the AGL showed that EwE has been applied only on Lakes Malawi, Kivu, Victoria, Tanganyika, and Turkana; no study using EwE was retrieved for Lakes Albert and Edward, which are all shared by Uganda and DRC (Figure 7.1). All the publications presented steady-state models, describing the trophic structure of the modelled areas and periods. Only four of the publications (Downing et al., 2012; Matsuishi et al., 2006; Nsiku, 1999; Villanueva and Moreau, 2002) (Table 7.2) extended the "snap-short" Ecopath models to explore different management options using the Ecosim component of EwE. No publication, so far, has utilized Ecospace and Ecotracer routines of the EwE modelling platform on the AGL, indicating that EwE has not been utilized to inform decisions on protected areas, one of the fisheries management tool promoted by EBFM, and predict movement and accumulation of contaminants and tracers. Only two EwE models were developed for a whole lake system, i.e. Nsiku (1999) for Lake Malawi and Matsuishi et al. (2006) for Victoria. The rest of the models were developed for localized parts within the water bodies considered in the model.

Another interesting feature of the publications was the authorship. Except for the thesis of Nsiku (1999), the lead authors on all the publications using EwE were affiliated to institutions out of the AGL region, i.e., in countries like the United Kingdom, France, and Denmark (Table 7.3). Of the 10 publications that had more than one author, only five publications had at least one African as a co-author or co-authors, affiliated

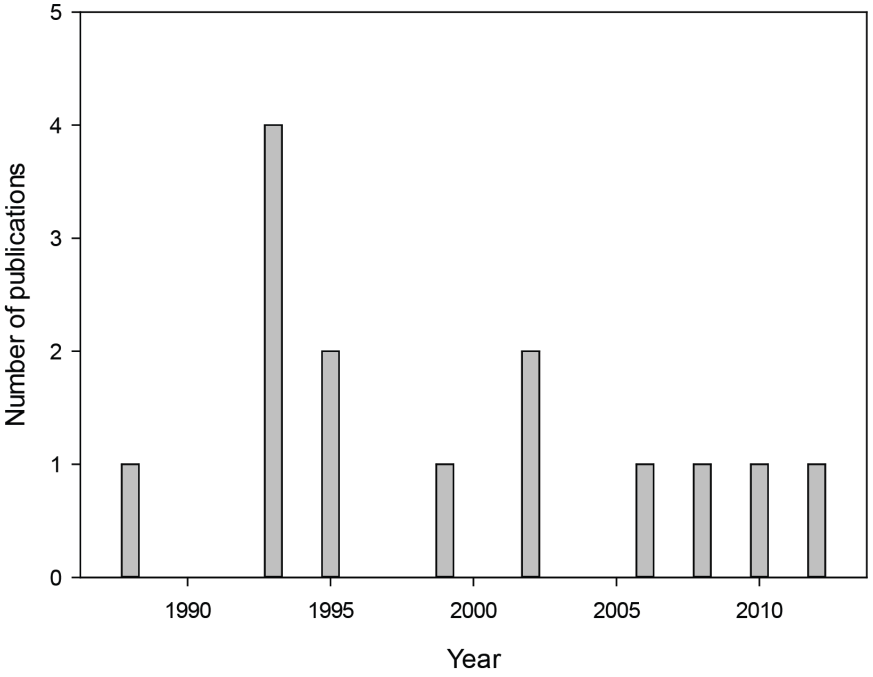

Figure 7.2: Trend in the number of publications since 1988 in which the Ecopath with Ecosim (EwE) modelling approach has been applied on the African Great Lakes (AGL).

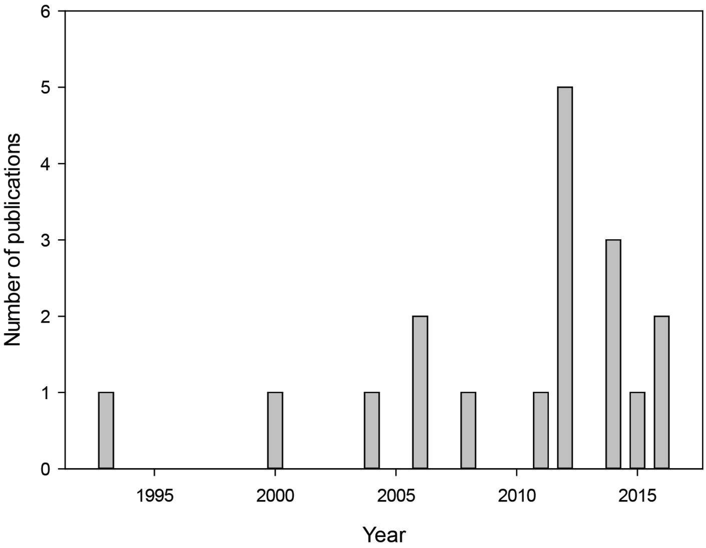

Figure 7.3: Trend in the number of publications in which the Ecopath with Ecosim (EwE) modelling approach has been applied on the American Great Lakes since 1993. Sources: Kitchell, J.F. et al., 2000. Ecosystems, 3: 545-560; Langseth, B.J. et al., 2012. Ecological Modelling, 247, 251-261; Stewart, T.J. and Sprules, W.G. 2011. Ecological Modelling, 222(3), 692-708; Cox, S·P and Kitchell, J.F. 2004. Bulletin of Marine Science, 74(3): 671-683; Hossain, M. et al., 2012. Journal of Great Lakes Research, 38(4), 628-642; Langseth, B.J. et al., 2014. Ecological Modelling, 273, 44-54; Yu-Chun, K. et al., 2014. Journal of Great Lakes Research, 40(1), 35-52; Zhang, H. et al., 2016. Transactions of the American Fisheries Society, 145,136-162; Rogers, M.W. et al., 2014. Can. J. Fish. Aquat. Sci., 71, 1072-1086; Koops, M.A. et al., 2006. Comparative modelling of the ecosystem impacts of exotic invertebrates and productivity changes on fisheries in the Bay of Quinte and Oneida Lake. In: Project Completion Report. Great Lakes Fishery Commission, Ann Arbor.; Langseth, B.J. 2012. An Assessment of Harvest Policies for a Multi-Species Fishery in Lake Huron Using a Food-Web Model. PhD Thesis, Michigan State University; Blukacz-Richards, E.A. and Koops, M.A. 2012. Aquatic Ecosystem Health and Management, 15(4):464-472; Yu-Chun, K. et al., 2016. Ecosystems, 19: 803-831; Yu-Chun, K. 2015. Modeling the Effects of Climate Change, Nutrients, and Invasive Species on Lake Huron Food Webs. PhD thesis, University of Michigan; Halfon E., and Schito N. (1993). Lake Ontario Food Web, an Energetic Mass Balance. pp. 29-39 In Christensen V., Pauly D., (eds). ICLARM Conf. Proc.; Jaeger, A.L. 2006. Invasive Species Impacts on Ecosystem Structure and Function. MSc. Thesis, Department of Fisheries and Wildlife, Michigan State University; Currie et al., 2012. Modelling Spread, Establishment and Impact of Bighead and Silver Carps in the Great Lakes. DFO Can. Sci. Advis. Sec. Res. Doc. 2011/113. vi + 74 p.

to institutions within the AGL region, where the lakes are located. The African co-authors were affiliated to only six institutions from only seven regional countries, namely Kenya, Tanzania, Uganda, Burundi, Zambia and DRC (Table 7.3).

Table 7.3: Affiliation of first and co-authors, where applicable, of publications (excluding thesis) applying Ecopath with Ecosim (EwE) modelling approach on the African Great Lakes. The affiliation stated is that at the time of publication.

Reference	First author affiliation	Country of affiliation	Number of native co-authors	Number of native institutions	Country(ies) of native institutions
Darwall et al. (2010)	Non-native	United Kingdom	0	0	-
Villanueva et al. (2007)	Non-native	France	2	1	DRC
Moreau et al. (1993a)	Non-native	France	0	0	-
Degnbol (1993)	Non-native	Denmark	N/A	N/A	N/A
Moreau et al. (1993b)	Non-native	France	2	2	Burundi and Zambia
Moreau and Nyakageni (1988)	Non-native	France	1	1	Burundi
Kolding (1993)	Non-native	Norway	N/A	N/A	N/A
Moreau and Villanueva (2002)	Non-native	France	0	0	-
Villanueva and Moreau (2002)	Non-native	France	0	0	-
Downing et al. (2012)	Non-native	Netherlands	0	0	-
Matsuishi et al. (2006)	Non-native	Japan	6	3	Uganda, Tanzania and Kenya
Allison et al. (1995)	Non-native		0	0	-
Moreau (1995)	Non-native	France	N/A	N/A	-

7.1.3 Deficiencies in data eminent in existing EwE models

Because no single publication was retrieved for Atlantis, the analyses on data deficiencies in existing models were based only on the EwE modelling platform. Data gaps identified in the published models were consolidated, enabling the provision of information on data deficiencies on the AGL that could be limiting ecosystem modelling. The data gaps were scrutinized in line with generic data requirements for EwE, obtained from the most recent user-guide (Christensen et al., 2008), and the best practices for developing EwE models (Heymans et al., 2016).

Data for input parameters of EwE models can be obtained from several sources, including field data collection surveys, published literature, where it occurs in sources including stock assessments and ecological studies for the systems being modelled or closely related systems (Christensen et al., 2008). The models on the AGL combined several data sources and, because of data limitations, no model utilized data exclusively within the modelled area or model period. Instead, where data were not collected or available in the literature for the modelled areas or within the periods modelled, the modellers relied on data from outside the modelled areas or periods, obtained from literature, general knowledge and assumptions, or, in inappropriate modelling practice (Ainsworth and Walters, 2015), left key input parameters such as biomass of top predators to be estimated by the model. The use of data from other systems and periods other than those modelled was prevalent in most of the existing models on the AGL. Nsiku (1999) used input values for parameters, including production to biomass ratio (P/B), consumption to biomass ratio (Q/B), and ecotrophic efficiency (EE) for some functional groups in the Lake Malawi model from other lakes such as Lake Etang de Thau (in France), Lake George (in Uganda), and Lake Kinneret (in Israel), all of which lie in different geographical areas and probably have different environmental conditions compared to Lake Malawi. Other models on the AGL that relied on data from other areas include the models of Lakes Turkana (Kolding, 1993), Malawi (Darwall et al., 2010), Victoria (Downing et al., 2012), and Kivu (Villanueva et al., 2007).

Assumptions that are perhaps unrealistic were also prevalent in the models. Nsiku (1999), while constructing the EwE model for Lake Malawi, assumed no significant difference in biomass of deepwater catfishes in different regions of the lake in order to estimate their biomass for the whole lake and differentiate clariid catfishes into two groups based on the proportions of the catfishes in trawl catches from small areas in the lake. This assumption could be invalid because Lake Malawi exhibits a non-uniform distribution of fish species in its diverse habitats (Fryer, 1959; Lowe-McConnel, 1975). As a result, the biomass of the catfish fishes in the whole lake could have been poorly estimated in the model. Some existing models assumed no change in some input parameters such as biomass, diet composition, and P/B for functional groups between periods due to unavailability of data, which could potentially underestimate or overestimate the parameter values. For instance, Kolding (1993) assumed no changes in diet composition of all fish groups in the model for Lake Turkana, except the one between 1973 and 1987, a period spanning more than one decade. Matsuishi et al. (2006) assumed no change in values for most of the input parameters used in the historical (the 1970s and 1980s) models of Lake Victoria (Moreau et al., 1993a; Villanueva and Moreau, 2002), and used them in the models for 2000. Other inappropriate practices prevalent in the models due to data deficiencies included assuming EE for functional groups whose P/B or biomass were unknown (for example, Kolding, 1993), grouping together into one functional group species that would otherwise be different functional groups if data were available (for example, Kolding, 1993; Nsiku, 1999), and excluding some species in functional groups (for example, Nsiku, 1999).

Although reliance on data from other areas, models, and periods, other than the system being modelled, and on assumptions and general knowledge can be acceptable, when necessary, it is an indicator of data deficiency that should be addressed because, for best practice in EwE, data for model parameterization should preferably come from an area or ecosystem of concern, and models should be based on parameters averaged for a given period being modelled (Ainsworth and Walters, 2015;

Heymans et al., 2016). Regarding this requirement, some level of best practice among the existing models for the AGL was observed in Degnbol (1993) and Allison et al. (1995), where most of the data were for the modelled area and within the period covered by the model; also, biomass, production, and consumption for main functional groups in the model were annual averages for the modelled period.

7.2 Implications for ecosystem modelling

Although ecosystem models cannot exactly depict structures and dynamics in real ecosystems, models are built to ensure that they become the best possible representation of the basic features and dynamics of the ecosystems. The use of data from other sources, contrary to best practices, can lead to the use of inappropriate data for input parameters, leading to parametric errors in the models (Link et al., 2012). Because the majority of models for the AGL used such sources, their ability to provide the best picture of trophic interactions and ecosystem dynamics was degraded due to the use of inappropriate parameter values and assumptions (Fulton et al., 2011b). Indeed, Nsiku (1999) asserted that limited interpretations could be made from the model of Degnbol (1993) due to limitations and data gaps in zooplankton production dynamics, the role of detritus and organic matter, and fish mortalities. Kolding (2013), also, argued that Downing et al. (2012) contributed little to defining drivers of ecosystem function and changes in Lake Victoria because the outputs from their model presented conclusions that do not correspond with ecological reality, emanating from inappropriate parameter estimates. Also, due to data deficiencies, there are many known and unknown organisms, including fish species, which have not been included or misplaced in functional groups in the existing EwE models because they have either not been described in the lakes or are data deficient, further rendering the models weak.

The pedigree index (PI, Christensen and Walters, 2004a) has recently been incorporated in EwE to assess the reliability of data acquired from different sources and to judge the overall model quality. Darwall et al.

(2010) implemented the PI in the model of Malawi and obtained a value of 0.611. Although this is acceptable, the index indicated that many input values were obtained from other systems other than Lake Malawi. However, only one publication used the PI routine, making the assessment of the reliability of data sources in other models difficult.

Data deficiencies have also made most ecosystem models to be restricted to specific periods and areas. For instance, Kolding (1993) and Nsiku (1999) could not build time-series-fitted models for Lakes Turkana and Malawi, respectively, but limited their models to periods where data was available. Villanueva et al. (2007) considered the Bukavu basin of the Congolese sector of Lake Kivu for their model because data on biological communities and fisheries better presented it compared to the Rwandese part of the basin. Even in the most recent publications, the models were constructed for the periods for which most data were available (Downing et al., 2012). As a result, time series-calibrated models, and models of some lakes or parts of lake ecosystems, do not exist.

7.3 Implications for fishery management

Information from ecosystem models can be applied directly or indirectly to support decisions for fisheries management, particularly EBFM approach, which is important for rebuilding the fisheries resources that are affected by multiple stressors, including exploitation (Worm et al., 2009). From this analysis, it cannot be confirmed whether or not the information from the existing models was used to support decision making for fisheries management on the AGL. However, it is known that use of unrealistic models results into imprudent decisions because the parametric and structural model errors eminent in the models due to inaccurate parameter values and inappropriate assumptions inhibit proper decision making and fisheries management (Fulton et al., 2011b). Therefore, currently, no proper validated models exist on the AGL from which sound management decisions can be based. Lack of diversity in ecosystem models seems to be limiting EBFM on the AGL compared to other global water bodies, where EBFM is only limited by disagreements between experts and conflicting country management priorities and guidelines (Essington and Punt, 2011).

7.4 Strategies to improve ecosystem modelling on the AGL

Based on the observations presented here, the strategies needed to improve ecosystem modelling on the AGL may include (1) increasing local and regional capacity for ecosystem modelling to accelerate ecosystem modelling research activities on the lakes, and (2) improving availability of data for ecosystem modelling, which will require strengthening monitoring programs on the lakes.

7.4.1 Increasing local and regional capacity for ecosystem modelling and activating ecosystem modelling

The examination of publication trends indicated the limited capacity for ecosystem modelling, with all models led by foreign researchers (Table 7.3), and that ecosystem modelling research is inactive on the AGL (Figure 7.2). Interventions are required to increase the capacity, and consequently activate ecosystem modelling in the region. Christensen and Walters (2005) found that models applying EwE ecosystem modelling platform were increasing by 23% annually on a global scale due to the training courses and workshops, among other factors, that have been conducted around the world involving about 600 scientists by 2005. Therefore, short training sessions, which provide practical skills for ecosystem modelling platforms, could also increase capacity and activate ecosystem modelling on the African inland fisheries. A course "Introduction to the Atlantis Ecosystem Model" has been developed to equip learners with basic skills for ecosystem modelling using Atlantis and knowledge of ecosystem modelling and Management Strategy Evaluation. Such courses also exist for EwE. Unfortunately, to the best of our knowledge, no such training workshop has ever been conducted in Africa. The developers of these modelling platforms, conservation organizations, development agencies, and other stakeholders may also consider similar training in underdeveloped countries (including AGL region), and particularly among early-career scientists as a pathway to develop the capacity for ecosystem modelling and consequently promote EBFM. Increasing local capacity for ecosystem modelling may also require mainstreaming ecosystem modelling in training curricula for the tertiary institutions that conduct fisheries training, including local universities.

7.4.2 Improving data availability for ecosystem modelling

Although EBFM can commence with limited data, it is important to implement appropriate strategies to improve the availability of data on spatial and temporal scales. Data will improve the performance of models to provide knowledge of ecosystem status and interactions, promote EBFM, and monitor for its success (Pikitch et al., 2004). More data will also facilitate new ecosystem models, and refine and expand existing models to better depict real ecosystems and their physical, biotic, and human interactions (Murawski, 2007). Data collection surveys should be conducted to fill data gaps in the existing models. Such data, important for both EwE and Atlantis, include information on aquatic community composition, abundance per age class per year, growth rates of organisms, habitat preferences, migratory characteristics, biogenic habitats, the diet of organisms and food chain interactions, non-fish tertiary consumers such as birds and reptiles (for example crocodiles), import and export roles of other organisms (such as non-predatory birds and hippopotamus, which are frequent in freshwater aquatic systems), and describing unknown species of fish and invertebrates and their roles in the ecosystems. Indeed, some AGL, such as Lake Edward (Figure 7.1), have undescribed fish groups which may not be put into appropriate functional groups if ecosystem models were to be built in the systems. Current data collection surveys should also be integrated with data collection on primary variables that can be used to estimate some input parameters for the ecosystem modelling platforms using empirical equations (Heymans et al., 2016). For fish, these parameters include catch, biomass, length, weight, height and the surface area of the caudal fin, which are important in estimating P/B and Q/B for EwE. Some of these parameters are not available for some fish species and, for others, they are not routinely collected. Other parameters such as height and surface area of the caudal fin are not highlighted in standard guidelines for collecting biological information on fishes of Lake Victoria (LVFO, 2007b), and have, therefore, not been collected for many fish species for a long period. Also, volumetric and gravimetric methods that provide the best ways to express diet composition (weight or volume) in EwE (Christensen et al., 2008) should be used in estimating diet composition of fish, replacing the most common methods in the region (points method and frequency of occurrence) that express diet composition as present occurrence and dominance, which are of little use to quantify diets. Bycatch on the lakes is also increasingly becoming important and may need to be considered for proper estimates of parameters for some functional groups. For instance, on Lake Victoria, bycatch of fish, mainly haplochromines and juvenile Nile perch (*Lates niloticus*) and invertebrates, mainly freshwater shrimp (*Caridina nilotica*) and molluscs, is increasingly becoming important in the light fishery that primarily targets the silver cyprinid (*Rastrineobola argentea*) (Budeba and Cowx, 2007).

7.5 Conclusion

Successful application of EBFM is essential for sustainable management and exploitation of the AGL. For EBFM to be effective, regional capacity for ecosystem modelling in the AGL region must be strengthened as well as monitoring and research programmes that provide the basic input and validation data for ecosystem models such as EwE and Atlantis. Because the AGL lakes (and their fisheries) are among the most important and stressed in the world, the need for regional and global action is urgent to protect the regions' valuable fisheries and ecosystem values provided by the lakes, as well as to safeguard a substantial fraction of global freshwater biodiversity.

7.6 Acknowledgements

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8

Paper II

Exploring the structural and functional properties of the Lake Victoria food web, and the role of fisheries, using a mass balance model

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Abstract

Human and environmental factors have affected the Lake Victoria ecosystem, especially in the last four decades. However, the lake continues to support the World's largest freshwater fishery, currently producing ca. one million tons of fish per year and directly supporting livelihoods of ca. four million people in three riparian countries (Uganda, Kenya, and Tanzania). This study used the Ecopath component of Ecopath with Ecosim (EwE) modelling software to construct a new model reflecting ecosystem state in 2014 and to reparameterize two existing mass balance models for the periods 1971-1972 and 1985-1986. The aim was to assess the structural and functional properties of Lake Victoria food web and the role of fisheries on the ecosystem. Results showed a decrease in food web connectivity and productivity, in relation to biomass and respiration, and an increase in biomass cycling. The total system throughput (the sum of all flows) decreased fivefold between 1971-1972 and 1985-1986, but increased slightly in 2014, with a moderate shift from herbivory to detritivory. The implication of these changes on system maturity and resilience are discussed. The Trophic level of the catch (TLC) increased between 1971-1972 and 1985-1986 due to the addition of high Trophic level (TL) catches from the introduced piscivorous Nile perch (*Lates niloticus*). However, the decline in the TLC between 1985-1986 and 2014 seems to have been due to sequential addition of low TL catches, especially from the native silver cyprinid (*Rastrineobola argentea*) (i.e., "fishing through the food web"), as opposed to a decline in high TL catches (i.e., "fishing down the food web"). Currently, exploitation is concentrated on the least productive species/groups at the top of the food chain. The causes of this fishing pattern and the implication on species composition and size structure are discussed.

Keywords: Balanced fishing, Ecopath with Ecosim, Lake Victoria, Mass balance, Resilience

8.1 Introduction

Changes in biodiversity due to human activities have been more rapid in the past 50 years than at any time in human history (MEA, 2005). The global Living Planet Index, which measures trends in thousands of vertebrate species' populations, shows an average decline of 52% between 1970 and 2010; freshwater species have declined by 76%, while marine and terrestrial species have declined by 39% (World Wide Fund for Nature, 2014). These trends imply that, in less than two human generations, population sizes of vertebrate species have dropped by half. These changes in species abundance have implications for aquatic ecosystem stability, because of their role in energy cycling, as well as recovery from perturbations (Heymans et al., 2014; Vasconcellos et al., 1997).

Non-native invasive fish species (intentionally or accidentally introduced by humans) are increasingly recognized as a significant contributor to extinction threat in inland waters around the world, by adding and/or worsening the threats associated with habitat loss and fragmentation, hydrologic alteration, climate change, overexploitation, and pollution (Dudgeon et al., 2006). Whereas non-native species can also have positive outcomes, such as trophic subsidy, competitive release, and predatory release (Rodriguez, 2006; Schlaepfer et al., 2010), majority, when they become invasive, exert negative ecological and evolutionary impacts, ranging from behavioural shifts of native species in the presence of invaders to the complete restructuring of food webs (see, for example, the case of Nile perch *Lates Niloticus* in Lake Victoria Witte et al., 1992)).

The decline in aquatic biodiversity, but most importantly fish, is most felt by inland fisheries because of the immense contribution of fisheries to livelihoods; many people, mainly from developing and underdeveloped nations, rely on fish as a food staple (Traoré et al., 2012). Inland fisheries contribute >6% of the world's annual animal protein supplies for humans and about 94% of all freshwater fisheries occur in developing and underdeveloped countries (FAO, 2008). In Africa, inland fisheries generate about US$4,676 million from local, regional and international trade, employ >600,000 fishers (de Graaf and Garibaldi, 2014), and contribute at least 30% of total animal protein intake in most landlocked countries (FAO, 2008).

Africa's Lake Victoria supports one of the world's biggest inland fisheries, with total landings of about one million tons per year (Mkumbo and Marshall, 2015). The fishery directly employs ca. one million people in fishing and other value–chain related activities; when dependants are included, the fishery supports livelihoods of about four million people (Mkumbo and Marshall, 2015). Traditional fisheries (i.e. before the 1960s) harvested endemic tilapias, for example, Singida tilapia, *Oreochromis esculentus* (Graham, 1928), and Victoria tilapia, *O. variabilis* (Boulenger, 1906), and the small-bodied haplochromines. These species supported fisheries with only modest economic value. In an attempt to increase the economic value and use of fishes from the lake, the piscivorous Nile perch was introduced during the mid-1950s to convert the small bony haplochromine cichlids to fish flesh of commercial importance (Pringle, 2005). Between 1980 and 1990, Nile perch landings grew from almost nothing to 300,000 tons (making up 66% of the total landings), while the haplochromine fishery virtually collapsed due to predation (Mkumbo and Marshall, 2015; Witte et al., 1992) and environmental change (van Zwieten et al., 2015). The diverse fish community was reduced, leaving a system dominated by four species: the native silver cyprinid, *Rastrineobola argentea* (Pellegrin, 1904), locally known as dagaa, and the atyid prawn, *Caradina nilotica* (P. Roux, 1833), as well as the introduced Nile perch and Nile tilapia, *O. niloticus* (Linnaeus, 1758) (Goudswaard et al., 2008). The original complex food web (Moreau et al., 1993a) was also simplified, with Nile perch, the top predator, feeding mainly on the atyid prawn (primary consumer), dagaa, and juvenile Nile perch (both secondary consumers) (Ogutu-ohwayo, 1990a).

Demographic changes in Nile perch population post-1990, i.e., reduction in fish abundance due to intensive fishing, contributed to the recovery of few haplochromines groups, notably zooplanktivores (*Yssichromis pyrrhocephalus* Witte and Witte-Maas, 1987 and *Y. laparogramma* Greenwood and Gee 1969) and detritivores (*Haplochromis* sp.

'paropius-like', *H.* sp. 'straight head dusky', *H.* sp. 'cinctus-like', and *Enterochromis antleter* Mietes and Witte 2010) (Kishe-Machumu et al., 2014; Taabu-Munyaho et al., 2016). Consequently, a reorganisation of the food web was expected (to some extent). Indeed, Downing et al. (2012) noted that by 2005, the biomass distribution over the primary trophic levels (TLs) in the Mwanza Gulf had recovered to the historical (pre-1980) levels, although biodiversity remained low. However, the findings were questioned on the basis that the parameters used in the Ecopath models were unrealistic (Kolding, 2013). Additional investigations are required to understand the evolution of the Lake Victoria food web, especially following the major perturbations in the 1980s. In this study, two existing Ecopath models for the Nyanza Gulf for periods 1971-1972 and 1985-1986 are reparameterized, and a new model constructed for the whole lake for the period 2014. This study aims to assess the evolution of biomass flows over the main TLs and to understand the structural and functional properties of the Lake Victoria food web and the role of fisheries on the ecosystem. Pre-balance (PREBAL) diagnostics (Link, 2010) are used to ensure that all the parameters fall within the ranges expected from literature (Christensen et al., 2008).

8.2 Material and methods

8.2.1 Study area

Lake Victoria (Figure 8.1) is the world's second-largest freshwater body and the largest tropical lake in terms of surface area (68,800 km^2). However, with a maximum depth = 79 m and average depth = 40 m, the lake is shallower compared to other East African Great Lakes (Ogutu-ohwayo et al., 2016). Lake Victoria has an indented shoreline with numerous islands, bays, channels, and wetlands. The lake has undergone major transformations, especially after the 1970s, both in limnology and fisheries, including changes in trophic status, stratification pattern, water temperature, seasonality, and fish community (Hecky et al., 2010; Kolding et al., 2014,0; MacIntyre et al., 2014; van Zwieten et al., 2015). Despite the changes, the lake continues to support the World's largest freshwater fishery, currently producing ca. one million tons of fish per year and directly supporting livelihoods of ca. four million people in three riparian countries (Mkumbo and Marshall, 2015).

8.2.2 Model formulation

Mass-balance models were constructed using Ecopath component of the Ecopath with Ecosim (EwE) software (`www.ecopath.org`). Using Ecopath, a system is partitioned into functional groups comprising species having either a common physical habitat, similar diet, or life history characteristics (Christensen and Pauly, 1992; Christensen and Walters, 2004a; Pauly et al., 2000). In a given ecosystem, the functional groups are regulated by gains (consumption, production, and immigration) and losses (mortality and emigration). Production for each functional group i, P_i, is the sum of fishery catches (Y_i), predation mortality ($M2_i$), biomass accumulation (BA_i), net migration (E_i), and other mortality (MO_i) as shown in Equation (8.1).

$$P_i = Y_i + B_i \cdot M2_i + E_i + BA_i + P_i \cdot (1 - EE_i) \tag{8.1}$$

where, EE_i is ecotrophic efficiency (the proportion of the production that is utilized in the system). The term $P_1 \cdot (1 - EE_i)$ is an expression of 'other mortality', MO_i, representing mortality other than that caused by predation or fishing.

For parameterisation, Equation 8.1 can be re-expressed as:

$$B_i \cdot (\frac{P}{B})_i = \sum_{j=1}^{n} B_j \cdot (\frac{Q}{B})_j \cdot DC_{ji} + B_i \cdot (\frac{P}{B})_i \cdot (1 - EE_i) + Y_i + E_i + BA_i \tag{8.2}$$

where, for each functional group i, P/B stands for the production rate per unit of biomass, Q/B stands for the consumption rate per unit of biomass of predator j, and DC_{ji} is the fraction of prey i in the average diet of predator j.

Equation (8.2) suggests that the net production of a functional group

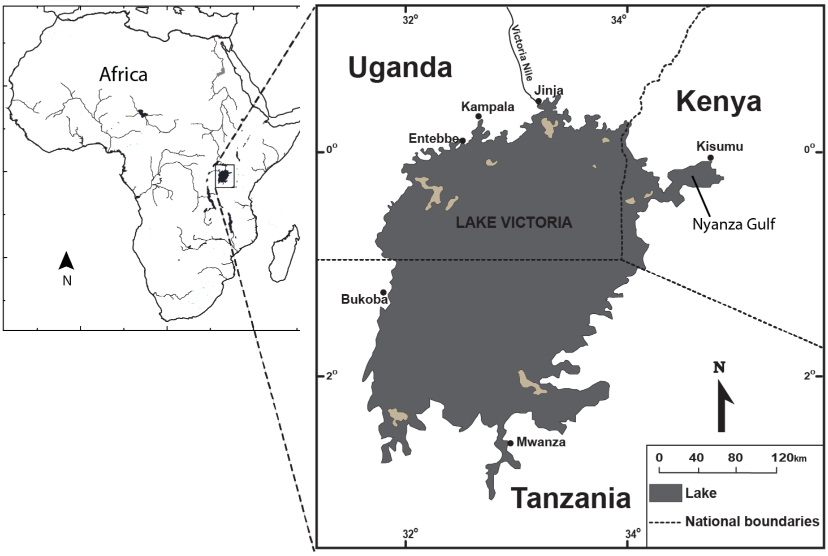

Figure 8.1: Lake Victoria, East Africa, and location of the Nyanza Gulf.

i equals the sum of (1) the total mass removed by predators and fishing, (2) the net biomass accumulation of the group, (3) the net migration of the group's biomass, and (4) the mass flowing to detritus. Therefore, achieving mass balances requires that energy input and output of all biomass compartments balance, as shown in Equation (8.3).

$$Q = P + R + U \tag{8.3}$$

where, R is respiration, and U is unassimilated diet. Respiration is rarely measured in fisheries analysis, but it can easily be computed as the difference between consumption and production (plus unassimilated food).

8.2.3 Model groups

Table 8.1 shows a description of the different functional groups used in the three Ecopath models. Not all the functional groups were considered in the three models. For instance, fish-eating birds were not considered in the existing models, while Nile perch was modelled as one group (Moreau et al., 1993a). The same groups were maintained, except that the haplochromines were merged in the 1985-1986 model (where they had virtually collapsed). In the new model, Nile perch was separated into adult and juvenile groups to account for the ontogenetic diet shifts between life stages (Kishe-machumu et al., 2012a; Nkalubo et al., 2014). Fish-eating birds were also considered using data from Villanueva and Moreau (2002).

8.2.4 Model parameterization

To parameterize an Ecopath model mandatory data are needed on B, P/B, Q/B, DC, and Y. Data on other parameters, such as discards, landings values, and fishing costs, can be included. A detailed explanation of data requirements of EWe models can be found in the literature (Christensen and Walters, 2004a; Pauly et al., 2000).

Biomass (t/km^2/year)

The models of (Moreau et al., 1993a) used biomasses calculated within the software by assuming some values of EE. Except for the 1985-1986 model, this study aimed at entering biomasses of all fish groups as input to the models since EE is hardly measured experimentally. For the 1971-1972 model, biomasses for the fish groups were obtained from trawl surveys conducted between 1969 and 1971 during the implementation of the Lake Victoria Fisheries Research Project (LVFRP) (Kudhongania and Cordone, 1974). Biomasses in the 1985-1986 model, however, were estimated by the model; EE was fixed at 0.95 for the groups for which biomass data were not available. For the 2014 model, biomasses of Nile perch, dagaa, and haplochromines were taken from the lake-wide hydroacoustic survey (LVFO, 2015). The juvenile-adult threshold of 40 cm was set following Nyamweya (2012); 10% of the biomass was apportioned to adult Nile perch and 90% to the small-sized Nile perch. These proportions are consistent with single target detections data from hydroacoustic surveys where Nile perch <50 cm total length constitute more than 90% of Nile perch numbers (LVFO, 2018). Separation of haplochromines into zooplanktivore, detritivore, and ’other guilds, was done using pro-

Table 8.1: Biological groups used in the Ecopath mass balance models

No.	Group	Description
1	Birds	Fish-eating birds, including the Cormorants, African fish eagle, White-winged black tern, and Pied kingfisher
2	Adult Nile perch	Nile perch >40 cm total length (based on Nyamweya, 2012)
3	Juvenile Nile perch	Nile perch <40 cm total length (based on Nyamweya, 2012)
4	Catfishes	*Bagrus* spp. and *Clarias* spp.
5	Marbled lungfish	The only lungfish representative in the lake
6	Snout fishes and squeakers	*Synodontis* spp. and family momyridae
7	Zooplanktivorous haplochromines	This group includes *Haplochromis pyrrhocephalus* and *H. laparogramma*, which constitute about 71% of the recovering haplochromine standing stock (Kishe-Machumu et al., 2015)
8	Detritivorous haplochromines	This group includes *H.* 'paropius-like' *H.* 'cinctus-like', *H. antleter*, which constitute 21% of the recovering haplochromine standing stock (Kishe-Machumu et al., 2015)
9	Other haplochromines	Other trophic groups that constitute less than 10% of haplochromine biomass
10	Dagaa	*R. argentea*: represents the only native pelagic fishery that persisted the ecosystem recession after species introductions in the 1980s
11	Nile tilapia	This species was previously known to be herbivorous, exclusively feeding on algae, but has recently diversified its diet to include fish and invertebrates (Njiru et al., 2008)
12	Other tilapias and cyprinids	Red belly tilapia (*Coptodon zillii*), Red breast tilapia (*Coptodon rendalii*), Blue spotted tilapia (*Oreochromis leucostictus*), and *Barbus* spp.
13	Lake prawn	Atyd prawn (*Caridina nilotica*)
14	Insects and Molluscs	This group includes diptera (especially the midge, *Chironomus*, and the phantom midge, *Chaoborus* larvae), odonata and ephemeroptera nymphs, bivalves, amphipods and gastropods.
15	Zooplankton	Copepoda, Ostracoda, Cladocera, and Rotifera
16	Phytoplankton	Major algae groups, including Cyanobacteria, diatoms, and Green algae
17	Benthic producers	Macrophytes, periphyton, epiphyton
18	Detritus	Cycling group composed of decaying organic matter

portions in the literature (Kishe-Machumu et al., 2015). Biomasses of fish groups not captured in the hydroacoustic survey (for example, catfishes and Marbled lungfish) were obtained from bottom trawl surveys conducted in 2008 during the Implementation of Fisheries Management Plan (IFMP) project (NaFIRRI unpublished data). Biomass for Nile tilapia was estimated as the ratio of annual catch (for LVFO, 2014) to fishing mortality (F=1.32 year^{-1}, Njiru et al. (2006)). Biomasses for phytoplankton and fish-eating birds were obtained from the literature (Villanueva and Moreau, 2002; Witte et al., 2012). Biomasses of other lower TLs were estimated by the model.

Production/Biomass ratio (per year)

At steady states, P/B is approximately equal to the instantaneous rate of total annual mortality (Z) (Allen, 1971). For the 1971-1972 and 1985-1986 models, P/B values for dagaa were increased from 1.8 and 2.2 per year to 3.9 and 4.0 per year, respectively, basing on data in Wandera and Wanink (1995) and Njiru (1995), respectively. For the marbled lungfish, data on landings (0.42 t/km^2/year, Moreau et al. (1993a)) and biomass data from trawl survey for the same period (0.38 t/km^2) were used to estimate F (i.e., 1.1 per year). Consequently, Z was increased from 0.3 per year, which was originally used in the 1971-1972 model (Moreau et al., 1993a), to 1.7 per year in the reparameterized models (assuming natural mortality, M, of 0.4 per year from FishBase (Froese and Pauly, 2016). All other values of P/B in Moreau et al. (1993a) were maintained in the reparameterized models. For the new (2014) model, the Z for fish groups was calculated by adding M and F. Natural mortality was calculated using an empirical relationship Pauly (1980) linking M to the two parameters of the von Bertalanffy Growth Function (VBGF) and mean environmental temperature (Equation (8.4)).

$$M = K^{0.65} \cdot L_{\infty}^{-0.279} \cdot T^{0.463} \tag{8.4}$$

where, L_{∞} is the asymptotic length, i.e., the mean length that the individuals in the population would reach if they were to live and grow indefinitely, calculated according to the formula:

$$\log L_\infty = 0.044 + 0.9841 \log L_{max} \tag{8.5}$$

where, L_{max} is maximum length in the population (Froese and Binohlan, 2000), K is the VBGF curvature parameter (expressing the rate at which L_∞ is approached, and calculated using the empirical relationships (Froese and Pauly, 2016)), and T is the mean environmental temperature (^{o}C). An average temperature of 25.88 ^{o}C (Marshall et al., 2013) was used. Data on growth parameters used in the calculation of M, and catches used in the calculation of F, as well as their sources, are provided in the supplementary material (Supplementary Table S1). The P/B ratios for fish-eating birds and other low TL groups were taken from the literature (Villanueva and Moreau, 2002).

Consumption/biomass ratio (per year)

The Q/B ratio for fish groups, except the marbled lungfish, whose aspect ratio (A) of the caudal fin could not be determined, was estimated using an empirical formula that relates Q/B with one parameter of the VBGF, habitat temperature, morphological variables, and food type (Palomares and Pauly, 1998) as shown in Equation (8.6).

$$\log \frac{Q}{B} = 7.964 - 0.204 log W_\infty - 1.965T' + 0.083A + 0.532h + 0.395d \tag{8.6}$$

where, A is the aspect ratio of the caudal fin (approximately equal to 1.32 and 1.9 for fish with round and forked tails, respectively Froese and Pauly (2016)), h is a dummy variable expressing food type (i.e., 1 for herbivores, and 0 for detritivores and carnivores), and d is a dummy variable also expressing food type (i.e., 1 for detritivores, and 0 for herbivores and carnivores), W_∞ is the asymptotic weight (g), calculated using the formula

$$W_\infty = qL_\infty^3 \tag{8.7}$$

where, q is the expression of condition factor in gram per cubic centimetre of fish (Sparre and Venema, 1998)). T' in Equation (8.6) is an expression for the mean annual temperature of the water body, calculated using the formula

$$T' = \frac{1000}{T + 273.15} \tag{8.8}$$

where, T is average water temperature (^{o}C)). Information on W_∞ in Moreau et al. (1993a) were used in the calculation of Q/B for both 1971-72 and 1985-86 reparameterized models. Mean annual temperature of 25^{o}C (Talling, 1987) was used in both cases. For the 2014 model, however, W_∞ data used in the calculation of Q/B, and their sources, are given in supplementary material (Supplementary Table S1). An average temperature of 25.88^{o}C (Marshall et al., 2013) was used. For the marbled lungfish, whose Q/B ratio could not be calculated from equation 8.6, and the non-fish groups, Q/B were obtained from literature (Villanueva and Moreau, 2002).

Exports (catches, t/km^2/year)

Data on catches in Moreau et al. (1993a) were used in the reparametrized models. For the new model, data on catches were based on the catch assessment surveys (LVFO, 2014) (Supplementary Table S2). Data were separated by fishing gear to permit assessment of gear-specific fishing impacts when analysing mixed tropic impacts (MTI). Nile perch catches were also separated for the juvenile and adult stages based on proportions in Mkumbo and Marshall (2015): 30% allocated to the adult group ($>$40 cm total length) and 70% to the juvenile group ($<$40 cm total length). Also, in the new model, atyid prawn was included in exports because they are harvested as bycatch in small seines alongside dagaa and are not discarded into the lake (Budeba and Cowx, 2007). Approximately 10% of the fish caught in small seines was considered to be atyid prawn basing on data from the Tanzanian part of the lake (Budeba and Cowx, 2007).

Diet composition (DC) and unassimilated food (U)

The diet compositions in the 1971-1972 and 1985-1986 models of Moreau et al. (1993a) were maintained (Supplementary Tables S3-S4). For the new model, diet compositions of both Nile perch and Nile tilapia were based on stomach content analyses (Kishe-machumu et al., 2012b; Njiru et al., 2008). Information on the diet for other groups was obtained from the literature (Downing et al., 2012; Villanueva and Moreau, 2002). The final diet matrices for the mass-balanced models are provided with the supplementary material (Supplementary Table S5). For the unassimilated food, default Ecopath values were used; however, these values were doubled for herbivores (Christensen et al., 2008).

8.2.5 PREBAL diagnostics

Once all input parameters, as estimated from original data or obtained from literature, were entered into EwE software, underlying assumptions were tested using PREBAL diagnostics (Link, 2010). Several diagnostics were considered, including biomass and vital rates across taxa. Biomass and vital rates are expected to decrease with increasing TLs, reflecting the lower abundance of larger-sized organisms at upper TLs (Heymans et al., 2016).

8.2.6 Balancing Ecopath models

The models were considered to be mass-balanced when the following five physiological constraints (Darwall et al., 2010; Heymans et al., 2016) were met simultaneously:

- EE ≤ 1 for every functional group and consistent with group's mortality rate, i.e., EE approaching 1.0 when the main part of production is consumed by predators or exported from the system through fishing and nearing 0.0 for groups that suffer no predation and are not exploited by the fishery, for example, fish-eating birds (apex predators).

- $0.1 \leq P/Q \leq 0.35$, except for fast-growing groups with higher values, and top predators with lower values.
- Net efficiency $< 1.0 <$ Production/Consumption (P/Q) because net efficiency is the value for food conversion after accounting for U and, therefore, cannot exceed GE.
- Respiration/Assimilation (R/A) <1.0, because the proportion of biomass lost through respiration should not exceed the biomass of food assimilated, and consistent with groups strategies for energy allocation, i.e., R/A close to 1.0 for K-selected species and top predators, which invest more energy on growth and reproduction, and $R/A<<<1.0$ for r-selected species that invest less energy on reproduction).
- Respiration/Biomass ratio (R/B), i.e., the metabolic activity level of a group consistent with the group activities. Generally, R/B ratios are expected to be within 1-10 /year for fish, but they can be as high as 50-100 /year for groups with higher turnover such as zooplankton.

During model balancing, only the diet composition matrices were modified to ensure that all the above requirements were met. However, modification of diet compositions was done pragmatically so that the final diet composition matrix for each model (see supplementary material) was still in the same range as that reported from most stomach content analyses on the lake.

8.2.7 Assessing ecosystem indices that relate to maturity and stability

Various ecological attributes that are useful for analysing the ecological role of the different ecosystem components are incorporated in EwE. The following metrics were considered in this study. (i) Total System Throughput (T), the measure of the size of the entire system in terms of the summation of biomass flows from total consumption, respiration, export, and flows to detritus. (ii) Total Primary Production (PP), the summed primary production from all producers). (iii) Net System Production (NSP), the difference between PP and total respiration). (iv) Primary Production/Respiration (PP/R), the measure of system maturity that is expected to approach one as the system matures. (v) Trophic transfer efficiency (TE), the percentage of T entering a TL that is subsequently passed on to the next TL or harvested. (vi) Connectance Index (CI), the ratio of the number of actual links to the number of possible links in the food web. (vii) System Omnivory Index (SOI), the average omnivory index of all consumers weighted by the logarithm of each consumer's food intake). (viii) Ascendency (A), quantifying both the level of activity and the degree of the organization of the system. The mathematical upper limit of A is the development capacity (DC), representing the scope of the system for further development, while the difference between the DC and A is the System Overhead (O), representing the ecosystem's potential for recovery. These indices describe the relative impacts of different drivers of change, including fishing and environmental forcing, on system maturity, productivity, efficiency, and stability(Christensen and Pauly, 1992; Christensen et al., 2008; Odum, 1969; Ulanowicz, 1986, 2004; Ulanowicz and Puccia, 1990). These indices were compared with other systems in the region to understand the relative state of system development.

In addition to the above indices, the new model was used to identify keystone species, a species or groups of species, usually predators, with a disproportionately stronger impact on other groups in the food web compared to their biomass (Valls et al., 2015). Knowing keystone species may allow for the management of a single focal species to maintain the whole ecosystem. Three keystone (KS) indices exist in EwE, but this study considered only KS3 (Valls et al., 2015), which balances contributions between trophic impact and biomass components in the estimation of species' keystoneness, without over-representing abundant or rare species, to identify keystones.

8.2.8 Assessing the role of fisheries

Some indices were computed to identify the current focus of fisheries, including:

- Mean trophic level of the catch (TLC). This index reflects the overall strategy of a fishery. It is calculated by weighting the proportions of each fish/fish group from the catch by their respective TLs. The TLC decreases as fishing impacts increase in the ecosystem since fishing tends to remove the higher TL organisms first (Pauly et al., 1998).

- Primary production required (PPR). This index represents the PP that is required to sustain the catches. It is calculated from both primary producers and detritus to evaluate the sustainability of fisheries in terms of energy. PPR is calculated using empirical formula linking PPR to fish catches, TE, and TL (Pauly and Christensen, 1995) according to the following equation:

$$PPR = \frac{1}{9} \cdot \sum_i Y_i \cdot (\frac{1}{TE})^{TL_i - 1} \tag{8.9}$$

- Gross fishing efficiency (GFE). This index is computed as the sum of all fisheries catches divided by PP. The index shows high values for systems with more efficient use of the system's production (i.e., harvesting fish low in the food web), and low values in systems whose fish stocks are underexploited, or where the fishery is concentrated on apex predators.

This study also assessed whether the current fishing pattern is consistent with the recently proposed balanced harvest (BH) strategy, i.e., exploitation covering a broad range of species in proportion to their natural productivity (Garcia et al., 2015). This analysis was done using catch and production data from the 2014 mass-balanced Ecopath model, following the method of Kolding et al. (2016a). From the definition of Garcia et al. (2015), a balanced fishing pattern is achieved when all exploited fish groups have the same exploitation rates (E). This method follows that if all the fishes that are exploited through fishing have the same E, a linear regression of catches (Y) against production (P) (both on logarithm scale) would have a slope of $b = 1$ and an intercept of $a = log(E)$ (Kolding et al., 2016a). Any deviations from a slope of 1 would show regular differences in E among fishes, and the magnitude of the difference from the slope of 1 would indicate how unbalanced the fishing pattern is. The higher the deviation around the slope, the more inconsistent (i.e., unbalanced) is the exploitation pattern. Also, because the intercept a of the linear regression on of Y against P (both on logarithm scale) represents the log average E, the closer the points lie to the $Y = P$ line, in other words, $E = 1$, the higher the fishing pressure and vice versa. The data used in this analysis are catches and annual production for each of the exploited functional groups. Annual production (P) for each functional group i was calculated as $P_i = (P/B)_i \cdot B_i$. Both P/B and B are available in the 2014 mass-balanced model (see Table 8.4). Data on catches for the same model period is provided in the supplementary material (Supplementary Table S2).

8.3 Results

8.3.1 PREBAL and mass balances

The parameters and key outputs from the balanced models are given in Tables 8.2-8.4, while the main trophic flows are presented in Figure 8.2. Generally, biomass was found to decline with increasing TL, except in the new model, where mid-TL groups (haplochromines, dagaa, and juvenile Nile perch) had higher biomass than lower TL groups. Biomass for these groups was not changed because of the following reasons. (i) Data on these pelagic fisheries were obtained from local sampling, including hydroacoustic surveys (LVFO, 2015). (ii) Nile perch is an invasive species, and its higher biomass compared to low TL counterparts is expected. (iii) the high biomass of haplochromines is also expected as the group has been recovering since the 1990s (Witte et al., 2000). Nonetheless, all the vital rates, including P/B, Q/B, and R/B, were observed to decline with increasing TL. Also, except for the 1985-1986 model, where EE values were pre-defined, biomass utilization for every taxon was lower than biomass production, and EE was consistent with the group's mortality rate. Fish-eating birds (top predators) are neither harvested nor consumed in the system; the EE of zero was expected. Also, total human removals were less than total production. These observations suggest that the models are generally consistent thermodynamic principles (Darwall et al., 2010; Heymans et al., 2016; Link, 2010).

Table 8.2: Input parameters: biomass (t/km^2), production/biomass (P/B /year), consumption/biomass (Q/B, /year), ecotrophic effeciency (EE), and key outputs: trophic level (TL), production/consumption (P/Q), net efficiency (NE), and omnivory index (OI) for the 1971-1972 Ecopath model. Parameters in italics were estimated by EwE software to balance the model. Values of EE in parentheses were entered directly to balance the model where biomass data were not available. Flows to detritus are expressed in t/km^2/year. 'Haps' refer to haplochromine fishes.

Group name	TL	B	P/B	Q/B	EE	P/Q	Flow to detritus	NE	OI
Nile perch	4.09	0.26	0.39	2.52	0.07	0.15	0.22	0.19	0.408
Catfishes	3.48	1.41	0.79	6.74	0.79	0.11	2.12	0.14	0.23
Marbled lungfish	3.18	0.38	1.75	4.8	(0.98)	0.36	0.37	0.45	0.28
Snout fishes and squeakers	3.39	0.3	1	9.96	0.99	0.10	0.59	0.12	0.17
Other 'Haps'	3.68	5.21	1.4	10.73	0.90	0.13	11.89	0.16	0.21
Planktivorous 'Haps'	2.04	5.21	2.5	52	0.56	0.04	59.91	0.06	0.05
Benthivorous 'Haps'	3.10	15.65	2.5	37.4	0.31	0.06	143.75	0.08	0.14
Dagaa	2.61	6.95	3.9	23.5	(0.95)	0.16	34.05	0.20	0.313
Nile tilapia	2.058	0.06	0.65	22.95	0.68	0.02	0.56	0.047	0.06
Other tilapias	2.05	1.88	1	29.9	0.73	0.03	22.97	0.05	0.06
Lake prawn	2.48	12.13	14	64	(0.7)	0.21	206.2	0.27	0.28
Macrozoobenthos	2.24	183.8	5	25	(0.95)	0.2	965.14	0.25	0.22
Zooplankton	2.052	59.04	33.5	140	(0.7)	0.23	3899.9	0.39	0.052
Phytoplankton	1	27.01	365		(0.85)		1478.8		
Benthic producers	1	113.04	25		(0.85)		423.9		
Detritus	1	10			0.21				

Table 8.3: Input parameters: biomass (t/km^2), production/biomass (P/B /year), consumption/biomass (Q/B, /year), ecotrophic effeciency (EE), and key outputs: trophic level (TL), production/consumption (P/Q), net efficiency (NE), and omnivory index (OI) for the 1985-1986 Ecopath model. Parameters in italics were estimated by EwE software to balance the model. Values of EE in parentheses were entered directly to balance the model where biomass data were not available. Flows to detritus are expressed in t/km^2/year. 'Haps' refer to haplochromine fishes.

Group name	TL	B	P/B	Q/B	EE	P/Q	Flow to detritus	NE	OI
Nile perch	3.51	12.58	0.98	2.4	(0.95)	0.40	6.65	0.51	0.09
Catfishes	3.34	0.69	0.85	6.74	(0.95)	0.12	0.96	0.15	0.16
Marbled lungfish	3.16	0.83	0.3	4.8	(0.95)	0.06	0.81	0.07	0.20
Squeakers and snoutfishes	3.20	0.27	0.9	9.96	(0.95)	0.09	0.56	0.11	0.13
Haplochromines	3.10	0.13	2.83	33.37	(0.95)	0.08	0.91	0.105	0.14
Dagaa	2.61	2.10	4	23.5	(0.95)	0.17	10.33	0.21	0.31
Nile tilapia	2.06	5.67	0.82	22.95	(0.95)	0.03	52.36	0.059	0.08
Other tilapias	2.06	0.516	1.2	29.9	(0.95)	0.04	6.20	0.06	0.07
Lake prawn	2.48	2.61	16	64	(0.95)	0.25	35.58	0.31	0.28
Macrozoobenthos	2.24	43.48	5	25	(0.6)	0.2	304.41	0.25	0.22
Zooplankton	2.05	10.26	33.5	140	(0.8)	0.23	643.53	0.39	0.05
Phytoplankton	1	4.53	365		(0.95)		82.70		
Benthic producers	1	25.66	25		(0.85)		96.23		
Detritus	1	10			0.29				

Table 8.4: Input parameters: biomass (t/km^2), production/biomass (P/B /year), consumption/biomass (Q/B, /year), ecotrophic effeciency (EE), and key outputs: trophic level (TL), production/consumption (P/Q), net efficiency (NE), and omnivory index (OI) for the 2014 Ecopath model. Parameters in italics were estimated by EwE software to balance the model. Values of EE in parentheses were entered directly to balance the model where biomass data were not available. Flows to detritus are expressed in t/km^2/year. 'Haps' refer to haplochromine fishes.

Group name	TL	B	P/B	Q/B	EE	P/Q	Flow to detritus	NE	OI
Fish-eating birds	3.897	0.005	0.3	60	0.0	0.005	0.06	0.006	0.142
Adult Nile perch	3.837	1.82	0.922	4.811	0.65	0.19	2.33	0.239	0.20
Juvenile Nile perch	3.335	16.2	3.5	11.73	0.17	0.29	84.51	0.372	0.12
Catfishes	3.206	0.093	0.991	6.009	0.99	0.16	0.11	0.20	0.09
Lungfish	3.242	0.076	1.12	4.3	0.79	0.26	0.082	0.326	0.243
Squeakers and snout fishes	3.061	0.276	1	8.76	(0.95)	0.11	0.49	0.14	0.13
Zooplanktivorous 'Haps'	3.040	9	2.7	21.58	0.981	0.12	39.32	0.15	0.002
Detritivorus 'Haps'	2	2.438	2.53	47.96	0.83	0.05	24.40	0.06	
Other 'Haps'	3.463	0.928	1.83	13.45	0.86	0.13	2.72	0.17	0.16
Dagaa	2.56	19.1	3.93	30.79	0.82	0.12	131.04	0.159	0.25
Nile tilapia	2.568	0.624	2.02	19.6	0.91	0.10	5.00	0.172	0.50
Other tilapias and cyprinids	2.052	0.232	2.37	33.42	(0.95)	0.07	3.12	0.118	0.051
Lake prawn	2.1	13.75	16	64	(0.98)	0.25	180.4	0.312	0.09
Insects and molluscs	2.106	17.47	5	25	(0.8)	0.2	104.8	0.25	0.101
Zooplankton	2	15.24	34	140	(0.95)	0.24	879.56	0.404	
Phytoplankton	1	7.1	373.45		(0.95)		132.5		
Benthic producers	1	13.40	25		0.57		142.9		
Detritus	1	10			0.57				

The modelling procedure assigns a TL of 1 to primary producers and detritus, and a TL of 1 + weighted average of the preys' TL to consumers, resulting in TLs that are not necessarily integers (*sensu* Odum, 1969). The highest TL in the lake was occupied by Nile perch, except where fish-eating birds were included. Nile tilapia, other tilapias, detritivorous and planktivorous haplochromines, and zooplankton occupied the lowest TLs among the consumers, except in the new model, where TL of Nile tilapia was comparatively higher due to the shift from a herbivorous diet to an omnivorous diet (Tables 8.2-8.4, Figure 8.2). The trophic omnivory of Nile perch decreased significantly between 1971-1972 and 1985-1986, as shown by a sharp decrease in omnivory index (OI), while the opposite happened for Nile tilapia, which exhibited the greatest shift in feeding spectrum, with an increase in OI from 0.06 and 0.08 in the 1971-1972 and 1985-1986 models, respectively, to 0.5 in the 2014 model.

Figure 8.3 shows the Lindeman spines for the three models (excluding TLs >IV). The main flows, including detritus, occurred within TLI and TLII, generating 90-93% of T. Although the amount of total net PP consumed by herbivores increased from 85% in 1971-1972 to 92% in 1985-1986, and decreased slightly to 90% in 2014, with the remaining portion of PP, respectively, flowing to the detritus compartment, the detritivory to herbivory ratio doubled from 12-14% between 1971-1972 and 1985-1986 to 27% in 2014 (Figure 8.3). Transfer efficiencies (TEs), which tend to decrease as one ascends the trophic pyramid (Christensen and Pauly, 1993), increased in each successive TL in the 1985-1986 model, resulting into mean TE of 13.74% that deviated from the 10% Lindeman rule of trophic transfer efficiency.

8.3.2 Ecosystem indices

Table 8.5 shows the summary statistics of energy flows and biomasses in Lake Victoria over time, compared with other lakes in the region. Total production, consumption, exports, respiratory flows, and flows to detritus decreased more than sevenfold between 1971-1972 and 1985-1986, and either increased slightly (for example, consumption, exports, and respira-

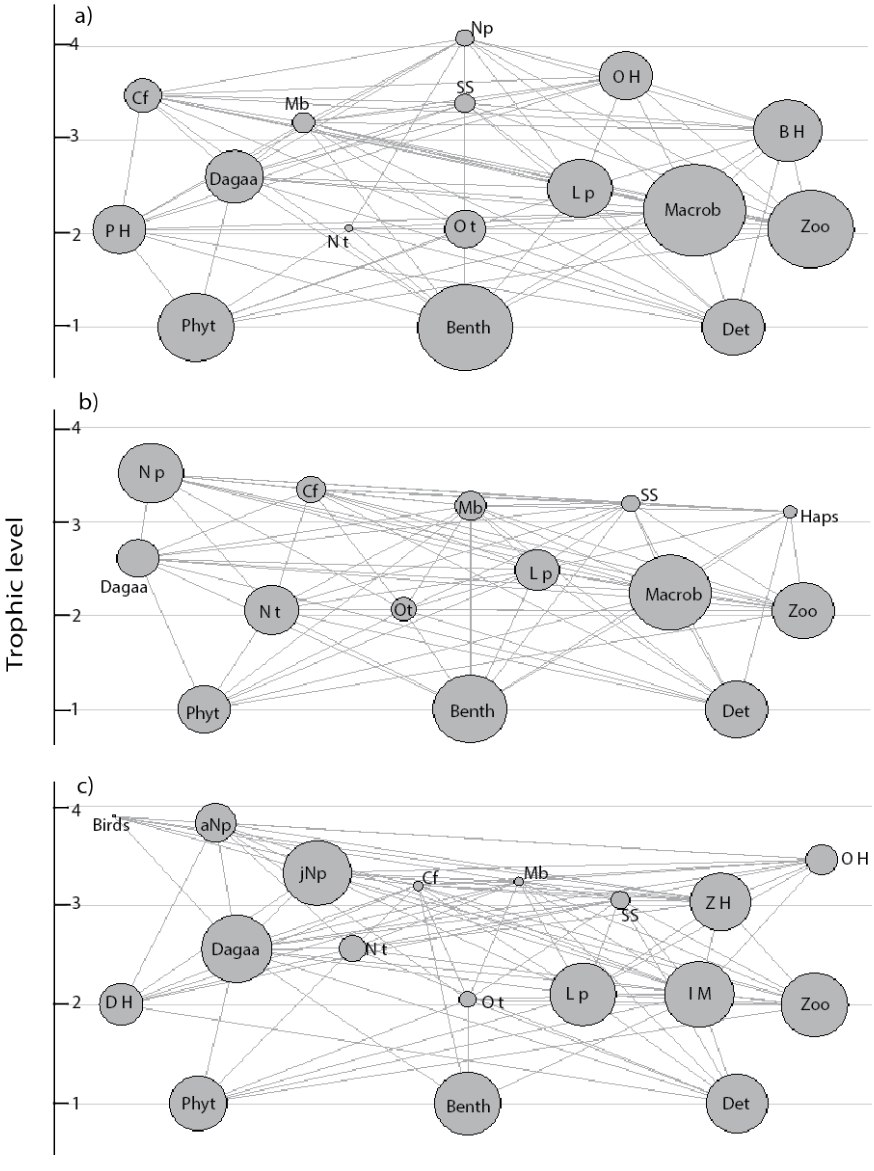

Figure 8.2: Flow diagrams of the Lake Victoria Ecopath models for three periods: (a) 1971-1972, (b) 1985-1986, and (c) 2014, organized by compartments at different trophic levels. Circles are proportional to the magnitude of biomass. Abbreviations stand for Phytoplankton (Phyt), Benthic producers (Benth), Detritus (Det), Zooplankton (Zoo), Detritivorous haplochromines (DH), Lake prawn (Lp), Insects and Molluscs (IM), Other tilapias (Ot), Nile tilapia (Nt), Nile perch (Np), juvenile Nile perch (jNp), adult Nile perch (aNp), Other haplochromines (OH), Planktivorous haplochromines (PH), haplochromines (Haps), catfishes (cf), marbled lungfish (Mb), and snout fishes and Squeakers (SS).

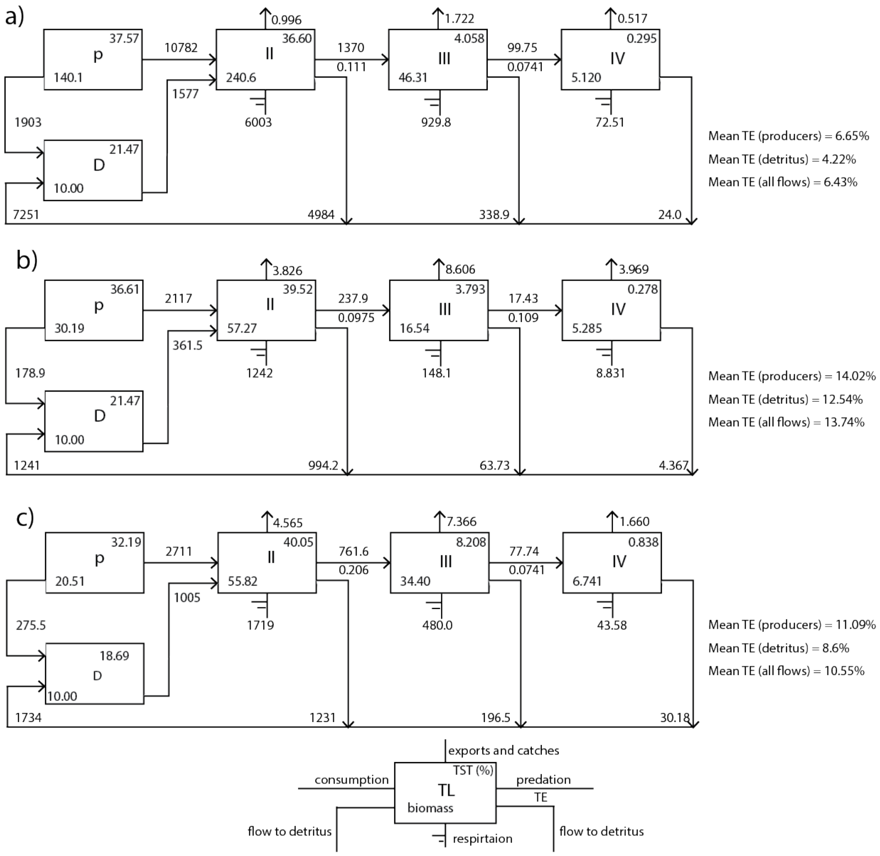

Figure 8.3: Lindeman spine for Lake Victoria food web during a) 1971-1972, b) 1985-1986, and c) 2014, with discrete trophic levels (TLs), showing flows and biomasses. All flows and biomasses are expressed in t/km^2/year. P stands for producers, D for detritus, and TE for trophic transfer efficiency.

tory flows) or decreased further (for example, flows to detritus) between 1985-1986 and 2014. The T also decreased fivefold between 1971-1972 and 1985-1986, and increased only slightly between 1985-1986 and 2014; however, the current value of T is comparable to Lakes Kivu, Tana, and Ébrié. During the three periods: 1971-1972, 1985-1986, and 2014, the proportion of T consumed by predation, respectively, increased from 40.9 to 43.5 to 49.1%; the proportion of T dissipated by respiration increased from 20.7 to 22.3 to 24.1%; the proportion of T exported (through catches) decreased from 16.8 to 14.2 to 8%; the flows to detritus decreased from 21.4 to 19.7 to 18.6%.

All the indicators used to assess the ecosystem status, including PP/R, PP/B, B/T, CI, Finn's cycling index, and Finn's path length, showed a system that is maturing, with relatively high productivity in relation with the total biomass and respiration, despite having low connectivity and biomass in relation with the total flows. Productivity in relation to biomass and respiration decreased over time. Food web connectivity (as shown by CI and SOI) also decreased over time. Biomass cycling (as shown by Finn's cycling index and Finn's path length), on the other hand, increased, with a reduction in the number of groups that a 'flow' passes through. On the food web organisation descriptors, both the system's A and O decreased fivefold between 1971-1972 and 1985-1986, but these slightly increased between 1985-1986 and 2014. The system's redundancy (O/DC) fluctuated between 66 and 70%.

Table 8.5: Summary of ecosystem attribute statistics related to biomass flows and systems organisation for Lake Victoria compared with other lake ecosystems in the region. Abbreviations stand for: total primary production (PP), total respiration (R), and total biomass (B). Ecosystem statistics for other lakes are for: Kivu (Villanueva et al., 2007), Awassa (Fetahi and Mengistou, 2006), Tana (Wondie et al., 2012), and Ebrie and Nokoue (Villanueva et al., 2007). Most flows for Lake Awassa have been omitted because of different units used.

Parameter/Lake	Victoria			Kivu	Awassa	Tana	Ebrie	Nokoue	
	1971-72	1985-86	2014						units
Sum of all production	15842.6	2926.2	3980.4	3040			2902	19595	$t/km^2/yr$
Sum of all consumption	14787	2933.1	4585.6	2190		760.7	1207.6	25731.4	$t/km^2/yr$
Sum of all exports	5677.2	896.2	742.6	1499.8		2530.2	2119.7	1327.4	$t/km^2/yr$
Sum of all respiratory flows	7007.6	1399.3	2243.9	1233.9		498.9	510.9	10498.5	$t/km^2/yr$
Sum of all flows into detritus	7250.5	1241.3	1733.6	1762.1		2657	2402.9	20410	$t/km^2/yr$
Total system throughput (T)	34723.2	6469.9	9305.8	6686		6447	6240	57967	$t/km^2/yr$
Total net primary production	12684.8	2295.5	2986.7	2733.8		3028.9	2629.9	11826	$t/km^2/yr$
PP/R	1.81	1.64	1.33	2.21	5.83	6.07	5.15	1.126	
Net system production (NSP)	5677.2	896.3	742.7	1499.5		2530.1	2119	1327.4	$t/km^2/yr$
PP/B	29.3	20.9	25.3	52.22	28.6	39.8	41.6	23.7	
B/T	0.012	0.016	0.012	0.008	0.016	0.012	0.01	0.009	/year
B (excluding detritus)	432.4	109.4	117.7	52.2		76.04	63.3	497.1	t/km^2
Connectance Index (CI)	0.41	0.49	0.32	0.396			0.191	0.266	
Finn's cycling index	4.33	5.84	4.75				2.57	34	%TST
Finn's path length	2.74	2.82	3.12				2.37	4.9	
System Omnivory Index (SOI)	0.17	0.16	0.12	0.148			0.145	0.156	
Ascendency (A)	44502	8310	12110				7656.1	47224	Flowbits
Overhead (O)	88200	17174	28189				3876.7	186154.3	Flowbits

Figure 8.4 shows the keystone index and the relative total impact of the different functional groups in the 2014 Ecopath model. Keystone indices were high for adult Nile perch, phytoplankton, and atyid prawn, but only adult Nile perch had low biomass and highest relative trophic impact.

8.3.3 The focus of fisheries

Total fish biomass decreased from 37.3 t/km^2 (out of which 70% were haplochromines) in 1971-1972 to 22.8 t/km^2 (out of which 80% were the introduced Nile perch and Nile tilapia) in 1985-1986. The 2014 model showed the total fish biomass to be 50.7 t/km^2, with the three groups (Nile perch, dagaa, and Haplochromines) constituting 97% of the total fish biomass. The proportion of total PPR increased from 5.89 to 19.59% between 1971-1972 and 1985-1986, and this further increased to 22.16 by 2014. During 1985-1986 and 2014, when PPR was highest, Nile perch (adult and juvenile combined) was responsible for about 70% of the total PPR. Specifically, adult Nile perch in the 2014 model was responsible for 60% of the total PPR to sustain the entire catch. GFE increased from 0.00025 to 0.0072 between 1971-1972 and 1985-1986, but it later decreased to 0.0045 during 2014.

The TLC increased from 2.9 to 3.1 between 1971-1972 and 1985-1986, but it declined to 2.8 by 2014. The initial increase in TLC coincided with the Nile perch (an introduced high TL invasive species) boom during the 1980s (Figure 8.5). The trends in catches of two predominant fisheries, a high TL species (Nile perch) and a low TL species (dagaa), were examined to get insight into the causes for the decline in TLC between 1985-1986 and 2014, i.e., whether the decline in TLC was due to the decline in catches of the high TL (predatory) fish(es), in line with 'fishing down' the food web (Pauly et al., 1998), or progressive increase in catches of low TL fishes, in line with 'fishing through' the food web (Essington et al., 2006; Stergiou and Tsikliras, 2011). The decline in TLC coincided with a threefold increase in catches of dagaa, a small pelagic species that occupies TL of 2.56, with no indication of a change in Nile perch catches

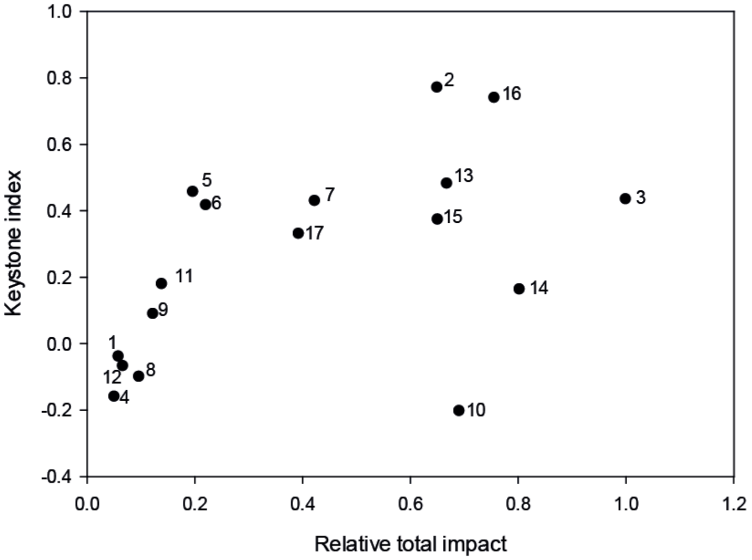

Figure 8.4: Keystone index and relative overall effect of each functional group from the mass balance Ecopath model of the Lake Victoria parameterized to represent ecosystem status in 2014. The numbers represent functional groups in the Ecopath model (Table 8.1).

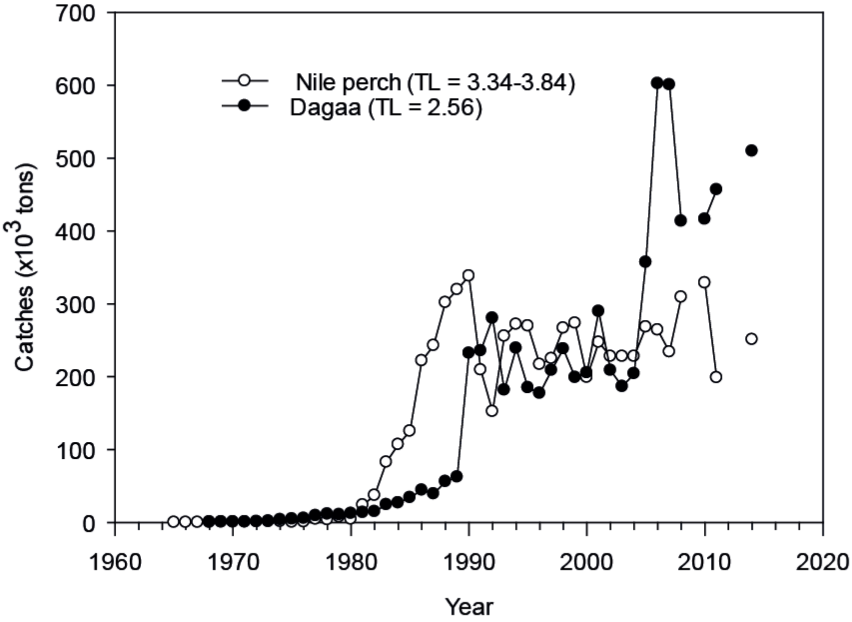

Figure 8.5: Total catch (tons) of two predominant fisheries, Nile perch and dagaa, plotted versus years in Lake Victoria. Data from Kolding et al. (2014), supplemented by LVFO (2014) from 2010 to 2014.

(Figure 8.5).

Figure 8.6 shows the fishing pattern in Lake Victoria, expressed as yield (kg/km^2) versus production (both on a logarithm scale) from an Ecopath model of 2014. The E of small pelagic groups (for example, juvenile Nile perch, dagaa, and haplochromines) were less than 15% of total annual production. However, large demersal/benthopelagic groups (for example, adult Nile perch, Nile tilapia, catfishes, mormyrids and squeakers, and marbled lungfish) had high E (>50%) relative to production. From a BH perspective, if all the fished groups have the same E, they should be on a straight line, with a slope $b = 1$ and with the intercept $a = log(F/Z)$; the intercept a represents the average fishing pressure (Kolding et al., 2016a). Because the ratio of slope between yield and production was significantly different from 1, implying that E was not evenly distributed across TLs, fishing on Lake Victoria is inconsistent with the BH strategy.

Figure 8.7 shows the fishing intensity in Lake Victoria, expressed as average E per 0.4 TL intervals, compared with the total average production (kg/km^2, on a logarithm scale) from an Ecopath model of 2014. Exploitation was skewed to the least productive species/groups at higher TLs, with significantly less fishing ($E < 15\%$) occurring in the highly productive, low TL species/groups. This analysis, however, only includes species or groups above TL 2, which are exploitable, and therefore it does not include all functional groups in the ecosystem.

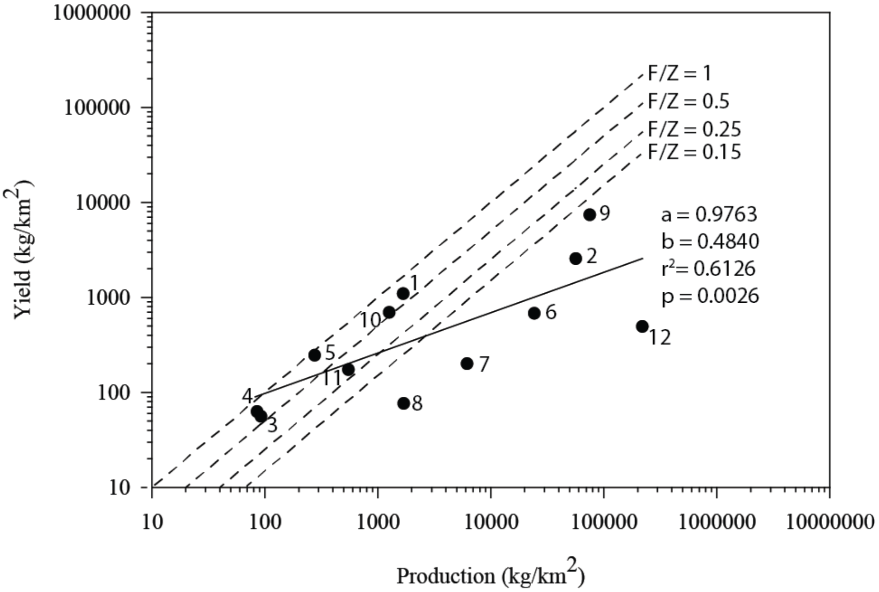

Figure 8.6: Harvest relative to production (on logarithm scales) for stocks or groups harvested in Lake Victoria using data extracted from an Ecopath model (see Table 8.4) parameterized to reflect ecosystem state and fisheries in year 2014. The more the slope deviates from the 1:1 line between yield and production (i.e. E = F/Z = Y/P = 1), the more “unbalanced” Garcia et al. (*sensu* 2012) the fishery is. Exploitation rates equivalent to 15, 25 and 50% of production are given as dotted parallel lines. p-value gives the test of slope $\neq 1$. Numbers represent species/functional groups: adult Nile perch(1), juvenile Nile perch (2), catfishes (3), marbled lungfish (4), squeakers and snoutfishes (5), zooplanktivorous haplochromines (6), detritivorous haplochromines (7),other haplochromines (8), Dagaa (9), Nile tilapia (10), other tilapias (11), and Lake prawn (12).

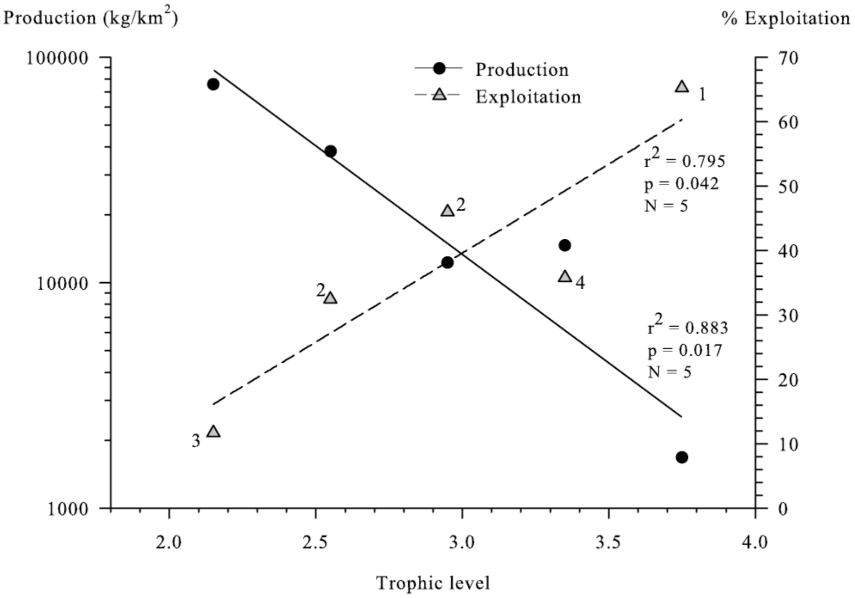

Figure 8.7: Production (kg/km^2) (on logarithm scale) and exploitation rate (%) per Trophic level (binned in 0.4 TL intervals). Numbers represent the total number of exploited trophic groups in each interval. Black circles = production and grey triangles = exploitation rate. Superimposed are linear trends for exploitation (ascending black line) and production (descending black line).

8.4 Discussion

8.4.1 Data limitations and model caveats

Ecopath, like any other model, has shortfalls and limitations, most of which have been discussed in literature (Christensen and Walters, 2004a; Plagányi and Butterworth, 2010). Perhaps, the major limitation of any ecosystem model is the quantity and quality of data available to parameterize the model. Whereas effort was made to include data collected at the model location to estimate input parameters, not all the functional groups are assessed during surveys with equal intensity and precision. Commercially important species (for example, Nile perch, Nile tilapia, and dagaa) are given more attention than other groups, which are often condensed into 'others'. This practice often promotes merging of functional groups that would, otherwise, be modelled in separate groups (Musinguzi et al., 2017), thereby affecting the overall quality of the model.

PREBAL diagnostics (metrics), including changes in biomass and vital rates across TLs, were checked to ensure that the parameters were consistent with thermodynamic principals (Link, 2010). Most of the metrics showed consistency with principle ecological and physiological rules, i.e., biomass utilization for every group lower or equal to biomass production of that group; gross GE varying between 0.1 and 0.4, especially in the new model; R/B higher for small organisms and top predators compared to lower trophic levels; R/A <1, and high for top predators; net efficiency <1 (Christensen et al., 2008; Heymans et al., 2016).

8.4.2 Mass balances

The values of GE, the physiological capacity to convert consumed food (Q) into tissue (P), were lower than 10%, i.e., the minimum amount of food consumed that is expected to be converted into tissue growth in finfish (Christensen et al., 2008), especially in the reparameterized models, for planktivorous and detritivorous haplochromines and other tilapias. The low GE can be attributed to both the lower values of productivity and assimilation efficiency used for the groups that feed on phytoplankton and detritus in the model. Nile tilapia, which fed on the similar phytoplankton-dominated diet in the 1970s and 1980s, had similar low GE values in the 1971-1972 and 1985-1986 models, but the value of GE increased and was in the expected range in the 2014 model, coinciding with a shift to a more diversified diet comprising of including insects and fish during in the 1990s and 2000s (Njiru et al., 2008). This trend is also reflected in the upward shift in omnivory index from 0.06-0.08 during the 1970s and 1980s to 0.5 in 2014.

The values of GE in this study deviate from those in the previous models. For instance, Downing et al. (2012) reported GE of 0.66 for Nile tilapia and 0.61% for juvenile Nile perch in 2005 for the model Mwanza Gulf. High values of GE in (Downing et al., 2012) imply a more efficient food web, where both Nile perch and Nile tilapia can convert more than 60% of what they consume into tissue growth. Generally, GE is expected to be lower than 35% for most fish groups (Darwall et al., 2010; Heymans et al., 2016), and the high GE reported in previous studies could have been due to overestimation of production (Kolding, 2013).

8.4.3 Ecosystem development and stability

Ecosystem development or succession is the process by which an ecosystem progresses towards a mature state, and it involves a directional, orderly, and predictable process that results in maximization of biomass and optimization of energy (Odum, 1969). This study used network analysis to characterize the Lake Victoria ecosystem maturity status, compared with other lakes in the region. The decrease in food web connectivity and productivity in relation with biomass and respiration, and the increase in biomass cycling, are characteristic of a system that is still developing. However, it may be in advanced stages of development compared to other systems in the region such as Lakes Kivu, Awassa, Tana, and Ebrie (Table 8.5).

Trophic connections are expected to evolve from linear to web-like structures as the system matures (Odum, 1969). The decrease in CI and the increase in biomass cycling, therefore, suggest that the system is still developing. Other attributes of food web connectivity (Finn's cycling index and Finn's path length) have increased, especially between 1985-1986 and 2014. Despite the diminished biodiversity, these indicators suggest that the system is relatively stable (Ulanowicz, 1986). Finn's mean path length is also related to the recovery time of the ecosystem (Vasconcellos et al., 1997), and the index value in the 2014 model suggests that the current ecosystem would likely recover more quickly than one of the 1970s or 1980s. The current level of food web connectivity is also comparable with other maturing ecosystem in the region (Table 8.5). However, anthropogenic and natural stressors can limit the maturity level an ecosystem can reach (for example, Christensen, 1995); therefore, the multiple stressors that Lake Victoria continues to endure (Hecky et al., 2010) may undermine the level of maturity the system can reach.

Before the introduction of an invasive fish predator, Nile perch, into Lake Victoria, a diverse fish community dominated by >500 haplochromine cichlids, which formed more than 80% of the fish biomass, was eminent (Kaufman et al., 1997; Seehausen, 1996). Moreau (1995) described the major food chains that formed key functional groups follows. (i) Zooplankton to herbivorous haplochromines and dagaa) to the top predators (catfishes and piscivorous Haplochromines). (ii) Zooplankton, insect larvae, and molluscs to zoophagous fish taxa (haplochromines, Mormyridae, *Barbus* spp., *Alestes* spp., *Synodontis* spp., and marbled lungfish to top predators. (iii) A direct flow to several herbivorous *Tilapia* spp. and haplochromines. After the Nile perch establishment in the 1980s, the complex food web, with biomass flows (T) totalling 34723.2 t/km^2/year, was simplified, reducing T by fivefold. The fish community was also reduced to only four dominant species: the two introduced Nile perch and Nile tilapia, and the native dagaa and lake prawn. Following the demographic changes in Nile perch numbers after the 1990s, aided by intensive fishing fishing (Mkumbo and Marshall, 2015), some trophic groups recovered, although biomass remained low. These results suggest that the trophic structure has not fully recovered, mainly at the functional group level, which is agreement with Downing et al. (2012). The food web is still simple and less diversified, with few groups that 'flows' pass through, as well as high biomass cycling.

Further evidence of a simplified food web can be seen from the results of ascendency, overhead, and development capacity (Table 8.5). A system with high ascendency usually is developed and much diversified, while a system with high overhead is more resilient and has strength in reserve to respond to perturbations (Christensen, 1995). The system's ascendency and overhead decreased ca. fivefold between 1971-1972 and 1985-1986, and increased only slightly between 1985-1986 and 2014. The 1971-1972 ecosystem was more diversified and resilient than 1985 and 2014 ecosystems. Nonetheless, the relative redundancy (O/DC), which is also used as a measure of the system's strength to meet unexpected perturbations (Christensen, 1995) suggests that the system can still bounce back even when it is not yet in an ecological climax state.

In immature systems, primary production is expected to exceed respiration (Odum, 1969). The PP/R ratio is related to community energetics, and it is expected to decrease as a system matures due to the accumulation of biomass in mature systems. Elsewhere, PP/R has been observed to vary between 0.8 and 3.2 (Christensen and Pauly, 1993). Downing et al. (2012) reported PP/R ratios in Mwanza Gulf that were approximately 800fold higher than those observed in the literature, which may have been overestimated (Kolding, 2013). This study showed a decline in productivity in relation to respiration, but the PP/R ratios (1.33-1.81) were within the expected range for developing systems. The increase in detritivory over time (Figure 8.3) is also indicative of maturing systems (Christensen, 1995; Odum, 1969).

On the keystone species, adult Nile perch had low biomass with disproportionately stronger influence on food web structure. This group had a disproportionately higher trophic impact compared to its biomass, and could, by definition (see Valls et al., 2015), be a keystone. Keystone properties were also exhibited by low TL groups, such as phytoplankton (Figure 8.4), although these groups had a low trophic impact. This heterogeneity in terms of TLs is suggestive of mixed control by top-bottom and bottom-up mechanisms in the food web, where a core set of ecosystem components has a predominant role on the control of biotic interactions exerted by both top-down (for example, Nile perch) and bottom-up (for example phytoplankton) mechanisms (Libralato et al., 2005). The aspect of mixed control mechanisms was also observed in mixed trophic impacts. Majority of the fish groups had minimal or no impact on the other groups, except Nile perch, which exerted a negative impact on all groups, and lower TL groups (for example, phytoplankton), which exerted a positive impact on the majority of functional groups. Therefore, an increase in biomass of adult Nile perch has a higher potential to destabilize the whole ecosystem, similar to the occurrence in the 1980s.

8.4.4 The focus and impact of fisheries

The higher percentage of total PPR for the fishery in the 1985-1986 and 2014 models reflects the higher landings (13.7-16.4 tons/km^2/year) compared to 1971-1972 (3.3 tons/km^2/year). In particular, the PPR to sustain Nile perch was higher during the 1985-1986 and 2014 model periods because their abundance was much higher relative to that of their prey compared to the 1971-1972 model period. The lower PPR to sustain Nile perch fishery in 1985-1986 compared with 2014 could be attributed to Nile perch feeding at lower trophic levels, during the period it shifted its diet from haplochromines to lake prawn, after the disappearance of the former (Moreau et al., 1993a), and the increase in TE, leading to energy optimization, compensating for the exploitation of fish at high trophic levels (Jarre-Teichmann, 1998). The exploitation of fish at lower TLs may also compensate for the inefficient transfer of energy from one TL to the next and make the fishery ecologically less expensive (Jarre-Teichmann, 1998). This explanation also applies to the low fraction of PPR in the 1971-1972 model, even when TE was the lower than the commonly referred Lindeman's 10%, and the lower fraction of PPR to sustain dagaa fishery (which constituted >50% of the total catches) compared to the adult Nile perch fishery (which constituted only 8% of the total catches) in the 2014 model.

The mean TLC is one of the most widely used indices for assessing the impact of fisheries on ecosystems (Pauly, 2010; Stergiou and Tsikliras, 2011), although it may be influenced by other factors such as an increasing abundance of low TL species (Branch et al., 2010; Essington et al., 2006). In Lake Victoria, landings of Nile perch (TL = 3.3-3.9) have remained stable since the 1990s, while landings of dagaa (TL = 2.56) have increased almost threefold (Figure 8.5, LVFO, 2014). The biomass of dagaa doubled between 1999-2002 and 2008-2011 (Taabu-Munyaho et al., 2016) and, in some coastal areas of the lake, densities of up to 40 tons/km^2 have been recorded (LVFO, 2015). Data from hydroacoustic surveys also show that the biomass of Nile perch has increased since 2007 (LVFO, 2015). The decline in the mean TLC may, therefore, be attributed to the sequential addition of low TL catches (dagaa), i.e., “fishing through” the food web (Essington et al., 2006), instead of a decline in catches of high TL species (Nile perch) as hypothesized by Pauly et al. (1998).

Analysis of fishing patterns in relation to the recently proposed BH strategy, showed exploitation to be concentrated at high TLs, and hence inconsistent with BH. This (selective) fishing pattern is consistent with most fisheries across the globe, where the focus of fisheries is on maximizing profit (Kolding et al., 2016a). Previous studies have shown that BH may increase overall yield, with the least change in the relative biomass composition of the fish community (Jacobsen et al., 2013; Kolding et al., 2016c). Other studies have shown that BH can emerge from individual decisions of fishers (Plank et al., 2016). These claims still need more investigations, especially in medium to large scale fisheries.

8.5 Conclusions

Lake Victoria’s food web is still simple with low connectivity; the trophic structure has not fully recovered after the disruptions during the 1980s, despite the recovery of some haplochromines. The large biomass flowing into detritus at the consumer level, especially in the mid-TLs, seem to suggest that the groups are less exploited by fisheries. Despite the high TE, efficient utilization of primary production, and an increase in biomass cycling and detritivory over time, the system is still developing. However, it is stable and has enough strength in reserve to respond to perturbations. With regards to fisheries, the food energy value of the system may be underutilized, given that exploitation pattern is not balanced across a wide range of TLs. In particular, juvenile Nile perch, dagaa, and all haplochromine groups, with higher production, could be under-exploited, while the adult Nile perch, Nile tilapia, catfishes and marbled lungfish may be over-exploited (i.e., E $>$ 50% of production). This particular fishing pattern could probably impact on the overall yield of the system as well as ecosystem functioning (Jacobsen et al., 2013), and could be responsible for the changes in the size structure of commercially-valuable species (Nile perch and Nile tilapia).

8.6 Acknowledgement

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8.7 Supplementary data

Supplementary data to this paper can be found at `https://www.dropbox.com/s/9rlbml2jiihn7i4/Supplementary_material.docx?dl=0`

9

Paper III

Ecosystem modelling of data-limited fisheries: how reliable are Ecopath with Ecosim models without historical time series fitting?

Vianny Natugonza, Cameron Ainsworth, Erla Sturludóttir, Laban Musinguzi, Richard Ogutu-Ohwayo, Tumi Tomasson, Chrispine Nyamweya, Gunnar Stefansson

Abstract

Long-term time series data is not available for many of the African Great Lakes. This gap precludes fitting ecosystem model parameters to time series data, and it is not known how reliable non-fitted models are compared to fitted ones in terms of predicting consequences of alternative management strategies. To investigate this, a historical Ecopath with Ecosim (EwE) model, fitted to time series data (1980-2015), and a present-day EwE model, representing average conditions for the period 2010-2015, are generated for Lake Victoria (East Africa). Afterwards, scenario simulations are run using the present-day model and the comparable 2015 end-state of the historical model, testing if incorporating information on short-term biomass trends by adjusting biomass accumulation (BA) parameter in the present-day model increases its reliability. Results show differences in model predictions, but those differences can be lessened by adjusting BA terms in the present-day model to reflect biomass trends from short-term empirical data near the models' initialisation year. Also, the study compares the models with and without fitted vulnerability parameters. The models generally give comparable results for the main commercial fisheries at low fishing pressure; when fishing mortality is increased, the models give variable predictions. This study adds to our current understanding of the limitations of EwE models that are not challenged to reproduce long-term historical fishery responses to perturbations. In conclusion, for the less productive groups, as well as groups that suffer heavy mortality (either due to predation or fisheries), it may be appropriate to use negative BA as the first draft assumption in present-day models that lack time series data.

Keywords: Ecopath with Ecosim, Ecosystem-based management, Lake Victoria, model comparison, model fitting

9.1 Introduction

The demand for ecosystem-based fisheries management (EBFM) in recent years has stimulated the development of multi-species and ecosystem models (Essington and Punt, 2011). Ecosystem models are preferred over single-species models for long-term strategic management because of their potential ability to predict (quantitatively) the consequences of future fishing scenarios by integrating available knowledge about the ecosystem across different scales (Patrick and Link, 2015). In particular, end-to-end ecosystem simulation models have become prominent because of their ability to integrate ecosystem and human components, which are all important in EBFM (Collie et al., 2016; Rose, 2012). At the heart of the EBFM discussions is the notion that well-calibrated models (i.e., models that are fitted to historical observations and mimic true ecosystems) are best suited for informing EBFM (Grüss et al., 2017; Rose et al., 2015). Consequently, model validation and skill assessment have become an important aspect of ecosystem modelling (Olsen et al., 2016; Stow et al., 2009).

Unlike single-species models, whose parameters can be estimated and tested statistically for their performance within the model, ecosystem models are multidimensional, with no computationally feasible means for determining key model parameters internally. Instead, validation of ecosystem model parameters relies on fitting the model to time series data until there are reasonable agreements between model predictions and observed long-term fishery dynamics (Grüss et al., 2017; Heymans et al., 2016). Unfortunately, model fitting is not always possible in data-limited fisheries. This gap precludes fitting ecosystem model parameters to time series data, and it is not know how reliable non-fitted models are compared to fitted ones in terms of predicting consequences of alternative management strategies.

Ecopath with Ecosim (EwE, Christensen and Pauly, 1992) is the most widely used ecosystem modelling tool globally, with over 400 models (Colleter et al., 2015). The modelling tool combines routines for ecosystem trophic mass balance analysis (Ecopath) with the dynamic and spatial modelling capabilities (Ecosim and Ecospace) to explore past and future impacts of fishing and the environment (Christensen and Walters, 2004a). Due to the relative paucity of fisheries data, less than 15% of the EwE models that exist globally are calibrated by fitting to time-series observational data (Heymans et al., 2014). The situation is worse for the inland fisheries, especially in the underdeveloped nations. Musinguzi et al. (2017) analysed all the EwE models that exist on the African Great Lakes (AGLs) and found that none of the 20 models was calibrated by fitting the model to time series data. The level of confidence that can be associated with predictions from these models is not known, and this is likely to be contributing to the limited utilization of EwE models for management applications (Christensen and Walters, 2005).

The EwE modelling framework quantifies energy flows among biological groups (or species) and provides predictions of biomass and catch rates of each species/group as affected by fishing, predation, and change in food availability (Christensen and Walters, 2004a). The main parameters in Ecopath are biomass per unit of habitat area (B), production per unit of biomass (P/B), consumption per unit of biomass (Q/B), ecotrophic efficiency (EE, the proportion of production used in the system), and biomass accumulation (BA, the instantaneous rate of biomass change EwE, which represents the degree of imbalance between losses, i.e., from predation and fisheries, and production) (Christensen et al., 2008). In Ecosim, vulnerability (the value assigned to a given predator-prey interaction, representing the factor by which an increase in the predator biomass will cause predation mortality on the prey) is one of the most influential parameters (Mackinson et al., 2003). However, it is also difficult to quantitatively estimate in the real world. The vulnerability parameter determines if the populations' dynamics are predominantly controlled by top-down (vulnerability >2), bottom-up (vulnerability <2), or mixed trophic control mechanisms, where neither bottom-up nor do top-down processes dominantly control groups' dynamics (vulnerability $= 2$) (Christensen et al., 2008). Other parameters, such as feeding time adjustment rate, predator effect on feeding time, and switching power, are also important (Mackinson et al., 2003), but these are often maintained at default Ecosim settings even in models that are fitted to time series data.

The validity of EwE models is often affirmed by a combination of ‘pretty fit’ (the model’s ability to reproduce long-term times series observations) and credible model behaviour (ecological accuracy of parameters used)(Heymans et al., 2016). In cases where historical data are lacking, or for models of the present-day that have no future observations, model validation is based on other criteria such as pre-balance (PREBAL) diagnostics (Link, 2010) and data "Pedigree" (Christensen and Walters, 2004a). Modellers of present-day models parameterize BA and the vulnerability matrix, which are estimated while fitting the model to historical observations, by more straightforward means: for example, by assuming zero BA rates, which results in a stable equilibrium, and by using the default global vulnerability setting of 2. BA of zero can result in overestimation of safe harvest rates for groups that suffer substantial mortality due to predation and fisheries (Ainsworth and Walters, 2015). At the same time, the global vulnerability setting of 2 tends to ignore prior exploitation histories of predators (Plagányi and Butterworth, 2010) and may not be conservative enough to aid precautionary management (Bundy, 2004). Although most of the limitations underlying the use of default parameter settings have been discussed in the literature (for example, Ainsworth and Walters, 2015; Heymans et al., 2016), there is still limited understanding on how reliable non-fitted models are compared to fitted ones in terms of predicting consequences of alternative management strategies.

This study aims to test how much adjusting EwE parameters from default values by fitting to time series data changes the reliability of model predictions (model skill and parameter uncertainty). To investigate this, a historical model, fitted to time series data (1980-2015), and a present-day model, representing average conditions for the period 2010-2015, are generated for Lake Victoria (East Africa). Then, through scenario simulations, the present-day model is compared with the comparable 2015 end-state of the historical model. The study tests if incorporating information on short-term biomass trends by adjusting BA parameter in the present-day model increases its reliability. Preliminary tests involve comparing the models to determine if the simulated biomasses, diets, and catches in end-state of the historical model are sufficiently similar to the present-day model so that differences in their scenario projections are only attributable to calibration (fitting the model to time series data). Due to the lack of consistent historical biomass data, Atlantis model of Lake Victoria (Nyamweya et al., 2016b) is used as the “true ecosystem", i.e., the time series of biomass simulated by Atlantis model are used "observations" to validate the fitted EwE model. Atlantis is a whole of ecosystem model that is age- and size-structured, and spatially-resolved, accounting for both physical (bathymetry, hydrography) and biological (species life history and distribution) components in a heterogeneous environment (Fulton et al., 2011a). Additional information about the Atlantis modelling software can be found in elsewhere (for example, Audzijonyte et al., 2017a,1). The presence of Atlantis model ("the Atlantis ecosystem") provides an opportunity to test the performance of simpler models (Sturludottir, 2017; Weijerman et al., 2016). The validity of the Atlantis model of Lake Victoria is affirmed by its ability to simulate distributions of nutrients, primary production and main commercial fish species, and temporal trends of biomass and catch that match well with observed data and community shifts reported in the literature (Nyamweya et al., 2016b). These aspects of model validity, however, do not imply that Atlantis is a true reflection of the total biomass or catch amounts; therefore, more emphasis is put on fitting the trends rather than absolute values.

9.2 Material and methods

9.2.1 Study area

The study focused on Lake Victoria, East Africa (Figure 9.1). Lake Victoria is the world’s second-largest freshwater lake in terms of surface area (68,800 km^2). The lake shoreline, which extends about 7,142 km, is highly indented with numerous islands, bays, and wetlands. However, with a maximum depth of 80 m (and an average depth of 40 m), the lake is shallower compared to the rest of the AGLs (Ogutu-ohwayo et al., 2016). Lake Victoria has received considerable attention in terms of ecosystem modelling, more than any other AGL. Out of the 20 EwE models that exist on the AGLs, 50% of the models are on Lake Victoria, either representing a particular section of the lake or the whole lake and for a particular year chosen by the modeller (Musinguzi et al., 2017).

Over the past five decades, the lake has endured multiple stresses, including new species introductions, intensive fishing, habitat degradation, invasive weeds, and climate variability, which have been accompanied by changes in lake size, limnological conditions, and fish species composition (Awange et al., 2019; Hecky et al., 2010). The original fishery (before the 1960s) was dominated by demersal and benthopelagic species, notably haplochromines, the catfishes (i.e., North African catfish (*Clarias garepinus*), Semutundu (*Bagrus docmak*), silver catfish (*Schilbe intermedius*), and squeakers (*Synodontis* spp.) and marbled lungfish (*Protopterus aethiopicus*) (Table 9.1, Ogutu-ohwayo, 1990b). The present-day commercial fishery, however, is dominated by the introduced Nile perch (*Lates niloticus*) and Nile tilapia (*Oreochromis niloticus*) and the native silver cyprinid (*Rastrineobola argentea*) (LVFO, 2016b). Haplochromines have been slowly recovering following a drastic decline in the mid-1980s (Witte et al., 2007), and currently constitute the major prey for the introduced Nile perch (Kishe-machumu et al., 2012b). However, the rest of the native species never recovered, and their commercial importance for the fisheries in the lake is considered negligible (Goudswaard and Hecky, 1997).

9.2.2 Modelling framework

EwE has a static trophic mass balance routine (Ecopath), which quantifies the energy flows among the functional groups included in the model (Christensen and Walters, 2004a). The functional groups are user-defined based on ecological roles and feeding interactions. Biomass flows in an ecosystem are regulated by gains (consumption, production, and immi-

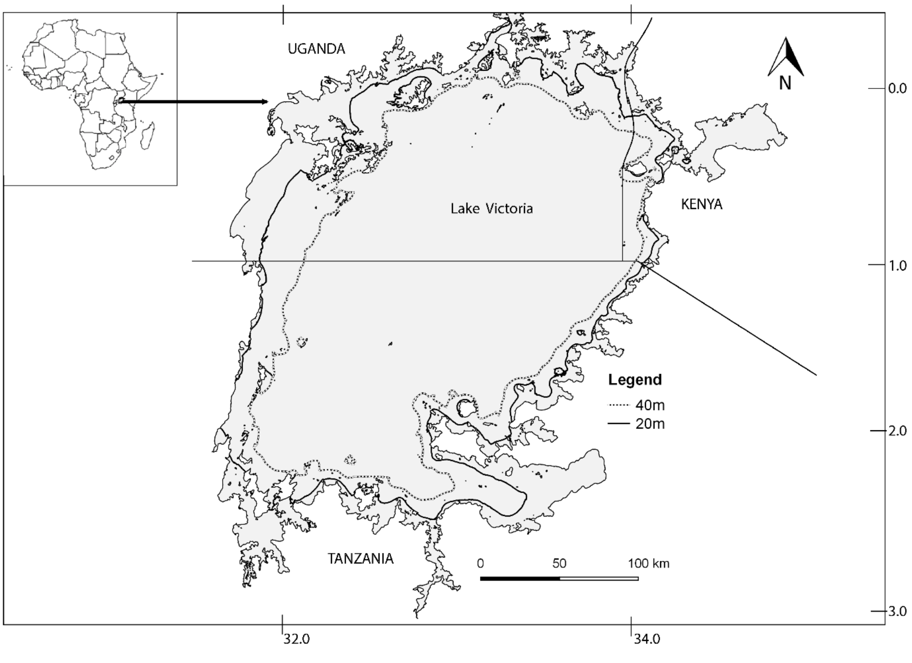

Figure 9.1: Lake Victoria in East Africa (extent of the modelled area). Depth contours show inshore (<20 m), coastal (20-40 m) and deep (>40 m) areas.

gration) and losses (mortality and emigration), through predator-prey relationships as shown in Equation 9.1.

$$B_i \cdot (\frac{P}{B})_i = \sum_{j=1}^{n} B_j \cdot (\frac{Q}{B})_j \cdot DC_{ji} + B_i \cdot (\frac{P}{B})_i \cdot (1 - EE_i) + Y_i + E_i + BA_i \quad (9.1)$$

where, DC_{ji} is the fraction of prey i in the average diet of predator j, Y_i is the total fishery catch rate of group i, and E_i is the net migration rate (emigration-immigration) of group i. The term $B_i \cdot (P/B)_i \cdot (1 - EE_i)$ is an expression of "other mortality", MO, representing mortality other than that caused by predation and fishing. To balance energy input and output of all biomass compartments, consumption rate must equal the sum of production rate, unassimilated food (UA) and respiration (R) as shown in Equation 9.2.

$$B_i \cdot (\frac{Q}{B})_i = B_i \cdot (\frac{P}{B})_i + R_i + UA_i \quad (9.2)$$

Ecosim is the time dynamic routine of EwE that uses Ecopath parameters to provide predictions of biomass and catch rates of each group in relation to fishing, predation, and food availability (Christensen and Walters (2004a) as shown in Equation 9.3).

$$\frac{dB_i}{dt} = g_i \cdot \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - B_i \cdot (MO_i + F_i + e_i) \quad (9.3)$$

where, for each functional group i, dB/dt is the change in biomass over time, g is the net growth efficiency (the ratio of production to consumption), Q_{ji} is the consumption rate on group j, Q_{ij} is the predation mortality rate by group j, F is fishing mortality rate, e is emigration rate, and I is the immigration rate. The consumption rates, $Q_j i$, are calculated based on the 'foraging arena' concept (Ahrens et al., 2012), where the biomasses of prey species, $Bi's$, are divided into vulnerable and invulnerable pools, with the vulnerability parameter representing the transfer rate at which prey move from an invulnerable state to a vulnerable state (Equation 9.4). During model fitting, Ecosim iteratively adjusts the vulnerability matrix for each predator-prey interaction to minimize the sum of squared deviations (SS) between predicted and observed biomass and catch data. Consumption is computed using the formula:

$$Q_{ij} = \frac{v_{ij} \cdot a_{ij} \cdot B_i \cdot B_j \cdot T_i \cdot T_j \cdot S_{ij} \cdot \frac{M_{ij}}{D_j}}{v_{ij} + v_{ij} \cdot T_i \cdot M_{ij} + a_{ij} \cdot M_{ij} \cdot B_j \cdot S_j \cdot \frac{T_j}{D_j}} \tag{9.4}$$

where, v_{ij} is the vulnerability of prey i to predator j, a_{ij} is the rate of effective search of i by j, T_i is the relative feeding time of i, T_j is the relative feeding time of j, S_j is the representation of seasonal or long-term forcing effects and D_j is the impact of handling time as the limit of consumption.

9.2.3 Model domain and functional groups

The historical and present-day EwE models were similar in spatial extent (3.05°S to 0.55°N and 31.5° to 34.88°E), covering the area of the entire lake, despite not being spatially resolved. The models were constructed with 23 functional groups organised either in single species or multispecies groups depending on habitat, feeding behaviour, economic importance or availability of data. These included: 15 fish groups, one fish-eating birds group, one reptile group, three invertebrate groups, two primary producers (phytoplankton and macrophytes), and one detritus group (Table 9.1). The species/groups that are important either for commercial purposes or for food were harvested in the model by a specific fishing fleet. The models included four commonly used fishing gears on the lake. i) Gillnets, targeting most species except small fishes such as Silver cyprinid. ii) Longlines, targeting Nile perch and other demersal and benthopelagic species (Table 9.1). iii) Small seines, targeting silver cyprinid, with freshwater shrimp (*Caridina nilotica*) and haplochromines as by-catch. iv) 'Others', an aggregation of gears (for example, beach seines, cast nets, traps) targeting a variety of fish species from shallow inshore regions.

Table 9.1: Functional groups in the EwE models. For the fish groups, information on common and scientific names, occurrence, habitat, and feeding mode is from Froese et al. (2016). Corm. and Biv. stand for Cormorant and Bivalvia, respectively.

ID.	Species/taxa included	Common name	Occurrence	Habitat	Feeding mode
BD	Haliaeetus vocifer, Ceryle rudis, Corm.	Fish-eating birds	Native	Domain	Piscivore
CD	*Crocodylus niloticus*	Crocodiles	Native	Domain	Carnivore
NP	*Lates niloticus*	Nile perch	Introduced	Dermersal	Piscivore
AC	*Clarias gariepinus*	North African catfish	Native	Benthopelagic	Omnivore
SM	*Bagrus docmak*	Semutundu	Native	Benthopelagic	Omnivore
ML	*Protopterus aethiopicus*	Marbled lungfish	Native	Demersal	Molluscivore
SQ	*Synodontis victoriae, S. afrofisheri*	Squeakers	Native	Benthopelagic	Insectivore
SF	*Momyrus kanume, G. longibarbis*	Snout fishes	Native	Demersal	Insectivore
SC	*Schilbe intermedius*	Silver catfish	Native	Pelagic	Piscivore
RB	*Labeobarbus altianalis*	Rippon barbell	Native	Benthopelagic	Omnivore
SB	*Enteromiuss* spp.	Small barbs	Native	Benthopelagic	Omnivore
RO	*Brycinus jacksoni, B. sadleri*	Robbers	Native	Pelagic	Omnivore
NG	*Labeo victorianus*	Ningu	Native	Demersal	Phytoplanktivore
HP	*Haplochromis* spp.	Haplochromines	Native	Demersal/Pelagic	Variable[a]
SD	*Rastrineobola argentea*	Silver cyprinid	Native	Pelagic (schooling)	zooplanktivore
NT	*Oreochromis niloticus*	Nile tilapia	Introduced	Benthopelagic	Omnivore
OT	*O. esculentus* and *O. variabilis*	Other tilapias	Native	Benthopelagic	Herbivore
FS	*Caridina nilotica*	Freshwater shrimp	Native	Benthic	Detritivore
IM	Diptera, Odonata, Ephemeroptera, Biv.	Insects and molluscs		Domain	Detritivore
ZP	Copepoda, Ostracoda, Cladocera, Rotifera	Zooplankton		Pelagic	Phytoplanktivore
PP	Cyanobacteria, diatoms, green algae	Phytoplankton		Pelagic	
MC	Periphyton, epiphyton	Macrophytes		Domain	
DT		Detritus		Benthic	

[a] More than 15 trophic groups (Witte and van Densen, 1995)

9.2.4 Input data and "pedigree"

The initial conditions in the historical model were set to represent the food web dynamics in 1980 when most of the non-native species had become established. Biomass estimates for fish groups, except for the silver cyprinid and Ningu (*Labeo victorianus*), were based on lake-wide bottom trawl surveys (at the model's initialisation year or for the next year) (NaFIRRI unpublished data: Supplementary Figure S1). For the silver cyprinid (a pelagic species) and Ningu (a riverine species), which may not be adequately sampled by the bottom trawls, their initial biomass estimates were obtained from another model (i.e., Atlantis, (Nyamweya et al., 2016b)). Initial biomass for fish-eating birds, reptiles, and lower trophic level (TL) groups, i.e., invertebrates (except freshwater shrimp and zooplankton) and producer groups, were also taken from Atlantis model (Nyamweya et al., 2016b). Biomass estimates for freshwater shrimp (*Caridina nilotica*) and zooplankton were entered as 'best guesses' (based on the most commonly used values in published EwE models) given that assuming EE is more subjective than assuming a certain biomass (Ainsworth and Walters, 2015). Basic parameters, such as P/B and Q/B, were based on empirical relationships (Supplementary Table S1). Diet composition for fish groups (except for haplochromines) was based on information from literature (Corbet, 1961; Ogutu-ohwayo, 1990a; Trewavas, 1983). For the haplochromines, diet composition was based on the most abundant trophic groups before Nile perch establishment, i.e., detritivores, zooplanktivores, phytoplanktivores and insectivores (Witte et al., 2007). Information on catch was derived from (Nyamweya et al., 2016b). The proportion of food that is not assimilated by predators was set at default Ecopath value (i.e., 20%), except for Nile tilapia and other tilapias, and zooplankton, whose values were doubled to account for assimilation deficiencies in plant-dominated diets (Christensen et al., 2008). Other parameters such as E and BA were maintained at default Ecopath values to balance the model (Christensen et al., 2008).

In the present-day model, the initial conditions were set to represent the average conditions for the period 2010-2015. The present-day model was modified from the existing model of (Natugonza et al., 2016), which only considered data for one year (2014). The significant changes to the model of Natugonza et al. (2016) included: separation of catfishes into three groups, i.e., North African catfish, Semutundu, and silver catfish; separation of squeakers and snout fishes (Mormyridae); separation of other tilapias and cyprinids into five groups, i.e., Ningu, Rippon barbell *(Labeobarbus altianalis*), small barbs (*Enteromius* spp.), 'robbers' (*Brycinus* spp.), and 'other tilapias' (see Table 9.1 for example species); merging of three haplochromine groups into one group; merging of the juvenile and adult Nile perch groups into one group. These changes were aimed at ensuring a comparable representation of functional groups and feeding interactions in the two models. Biomass data for Nile perch, silver cyprinid, haplochromines, and freshwater shrimp were based on hydroacoustic surveys (Supplementary Figure S1, LVFO, 2015,1). Biomass data for other fish groups were based on bottom trawl surveys conducted only on the Ugandan side of the lake (Supplementary Figure S1). Data on catches for the leading commercial fisheries (Nile perch, silver cyprinid, Nile tilapia, and haplochromines) were based on catch assessment surveys (LVFO, 2016b), and these were apportioned to different gears based on the data from a frame survey conducted in 2014 (LVFO, 2016c). Because the landings of other groups that constitute less than 5% are often merged and not reported at species/genus level, data simulated by another model (Nyamweya et al., 2016b) were used to represent their catches.

The 'pedigree' routine of EwE (Christensen and Walters, 2004a) was used to assess the uncertainty of data and parameters used in the models. The pedigree routine gives an overall pedigree index, which varies between 0 (low-quality model, arising from parameters that are guestimates) and 1 (high-quality model, arising from an accurate sampling of the modelled system). The pedigree index allows a description of the quality of the model, which can be compared to other models (Morissette, 2007). Also, the pedigree information is used to determine uncertain parameters, which can be modified during the balancing procedure (Christensen and Walters, 2004a). Once the Ecopath data and parameters were entered into the software, the origin and the perceived quality of the data were recorded and assigned to each input a data pedigree value using the values specified in the Ecopath version 6.5 (`www.ecopath.org`). The index values that were assigned to parameters and input data for each functional group are given in supplementary material (Table S2). The model's consistency with the physiological constraints, such as the general decline in biomass and vital rates with increasing TL, was also checked using PREBAL diagnostics (Link, 2010).

9.2.5 Model balancing

Balancing Ecopath models was done by manually adjusting input data to ensure that the models were coherent with basic ecological and thermodynamic rules, i.e., EE's for every group to be less than 1, P/Q in a range of 0.1 to 0.3, respiration to assimilation and production to assimilation ratios less than 1 (Darwall et al., 2010; Heymans et al., 2016). In the historical model, except for haplochromines that had comparatively higher biomass (accounting for >80% of the total demersal fish biomass), most demersal and benthopelagic groups had values of EE>1.0. P/B values for these groups were adjusted upwards until all EEs were less than 1, given that their pedigree values were low. In the present-day model, problematic groups during balancing were haplochromines and freshwater shrimp (due to high predation pressure exerted by Nile perch) and all demersal fish groups (due to low biomass and turnover rates). Given that the diet composition of the main predator for these groups (Nile perch) was based on robust stomach content data (Kishe-machumu et al., 2012b), only P/B for haplochromines and biomass for the freshwater shrimp were increased. For the demersal groups, biomass was also adjusted upwards since pedigree index values were suggestive of high uncertainty in data.

9.2.6 Ecosystem indices

Several indices from Ecopath mass balances in the historical and present-day models were compared to get insight into changes in system maturity, productivity, and stability over time. The indices are based on works of Odum (1969), Ulanowicz and Puccia (1990), Pauly and Christensen (1995), Pauly et al. (1998), and Libralato et al. (2005). (1) Total Primary Production (PP): the summed primary production from all producers. Primary Production/Respiration (PP/R): a measure of system maturity, which is expected to approach one as the system matures. (2) Primary Production/Biomass (PP/B): a measure of system maturity, and decreases as the system matures. (3) Mean trophic level of the catch (TLC): the average TL of model groups, weighted by their catch; this index decreases either with the preferential depletion of higher TL species (Pauly et al., 1998), or addition of low TL species to the catches, i.e., fishing through the food web (Essington et al., 2006). (4) Primary production required (PPR): the PP that is required to sustain the catches; this is calculated from both primary producers and detritus to evaluate the sustainability of fisheries in terms of energy. (5) Mixed trophic impacts (MTI): a measure direct and indirect trophic interactions among functional groups showing the positive or negative impact that a hypothetical increase in the biomass of a functional group would have on another group in the system

9.2.7 Ecosystem dynamics (Ecosim)

The historical EwE model was fitted to both biomass data simulated by Atlantis model (Nyamweya et al., 2016b) and observed landings for the period 1980-2015. The application of complex models, such as Atlantis, to test parameters in simpler models is relatively new, but this has already shown promising results (Sturludottir, 2017; Weijerman et al., 2016). The Atlantis model of Lake Victoria was developed in a rigorous and transparent manner. The temporal trends of simulated biomass and catch of fish species match well with the changes in reported catch per unit effort (CPUE) and landings, respectively. Also, the metrics used in skill assessment (Pearson's correlation, modelling efficiency, and coefficient of variation) suggest that the model performed well against historical observations. The model was retrieved from `https://doi.org/10.6084/m9.figshare.4036077.v1`, but readers are encouraged to see Nyamweya et al. (2016b) for details about set-up, parameterisation, and calibration.

In Ecosim, fishing mortality (F) time-series data, generated from annual landings and Atlantis-simulated biomasses (F = catch/biomass), were used as a driver. Fitting the model to time-series data followed an iterative, stepwise procedure. (i) Time series data in Excel CSV file were read and stored in the EwE database. (ii) The model was projected forward in a null case, using the catches and F from the balanced Ecopath model and default vulnerabilities and BA rates to ensure the model was stable over a long period. (iii) The sensitivity of the sum of squares (SS) to vulnerability parameters was searched using prey-predator pairs. (iv) Vulnerabilities that minimize the SS of differences between model predictions and observations were searched using the 'vulnerability search routine'. (v) BA rates for the introduced fish groups and silver cyprinid (whose fisheries expanded by more than 200-fold during the initial ten years of the historical simulation period) were iteratively adjusted, searching for vulnerabilities again until the SS were lowest. (vi) The diet matrix was adjusted manually to fine-tune trends, and to ensure that the predicted biomass and catch for each functional group matched (as much as possible) the reference data. The fitted model can be found at `https://doi.org/10.6084/m9.figshare.7306820.v6`.

9.2.8 Skill assessment

Skill assessment was conducted to measure how well the predicted biomass and catch fit to the Atlantis-simulated biomasses and observed fish landings, respectively. Olsen et al. (2016) proposed several metrics that can be used to evaluate model skill. In this study, three skill assessment metrics, which demonstrate in different ways how the model fits to reference data, were used: modelling efficiency (MEF, Equation 9.5), reliability index (RI, Equation 9.6), and Pearson correlation (r, Equation 9.7).

$$MEF = \frac{\sum_{i=1}^{n}(O_i - \bar{O})^2 - \sum_{i=1}^{n}(P_i - O_i)^2}{\sum_{i=1}^{n}(O_i - \bar{O})^2} \tag{9.5}$$

$$RI = \exp \sqrt{\frac{1}{n}\sum_{i=1}^{n}(log\frac{O_i}{P_i})^2} \tag{9.6}$$

$$r = \frac{\sum_{i=1}^{n}(O_i - \bar{O})(P_i - \bar{P})}{\sqrt{\sum_{i=1}^{n}(O_i - \bar{O})^2 - \sum_{i=1}^{n}(P_i - \bar{P})^2}} \tag{9.7}$$

where, O_i and P_i are the i^{th} of n observations and predictions, respectively, and the $\bar{O}$ and $\bar{P}$ are the corresponding averages. MEF measures how well the model fits the data compared to the average; values close to 1 suggests a perfect fit, 0 means that the model is no better than using the average of the data points, while negative values suggest that the model is worse than simply using the average of the data in terms of providing direct biomass estimates. However, a negative MEF may be due to predictions and reference data differing in magnitude, despite the simulations following the same trend as data. Therefore, a model with negative MEF may still be useful if the correlation is positive (i.e., the model has the same trend as the data). RI measures how far, on average, the predictions and the observations are from each other. RI closer to 1 corresponds to perfect fit, while values far away from 1 suggest poor fits: a value of 1.2, for instance, would that the model simulates the reference values with a 20% difference in magnitude. The correlation ranges between -1 and 1. Values close or equal to 1 represent a perfectly positive, linear association; 0 represent no linear association and; -1 represents is a perfect negative, linear association. Generally, the closer r is to 1, the better the model. However, correlation ought to be cautiously interpreted because it can be one even if the model is far from the observations, i.e., when the predictions differ from the observations by a constant factor.

In addition to skill assessment, model validity was also tested by comparing the simulated diet composition and ecosystem metrics (such as TL of catch, total system biomass, and landings) with those estimated directly from recent data.

9.2.9 Model comparison

Two model types were compared: the historical model end-state (A) and the present-day model representing average conditions for the period 2010-2015 (B). First, simulated biomasses, diet composition, TL of catch, and total catches of model A were compared with those of model B to ensure the models were comparable, and that any of the differences in their projections were attributable to model calibration. Correlation of diet matrices was used to compare diet compositions in model A (Supplementary Table S3) and model B (Supplementary Table S4). Second, forward simulations were performed using models A and B under different assumptions of vulnerability and BA. In model A, projections were run using fitted vulnerabilities (A1) and default vulnerabilities (A2). In model B, projections were run using default Ecopath BA rates (B1) and empirically-derived BA rates (B2). BA rates in model B2 were derived as $(B_{2015} - B_{2010})/n$, where B_{2010} and B_{2015} are biomass estimates in 2010 and 2015, respectively; and n is the number of years covered by the present-day model. Biomass estimates for Nile perch, silver cyprinid and haplochromines were based on hydro-acoustic surveys (LVFO, 2015,1). For the rest of the fish groups, biomass estimates were derived from another model (Nyamweya et al., 2016b). In both B1 and B2, vulnerabilities were maintained at default values. In all simulations (i.e., involving models A1, A2, B1, B2), all other parameters in Ecosim (for example, feeding time adjustment rate, predator effect on feeding time, switching power) were maintained at their default values.

Each model was projected forward for 20 years, starting from 2015 (the baseline), under five different fishing scenarios. The scenarios focused on functional groups with the highest ecological and economic importance in the system, i.e., Nile perch (high TL piscivore; high commercial value) and haplochromines (mid-TL forage fish). The scenarios included: reducing Nile perch fishing mortality F by 60% from the baseline level ($NP : 0.4F$); increasing Nile perch F by 60% from the baseline level ($NP : 1.6F$); reducing F for haplochromines to zero ($HP : 0.0F$); increasing F for haplochromines by 200% ($HP : 3.0F$); maintaining F for all functional groups at the baseline level (status quo, SQ). In each run, F values were held constant at either the prescribed (scenario) test values or the Ecopath base values. For model A, F rates were held constant at the 2015 level (i.e., the last year of the historical simulation), while in model B, Ecopath base F values were used as the baseline.

The impact of each fishing pressure scenario on species biomass was assessed by calculating the percentage change in biomass for each scenario relative to the baseline (Equation 9.8).

$$100 \cdot (\frac{B_{end}}{B_{start}} - 1) \tag{9.8}$$

where B_start and B_end are biomasses at the beginning and end of the simulation, respectively. All outcomes of fishing scenarios were compared at the end of 20 years; a percentage change of zero indicated no change in biomass relative to baseline. Interpretation of results followed that models gave consistent qualitative results if the direction of change in predicted biomass was the same (either increase or decrease relative to baseline values), while consistent quantitative results were to be indicated by predictions with similar direction and magnitude.

9.3 Results

9.3.1 The historical model

The initial conditions of the Ecopath model were balanced with key parameters shown in Table 9.2. The underlying mass balance assumptions and thermodynamic rules were checked using key indices (EE, P/Q, PP/R, respiration/assimilation (R/A)), which ranged within values described in literature (Heymans et al., 2016). PREBAL diagnostics (Link, 2010) also showed declining biomass and vital rates through higher TL, with few exceptions (e.g., Ningu, Robbers, Nile tilapia, and other tilapias) that had low biomass relative to the TL. Fish-eating birds also had exceptionally high Q/B value considering the trophic position of the group. The overall Ecopath pedigree index was 0.53.

Table 9.2: Input parameters and some key outputs for the historical model. For each functional group are inputs: biomass (B; t/km^2), production/biomass ratio (P/B; y^{-1}), consumption/biomass ratio (Q/B; y^{-1}), annual landings (Y; t/km^2); outputs: trophic level (TL), ecotrophic efficiency (EE; values in parentheses are entered to estimate BA at the start of model run), production/consumption (P/Q), fishing exploitation rate (E). BA$_{start}$ and BA$_{end}$ represent biomass accumulation (t/km^2/y) at the start (1980) and end (2015) of the historical simulation, respectively, estimated by Ecopath.

Group name	TL	B	P/B	Q/B	Y	EE	P/Q	F/Z	BA$_{start}$	BA$_{end}$
Fish-eating birds	3.63	0.0077	0.3	100.3		0.0	0.003			0.0005
Crocodiles	4.09	0.046	0.3	4.0		0.0	0.075			0.0027
Nile perch	3.44	1.997	1.70	6.34	0.0645	(0.98)	0.268	0.01	3.44	0.238
North African catfish	3.37	0.188	0.65	3.56	0.0892	0.97	0.182	0.72		-0.003
Semutundu	3.37	0.785	0.55	4.20	0.24	0.926	0.130	0.55		-0.019
Marbled lungfish	3.06	0.37	0.44	3.95	0.118	0.894	0.111	0.72		-0.01
Squeakers	3.26	0.527	0.40	3.80	0.0697	0.751	0.106	0.32		-0.012
Snout fishes	3.13	0.089	0.4	3.66	0.009	0.860	0.109	0.25		-0.002
Silver catfish	3.35	0.478	0.39	3.66	0.0975	0.853	0.108	0.51		-0.012
Rippon barbell	2.99	0.533	0.39	3.87	0.0133	0.756	0.10	0.06		-0.014
Small barbs	3.05	0.0925	2.49	12.85		0.804	0.193			-0.00002
Robbers	3.13	0.0026	0.45	3.47	0.0003	0.874	0.132		0.28	0.00002
Ningu	2.0	2.087	0.37	3.66	0.24	0.539	0.102	0.30		-0.051
Haplochromines	2.48	25.0	1.5	14.29	0.0542	0.331	0.105	0.001		-0.474
Silver cyprinid	3.05	5.243	2.51	17.27	0.179	(0.96)	0.145	0.01	8.46	0.418
Nile tilapia	2.44	0.367	1.5	6.81	0.0516	(0.99)	0.220	0.09	0.46	0.041
Other tilapias	2.0	1.824	0.66	6.16	0.887	0.862	0.108	0.72		-0.047
Shrimp	2.21	19.0	5.47	34.0		0.396	0.161			0.123
Insects and molluscs	2.31	36.0	4.32	30.0		0.268	0.144			0.167
Zooplankton	2.05	45.0	35.22	120.0		0.559	0.293			-0.07
Phytoplankton	1.0	80.0	120.0			0.565				0.08
Macrophytes	1.0	55.0	15.0			0.134				-0.05
Detritus	1.0	267.5				0.130				0.03

The system was phytoplanktivore-dominated, with biomass flow from detritus five times lower than the flow from primary producers. Total system production (TSP) was 12,328 t/km^2/year. PP was 10,425 t/km^2/year and R was 3113 t/km^2/year, resulting in PP to R ratio of 3.3, which is consistent with maturing systems (Odum, 1969). The PP to biomass ratio was 37.9, while PPR was 7% of the total PP. MTI showed that introduced Nile perch and haplochromines had the greatest negative impact on other species, the former directly impacting other groups through predation and the latter through competition with mid-TL groups for the same prey.

The TL$_C$ at initial conditions was 2.56. Exploitation rates (F/Z) were relatively higher (i.e., above 0.5) for the native fisheries (North African catfish, semutundu, marbled lungfish, silver catfish, and other tilapias), and fishing accounted for most of the production for these groups (Table 9.2). The silver cyprinid and haplochromines were an exception with substantially low exploitation rate relative to production (i.e., F/Z less than 1%) as these were less targeted by fisheries in the 1980s. The introduced groups (Nile perch and Nile tilapia) also had low exploitation rates (i.e., 1% and 9% for Nile perch and Nile tilapia, respectively) as they had not yet become established.

Dynamic simulations in Ecosim showed a massive change in fish composition, but the total fish biomass at the beginning and end of simulation was relatively the same. The total fish biomass was about 2.77 million tonnes at the start of the model run (with haplochromines accounting for more than 65% of the fish biomass) and 2.86 million tonnes at the end of the simulation (with the silver cyprinid and the introduced Nile perch accounting for 75% of the fish biomass). However, the landings increased substantially, i.e., from about 170,000 tonnes at the start of the model run (with landings dominated by native tilapias, Ningu, and catfishes) to nearly one million tonnes at the end of the simulation (with landings dominated by introduced Nile perch and the native silver cyprinid). TL$_C$ also increased from 2.56 at the start of the model run to 3.2 in the late 1980s and 1990s, following a shift in fisheries to high TL species (dominated by the introduced Nile perch), but started declining after 2003 and was 3.0 by 2015. The decline in TL_C may be attributed to the sequential addition of low TL catches (especially silver cyprinid) as opposed to the preferential depletion of high TL species hypothesized in Pauly et al. (1998), given that the overall landings of Nile perch (high TL species) have remained stable since the 1990s (Kolding et al., 2014; Taabu-Munyaho et al., 2016).

Generally, most of the groups had their biomass decrease substantially either immediately at the start of the simulation (for example, all native fisheries, except silver cyprinid) or towards the end of the model run (for the case of introduced species) (Figure 9.2). The groups whose biomass declined at the start of the model run were also close to extinction, except for the haplochromines, and had negative BA values at the end of the simulation (Table 9.2). For haplochromines, the biomass decreased by more than 60% during the first five years of the simulation, due to the increased predation pressure exerted by the introduced Nile perch, but the group later stabilised as Nile perch switched to the more abundant prey (the freshwater shrimp). The biomass of introduced species increased at the start of the model run, but it declined during the 1990s and stabilised at low numbers when fishing intensified (Figure 9.2). However, the BA rate for these groups was positive at the end of the simulation (Table 9.3).

The simulated biomass trajectories of 14 functional groups were compared with reference data, and results showed reasonable agreements for most groups (Figure 9.2). Table 9.3 shows the results of skill assessment using three metrics: MEF, RI, and r. These metrics were positive and close to 1 for most of the groups, suggesting good fit to the reference data. Exceptions were for the ‘robbers’, haplochromines and other tilapias where values of MEF were negative. Nonetheless, r values for haplochromines and other tilapias were positive, suggesting that the simulated biomass trajectories had the same trend as reference data despite the differences in magnitude. Also, whereas the model showed poor fit to reference data for the ’robbers’, with both MEF and r being negative

Table 9.3: Skill assessment for predicted and observed biomass and landings. The metrics used are modelling efficiency (MEF), reliability index (RI), and Pearson correlation (r) (see equations 9.5-9.7).

	Biomass			Landings		
Group	MEF	RI	r	MEF	RI	r
Nile perch	0.71	1.14	0.90	0.44	1.15	0.85
North African catfish	0.79	1.15	0.89	0.75	1.17	0.86
Semutundu	0.53	7.77	0.83	0.44	1.71	0.77
Marbled lungfish	0.81	1.78	0.98	0.93	1.13	0.96
Squeakers	0.74	1.26	0.92	0.60	1.87	0.88
Snout fishes	0.97	2.35	0.98	0.66	1.87	0.88
Silver catfish	0.93	1.29	0.98	0.89	1.26	0.97
Rippon barbell	0.9	1.84	0.98	0.30	1.78	0.61
Robbers	-18.3	1.42	-0.44	0.16	2.88	0.18
Ningu	0.65	1.90	0.87	0.58	3.49	0.86
Haplochromines	-0.07	1.29	0.74	0.74	1.32	0.95
Silver cyprinid	0.35	1.18	0.64	-0.07	1.19	0.95
Nile tilapia	0.41	1.17	0.70	0.47	1.20	0.81
Other tilapias	-13.02	1.61	0.47	-3.21	2.28	0.31

and far from 1 for the simulated biomass and landings, respectively, RI suggests that the model simulated reference biomass data with a 42% difference in magnitude. This index was better than that of several groups with positive values of MEF and r (for example, semutundu, marbled lungfish, Ripon barbel, and Ningu) (Table 9.3). Note that RI is sensitive if there are few years where the magnitude is incorrect, as seen in the case of some native groups, for example, semutundu, marbled lungfish, and Ripon barbel, where the biomass and landings were very low. Here, the total difference in tons was not high (Figure 9.2), but because of the small numbers, the difference in magnitude could be substantial. This observation underscores the importance of using multiple metrics when evaluating model skill (Olsen et al., 2016).

The model was also compared with time series landings data for the 14 harvested groups (Figure 9.3), and its predictive skill is also shown

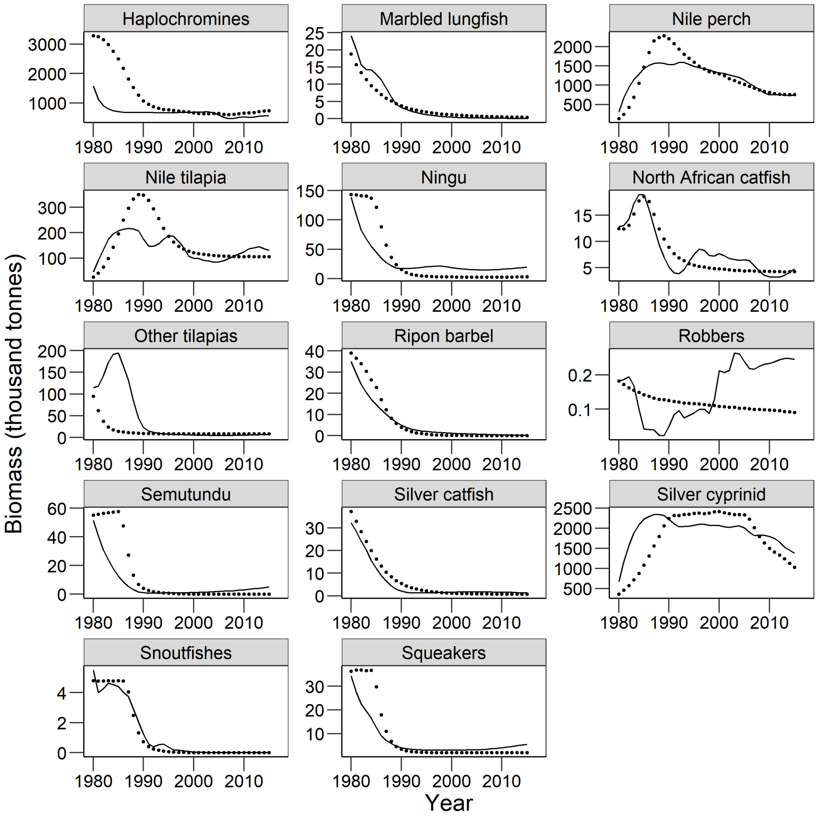

Figure 9.2: Simulated biomass from the historical EwE model (lines) compared to reference biomass estimates from the Atlantis model of Lake Victoria (dots) for 14 fish groups.

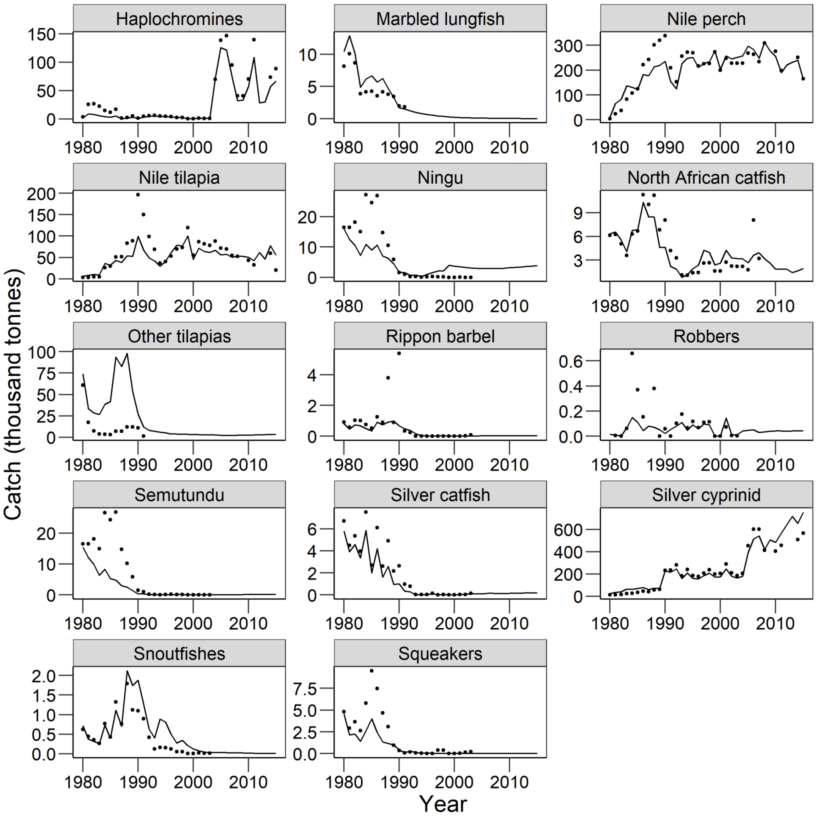

Figure 9.3: Simulated landings from the historical EwE model (lines) compared to landings data (dots) for 14 fish groups.

in Table 9.3. All groups had positive MEF, except silver cyprinid and other tilapias. RI values showed that eight of the groups, including the dominant commercial fisheries (Nile perch, silver cyprinid, Nile tilapia, and haplochromines) were within 30% difference in magnitude from their observed values Table 9.3. The correlation coefficient was also positive for all groups, despite being very low for ‘robbers’ and other tilapias. Generally, the model overestimated landings for other tilapias and underestimated landings for Ningu, semutundu, and squeakers at the start of the model run.

9.3.2 The present-day model

The parameters and selected outputs of the balanced Ecopath model are shown in Table 9.4. Ecopath PREBAL diagnostics showed that Nile perch (high TL group) and haplochromines and silver cyprinid (mid-TL groups) had exceptionally higher biomass than low TL counterparts. The three groups constitute more than 90% of the total fish biomass LVFO (2015); and, therefore, the biomass estimates for the other fish groups were not changed because of the low abundance reflected in surveys. The vital rates were fairly consistent with the PREBAL rules, generally increasing with decreasing TL. The overall Ecopath model pedigree index was 0.39.

The system was still phytoplanktivore-dominated, with biomass 'flow' from detritus lower than the 'flows' from primary producers; TSP and PP were comparable to the historical Ecopath model. The PP/R ratio was 2.5, which was about 24% lower than the value in the historical Ecopath model, and hence consistent with maturing systems. PP/B ratio (41.5), on the other hand, was slightly higher compared to the historical model. The PPR to sustain the catch was 21% of the total PP, representing a three-fold increase from the historical model. The MTI showed that the introduced Nile perch negatively impacted most fish groups except silver cyprinid, possibly due to competition release from haplochromines.

Fisheries were dominated by the two introduced species (Nile perch and Nile tilapia) and two native groups (haplochromines and silver cyprinid), corresponding to the end-state of the historical model (Supplementary Table S5). Other native fisheries constituted less than 5% of the landings; however, the exploitation rate (F/Z) for these groups, except semutundu and snout fishes, was substantially high (i.e., above 0.5). The BA for most native groups was also negative, except for the squeakers, Ningu, and other tilapias (Table 9.4).

Table 9.4: Ecopath parameters and main outputs for the present-day model. Abbreviations denote: trophic level (TL), biomass (B; t/km^2), production/biomass ratio (P/B; yr^{-1}), consumption/biomass ratio (Q/B; yr^{-1}), landings (Y; t/km^2), biomass accumulation (BA, t/km^2/yr), ecotrophic efficiency (EE$_{BA}$, where the model uses empirically-derived BA, and EE$_{BA=0}$, where Ecopath default value of BA is used), production/consumption (P/Q), and exploitation rate (F/Z).

Group name	TL	B	P/B	Q/B	Y	BA	EE$_{BA}$	EE$_{BA=0}$	P/Q	F/Z
Fish eating birds	3.98	0.0001	0.3	100.25			0.0	0.0	0.003	
Crocodiles	3.99	0.001	0.3	2.0			0.0	0.0	0.15	
Nile perch	3.59	9.36	0.92	3.90	3.238	0.24	0.40	0.37	0.23	0.37
North African catfish	3.13	0.008	0.71	3.66	0.0375	-0.000165	0.93	0.93	0.19	0.85
Semutundu	3.31	0.0012	0.43	4.26	0.000008	-0.0000026	0.66	0.67	0.10	0.01
Marbled lungfish	3.11	0.036	0.71	3.55	0.00449	-0.00033	0.91	0.98	0.20	0.98
Squeakers	3.17	0.0083	0.43	4.20	0.017	0.0000064	0.97	0.97	0.10	0.86
Snoutfishes	3.09	0.0006	0.65	4.73	0.000001	-0.0000005	0.79	0.88	0.14	0.22
Silver catfish	3.55	0.00052	0.45	4.47	0.00703	-0.00014	0.98	0.99	0.14	0.97
Rippon barbell	2.86	0.0012	0.34	3.37	0.00017	-0.000045	0.86	0.96	0.16	0.38
Small barbs	2.71	0.00002	1.66	14.85			0.80	0.80	0.11	
Robbers	3.07	0.00009	1.35	8.96	0.00093	-0.000017	0.49	0.50	0.15	0.50
Ningu	2.10	0.00127	0.55	5.46	0.0198	0.00053	0.92	0.90	0.10	0.89
Haplochromines	2.82	8.61	2.73	17.14	1.354	0.12	0.92	0.92	0.16	0.05
Silver cyprinid	3.02	17.0	3.93	26.21	7.038	1.41	0.35	0.33	0.15	0.10
Nile tilapia	2.53	1.2	0.78	6.81	0.568	-0.00023	0.96	0.96	0.11	0.96
Other tilapias	2.0	0.0054	0.84	5.63	0.076	0.00013	0.77	0.77	0.15	0.74
Lake prawn	2.20	12.39	11.47	35.0			0.21	0.22	0.32	
Other macroinvertebrates	2.05	35.0	4.5	30.0			0.16	0.16	0.15	
Zooplankton	2.02	45.0	28.0	120.0			0.59	0.59	0.23	
Phytoplankton	1.0	85.0	120.0				0.55	0.55		
Macrophytes	1.0	50.0	15.0				0.25	0.25		
Detritus	1.0	250.0					0.10	0.11		

9.3.3 Model comparison

Comparison of the historical model end-state (model A, Supplementary Table S5) with the present-day model (Model B, Table 9.4) showed minimal variation (i.e., in the order of 1-17%) in key indices such as TL_C, biomass, and catch. Generally, biomass and landings were slightly higher in model A than in model B, while TLC was comparable across models (i.e., 3.05 and 3.1 in A and B, respectively). Exploitation rates (F/Z) were also higher in model A compared to model B, especially for the major fisheries, i.e., Nile perch and silver cyprinid, which account for more than 75% of the total landings. Correlation of diet matrices (Supplementary Table S6) showed the simulated diet composition for the predators in model A to be consistent with the diet composition from stomach content analyses in model B, especially for the most ecologically important and well-studied groups, i.e., Nile perch, silver cyprinid and Nile tilapia. With regards to BA, however, there were substantial differences between the two models, except for the Nile perch (see 'Table 9.2 versus Table 9.4'). Although the BA rates for most native groups were negative in both models, these values were lower by more than two orders magnitude for most groups in model A compared to model B. For the 'robbers' and Nile tilapia, BA was positive in the model A and negative in model B. For squeakers, Ningu, haplochromines, and other tilapia, the BA was negative in model A and positive in model B.

Figure 9.4 shows the relative change in biomass over a 20-year projection using the historical and present-day model. Generally, biomass projections were consistent across models (in terms of the direction of change) for the direct fishing-induced effects on target species. However, the consequent impact of changes in target groups on their respective prey/predators groups ("indirect trophic effects") were variable, depending on the strength of diet interactions and assumption regarding BA parameter. For example, under the two haplochromine fishing scenarios, $HP : 0.0F$ and $HP : 3.0F$, a steady increase and decrease in haplochromine biomass, respectively, accompanied by the rise and decline in the biomass of its primary predator (Nile perch), were observed.

Similar changes were found in the biomass of haplochromines when Nile perch baseline fishing mortality was changed (i.e., under $NP : 0.4F$ and $NP : 1.6F$ scenarios). The indirect trophic effects were mostly different, primarily when the steady-state assumption (BA = 0, B1) was used. However, when short-term empirically-derived BA rates were applied to the present-day model (B2), the direction of change was consistent across the two models (A1 and B2) for most groups, for example, marbled lungfish, Ningu, Ripon barbel, silver catfish, and snout fishes (Figure 9.4).

Despite the qualitative similarities between models, especially for the direct fishing-induced effects, the magnitude of change in predicted fish biomass was different between the models (Figure 9.4), mainly emanating from the differences in BA rates and vulnerabilities. The BA rates were much lower in model A1 than models B1 and B2, which may account for the higher sensitivity of model A1 to fishing compared to models B1 and B2. Exceptions were Nile perch (where BA was the same in A1 and B2), silver cyprinid (where BA was 3-times higher in B2 than A1), and haplochromines (where BA was negative in A1 and positive in B21). For haplochromines, the higher response (relative change in biomass) in model A1 than models B1 and B2 is expected as both fishing (scenarios $HP : 0.0F$ and $HP : 3.0F$) and predation by Nile perch (scenarios $NP : 0.4F$ and $NP : 0.4F$) affected a group whose biomass was already in decline. On the other hand, the higher response for Nile perch and silver cyprinid in model A1 compared to other models (B1 and B2) is linked to the differences in the vulnerability matrix (see Supplementary Table S7 for the fitted vulnerability matrix of model A1). In model A1, the vulnerability of haplochromines to Nile perch was 3.67 compared to the default value of 2 in models B1 and B2. Similarly, the vulnerability of silver cyprinid to haplochromines in model A1 was higher (54.3) compared to the default value of 2 in B1 and B2.

Generally, the vulnerability parameter was observed to exert a strong influence, especially for the groups with strong diet interactions (for example, Nile perch and haplochromines) at high fishing pressure (Figure 9.5). At low fishing pressure (for example, in the $NP : 0.4F$ and $HP :$

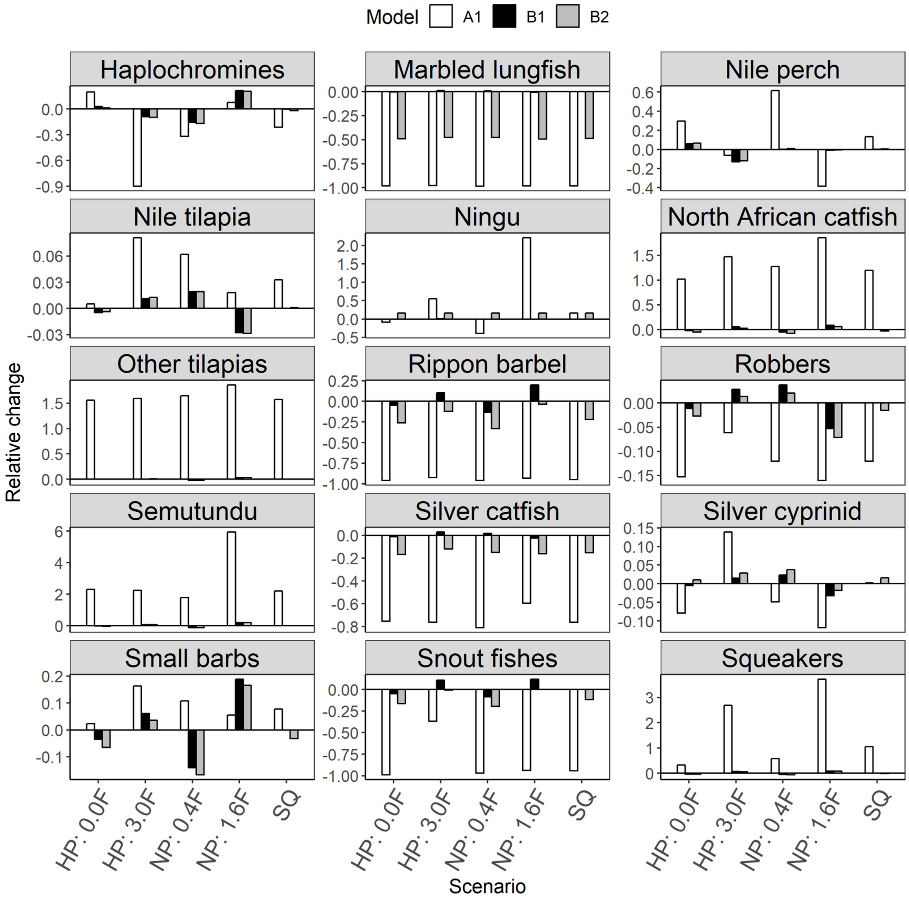

Figure 9.4: Percentage change (2035 relative to 2015) in biomass of functional groups as predicted by the historical model end-state (A1) and present-day models: B1 (using default biomass acummulation) and B2 (using empirically-derived BA biomass accumulation rates). Bars on the same side of zero line (either positive or negative) indicate qualitative agreements between models.

$0.0F$ scenarios), the response of both Nile perch and haplochromines in models A1 and A2 was mostly the same, except that haplochromines responded in a different direction when fishing was halted ($HP : 0.0F$ scenario). At high fishing pressure (for example, in the $NP : 1.6F$ scenario), biomass change for Nile perch and its primary prey (haplochromines) was about three times higher in A2 compared to A1. However, under the $HP : 3.0F$ scenario, the relative changes in the biomass of haplochromines and Nile perch were three times higher under fitted vulnerabilities than default vulnerabilities. The indirect trophic effects in the system were variable, but predictions were consistent for marbled lungfish, Ningu, Ripon barbel, and semutundu.

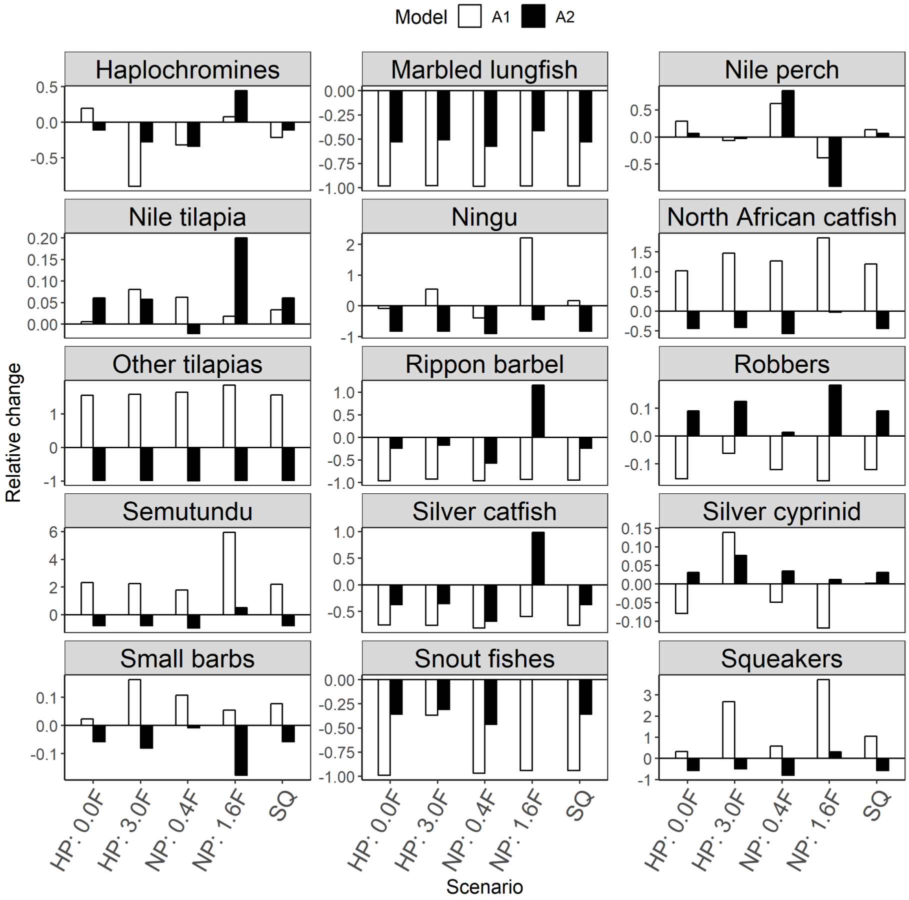

Figure 9.5: Percentage change (2035 relative to 2015) in biomass of functional groups as predicted under default (A1) and fitted vulnerabilities (A2). Qualitative similarities between models are indicated by bars on the same side of zero line.

9.4 Discussion

This study aimed to test ecosystem model skill and the influence of parameter uncertainty on model projections in data-poor situations. A present-day model was compared with the comparable 2015 end-state of the historical model, testing if incorporating information on short-term biomass trends by adjusting BA parameters in the present-day model increases its reliability. Results showed some major differences in model predictions, but those differences were lower when BA terms in the present-day model were adjusted to reflect biomass trends from short-term empirical data. The models were also compared with and without fitted vulnerability parameters. Results showed vulnerability to exert a stronger influence on model predictions at high fishing pressure than at low fishing pressure, especially for groups with strong diet interactions. Results also showed low vulnerabilities to be associated with low model responsiveness, especially for the key prey groups. These findings are generally consistent with those reported in literature (Ainsworth and Walters, 2015; Heymans et al., 2016,1; Mackinson et al., 2003) and have an important implication for ecosystem modelling in data-limited situations.

9.4.1 Data pedigree

The pedigree criterion was used to assess the uncertainty of parameters and data used in the models. Ecopath models with pedigree index values close to one are perceived to be of high quality, while those of low quality have index values close to zero (Christensen and Walters, 2004a). High quality means the model is constructed using precise estimates based on field data obtained from the system represented by the model, while poor quality means the model is not rooted in precise data. Morissette (2007) analysed existing EwE models in EcoBase and found pedigree index values ranging between 0.16 and 0.67, although higher values of up to 0.74 have been reported in most recent studies with improved data collection (Agnetta et al., 2019). The values obtained both for the historical and present-day models in the present study, therefore, place the data quality in the intermediate range.

The overall model pedigree index was expected to be higher in the present-day model, with more recent data collection efforts, compared to the historical model. On the contrary, the pedigree index was higher in the historical model than the present-day model. The low pedigree index in the present-day model can be attributed to the lopsided research in recent years, mainly focusing on commercially important species, for example, Nile perch, Nile tilapia and silver cyprinid. For instance, the diet composition for all the native (except haplochromines) and introduced fisheries in the historical model were based on detailed (lake-wide) quantitative stomach content analyses (Corbet, 1961; Ogutu-ohwayo, 1990a; Trewavas, 1983). No studies of comparable magnitude have been conducted recently. Yet the diet is one of the major components in food web models, and it has been observed to change over the years (Kishe-Machumu et al., 2017; Kishe-machumu et al., 2012b; Njiru et al., 2010). Even where some data on the diet of fish is available, it is opportunistically collected based on the frequency of occurrence, which expresses diet composition based on dominant prey items and hence not directly used in EwE. The groups that are considered to be of less commercial value are part of the ecosystem, forming a vital nearshore subsistence fishery (Njiru et al., 2018), and need to be considered when bridging the data gaps.

In the historical model, the biomass estimates are based on bottom trawl surveys. Although bottom trawling could have been efficient for the demersal and benthopelagic groups, which were the dominant fisheries, the method likely underestimates fish biomass in the nontrawlable inshore areas, which are inhabited by a majority of these groups (Kolding et al., 2014). During the Ecopath model balancing, biomass estimates for these (demersal/benthopelagic) groups were adjusted upwards, which affected the overall pedigree index even when the data were based on local sampling. The same applies to the present-day model, where, even when the biomass inputs for well-studied groups (for example, silver cyprinid and haplochromines) were based on sound survey data, there are still gaps associated with separating species as well as under-representation of inshore areas during hydro-acoustic surveys. With regards to harvests, recent data on annual landings are only disaggregated to species/genus level for the commercial species/groups: Nile perch, Nile tilapia, silver cyprinid, and haplochromines (LVFO, 2016b). The rest of the fish groups are reported as “others” (LVFO, 2016b); as a result, landings simulated by another model (Atlantis Nyamweya et al., 2016b) were used, which could have also contributed to the low pedigree index for the present-day model.

Significant gaps in data still exist, and these gaps need to be filled to promote ecosystem modelling on Lake Victoria. The historical model presented here represents the first attempt to fit the EwE model for Lake Victoria to time-series data, depicting the historical changes in fisheries. Due to the lack of consistent time series biomass data from surveys, we have employed a different calibration approach, where the EwE model was fitted to data simulated by the Atlantis modelling framework. This approach is relatively new, but it is equally robust, given that the real ecosystem is never really known, but only the data from those systems. Some studies have shown that complex end-to-end models such as Atlantis can be used to test parameters in simple ecosystem models (Sturludottir, 2017; Weijerman et al., 2016), and this study is one example of such applications. Nonetheless, actual data are needed to refine and expand this model to better depict real ecosystems and their physical, biotic and human interactions.

9.4.2 Model validation

Fitting ecosystem models to time series data is a critical step in the development of credible models for policy analysis as it shows how best the model can reproduce observed historical responses to disturbances such as fishing (Grüss et al., 2017; Heymans et al., 2016; Rose et al., 2015). Skill assessment using multiple metrics has been recommended to be incorporated in every ecosystem model intended for such purpose (Olsen et al., 2016). Consequently, skill assessment has now been conducted for most recent ecosystem models, especially Atlantis (Nyamweya et al., 2016b; Olsen et al., 2016; Ortega-Cisneros et al., 2017; Sturludottir et al., 2018). These authors have reported correlation higher than 0.5, as well as positive MEF, using either biomasses or landings or both, for most groups, which are comparable to values reported in the present model (Table 8.3). While this study included metrics that measure scale mismatch (ME and RI), more emphasis was on emulating trends rather than the absolute values in reference time series. The values of correlation obtained in this study suggest that the model performed well in emulating historical trends in fisheries. Nevertheless, ecosystem models need constant improvement as new data become available, which is the case with the current model. The skill assessment conducted in this study will allow the model to be judged for its reliability in assessments and projections, and in identifying areas that need further improvement.

The historical model starts in 1980, allowing visualisation of impacts of multiple stressors on the ecosystem. The model can reproduce major past events documented in the literature (Marshall, 2018; Taabu-Munyaho et al., 2016)(Supplementary Figure S1), which include the following. (i) The establishment of introduced species in the 1980s. (ii) The decline/collapse of most native species/groups during the 1980s. (iii) The decline of haplochromines following the establishment of Nile perch. (iv) The decline of introduced species during the 1990s due to intensive fishing, and stability at low numbers starting from 2000. (vi) The resurgence of haplochromines beginning from late 1990s through 2000s, following the decline in Nile perch .

Several studies have attributed the decline/collapse of most native fishes to intensive fishing and predation from the introduced Nile perch (Ogutu-ohwayo, 1990b). For the native tilapias (referred to as “other tilapias" in our models), studies also suggest that competition from the introduced Nile tilapia further suppressed the intensively fished native stocks (Njiru et al., 2010). The outputs of the developed historical model are consistent with these hypotheses. All the native fisheries, except silver cyprinid, started declining at the beginning of the simulation because their exploitation rates were already too high to be sustainable (i.e., F/Z >0.5; Table 8.2). The decline of haplochromines due to Nile perch predation could also have narrowed their prey base and further suppressed the stocks (Goudswaard and Hecky, 1997).

However, the rate of decline of haplochromines in the historical model is not as prominent as the reference time series data, despite the 60% decline within the first five years of the historical simulation. Whereas haplochromines constituted more than 80% of the demersal fish biomass in the 1970s (Kudhongania and Cordone, 1974), the total fish biomass may not have exceeded 1.5 million tonnes (Taabu-Munyaho et al., 2016). Therefore, the model was initialised using the upper limit of the biomass estimates from the trawl surveys conducted at the beginning of the 1980s (Supplementary Figure S1) and not the reference data from Atlantis. The trend for haplochromines observed in Figure 8.2 may, therefore, be regarded as a compromise between 'pretty fit' and credible model behaviour (Heymans et al., 2016), considering that model fits the reference data at the end of the simulation and that the overall trends are comparable. Also, the model fails to emulate the pattern of 'robbers' and overestimates the group's biomass at the end of the simulation. 'Robbers' are less abundant and do not exert substantial predation mortality on any of the forage fishes (especially haplochromines). Therefore, the overestimated biomass is not likely to destabilise the system or affect the behaviour of the model during projections.

9.4.3 Model comparison

Multi-species ecosystem models are designed to support EBFM by aiding evaluation of fisheries scenarios concerning the most important commercial or ecological species/groups (Grüss et al., 2017). Different models may not produce exactly similar quantitative results because of variation in parameters and baseline conditions; this study relates to whether the differences due to calibration are substantial to cause conflicting advice for management, i.e., the models predicting biomass changes in the opposite direction. Multispecies models are strategic decision support tools. Therefore, qualitative results, showing the direction of change in target and non-target species, are also important in the management context (Fulton et al., 2011a). Our results show some qualitative differences, especially for the indirect trophic effects, suggesting that calibration by fitting the model to time series data may have a major impact on policy simulations and present-day models should be used with caution.

However, some lessons can be learned from this study, which may improve predictions from present-day models when time-series data are entirely lacking to fit the model parameters. This study shows that the significant differences in model outputs emanate from the parameterization of BA and that some of those differences can be lessened by incorporating BA rates derived from short-term empirical data in present-day models. The BA values are the residuals of the mass-balance equation (i.e., the difference between production and mortality; Equation (1)) and are among the most influential parameters in the model (Ainsworth and Walters, 2015). In this study, the historical model shows that BA rates for most species are negative at the end of the historical simulation, which explains the decline in biomass in every fishing scenario during projections. It is, therefore, not surprising to see two models give opposite results for most of the groups under the steady-state assumption (BA = 0), but give consistent qualitative results after using short-term BA rates (also depicting a decline). Nonetheless, considerable quantitative differences still exist in the latter case because of the differences in the magnitude of BA values derived from long-term trends (historical model: Table 9.2) and short-trends (present-day model: Table 9.4), which explains the higher responsiveness of the historical model compared to the present-day model.

Negative BA rate generally indicates that depletion of the groups is in progress, and is characteristic of groups heavily exploited or predated upon (Ainsworth and Walters, 2015). The steady-state assumption, which is common in most Ecopath models, may not be appropriate in this situation. This study suggests that if a group is less productive, and is heavily fished or predated upon, assuming negative BA as a first draft assumption may be safer than assuming equilibrium conditions. For the high productivity groups or groups that are not heavily predated upon, negative BA is unlikely; for such groups, using zero BA rates may not be problematic and may instead result in precautionary advice.

Vulnerability is another influential parameter in Ecosim whose impacts on model dynamics have been widely discussed in previous studies (Christensen, 1998; Mackinson et al., 2003; Neira et al., 2014; Shannon et al., 2000). Vulnerability sets the maximum predation mortality in Ecosim, and its value ranges from one to infinity Christensen and Walters (2004a). In most present-day models, modellers assume low vulnerabilities as these are associated with more stable dynamics, but low vulnerability values may also over constrain the model and result in unrealistically stable resilient system Ainsworth and Walters (2015). Results from this study show that the effects of vulnerability may further manifest at different levels of high fishing pressure, especially for forage fishes. Unless the model is fitted to time series data, low vulnerabilities for primary prey may be cautiously used to avoid overstraining the responsiveness of prey to changes in predator abundance Martell et al. (2002), especially when testing high fishing pressure scenarios. Mackinson et al. (2003) also examined the effects of vulnerabilities on EwE dynamics and also found the system to be highly resilient under low vulnerabilities, with optimistic equilibrium yields, compared to high vulnerability settings. This study did not test the full range of vulnerability values, which range from one to infinity. There is still a need to examine a larger vulnerability space, and also to test the effects of other Ecosim parameters on system dynamics. Besides, other parameters in Ecosim, for example, foraging time, predator effect on feeding time, can influence the model results Mackinson et al. (2003). However, these were all kept at default Ecosim values in the present study and may need to be explored in future.

9.5 Conclusion

This study sought to understand the level of confidence that can be attached to policy advice from EwE models whenever historical time series observational data are not available. Many EwE models exist on Lake Victoria, but none of these has been validated by fitting to historical dynamics and tested for predictive skill. A historical EwE model has constructed for Lake Victoria, fitted to time series data for the period 1980-2015. The fitted model provides an opportunity to analyse trade-offs among alternative management goals for Lake Victoria (East Africa). The fitted model also highlights the important empirical data gaps to fill to improve ecosystem modelling on Lake Victoria. The model's reliability has been tested using multiple skill assessment metrics, with the temporal trends of predicted biomass and landings fairly matching with the historical fishery dynamics. Nonetheless, the parameters that achieved the best fits may not be regarded as the overall best Ecosim parameters, given that similar fits could be produced using different parameter combinations. Therefore, the model should be interpreted as the best working hypothesis rather than a definitive representation of the Lake Victoria ecosystem. The model is open to further improvements; in particular, assessing the sensitivity of EwE outputs to different input combinations.

A present-day model (representing average conditions for the period 2010-2015) has also been constructed and compared with the end-state of the historical model to test the influence of parameter uncertainty on future projections in data-poor situations. The differences between the model predictions are visible, but those differences may be lessened by incorporating information on short-term biomass trends in the present-day model. Therefore, when long-term time-series data are not available to fit a historical model, the present-day model may still provide reliable predictions if BA rates are set to reflect recent biomass trends near the model's initialization year. This approach is especially important for the less productive groups and those that suffer massive mortality (either due to predation or fisheries). For such groups, the use of negative BA as the first draft assumption in present-day models may be safer than assuming equilibrium conditions.

9.6 Acknowledgment

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9.7 Supplementary data

Supplementary data to this article can be found online at `https://doi.org/10.1016/j.jglr.2020.01.001`.

10

Paper IV

Ecosystem models of Lake Victoria (East Africa): can Ecopath with Ecosim and Atlantis predict similar policy outcomes?

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Abstract

Ecosystem simulation models are valuable quantitative decision tools for supporting ecosystem-based fisheries management. However, the application of ecosystem models in fisheries management is still undermined by the lack of simple procedures to test the effect of model uncertainty on policy outcomes. The use of multiple ecosystem models is viewed as "insurance" against the effects of uncertainty emanating from modelling complex systems, which calls for investigations to ascertain whether models with different structure and assumptions can give consistent policy evaluations. This study compared two structurally distinct ecosystem models, Ecopath with Ecosim (EwE) and Atlantis, for Lake Victoria by varying fishing mortality of the key functional groups: Nile perch (the top predator) and haplochromines (key prey species). The models were compared both at the ecosystem level and at the level of functional groups by evaluating changes in biomass of targeted groups and the consequent effects of changes in target groups on non-target groups. Results showed qualitative similarities (direction of change) for the major harvested groups; however, the cascading effects on non-target species varied across models, depending on the species interaction feedbacks. This study suggests that EwE and Atlantis, despite the huge differences in ecological processes between the models, can give consistent qualitative advice, which is needed for strategic management decisions. Consistency in the representation of trophic interactions may help to minimize variations in simulated fishery responses due to model structure. This study helps to highlight scenarios that are robust to model choice, and for which simpler models (such as EwE) could also provide reliable advice.

Keywords: EBFM, Ecosystem indicators, Lake Victoria, Model comparison, Multispecies models

10.1 Introduction

10.1.1 Ecosystem modelling for ecosystem-based fisheries management (EBFM)

In recent years, calls for the implementation of ecosystem-based fisheries management (EBFM) have increased (Fletcher, 2002), despite the slow progress towards its adoption (Essington and Punt, 2011; Pitcher et al., 2009). Many barriers have been identified as leading to the slow adoption of EBFM, including lack of inclusion of all stakeholders in the implementation process leading to misunderstandings about the approach (Nielsen et al., 2019; Patrick and Link, 2015; Trochta et al., 2018), conflicting nature of management objectives (Pope et al., 2019b), and institutional inertia, where institutions have historically been prepared to provide advice that seeks to reach narrowly defined targets, such as maximum sustainable yield (Ramirez-Monsalve et al., 2016). Despite these challenges, the advantages of EBFM approach are clearly understood: the approach considers fishing impacts entire ecosystem and fisheries and facilitates trade-offs between different fisheries and other aquatic resource stakeholders and their needs, through evaluation of alternative scenarios, when formulating strategic fisheries management plans and actions (Stefansson et al., 2019).

Ecosystem simulation models can be used to evaluate ecosystem properties and provide information on the potential effects that changes in EBFM practices would have on the ecosystem (Hollowed et al., 2000). Within the last two decades, both ecosystem and individual-based models (IBM) have become popular tools that are used to quantitatively predict the consequences of future fishing scenarios by integrating available knowledge about the ecosystem across different scales (DeAngelis and Gross, 2017; Grimm et al., 2017; Lehuta et al., 2016). However, the complex nature of the various available ecosystem models, coupled with the absence of simple procedures for critical evaluation of model performance and the lack of rigour in the treatment of uncertainties, have contributed to their limited operational use in practical fisheries management (Link et al., 2012; Rose, 2012).

The high levels of uncertainty in ecosystem-level processes mean that relying on a single ecosystem model to address all the questions under the EBFM framework is risky (Espinoza-Tenorio et al., 2012; Fulton et al., 2011a). Ecosystem models differ in detail of their biological processes and how they are represented, projection length, and solution time steps (Plagányi, 2007). Constructing models based on the knowledge of the system (minimal process uncertainty) and the best available data do not necessarily safeguard models from the uncertainty inherent in ecosystem-level processes (McElhany et al., 2010). As model complexity increases, tracking the impact of imperfect knowledge of model parameters, input data, or relationships among parameters on model results, and how these affect predictions and subsequent management decisions, becomes increasingly difficult. In ecosystem models such as Ecopath with Ecosim (EwE), a Monte Carlo approach can be taken to examine the sensitivity of simulation results to the initial input parameters (Christensen and Walters, 2004a). However, for more complex, multidimensional ecosystem models with thousands of parameters, for example, Atlantis (Fulton et al., 2011a), full-scale sensitivity analysis is not feasible unless it is done for individual model components (Ortega-Cisneros et al., 2017; Sturludottir et al., 2018). The confidence in outputs from these complex ecosystem models currently relies on how well the model fits observations through model skill assessment (Olsen et al., 2016; Stow et al., 2009). Yet, best fits may not necessarily mean the model captures well the natural processes and is, therefore, the right choice. Similar fits can be obtained with different parameter combinations that do not necessarily reflect the reality (Christensen and Walters, 2004a).

10.1.2 Use of multiple ecosystem models ("ensemble modelling approach")

Both scientists and managers have started recognizing that an *a priori* selection of one model to provide input for management, without an understanding of its associated biases and limitations, can result in misleading conclusions, and that multimodel simulations may provide some form of "insurance" against the increased risk of uncertainty emanating from modelling complex systems (Bauer et al., 2019; Collie et al., 2016; Espinoza-Tenorio et al., 2012). An ensemble modelling approach is helpful in (1) identifying key ecological mechanisms that may explain the differences in simulated fishery responses between models, (2) disentangling the uncertainty caused by differences in ecological model assumptions from the statistical uncertainty of future climate, and (3) identifying results that are common for the whole model ensemble and scenarios that may be robust to model choice (Gårdmark et al., 2013). Ensemble modelling can be benefit EBFM in two ways; first, the convergence of model results can increase confidence in the policy recommendations and; second, divergent results may help to highlight areas where different model considerations and assumptions may lead to varying predictions, which can guide further model development (Collie et al., 2016).

Model inter-comparisons have been performed for several systems to understand how modelled ecosystem impacts of fishing and climate vary across model structure using a suite of indicators (Bauer et al., 2019; Forrest et al., 2015; Fulton and Smith, 2004; Gårdmark et al., 2013; Pope et al., 2019a; Smith et al., 2015; Travers et al., 2010). At the broadest level, these studies have shown coherence in qualitative results across models (i.e., predictions in the same direction), especially for the target species ("single-species effects"), with considerable variations between model outcomes observed for the cascading effects on the non-target species ("multispecies effects"). The authors have concluded that: 1) structurally-distinct ecosystem models have the potential to provide qualitative advice; 2) the divergences in quantitative predictions and multispecies effects are due to the diverse environmental covariates and the different number of trophic relationships and their functional forms considered in the models. However, further investigations are needed to understand whether consistency in multispecies interactions, including similar choice of functional groups and representation of feeding interactions, would minimize variations in predictions due to model structure and assumptions.

The structural and functional differences between multispecies models are enormous. For example, EwE is a whole ecosystem, 0-dimensional biomass model; predation is regulated by explicit diet parameters (through a fixed diet matrix) and foraging vulnerability (Christensen and Walters, 2004a). On the other hand, Atlantis is a whole ecosystem, age- and size-structured, and 3-dimensional population model; predation is regulated by a diet preference matrix, although the actual resulting diet is subject to mouth-gape limitations and prey availability (Audzijonyte et al., 2017a,1). The two modelling approaches are designed to achieve the same ultimate goal, i.e., evaluating system-level trade-offs of alternative management strategies, but have no systematic variation in assumptions. An ensemble modelling approach involving such distinct models can provide vital insights into uncertainty around system structure and function.

10.1.3 Ecosystem models of Lake Victoria

Lake Victoria, East Africa (Figure 10.1), supports a lucrative fishery with annual total fishery production approaching one million tonnes which is worth US $600-900 million from the direct sale of fish at landing sites (LVFO, 2016b). The present-day Lake Victoria fish community is substantially different from that which existed before the introduction of new species, notably Nile perch (*Lates niloticus*) and Nile tilapia (*Oreochromis niloticus*), in the 1950s and 1960s. Before the introduction, the lake had 500+ species of haplochromines (Witte et al., 2007). Predation by the introduced Nile Perch, after successful establishment during the mid-1980s, reduced species diversity (to c. 200 spp. of haplochromines presently, Witte et al., 2007), but this predation fuelled a productive and lucrative Nile Perch fishery. Other native species (see Table 10.1) also declined/collapsed either directly from Nile perch predation or indirectly through competition for haplochromine prey (Ogutu-ohwayo, 1990b). However, demographic changes in Nile perch stock during the 1990s, attributed to intensive fishing, led to the resurgence of haplochromines (Witte et al., 2000). The rest of native species (notably the catfishes) have never recovered, and their commercial importance for the fisheries in the lake is considered negligible (Goudswaard and Hecky, 1997). Landings are currently dominated by the introduced Nile perch and Nile tilapia and the native silver cyprinid (*Rastrineobola argentea*) and haplochromines (LVFO, 2016b). The silver cyprinid constitutes the bulk of the catch (50%), followed by Nile perch (24%) and haplochromines (10%) (LVFO, 2016b). This trend is also reflected in the species' relative abundance from biomass surveys (Taabu-Munyaho et al., 2016). The main fishing gears used are long lines (especially for Nile perch), gill nets (for both Nile perch and Nile tilapia and other harvested species), and small seines for the silver cyprinid. These gears are operated mainly using paddled parachute canoes in shallow nearshore areas (i.e. less than 20 m) and sail/outboard engine-propelled Sesse boats in coastal and deep areas (greater than 20 m) (LVFO, 2016c).

Considerable attempts have been made towards modelling Lake Victoria's historical and present fishery dynamics, aimed at developing solutions that can be used to road-test the ecosystem-level effects of alternative fishery policies. Emphasis has also been put on the use of EwE and Atlantis modelling frameworks, possibly because of their popularity across the African Great Lakes (Musinguzi et al., 2017) and generally across the globe (Colleter et al., 2015; Fulton et al., 2011a). Most of the historical EwE models for Lake Victoria, however, considered short periods (one year) and specific sections of the lake (Musinguzi et al., 2017). A new EwE model for the whole lake that considers historical fishery dynamics, spanning a period of more than 50 years, has recently been developed (Natugonza, 2019). The new EwE model shares some basic similarities with the existing Atlantis model of Nyamweya et al. (2016b). (i) The historical simulation period in both models is the same. (ii) Both models are based on existing knowledge of the system and follow rigorous parameterization with the best available data. (iii) The choice of most vertebrate groups and representation of feeding interactions are comparable, with a few exceptions such as cannibalism in Nile perch and haplochromines (Figure 10.3). (iv) The models use similar forcing data

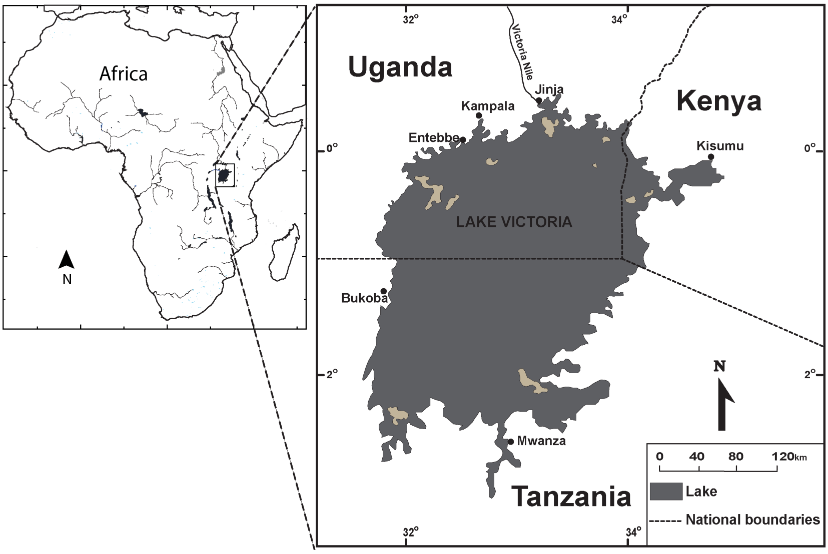

Figure 10.1: Location of Lake Victoria in East Africa.

(annual landings). These models are, therefore, good candidates for testing the effects the sensitivity of alternative fishing scenarios to model choice.

This study aims to compare the behaviour of EwE and Atlantis models, which differ in structure and assumptions, using fishing scenarios. The models are compared both at the ecosystem level, using globally-tested "robust" ecosystem indicators (Fulton et al., 2005), and also at the level of functional groups. The work described here is not intended to lead to the recommendation of one model over another. Instead, the main objective is to investigate how the ecosystem effects of fishing are sensitive to the model structure. Multispecies models are complex and typically generate extensive outputs. Biomass and catch predictions are aggregated into annual trends without spatial and size- and age-structure considerations to keep comparisons between models manageable.

10.2 Material and methods

10.2.1 The models

Ecopath with Ecosim (EwE)

EwE is a biomass model that is widely used in modelling food- web dynamics (Christensen and Walters, 2004a). The trophic mass balance routine (Ecopath) enables partitioning of an ecosystem into functional groups based on niche similarity and data availability. Biomass flows through functional groups are regulated by gains (consumption, production, and immigration) and losses (mortality and emigration), through predator-prey relationships. For each functional group, the net difference between gains and losses is equal to the instantaneous rate of biomass change, which is represented by the biomass accumulation (BA) parameter. Key model parameters include biomass per unit of habitat area, production rate per unit of biomass, consumption rate per unit of the biomass of predator, and ecotrophic efficiency (EE, the proportion of production that is utilized in the system). These parameters are manually tuned in the model. The software can use the input data along with algorithms and a routine for matrix inversion to estimate one missing basic parameter for each functional group, particularly EE, which is never estimated experimentally. The Trophic level (TL) of each functional group is calculated by the software based on average annual predation by aggregating diet data. Primary producers and detritus are assigned a TL of 1, and the TL of consumer groups is calculated as the biomass-weighted average TL of its prey + 1.

The time dynamic simulations are conducted in Ecosim, a routine of EwE that inherits Ecopath parameters to provide predictions of biomass and catch rates of each group as affected directly by fishing, predation, and change in food availability, and indirectly by fishing or predation on other groups in the system. Predation is governed by foraging arena theory (Ahrens et al., 2012), where functional groups are divided into vulnerable and non-vulnerable components, such that the overall feeding rate is somehow limited by prey density. The model parameterization is tested using fishery drivers (for example catch, effort, fishing mortality) and by adjusting foraging arena parameters (vulnerabilities) to ensure that predation mortality rates are within the tolerable limits given the prescribed groups' productivity (production per unit biomass).

The EwE model of Lake Victoria that was used in this study is described in Natugonza (2019), and a summary of its features is shown in Figure 10.2. The model can be accessed from `https://doi.org/10.6084/m9.figshare.7306820.v4`. Parameterisation and calibration of the model followed best practices documented in the literature (Heymans et al., 2016); thermodynamic inconsistencies were checked using PREBAL diagnostics (Link, 2010). The model's overall pedigree index is 0.53, which is suggestive of intermediate data quality. Model skill assessment using one of the correlation- based metrics described in Olsen et al. (2016) suggests that the predicted biomass and catch for the majority of harvested groups match well with the observations (see also Paper III).

The EwE model of Lake Victoria covers an area of approximately 68,800 km^2 (3.05^{o}S to 0.55^{o}N and 31.5^o to 34.88^{o}E, Figure 10.1) and the initial conditions represent the period when most of the non-native species had just been introduced, i.e., 1960. The model consists of 23 biological groups, organized either in single species or multispecies groups depending on habitat, feeding, economic importance or availability of data. The functional groups include 15 fish groups, one fish-eating birds group, one reptile group, three invertebrate groups, two primary producers (phytoplankton and macrophytes), and one detritus group (Table 10.1). The model is set-up in such a way that only fish groups are modelled in detail; the dynamics of invertebrate and producer groups are modelled superficially. Haplochromines, the principal prey for piscivores (Table 10.1), are modelled as one group due to lack of species-specific data. Nile perch, another group of focus in the fishing scenarios (see below), is also modelled as one group despite the species' dietary preferences related to size (Kishe-machumu et al., 2012b). Size-related dietary shifts are modelled implicitly by including all possible prey for juvenile and adult Nile perch in the same diet matrix.

Table 10.1: Functional groups used in Lake Victoria EwE and Atlantis models. For the fish groups, information on common and scientific names, occurrence, habitat, and feeding mode is retrieved from Fishbase: `www.fishbase.org`, version (10/2018). Abbreviations stand for: FF (forage fish); HTO (high turnover); and HHI (high commercial value).

Species/taxa included	Common name	Occurrence	Habitat	Feeding mode	Atlantis	EwE	FF	HTO	HCV
Haliaeetus vocifer, Ceryle rudis, Cormorants	Fish–eating birds		Native Domain	Piscivore	Yes	Yes			
Crocodylus niloticus	Crocodiles	Native	Domain	Carnivore	Yes	Yes			
Lates niloticus	Nile perch	Introduced	Demersal	Piscivore	Yes	Yes	No	Yes	Yes
Clarias gariepinus	North African catfish	Native	Benthopelagic	Omnivore	Yes	Yes	No	No	No
Bagrus docmak	Semutundu	Native	Benthopelagic	Omnivore	Yes	Yes	No	No	No
Protopterus aethiopicus	Marbled lungfish	Native	Demersal	Molluscivore	Yes	Yes	No	No	No
Synodontis victoriae, S. afrofisheri	Squeakers	Native	Benthopelagic	Insectivore	Yes	Yes	No	No	No
Momyrus kanume, *Gnathonemus* spp.	Snout fishes	Native	Demersal	Insectivore	Yes	Yes	No	No	No
Schilbe intermedius	Silver catfish	Native	Pelagic	Piscivore	Yes	Yes	No	No	No
Labeobarbus altianalis	Rippon barbell	Native	Benthopelagic	Omnivore	Yes	Yes	No	No	No
Enteromiuss spp.	Small barbs	Native	Benthopelagic	Omnivore	Yes	Yes	Yes	No	No
Brycinus jacksoni, B. sadleri	Robbers	Native	Pelagic	Omnivore	Yes	Yes	Yes	No	No
Labeo victorianus	Ningu	Native	Demersal	Phytoplanktivore	Yes	Yes	No	No	No
Haplochromis spp.	Haplochromines	Native	Benthopelagic	Variable[a]	3 groups	1 group	Yes	Yes	No
Rastrineobola argentea	Silver cyprinid	Native	Pelagic (schooling)	zooplanktivore	Yes	Yes	Yes	Yes	Yes
Oreochromis niloticus	Nile tilapia	Introduced	Benthopelagic	Omnivore	Yes	Yes	No	No	Yes
O. esculentus and *O. variabilis*	Other tilapias	Native	Benthopelagic	Herbivore	Yes	Yes	No	No	No
Caridina nilotica	Shrimp	Native	Demersal	Detritivore	Yes	Yes			
Macroinvertebrates	Insects and molluscs		Mainly demersal	Detritivore	5 groups	1 group			
Microzooplankton, Mesozooplankton	Zooplankton		Pelagic	Phytoplanktivore	2 groups	1 group			
Algal groups	Phytoplankton		Pelagic		4 groups	1 group			
Periphyton, epiphyton	Benthic producers		Domain		No	Yes			
Pelagic and sediment bacteria	Bacteria				Yes	No			
Labile and refractory detritus	Detritus		Benthic		2groups	1 group			

[a] More than 15 trophic groups (Witte and van Densen, 1995)

The species/groups that are important either for commercial purposes or for food are harvested in the model by a specific fishing fleet. The model includes four fishing gears commonly used on the lake, i.e., gillnets, longlines, small seines, and 'others'. Gillnets target most species, but the bulk of the catch is Nile perch and Nile tilapia. Longlines primarily target Nile perch, but other demersal and benthopelagic species (Table 10.1) are also included in this fleet. Small seines target silver cyprinid; freshwater shrimp (*Caridina nilotica*) and haplochromines are by-catches when the gear is deployed at night using light attraction and during the day without the aggregation lighting, respectively. The 'other' gear category is an aggregation of gears (e.g. beach seines, cast nets, traps) that target a variety of fish species from shallow inshore regions. The model is fitted to time series of biomass and landings for the harvested fish groups for the period 1960-2015 using fishing mortality (F) as a driver. Calibration is performed stepwise; first, by searching for vulnerabilities for each group with the time series from their default Ecosim values; and second, by adjusting diet composition to fine-tune predation mortality trends until best possible fits are achieved (Natugonza, 2019).

Atlantis

Atlantis is a deterministic, spatially resolved tool that is based on dynamically coupled biophysical and fisheries sub-models (production, consumption and predation, waste production and cycling, migration, reproduction and recruitment, habitat dependency and mortality) (Fulton et al., 2011a). A summary of the Atlantis modelling framework is included here, but a detailed description of the model set-up, process equations, parameterization and calibration procedures can be found elsewhere (for example, Audzijonyte et al., 2017a,b). The physical and biological processes are modelled in interconnected cells representing major features of the physical environment. The spatial domain is 3-dimensional, consisting of user-defined active regions and boundary layers that represent biogeographic features (hydrography, bathymetry and species distribution).

The biological model consists of functional groups that are defined based on ecological roles, ontogenetic behaviour and feeding interactions. Exchange of biomass occurs between regions according to seasonal migration and foraging behaviour, while water fluxes (which control advection of nutrients and plankton), heat, and salinity flux across boundaries are represented by a coupled hydrodynamic model. The flow of energy is tracked as nitrogen, which in all vertebrate groups is partitioned into structural and reserve nitrogen. Structural nitrogen determines growth, while reserve nitrogen (the amount of which varies depending on the food intake) is used for reproduction. Consumption is based on a modified Holling type II response, while recruitment is modelled using Beverton-Holt function. TL of each group is also computed based on average annual predation by aggregating diet data supplied through a preferential diet matrix.

The fisheries model simulates user-defined fishing fleets that are assigned to harvested groups with selectivity based on length. Most Atlantis models use imposed catch data to define fishing morality, especially when the objective is to understand the ecosystem dynamics given the specified catch biomass that the fisheries may want to take (Audzijonyte et al., 2017b).

Calibration is geared towards matching predicted and observed biomass trends, or diet, by varying initial conditions (particularly growth rates, consumption rates, natural mortality rates, and recruitment parameters) until size-at-age for age-structured groups is within 20% of initial conditions (Audzijonyte et al., 2017a).

The Atlantis model of Lake Victoria used in this study is described in Nyamweya et al. (2016b), and a summary of features applicable to this study is shown in Figure 10.2. The model can be accessed from `https://doi.org/10.6084/m9.figshare.4036077.v1`. The spatial extent covers the area of the entire lake (approximately 68,800 km^2), which is divided into 12 active regions (where the biology is modelled) and five boundary layers. Each region has up to three depth layers depending on the depth of the water column, i.e., inshore (less than 20 m), coastal (20-

40 m), and deep (higher than 40 m). The initial conditions represented the Lake Victoria ecosystem in 1958. The physical processes (temperature, salinity, and water fluxes) are modelled through a coupled Regional Oceanographic Model (ROMS, Nyamweya et al., 2016a). The biological model has 36 functional groups: one fish-eating birds group, one reptile group, 17 fish groups, nine invertebrate groups, four primary producers, two bacteria and two detritus groups (Table 10.1). The vertebrate groups are modelled as age-structured groups (with up to 10 age classes) while the rest of the lower TL groups are modelled as biomass pools. The fisheries model includes four fishing fleets: gill net, targeting most of the species except small fishes, such as silver cyprinid; longline, mainly targeting Nile perch and other demersal and benthopelagic fishes; small-seine, primarily targeting the silver cyprinid; and inshore fleet, which is an aggregation of gears (mostly illegal gears) targeting all species inhabiting shallow inshore habitats.

The model runs in 12 h time steps for the period 1958-2015. The model parameterisation is rigorous, utilizing the best available data and following best practices. Fishing mortality is varied with multiplication factors reflecting changes in the fishing effort during the simulation period, while final calibration is done by matching the predicted biomass and catch to the general trends of observed catch per unit effort (CPUE) and officially reported landings, respectively. Skill assessment uses two of the metrics described in Olsen et al. (2016): Modelling Efficiency (MEF), which measures scale mismatch between predictions and observations and Pearson correlation (r), which measures the relationship between predictions and observations. The values of MEF and r are all positive and above 0.5 for the majority of the functional group, suggesting that model predictions match well with observed data.

10.2.2 Fishing scenarios

Fishing scenarios were based on the two major groups: Nile perch and haplochromines, which are also emphasized in the Lake Victoria Fisheries Management Plan (LVFO, 2016a). These groups are of great economic

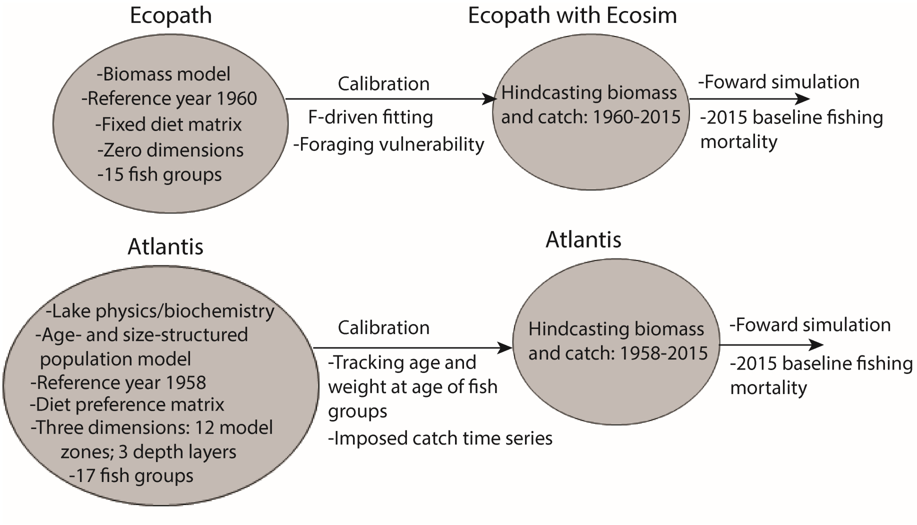

Figure 10.2: Schematic diagram showing the major features of EwE and Atlantis models for Lake Victoria. F stands for fishing mortality.

and ecological importance in the present-day Lake Victoria ecosystem. Nile perch is a voracious piscivore at the top of the food chain; the abundance of the species has considerable influence on the entire system (Marshall, 2018). Similarly, haplochromines are mid-TL forage fishes, whose abundance directly affects the commercially exploited fisheries at the top of the food chain. In terms of research, these groups are also the most studied. The representation of these groups in both models is expected to be fairly grounded in data; therefore, the projections are less likely to suffer from the effects of data uncertainty compared to less-studied groups.

Four fishing scenarios were tested as follows. (i) $NP : 0.6F$: Nile perch fishing mortality was reduced by 40% from the baseline level. (ii) $NP : 1.4F$: Nile perch fishing mortality was increased by 40% from the baseline level. (iii) $HP : 0.0F$: fishing mortality for haplochromines (the primary prey for Nile perch (Figure 10.3) was reduced to zero. (iv) Status quo (SQ): fishing mortality rates for all the harvested functional groups were maintained at the baseline levels. The baseline refers to model conditions at the end of the historical reconstruction simulation

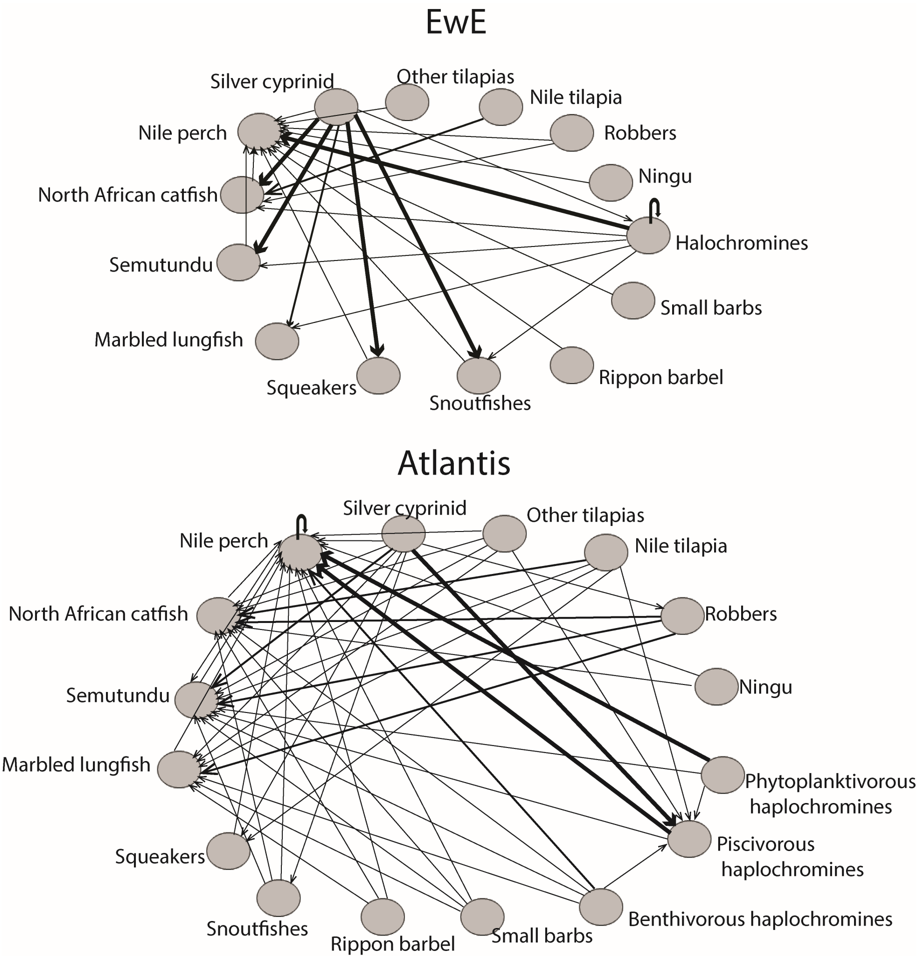

Figure 10.3: Schematic representation of predation interactions in EwE and Atlantis models of Lake Victoria. Model groups shown here are only for fish species, which are represented in both models, to ease comparisons. Note that arrows move towards the predators and arrow thickness is consistent with the contribution of prey to the predator's diet. Thick and black arrows indicate that the prey species constitute more than 30% of the predator's diet; thin arrows indicate that the prey species constitute less than 5% of the predator's diet.

(i.e. 2015). Table 10.2 shows baseline fishery conditions in the two models for the harvested fish groups, but readers can also get more information on the productivity of lower trophic levels via the links given to the models and their data. In each scenario, fishing mortality rates were held constant at the prescribed (scenario) test value, and the model projected for 20 years into the future. The SQ scenario was included because an ecosystem is expected to change under any level of fishing, and therefore, the results of the SQ scenario at the end of the projection period may not necessarily be the same as those at the start of the projection (Table 10.2; Supplementary Table S1).

Table 10.2: Baseline (2015) fisheries conditions in the Atlantis and EwE model used in the forward simulations. Biomass and catch values are presented in t/km^2. B and C stand for biomass and catch, respectively; F is fishing mortality approximated as catch/biomass.

Functional group	B (Atlantis)	C (Atlantis)	F	B (EwE)	C (EwE)	F
Nile perch	1.11E+01	3.46E+00	0.312	1.31E+01	4.44E+00	0.340
North African catfish	6.18E-02	3.74E-02	0.605	1.41E-01	5.72E-02	0.404
Semutundu	3.55E-06	2.91E-06	0.818	6.19E-01	1.67E-02	0.026
Marbled lungfish	5.77E-03	3.93E-03	0.681	7.56E-04	4.31E-04	0.569
Squeakers	3.04E-02	1.70E-02	0.558	4.28E-01	1.06E-03	0.002
Snout fishes	7.50E-07	5.23E-07	0.697	0.00E+00	0.00E+00	NA
Silver catfish	1.07E-02	6.83E-03	0.639	1.06E+00	1.45E-01	0.136
Ripon barbell	5.37E-04	1.44E-04	0.267	2.96E-01	2.37E-02	0.079
Small barbs	9.69E-02	7.36E-03	0.075	2.03E-02	0.00E+00	0.000
Robbers	1.34E-03	9.03E-04	0.672	5.86E-09	1.02E-09	0.173
Ningu	4.11E-02	2.06E-02	0.500	2.91E-01	5.82E-02	0.200
Haplochromines	1.05E+01	8.82E-01	0.083	9.57E+00	1.15E+00	0.120
Silver cyprinid	1.64E+01	5.42E+00	0.330	1.02E+01	5.62E+00	0.549
Nile tilapia	1.53E+00	5.55E-01	0.362	2.53E+00	1.08E+00	0.425
Other tilapias	1.21E-01	7.71E-02	0.635	3.53E-01	1.77E-01	0.500

10.2.3 Ecosystem indicators for comparison

Ecosystem indicators spanning a wide range of processes and biological groups have been used previously to detect a variety of impacts from fishing (Forrest et al., 2015; Fulton et al., 2005; Smith et al., 2015). Indicators can be evaluated at a functional group level, for example, biomass or catch of individual species, and at a community level, for example, the relative abundance of key functional groups (piscivores versus planktivores; pelagic versus demersal), mean TL of the community ($MTL_{biomass}$), or mean TL of catch (MTL_{catch}). Community-level indicators are perceived to be comparatively robust, responding to fishing pressure more predictably than individual species Fulton et al. (2005). For example, the relative biomasses of piscivores and planktivores can indicate a change in the trophic structure of the system, as can a shift in TL of the catch.

MTL$_{biomass}$ was calculated for each scenario as average TL of model groups, weighted by their biomass according to the formula:

$$MTL_{biomass} = \sum_i TL_i \cdot \frac{B_i}{B} \tag{10.1}$$

where, TL_i and B_i stand for the trophic level and biomass of model group i, respectively, and B is the total biomass of all the fish groups. The grouping of lower TL groups (zooplankton and phytoplankton) is considerably variable across models; therefore, only fish groups are considered to keep indicators comparable. Biomasses of planktonic groups can also vary greatly with environmental effects, and such fluctuations may not be relevant to fisheries management.

MTL$_{catch}$ was calculated for each scenario using the same approach as with MTL$_{biomass}$, but using the biomass of catch for each model group rather than stock biomass, i.e., as the mean TL of all landed fish, weighted by the biomass of catch as shown in Equation 10.2

$$MTL_{catch} = \sum_i TL_i \cdot \frac{B_{Ci}}{B_C} \tag{10.2}$$

where, B_{Ci} is the biomass of catch of model group i and BC is total catch. This indicator is perceived to signal the depletion of high TL species, i.e., 'fishing down the food web' (Pauly et al., 1998).

Each indicator was analyzed at the end of the projection relative to baseline values according to the formula:

$$100 \cdot (\frac{IV_{end}}{IV_{start}} - 1) \tag{10.3}$$

where, IV_{start} and IV_{end} are indicator values at the start and end of the projection, respectively. All outcomes of fishing scenarios were compared at the end of 20 years; a percentage change of zero indicated no change in indicator value relative to baseline. Interpretation of results followed that models gave consistent qualitative results if the direction of change in each prescribed indicator was the same (either increase or decrease relative to baseline values). Similarly, predictions with similar direction and magnitude indicated consistent quantitative results.

To ascertain whether similarities or discrepancies between models in the forward simulations (forecast) were linked to agreements or disagreements, respectively, between models in the historical simulations, both the direction and strength of the association between EwE- and Atlantis-simulated biomasses were assessed using Spearman rank correlation (r). The r was calculated using time-series predictions for each functional group during the last 20 years of the simulation (1996-2015), and compared values with those obtained using 20-year projected biomass time-series from the forecast (2016-2035).

10.3 Results

10.3.1 Species-level indicators

Comparison of EwE and Atlantis models in both the historical reconstruction simulations (Figure 10.4) and forward simulations under alternative fishing scenarios (Table 10.3, Supplementary Figure S1) showed variable results; however, overall qualitative agreements between models (positive correlations show similar direction of change) were observed for the dominant fisheries, especially Nile perch and silver cyprinid. However, not all the agreements between models in the historical simulations translated into agreements in the forward simulations. For instance, the models showed similar trends (although the correlations were weak) for haplochromines and Ningu in the historical simulation (Figure 10.4), but the forward simulations showed opposite trends in most of the scenarios (Table 10.3). Also, under the SQ scenario, Atlantis predicted an increase for Nile perch, but EwE instead predicted a decrease (Supplementary Figure S1). Strong disagreements between models (i.e., opposite trends in biomass predictions) were observed in the historical simulation for Nile tilapia, other tilapias, Ripon barbell, silver catfish, and small barbs (Figure 10.4). However, forward projections showed consistent qualitative results (similar direction) for these groups in most of the scenarios, except for Nile tilapia where the models predicted opposite trends in every scenario (Table 10.3). Interestingly, even when these groups showed weak or negative correlations for the entire simulation time series (Table 10.3), the end-state results (where biomass was evaluated at the end of the simulation relative to the baseline), including Nile tilapia, were generally consistent across models (Figure 10.4). This observation is important for management advice, i.e., whether advice can be based on end-state results (where in this case models agree) or predictions for the entire projection time series (Supplementary Figure S1), where the models differ).

Despite the qualitative similarities between model predictions, quantitative results (showing the sensitivity of groups to direct and indirect effects of fishing) were different in all scenarios, and the differences were not systematic across models (Figure 10.5). For instance, Nile perch increased and decreased in both models under the $NP : 0.6F$ and $NP : 1.4F$ fishing scenarios, respectively, but the sensitivity of the group to fishing was two times higher for EwE than Atlantis. The indirect effects on the non-target groups were variable. In the two fishing scenarios targeting Nile perch ($NP : 0.6F$ and $NP : 1.4F$), for instance, Atlantis was more responsive than EwE for haplochromines, silver cyprinid, semutundu, Ripon barbell, and other tilapias. The magnitude of change in biomass of Nile tilapia

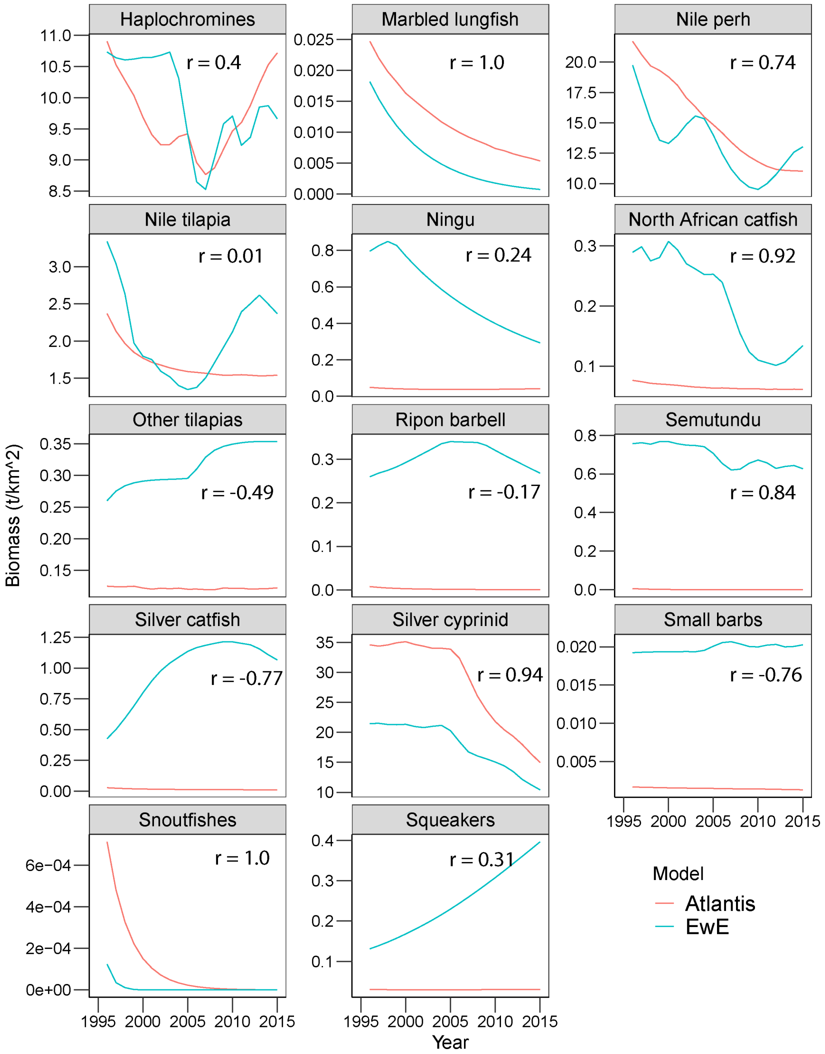

Figure 10.4: Biomass of fish groups simulated by EwE and Atlantis models of Lake Victoria in the historical reconstruction simulation (1996-2015). Trends are presented with values of Spearman rank correlation coefficient (r), showing the level of consistency between EwE and Atlantis predictions in the hindcast.

Table 10.3: Spearman rank correlation of EwE versus Atlantis-simulated biomass trends in the forward simulations (2015-2035). Scenarios are defined as: status quo (SQ); no fishing for haplochromines ($HP : 0.0F$); Nile perch fishing mortality reduced by 40% from baseline ($NP : 0.6F$); Nile perch fishing mortality increased by 40% from baseline ($NP : 1.4F$).

Species/scenario	SQ	HP:0.0F	NP:0.6F	NP:1.4F
Nile perch	-0.96	0.39	0.44	-0.44
African catfish	0.78	0.803	-0.13	0.95
Semutundu	1.0	0.44	1.0	1.0
Marbled lungfish	1.0	1.0	1.0	1.0
Squeakers	0.30	0.54	-0.86	0.91
Silver catfish	0.66	0.62	0.80	0.54
Rippon barbell	1.0	1.0	1.0	1.0
Small barbs	0.65	0.49	0.63	0.52
Ningu	-0.97	-0.97	0.99	-1.0
Haplochromines	-0.95	-0.14	0.99	-0.99
Silver cyprinid	1.0	0.99	0.99	1.0
Nile tilapia	-0.63	-0.64	-0.72	-0.45
Other tilapias	0.88	-0.17	0.83	0.90

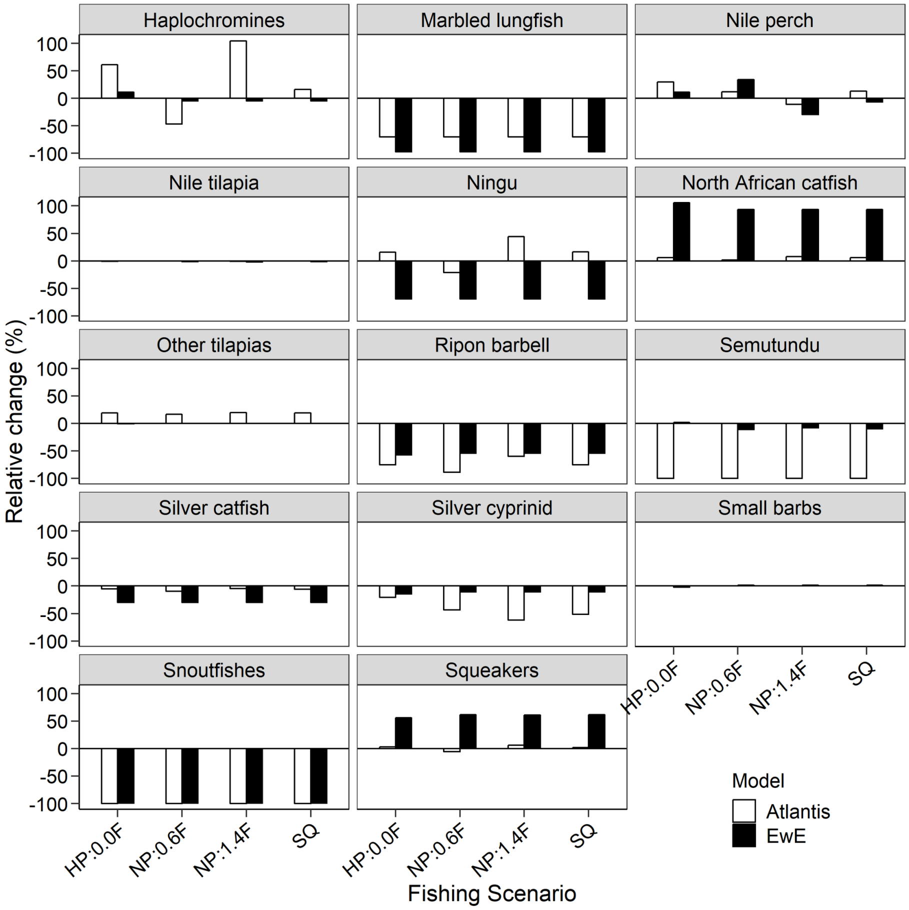

Figure 10.5: Percentage change (2035 relative to 2015) in biomass of functional groups as predicted by Atlantis and EwE models. Zero indicates no change. Bars on the same side of zero line (positive or negative) indicate qualitative agreements between models.

and small barbs was less than 2% in each model, while the snout fishes collapsed in each model before the end of the projection (Figure 10.5).

10.3.2 Community-level indicators

Changes in community-level indicators for the different fishing scenarios are shown in Figure 10.6. Four major patterns were observed. First, the magnitude of change in community-level indicators was generally smaller than species-level indicators. For instance, the maximum observed change in MTL biomass and MTL catch in all fishing scenarios was in the order of 0-5%. Second, the community level indicators showed more coherence in predictions between the models than species-level indicators. Exceptions were 1) biomass of demersal and piscivore guilds under SQ scenario, 2) biomass of forage fishes and ratios associated with feeding and habitat guilds, i.e., planktivorous/piscivorous and pelagic/demersal ratios, respectively, under the $NP : 1.4F$ scenario, and 3) biomass of high turnover and high commercial value species, and total biomass, under the $NP : 0.6F$ scenario. Third, the community-level indicators were generally more sensitive in Atlantis than in EwE. Exceptions were the biomasses of demersal and piscivorous guilds, where the responses were two times higher in EwE than in Atlantis under the two Nile perch scenarios ($NP : 0.6F$ and $NP : 1.4F$). This variation may be due to the individual influence of Nile perch in both scenarios, being the most dominant demersal and piscivorous species, and also being more sensitive in EwE than Atlantis. Fourth, trophic guilds showed unexpected results under high fishing pressure. For instance, a fishing-induced decline in the piscivore guild under the $NP : 1.4F$ scenario was expected to cause an increase in planktivore guild and forage fishes. However, the planktivore guild also declined in both models, while the overall biomass of forage fishes declined in EwE and remained relatively unchanged in Atlantis. At low fishing pressure (under $NP : 0.6F$ scenario), results followed the expected trend, where the increase in piscivore guild was accompanied by a decline in planktivore guild and forage fishes in both models.

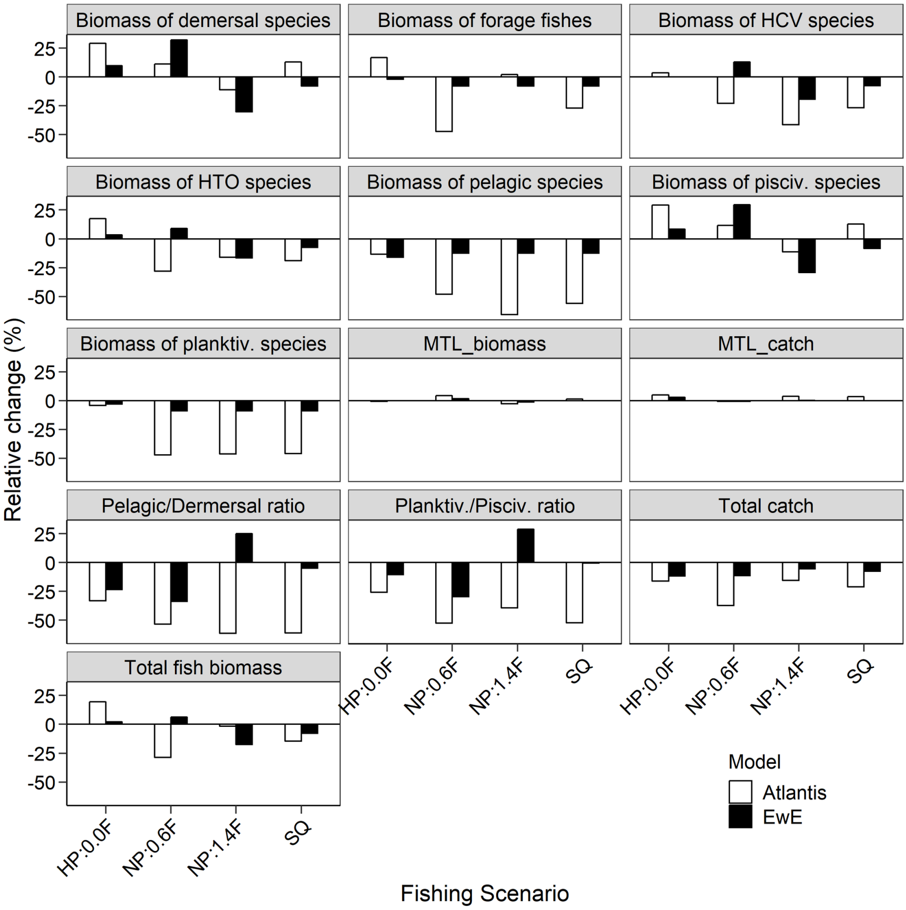

Figure 10.6: Indicators based on biomass and catch of fish groups as predicted by EwE and Atlantis. Values represent 2035 value of indicator under each fishing scenario relative to 2015 baseline value. Zero indicates no change. Abbreviations stand for piscivorous (pisciv.), planktivorous (planktiv.), high commercial value (HCV).

10.4 Discussion

The work described in this paper relates to the use of multimodel simulations in evaluating alternative fishing policy scenarios. The study provides insight into scenarios that are robust to the choice of modelling strategy, and for which simpler models (such as EwE) can also be used to provide reliable advice. Inconsistent predictions across the models of different structure have been the major challenge impeding the use of ecosystem models in management (Harwood and Stokes, 2003). Therefore, understanding the key ecological mechanisms responsible for the differences in simulated fishery responses between models is of great importance for management. This study used EwE and Atlantis models because of their widespread use across the globe (Colleter et al., 2015; Fulton et al., 2011a) as well as the African inland lakes (Musinguzi et al., 2017). Both modelling frameworks represent the food webs, abiotic environment (including climate impacts), and fisheries, but at different scales and varying levels of complexity (i.e., heterogeneity in lake habitats, physics, and algorithms of biomass elaboration and feeding). Atlantis, in particular, offers a more detailed and explicit representation of biochemistry, physical processes, and lower trophic level dynamics (Fulton et al., 2011a). The calibration process also differs between the models; Atlantis tracks the age structure and weight at age of fish groups, whereas calibration in EwE is mainly achieved through adjustment of foraging arena parameters. These differences, together with the species interaction feedbacks and baseline fishery conditions, were identified as the main drivers causing relatively large variations in quantitative results between the models (Figure 10.5). Despite that, the models gave consistent qualitative predictions, especially for the key targeted fisheries, which shows the potential of structurally-distinct ecosystem models to provide sound qualitative advice that is valuable for EBFM even when quantitative results differ.

10.4.1 Effect of trophic interactions on model agreement/ disagreement

The models gave consistent qualitative predictions under fishing scenarios related to Nile perch and the primary prey (haplochromines). In any multispecies system, fishery-induced changes in predator abundance (either increase or decrease) are expected to lead to corresponding shifts in prey abundance, except where competition among several prey species outweigh the effects of predation-release (May et al., 1979). The increase and decrease in Nile perch biomass in both models under the two different fishing pressure scenarios, $NP : 0.6F$ and $NP : 1.4F$, respectively, and the corresponding changes in the biomass of haplochromines (the main prey) were consistent with the expectation. Previous studies involving ecosystem model inter-comparisons have also shown qualitative agreements between models in relation with the direct effects fishing on target species and primary prey, except that the cascading effects of fishing target species on the non-target species (multispecies effects) have been found to be generally different (Bauer et al., 2019; Forrest et al., 2015; Fulton and Smith, 2004; Smith et al., 2015; Travers et al., 2010). The differences in multispecies effects have partly been attributed to the mismatch in the number of trophic links and their functional forms considered in the models. The choice of biological groupings and representation of diets influence the level of connectivity between groups, which is likely to affect the direction of one species' biomass or catch as affected by other species' fishing mortality. Attempt was made to minimise the effect of variation in functional groups by using models with comparable representation of functional groups and trophic connections, for most vertebrate groups (Figure 10.3), which, with a few exceptions, yielded consistent results for the non-target species. The observed qualitative differences in our study may be due to the mismatch in the representation of some groups (for example, haplochromines, which are modelled in three trophic groups in Atlantis and one group in EwE); inclusion of Nile perch cannibalism in Atlantis but not in EwE, and haplochromine cannibalism in EwE but not in Atlantis and; the overall differences in strength of diet dependencies, e.g., silver cyprinid as large diet item to snoutfish, North African catfish, semutundu and squeakers in EwE but not in Atlantis (Figure 10.3). These findings suggest that consistency in model set-up may help to minimize variations in predictions due to model structure and assumptions. In future studies, basic model considerations such as choice of functional groups and feeding interactions may need to be standardized before conducting model comparisons.

On the other hand, the models showed considerable variations in quantitative results. For example, under the two different Nile perch scenarios, $NP : 0.6F$ and $NP : 1.4F$, both models predicted an increase and decrease in Nile perch biomass, respectively, but the magnitude was 3-times higher in EwE than Atlantis. This observation is attributed to the differences in baseline F for Nile perch, which is higher in EwE than Atlantis. The differences in baseline conditions may also partly explain the higher responsiveness of groups such as semutundu, other tilapias, and Ripon barbell in Atlantis than EwE, given the comparatively higher baseline F in the former (Table 10.2). However, the variations in sensitivity of these groups to fishing across models can also be attributed to the differences in baseline abundance at the beginning of the projections. These groups, in addition to the North African catfish and squeakers, were virtually collapsed in the Atlantis model during the last 20 years of the historical simulation (Figure 10.4) and, therefore, were more sensitive to changes in predator/prey abundance in Atlantis than EwE. A similar situation can be seen from the absolute biomass predictions at the end of the simulation: even when the magnitude of change in relative biomass (i.e., biomass at the end of the projection relative to biomass at the start of the forecast) is higher in Atlantis than EwE, the absolute biomasses at the end of the projections are lower in the former (Supplementary Figure S1). Marbled lungfish and snout fishes, which showed similar patterns in the historical simulation, also exhibited similar patterns in the forecast, although this observation does not suggest that consistent results in hindcast necessarily translated into consistent results in the forecast (Table 10.3; Figure 10.4).

Variations in quantitative results for the rest of the groups (for example, haplochromines and silver cyprinid) that are not related to fishery drivers or baseline conditions, i.e., where the responsiveness was higher in Atlantis than EwE despite the lower F in the former, can be attributed to the strength of diet dependencies and the differences in mechanisms governing predation in each model outweighing the direct effects from fishing. In EwE, predation mortality is governed by the foraging arena theory, mainly through the vulnerability parameter (Ahrens et al., 2012; Walters et al., 1997), while in Atlantis, predation is modelled through the Holling type II functional response (Audzijonyte et al., 2017a). Low vulnerabilities in EwE (which usually represent bottom-up control) tend to constrain the responsiveness of the model and increase the resilience of prey to changes in predator abundance (Ainsworth and Walters, 2015; Christensen and Walters, 2004a). In the EwE model used in this study (`https://doi.org/10.6084/m9.figshare.7306820.v5`), the values representing the vulnerability of haplochromines and silver cyprinid to Nile perch (the primary predator) are all less than 2, which could be the main reason these groups are less responsive to changes in predator (Nile perch) abundance in EwE. While these low vulnerabilities can buffer against unrealistically high fluctuations associated with top-down (Lotka-Volterra) predator-prey relationships, they also tend to overestimate resilience of the system, and this may result in underestimation of extinction risk (Christensen and Walters, 2004a). For example, under the *NP:0.6F* scenario (Figure 10.5), when Nile perch biomass increases by 25% in Atlantis following a reduction in fishing pressure, the biomass of haplochromines (the principal prey) decreases by 50%. However, in EwE, a 50% increase in Nile perch biomass under the same scenario is accompanied by 10% decrease in haplochromine biomass. Subsequent improvements to the EwE model of Lake Victoria may need to reexamine the vulnerability matrix and ensure that the fitted vulnerabilities do not overconstrain the model.

The low responsiveness of haplochromines and silver cyprinid in EwE compared to Atlantis may also be linked to the difference in the assimilation efficiency (AE) of Nile perch (the main predator) in the two models.

In the EwE model, unassimilated food for Nile perch is set at 20%, while in Atlantis, unassimilated food is set at 40%. This imbalance in AE is likely to create higher predation mortality in Atlantis than EwE, leading to a higher sensitivity of prey to changes in predator abundance in the former. Future investigations may also attempt to recalibrate the EwE model with lower values of AE, but the productivity of Nile perch would need to be reduced to avoid crushing the prey.

Previous studies that have been conducted on this subject (inter-model comparisions) have found mixed results. Some studies have found EwE to be more responsive than Atlantis (for example, Forrest et al., 2015; Kaplan et al., 2013; Smith et al., 2011), which has been attributed to the "delaying" features incorporated in the Atlantis modelling framework, for example, age- and size-structure, life history stages and reproductive behaviour, with an effect of delaying the reproductive response of a population. In the present study, however, this explanation is only consistent with the smaller increase in biomass of Nile perch in Atlantis than in EwE under the *NP: 0.6F* scenario. Under the *NP: 1.4F* scenario (where fishing pressure on Nile perch is intensified), the delaying features in Atlantis would instead result in a rapid fishing-induced decline, as the population takes longer to recover, which is not the case. Other studies (for example, Smith et al., 2015) found Atlantis to be more responsive than EwE, even when Atlantis incorporated age-structure and life history, and attributed this to the relative strength of diet dependencies and competition outweighing delaying features. These findings (both in the present and previous studies) suggest absence of single key ecological mechanism explaining the differences in simulated fishery responses between structurally-distinct models, and that uncertainty in fishery responses may be more driven by biases and ecosystem- or group-specific considerations in individual models than the model structure. Ensemble modelling may, therefore, help to identify such areas before the models are used in management.

10.4.2 Effect of the environment and lower trophic dynamics on model predictions

The EwE model of Lake Victoria used in this study does not include the effects of non-fishing, anthropogenic changes such as limnological and other physical attributes (for example, nutrient inputs), which effect on Lake Victoria's ecosystem functioning (Downing et al., 2012; Hecky et al., 2010). Forrest et al. (2015) found the dynamics of several functional groups in Atlantis to be more influenced by bottom-up processes (i.e., fluctuations in primary production driven by the oceanographic components in the physical sub-model) than in EwE, where no explicit primary productivity drivers were included, which contributed to major deviations between model predictions. These differences in model detail and considerations could also have contributed to the differences in model predictions observed in this study. At the core of Lake Victoria's Atlantis model is a ROMS model, which provides hydrodynamic input (Nyamweya et al., 2016a). The model shows seasonal variation in lakes' physical processes and heterogeneity in nutrient concentrations, which are all positively correlated with fish species abundance (Nyamweya et al., 2016b). In contrast, the EwE model is used in its simplest, non-spatial form, which may be a shortcoming to this study, i.e., contrasting a 3-dimensional Atlantis model with a zero-dimensional EwE model. Nonetheless, comparisons were made between biomass and catch predictions that were aggregated into annual trends and for the entire lake, with no age- and size-structure considerations, and hence the conclusions for strategic management advice are expected to remain valid. Future studies may need to incorporate environmental and non-fishing anthropogenic factors into the EwE model, include the spatial effects using the Ecospace module (Christensen and Walters, 2004a), and evaluate alternative scenarios using the two models at habitat level (inshore versus coastal versus deep open waters).

10.4.3 Effect of species aggregation on model sensitivity

This study shows $\mathrm{MTL}_{biomass}$ to increase under the *NP: 0.6F* scenario and decrease under the *NP: 1.4F* scenario in both models. This observation is expected, given the influence of Nile perch (a piscivore) at the top of the food chain. Reducing fishing mortality of Nile perch in the *NP: 0.6F* scenario leads to an increase in biomass, and hence average TL of the community; the reverse occurs when fishing pressure on the predator is intensified (i.e., under the *NP: 1.4F* scenario). Nevertheless, the maximum observed shift is less than 5%, which is possibly caused by the higher biomass of silver cyprinid, a low TL pelagic zooplanktivore. In contrast, MTL_{catch} increases when fishing pressure is increased for the piscivorous fish (*NP: 1.4F* scenario) and reduces for the low-TL forage fishes (*HP: 0.0F* scenario). This observation is inconsistent with the expectation from the 'fishing down the food web' hypothesis (Pauly et al., 1998), where TL of the catch is expected to decline in response to preferential depletion of high TL species. However, the deviation could be due to the fact in both models, F remains constant (and relatively small) contrary to the progressive and sustained increase in fishing pressure depicted under the 'fishing down' hypothesis. Besides, the increase in catches of the predator in the short-term can increase TLC, which seems to be the case with the *NP: 1.4F* scenario, given the short projection period considered in the present study.

Shifts in community-level indicators were small compared to species-level indicators, and less sensitive in EwE compared to Atlantis. Travers et al. (2010) used two fishing scenarios (overfishing versus stock recovery) to compare relative change in selected ecosystem indicators in EwE and OSMOSE (Object Oriented Simulator of Marine Ecosystems, Shin and Cury, 2001), and found similar results. In EwE, the observed maximum change in $\text{MTL}_{biomass}$ and MTL_{catch} was less than 1% and about 1.5%, respectively, while in OSMOSE, $\text{MTL}_{biomass}$ and MTL_{catch} changed about 1% and 4%, respectively. Interestingly, these changes were only observed in the overfishing scenario; the recovery scenario showed no change. Smith et al. (2015) extended this comparison to three models by adding Atlantis and also found similar results: the maximum change was 2% for $\text{MTL}_{biomass}$ and 3% for MTL_{catch}, with EwE predicting the least change in all cases. However, these small changes may never be detected in real-world fisheries amidst multiple stressors (Branch et al., 2010).

By examining the feeding guilds, it was expected that a fishing-driven decline in the piscivore guild, due to increased fishing pressure on Nile perch (*NP: 1.4F*), would cause an increase in biomass of the main prey, especially haplochromines. Whereas results of Atlantis were consistent with this expectation, EwE predicted the opposite, owing to the low sensitivity of haplochromines to Nile perch predation. Under the same fishing scenario (*NP: 1.4F*), planktivore to piscivore ratio was also expected to increase following a fishing-driven decline in Nile perch. However, this indicator increased in EwE and decreased in Atlantis. The decrease in Atlantis can be attributed to a substantial reduction (i.e., by more than 50%) in the biomass of silver cyprinid, a dominant pelagic planktivore, possibly due to competition with haplochromines, whose biomass increases by 100% following a decline in the main predator (Nile perch). The sharp decline in silver cyprinid cancels out the effect of a decline in Nile perch on pisciviore abundance. When the indicator is recalculated under the same scenario, but without the silver cyprinid, it also shows an increase in Atlantis (i.e., by 93%), which is consistent with EwE prediction and the overall expectation, despite the difference in magnitude.

10.5 Conclusion

The question that motivated this work was: can EwE and Atlantis give similar policy evaluations? While considerable quantitative differences were observed in model predictions for individual species/groups, the models gave similar qualitative results for the major groups that are targeted by fisheries. The findings from this study illustrate the capacity of EwE and Atlantis models, which differ in structure and biological processes included in the models, to provide reliable qualitative advice that can support strategic management decisions. However, the present work uses scenarios concerning highly documented species (Nile perch and haplochromines). The behaviour of the models on fishing lesser-known species needs further investigation.

Ecosystem modelling is resource-intensive and the majority of ecosystem models that exist globally, including models of similar ecosystems, are constructed by independent research groups; practically, this situation will always be the same. Model inter-comparisons, therefore, should be emphasized to identify scenarios that are less sensitive to model choice and for which simpler models (for example, EwE) could still provide reliable advice for EBFM. Although multiple drivers can influence the simulated fishery responses across structurally-distinct models, this study suggests that minimizing the differences in the trophic linkages between the models, i.e., by using similar functional groupings and feeding interactions, may help to minimize variations in fishery responses due to model structure. Consequently, deliberate attempts should be made to improve the accuracy of diet data through rigorous stomach content analyses, especially for the non-charismatic groups that are always ignored during surveys.

Both species and community-level indicators are essential for ecosystem monitoring and assessment. However, aggregating results under community-level indicators may hide important information and mask actual ecosystem effects of fishing in cases where opposite trends in several biological groups cancel each other. Therefore, community-level indicators should always be used in combination with species-based indicators. Even where models tend to give different biomass predictions at a functional group level, tracking and identifying critical ecological processes that cause disparities in simulated responses to alternative scenarios becomes easy, as seen in the case of Nile perch in the present study.

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10.7 Supplementary data

Supplementary data to this article can be found at `https://doi.org/10.1016/j.jglr.2019.09.018`.

11

Paper V

Simulating trade-offs between socio-economic and conservation objectives in Lake Victoria (East Africa) using multispecies, multifleet ecosystem models

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Abstract

Most small scale inland fisheries worldwide are open access, and fishing provides the vital source of employment and livelihood for the riparian communities. Management of these fisheries requires information on trade-offs between fish production, profits from fishing, employment, and conservation objectives. Here, a non-linear optimization procedure in Ecopath with Ecosim (EwE) modelling package is used to the determine long-term gear-specific fishing effort that can maximize economic, social, and conservation objectives for Lake Victoria (East Africa). Then the resulting "optimal fishing effort" levels are applied in both EwE and Atlantis models to predict long-term changes in the ecosystem. Results show profit maximization to be more compatible with conservation objectives than is the maximization of catch (or employment). However, maximizing economic value, while maintaining ecosystem structure, would require a reduction in fishing effort of almost every fishing gear. This trade-off can be severe (high social cost) for fishing communities with limited alternative livelihoods. This study provides an understanding of relative risks and benefits of various management objectives, which will enable stakeholders and the public to conduct informed discussions on future management policies.

Keywords: conservation, Ecopath with Ecosim, Lake Victoria, optimal policy search, trade-offs, socio-economics

11.1 Introduction

Fisheries management globally relies predominantly on “tactical” advice, focusing on output control measures, such as quotas, and input controls, either in the form of gear limitations or closures of fishing areas (Stefansson and Rosenberg, 2005). The main goal is to maintain harvested stocks at levels that produce maximum sustainable yield (MSY, the highest equilibrium yield that can be continuously harvested from a stock under existing environmental conditions) (Tsikliras and Froese, 2018).). However, achieving this goal in multispecies fisheries is a challenge because the biological yield of predator and prey species can shift depending on the changes in abundance of their prey or predator species (Walters et al., 2005). For example, the fishing effort required to produce MSY for less vulnerable stocks, i.e., those with high turnover rate, can be high, thereby increasing the risk of over-exploiting or even collapsing the vulnerable stocks. The alternative strategy that is increasingly receiving attention towards addressing this challenge is ecosystem-based fisheries management (EBFM), which takes into account species interactions, feedbacks, and trade-offs within fished systems (FAO, 2003; Stefansson et al., 2019; Townsend et al., 2019).

Despite the growing popularity of EBFM, the actual adoption and implementation of the approach have remained slow globally (Pitcher et al., 2009). Many factors have been suggested as leading to the slow adoption of EBFM, but mainly the lack of inclusion of all stakeholders in the implementation process, leading to misunderstandings about the approach (Patrick and Link, 2015; Trochta et al., 2018). However, EBFM may also be hampered by the conflicting nature of management objectives. Previous studies have shown, for example, that total ecosystem yield may not be maximized without depleting some stocks and that protecting all exploited species from overfishing would require reducing fishing effort and catch (employment) in every fishing sector/fleet (Andersen et al., 2015; Forrest et al., 2015; Hilborn, 2007,1; Hilborn et al., 2004; Pascoe et al., 2013; Sparholt and Cook, 2010). Whereas these conclusions apply to many exploited fisheries across the globe, trade-offs can also be influenced by local conditions such as productivity (the rate of natural population increase) of the individual stocks and strength of species interactions (Shelton et al., 2014; Voss et al., 2014) and the socio-economic set-up of the fishing communities (Bene, 2009). Additional investigations, therefore, are needed on how to achieve a balance between fish production, profits from fishing, employment, and conservation objectives at the local scale.

Analysis of trade-offs between management objectives at the local scale is particularly important for small scale inland fisheries because of the level of dependence of riparian communities on these fisheries for livelihoods. These fisheries are generally open access, with fishing providing the vital source of employment and livelihood for the riparian communities (Cooke et al., 2016). In these fisheries, most fishers (boat crew) are underprivileged, and illegal fishing activities are rampant; also, the least productive species have been overexploited, and the stocks need rebuilding (Bene, 2009; FAO, 2018). However, reducing fishing effort and catch to levels appropriate for rebuilding the declining stocks may impose a high social cost, considering that most of these fisheries are in the underdeveloped nations that generally lack social benefit systems and alternative livelihoods (Bene et al., 2010). Managers of these fisheries need information on the potential risks associated with maintaining high fishing effort and catch against the long-term benefits associated with smaller, more profitable catch, but at the expense of livelihoods and employment.

11.1.1 Ecosystem models

Ecosystem models are essential decision support tools (DST) for EBFM (Collie et al., 2016; Stefansson et al., 2019; Townsend et al., 2019). Many ecosystem modelling tools exist globally, but the most widely used are Ecopath with Ecosim (EwE, Christensen and Walters, 2004a), with over 400 published models (Colleter et al., 2015), and Atlantis (Fulton et al., 2011a), which has been applied in all continents across the globe (CSIRO, 2020). These tools have also been used in many socio-ecological studies involving trade-offs between fisheries management objectives (Araújo et al., 2008; Cheung and Sumaila, 2008; Christensen and Walters, 2004b; Forrest et al., 2015).

Ecosystem models, however, often give contrasting results, although qualitative similarities have been observed in some comparative studies (Forrest et al., 2015; Natugonza et al., 2019; Pope et al., 2019a). This uncertainty is likely the main reason hampering the use of ecosystem models directly in fisheries management decision making and EBFM (Collie et al., 2016; Hyder et al., 2015; Link et al., 2012). Consequently, presenting model outputs with a realistic cognizance of their uncertainty has become a requirement for their use in EBFM (Grüss et al., 2017).

Model uncertainty takes multiple forms, including natural variability, observation error, inadequate communication (especially among scientists, decision-makers and stakeholders), outcome uncertainty, unclear or non-specific management objectives, or structural complexity of the model(s) (Link et al., 2012). These forms of uncertainty enter the modelling process at different stages, making it impossible to address all forms by a single technique. In models that are developed for exploring fishery policy scenarios, more emphasis is put on structural uncertainty, arising from parameter estimates (parametric uncertainty), model framework, functional form, spatial/temporal scaling, or complexity trade-off (Link et al., 2012). For parametric uncertainty, sensitivity analysis (Essington, 2007; Fennel et al., 2001; Klepper, 1997; Steenbeek et al., 2018; Wu et al., 2014), model fitting to time series data (Grüss et al., 2017; Heymans et al., 2016), and skill assessment (Olsen et al., 2016; Stow et al., 2009) are recommended to show how the model deviates from reality. However, due to the large number of parameters involved in some complex end-to-end models, such as Atlantis, full-scale sensitivity analysis is computationally prohibitive (Morzaria-Luna et al., 2018; Ortega-Cisneros et al., 2017; Sturludottir et al., 2018). Consequently, fitting the model to time series data and optimizing prediction skill remains the most widely used approaches for addressing uncertain parameters in complex ecosystem models (Grüss et al., 2017). For the remaining four subcategories of structural uncertainty (model framework, functional form, spatial/temporal scaling, and complexity trade-off), more emphasis has been put on ensemble/structured modelling, involving multimodel inference (Espinoza-Tenorio et al., 2012; Gårdmark et al., 2013). The rationale is that sound management decisions can be supported if multiple ecosystem models, despite their different assumptions, lead to consistent and converging results. Recent studies show that this approach has the potential to offer some 'insurance' against the uncertainty that comes with modelling complex ecosystem-level processes (Bauer et al., 2019; Pope et al., 2019a).

11.1.2 The case of Lake Victoria (East Africa)

Lake Victoria is the largest tropical freshwater lake in terms of surface area (about 68,800 km^2) which is shared by three countries, i.e., Uganda, Kenya and Tanzania. The catchment area has one of the highest population densities in Africa, approaching 500 people km^{-2} (Kolding et al., 2014).This population has put pressure on fishery resources, with indications that the fishery is experiencing effects of "Malthusian overfishing" (Pauly, 1990,9; Teh and Sumaila, 2007). The typical fishers (boat crew) around Lake Victoria have a poor financial savings culture, and, except for the few islands with agricultural activities, the only source of employment and livelihood for the resident communities is fishing (Johnson and Bakaaki, 2016; Nunan, 2014a). While the overall landings from the dominant species, for example, Nile perch (*Lates niloticus*), Nile tilapia (*Oreochromis niloticus*), and the Silver cyprinid (*Rastrineobola argentea*), locally called dagaa, have not plummeted, the catch rates (catch per unit effort, CPUE) for all the species have declined (LVFO, 2016b). Consequently, the use of illegal fishing gears and techniques, notably the small gillnets less than 5 inches (stretched mesh size), beach seine and monofilament gillnets, has increased during the past decade (LVFO, 2016c; Mpomwenda, 2018). The main focus of the current Lake Victoria Fisheries Management plan (LVFO, 2016a) is to halt or reverse this trend. However, the social cost associated with reducing fishing effort and rebuilding fisheries remains unknown.

Lake Victoria is generally open-access, with limited output restrictions. Approximately one million tonnes of fish are harvested from the lake each year; this catch is worth the US $600-850 million annually from the direct sales of fish at the landing sites (LVFO, 2016b). In terms of employment, the fishery directly employs about one million people through fishing and value chain activities; with the inclusion of their dependants, the lake supports livelihoods of approximately four million people (Mkumbo and Marshall, 2015). The decline in catch rates over the years suggests that the stocks are exhibiting the effects of intensive fishing (LVFO, 2016a; Mkumbo and Marshall, 2015), and that these multiple benefits (high yield and employment) may be short-lived.

Recently, the authorities on the Ugandan side of Lake Victoria have adopted a management objective aimed at maximizing net economic returns, through limiting access, as the primary management objective (Glaser, 2018; Johnson and Bakaaki, 2016). However, a wealth-dominated approach in small scale fisheries is known to target and disadvantage the poor, vulnerable fishers, especially those fishing for food in near-shore areas, whose overall impact on the fishery may be insignificant; also, it promotes illegal fishing activities (Bene et al., 2010). On Lake Victoria, these aspects will be exacerbated because the targeted groups of fishers have limited livelihood options and the wealth generated for governments may not necessarily be used to create alternative employment for the affected fishers (Johnson and Bakaaki, 2016; Nunan, 2014b). The need for information on how to achieve a balance between fish production, profits from fishing, employment, and conservation objectives is apparent and is the focus of this study.

11.1.3 Objective of the study

This study aims to explore the trade-offs between socio-economic and conservation objectives in fisheries management using Lake Victoria as a case study. The study involves estimating long-term, gear-specific fishing effort (optimal fishing effort) that can maximize pre-defined management objectives (economic, social, and conservation benefits) and assessing the response of the ecosystem to each management objective. By understanding the trade-off relationships between ecological, economic, and social objectives, managers will be in a position to weigh risks and benefits associated with each objective to make informed decisions. To minimize the effect of structural uncertainty associated with multispecies models, trade-offs are explored using two structurally-distinct modelling frameworks, EwE and Atlantis. For parametric uncertainty, although the sensitivity of outputs to different input parameter combinations in both EwE and Atlantis models of Lake Victoria is unknown, both models are fitted to time series data and their predictive skill can be assessed from the associated multiple skill assessment metrics (Natugonza et al., 2020; Nyamweya et al., 2016b). The values of the skill metrics (see below) can be used to judge how the models perform against data and any caution that may be applied while interpreting model outputs.

11.2 Materials and methods

11.2.1 Modelling software

EwE and Atlantis, the most widely used ecosystem modelling tools globally (Colleter et al., 2015; Fulton et al., 2011a) and on the African Great Lakes (Musinguzi et al., 2017), were the main modelling tools in this study. These modelling tools represent food webs, abiotic environment (including climate impacts), and fisheries, but at different scales and varying levels of complexity. EwE is 0-dimensional biomass model, where predation is regulated by explicit diet parameters (through a fixed diet matrix) and foraging vulnerability (Christensen and Walters, 2004a). Atlantis, on the other hand, offers a more detailed and explicit representation of biochemistry, physical processes, and lower trophic level dynamics. The model is age- and size-structured, the spatial domain is resolved in 3 dimensions; predation is regulated by a diet preference matrix, although the actual resulting diet is subject to mouth-gape limitations and prey availability (Audzijonyte et al., 2017a,b).Previous studies have shown that these modelling tools can give consistent qualitative policy evaluations, especially for the fishery-induced effects of the directly targeted species, although quantitative results differ (Forrest et al., 2015; Natugonza et al., 2019; Pope et al., 2019a; Smith et al., 2015). The two modelling tools have also been used extensively in studies linking fisheries socio-economics and ecology (Ainsworth and Pitcher, 2010; Araújo et al., 2008; Cheung and Sumaila, 2008; Christensen and Walters, 2004b; Heymans et al., 2009; Kaplan et al., 2014).

11.2.2 The models

The EwE and Atlantis models of Lake Victoria were parameterized independently. The EwE model is described in detail (mass balances, data sources and uncertainty, model fitting to time series data, and skill assessment) in (Natugonza et al., 2020). The model run file is freely accessible at `https://doi.org/10.6084/m9.figshare.7306820.v6`. For quick reference, the basic parameters are given in the electronic supplementary material (Supplementary Table S1). The Atlantis model is described in detail in (Nyamweya et al., 2016b). The model is also freely accessible at `https://doi.org/10.6084/m9.figshare.4036077.v1`. Key features highlighting the differences in structure and assumptions between the two models are given in Figure 11.1. The representation of functional differs for the lower trophic levels (TLs, i.e., biomass pools), but the vertebrate groups are comparable, except haplochromines, which are modelled as one group in EwE and three groups in Atlantis (Table 11.1). Feeding interactions are also fairly comparable; the main differences relate to the strength of the diet dependencies and representation of cannibalism in Nile perch and haplochromines (Figure 11.2). Despite these variations, the previous comparison of the two models using species-specific fishing scenarios (for example, doubling/halving the baseline fishing mortality of key functional groups: Nile perch and haplochromines) resulted in consistent qualitative predictions (Natugonza et al., 2019). What this study intends to explore is whether the models can give similar results for scenarios that involve changing, simultaneously, the fishing mortality of all fished groups in the system.

Some adjustments were made to the gear set-up in the EwE model to cater for variation in the cost of fishing associated with the fishing area and mode of operation of the fishing gear. The EwE model of (Natugonza et al., 2020) considered four gears: gillnets, longlines, small seines, and 'others. Gillnets target most species except small fishes such as silver cyprinid. Longlines target Nile perch and other demersal and benthopelagic species (Table 11.1). Small seines target silver cyprinid; freshwater shrimp (*Caridina nilotica*) and haplochromines are by-catch. ‘Others’ is an aggregation of gears (for example, beach seines, cast nets, traps), targeting a variety of fish species from shallow inshore regions. However, the mode of operation of the fishing gears used in Lake Victoria differs by region and water depth. In the shallow inshore waters ($<$20 m), gillnets and longlines are operated with small to medium-sized paddled canoes, while in coastal (20-40 m) and deep ($>$40 m) waters (Figure 11.3), both gears are operated with large sail/outboard engine-powered Sesse boats (LVFO, 2015). These fishing areas and mode of operation of fishing gear have implications for the fishing costs and net profit (Onyango, 2018), which are inputs in the optimization for economic benefits (see below). These gears were, therefore, separated into 12 distinct fleets, reflecting the actual mode of operation, using information from catch assessment and Frame surveys (Supplementary Table S2).

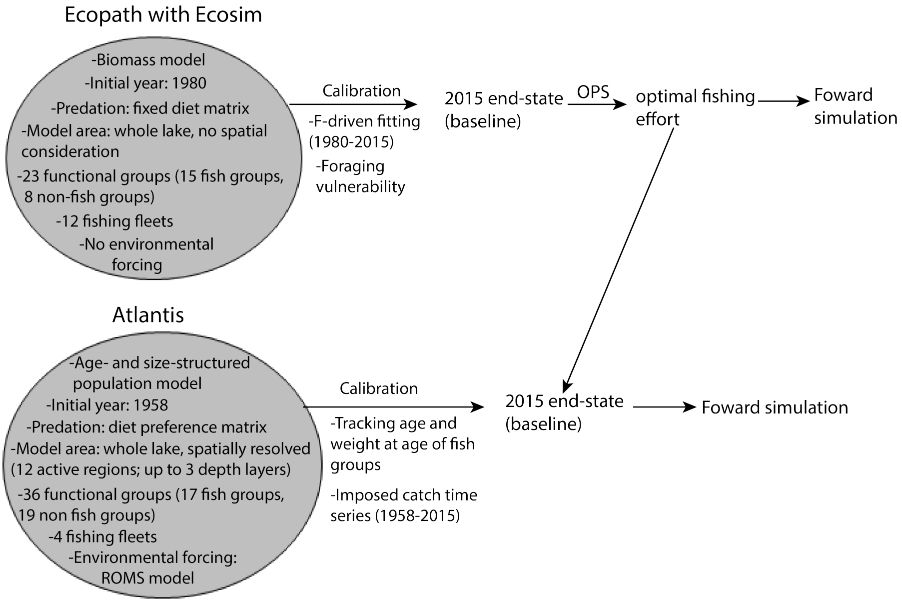

Figure 11.1: Schematic diagram showing the major features of EwE and Atlantis models for Lake Victoria. F stands for fishing mortality. Modified from (Natugonza et al., 2019).

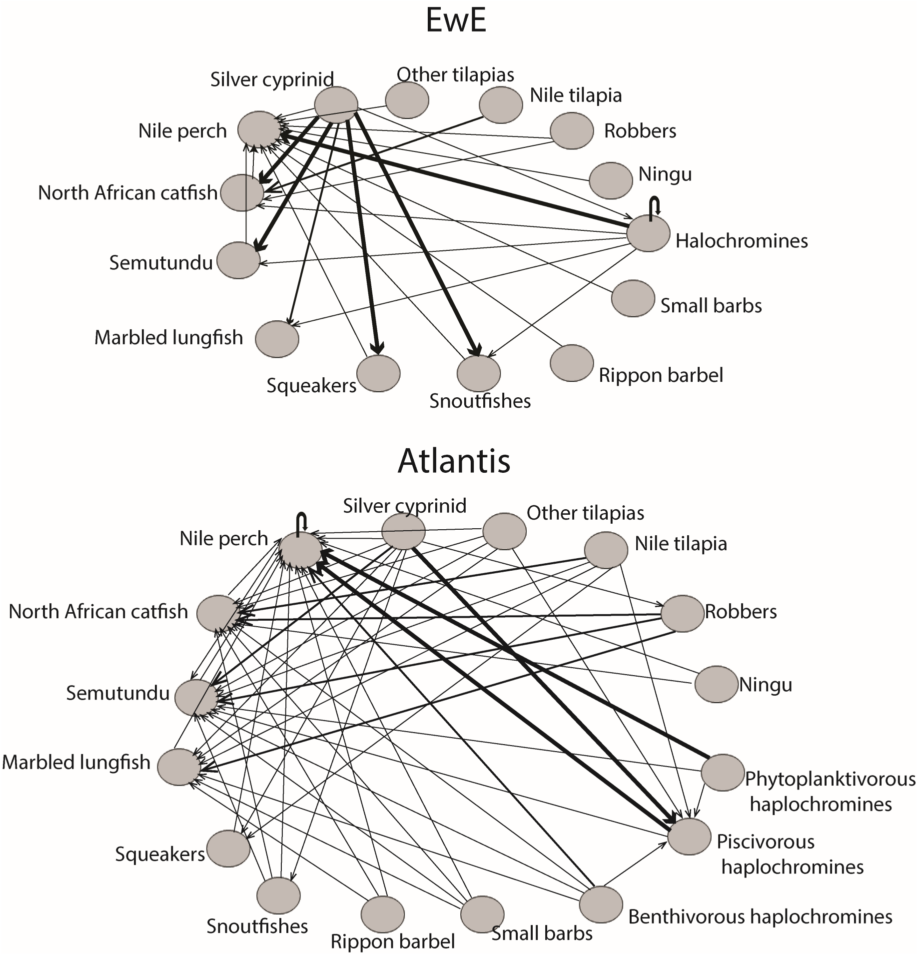

Figure 11.2: Schematic representation of predation interactions in EwE and Atlantis models of Lake Victoria. Model groups shown here are only for fish species, which are represented in both models, to ease comparisons. Note that arrows move towards the predators and arrow thickness is consistent with the contribution of prey to the predator's diet. Thick and black arrows indicate that the prey species makes up more than 30% of the predator's diet, while thin arrows indicate that the prey species makes up less than 5% of the predator's diet. From Natugonza et al. (2019).

Table 11.1: Functional groups used in Lake Victoria EwE and Atlantis models. For the fish groups, information on common and scientific names, occurrence, habitat, and feeding mode is retrieved from Fishbase: `www.fishbase.org`, version (10/2018). Abbreviations stand for: FF (forage fish); HTO (high turnover); and HHI (high commercial value).

Species/taxa included	Common name	Occurrence	Habitat	Feeding mode	Atlantis	EwE	FF	HTO	HCV
Haliaeetus vocifer, Ceryle rudis, Cormorants	Fish-eating birds		Native Domain	Piscivore	Yes	Yes			
Crocodylus niloticus	Crocodiles	Native	Domain	Carnivore	Yes	Yes			
Lates niloticus	Nile perch	Introduced	Demersal	Piscivore	Yes	Yes	No	Yes	Yes
Clarias gariepinus	North African catfish	Native	Benthopelagic	Omnivore	Yes	Yes	No	No	No
Bagrus docmak	Semutundu	Native	Benthopelagic	Omnivore	Yes	Yes	No	No	No
Protopterus aethiopicus	Marbled lungfish	Native	Demersal	Molluscivore	Yes	Yes	No	No	No
Synodontis victoriae, S. afrofisheri	Squeakers	Native	Benthopelagic	Insectivore	Yes	Yes	No	No	No
Momyrus kanume, Gnathonemus spp.	Snout fishes	Native	Demersal	Insectivore	Yes	Yes	No	No	No
Schilbe intermedius	Silver catfish	Native	Pelagic	Piscivore	Yes	Yes	No	No	No
Labeobarbus altianalis	Rippon barbell	Native	Benthopelagic	Omnivore	Yes	Yes	No	No	No
Enteromiuss spp.	Small barbs	Native	Benthopelagic	Omnivore	Yes	Yes	Yes	No	No
Brycinus jacksoni, B. sadleri	Robbers	Native	Pelagic	Omnivore	Yes	Yes	Yes	No	No
Labeo victorianus	Ningu	Native	Demersal	Phytoplanktivore	Yes	Yes	No	No	No
Haplochromis spp.	Haplochromines	Native	Benthopelagic	Variable[a]	3 groups	1 group	Yes	Yes	No
Rastrineobola argentea	Silver cyprinid	Native	Pelagic (schooling)	zooplanktivore	Yes	Yes	Yes	Yes	Yes
Oreochromis niloticus	Nile tilapia	Introduced	Benthopelagic	Omnivore	Yes	Yes	No	No	Yes
O. esculentus and *O. variabilis*	Other tilapias	Native	Benthopelagic	Herbivore	Yes	Yes	No	No	No
Caridina nilotica	Shrimp	Native	Demersal	Detritivore	Yes	Yes			
Macroinvertebrates	Insects and molluscs		Mainly demersal	Detritivore	5 groups	1 group			
Microzooplankton, Mesozooplankton	Zooplankton		Pelagic	Phytoplanktivore	2 groups	1 group			
Algal groups	Phytoplankton		Pelagic		4 groups	1 group			
Periphyton, epiphyton	Benthic producers		Domain		No	Yes			
Pelagic and sediment bacteria	Bacteria				Yes	No			
Labile and refractory detritus	Detritus		Benthic		2groups	1 group			

[a] More than 15 trophic groups (Witte and van Densen, 1995)

11.2.3 Model uncertainty

The sensitivity of model outputs to input parameters and data have not been explicitly analysed for both EwE and Atlantis models of Lake Victoria. Instead, model uncertainty has been assessed using proxy indicators, including pedigree criteria (Christensen and Walters, 2004a), model fit to time series data (Audzijonyte et al., 2017a; Scott et al., 2015), and prediction skill (Olsen et al., 2016; Stow et al., 2009). The pedigree criterion involves estimation of an index, the pedigree index (PI), showing whether the parameters are of low quality (uncertain), i.e., guestimates (PI =0) or of high quality, i.e., parameters arising from an accurate sampling of the modelled system (PI = 1). Skill assessment involves comparing model predictions with data using multiple metrics that measure both scale mismatch (magnitude of the difference between predictions and observations) and correlation (similarity of trends). The commonly used metrics are modelling efficiency (MEF), reliability index (RI), and coefficient of variation (CV), for scale mismatch, and Pearson correlation (r) for trend comparison (Ortega-Cisneros et al., 2017; Sturludottir et al., 2018).

The PI of Lake Victoria's EwE model is 0.53 (Natugonza et al., 2020). Based on PI values of all EwE models published in EcoBase (0.1-0.7), this value is suggestive of intermediate parameter/model quality (Morissette, 2007). Regarding prediction skill, Natugonza et al. (2020) used three metrics: MEF, RI, and r. The values of these metrics were positive and close to 1 for most of the groups, suggesting good fit to the reference data. Exceptions were the 'robbers', haplochromines, and other tilapias (see group definitions in Table 11.1), where values of MEF were negative; nonetheless, r values for haplochromines and other tilapias were positive, suggesting that the simulated biomass trajectories had the same trend as reference data despite the differences in magnitude. Also, the model simulated diet composition that somewhat resembled data from stomach content analyses (Natugonza et al., 2020). For Atlantis model, Nyamweya et al. (2016b) also used multiple metrics (MEF, r, and CV) to evaluate model prediction skill. All metrics were positive; also, for most of the functional group, values were close to 1, suggesting that model predic-

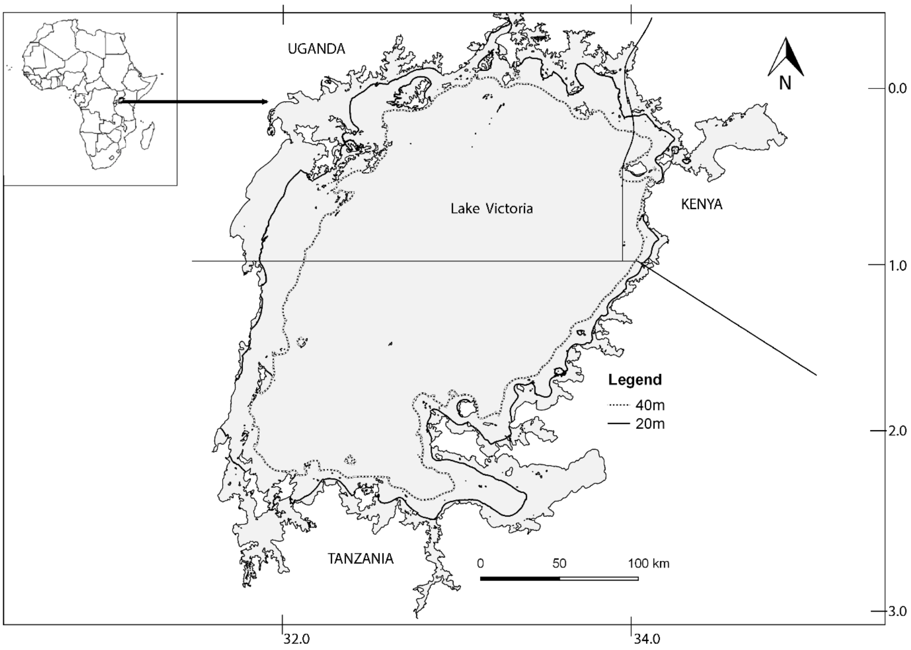

Figure 11.3: Lake Victoria in East Africa (extent of the modelled area). Depth contours show inshore (<20 m), coastal (20-40 m) and deep (>40 m) areas

tions were consistent with data (both in terms of magnitude and trend). Besides, the model simulates distributions of nutrients, primary production, and main commercial fish species that match well with the available data (Hecky et al., 2010), suggesting that the model also captures well the heterogeneous nature of the Lake Victoria ecosystem.

11.2.4 Study design

EwE includes a fisheries optimization routine, the optimal policy search (OPS), which is used in a calibrated model to search for long-term, gear-specific fishing effort (optimal fishing effort) that can maximize a user-defined management objective (Christensen and Walters, 2004a). Atlantis does not have a similar computationally-flexible procedure. For purposes of model comparison, a more straightforward approach, similar to that used in Forrest et al. (2015), was used. The OPS procedure was applied in EwE, where different weightings and objectives could be easily defined, and the resulting optimal fishing effort levels were then applied in both EwE and Atlantis to evaluate long-term changes in ecosystem structure. Also, EwE and Atlantis differ substantially in the way fleets are modelled. In this study, variations in predictions due to fleet representation and dynamics in Atlantis (Audzijonyte et al., 2017a) were minimised by controlling fishing mortality during projections at the level of functional groups.

11.2.5 Optimal policy search

The gear-specific optimal fishing rates for each objective were simulated using the OPS routine of the EwE software version 6.5 (freely available at `https://ecopath.org/`). The OPS routine uses a calibrated EwE model to probe an n-dimensional parameter space (a response surface) for zones that yield increased benefits, where n is equal to the number of gear types in the model (Christensen and Walters, 2004a). The routine uses the non-linear Davidon-Fletcher-Powell optimization procedure (Fletcher, 1987) to improve an objective function by changing relative fishing rates iteratively. This procedure uses a "conjugate-gradient" method, testing alternative parameter values to approximate the objective function locally as a quadratic function of the parameter values, which are updated stepwise. An optimal fleet-effort solution is generated that maximizes benefits over the simulation time horizon and manipulates the ecosystem into a maximally beneficial form. The benefits are defined by a multi-criterion objective function (OBJ), which, in our study, contained terms representing economic, social, and conservation (ecosystem maturity and biomass diversity) benefits as shown in Equation 11.1.

$$OBJ = W_{E}con\cdot\sum NPV_{ij} + W_{S}oc\cdot\sum Jobs_{jt} + W_{E}col\cdot\sum \frac{B}{P}_{it} + W_{B}iod\cdot\sum Q90_{ij} \tag{11.1}$$

where, W_{Econ}, W_{Soc}, W_{Ecol} and W_{Biod} are, respectively, relative weightings applied to economic, social, ecosystem maturity and biomass diversity criteria (see below). The summed terms evaluate the benefits of the harvest plan across each functional group i, gear type j, and simulation time step t; the latter is set by default at monthly intervals. For single-objective optimization, a weight of 1 is placed on either economic, social, or conservation criterion, and zero on all others. For a combined objective (mixed objective optimization), similar or different weights can be applied to the objectives, depending on the societal objectives (see below).

Maximizing economic benefits

The net present value (NPV) is the default metric for assessing the economic benefits of a harvest plan in EwE. The form of discounting is based on the intergenerational discounting approach (Sumaila, 2004; Sumaila and Walters, 2005). This approach considers a continuous interlacing of generations, where the discounting of future benefits is countered each year by the addition of 1/G stakeholders (Equation 11.2; G is generation time=20 years). These new entrants bring with them a renewed perspective on future earnings, partially resetting the discounting clock. NPV is calculated using the formula:

$$NPV = \begin{cases} \sum_{t=0}^{T} NB_t(d^t + \frac{d_{fg}\cdot d^{t-1}}{G}[\frac{1-(\frac{d_{fg}}{d})^t}{1-\frac{d_{fg}}{d}}]) & \text{if} \quad \delta \neq \delta_{fg} \\ \sum_{t=0}^{T} \frac{NB_t}{(1+\delta)^t} \cdot (1+\frac{t}{G}) & \text{otherwise.} \end{cases} \tag{11.2}$$

where, NB is net benefits (gross income minus operating costs) accruing in year t; d is a standard annual discount factor, calculated as

$$d = \frac{1}{1+\delta} \tag{11.3}$$

(δ is the annual discount rate); d_{fg} is a discount factor to evaluate benefits destined for future generations, *fg*, calculated as

$$d_{fg} = \frac{1}{1+\delta_{fg}} \tag{11.4}$$

With the IG approach, future benefits are less discounted and higher NPV is assigned to policies that spread out benefits over a long time (Sumaila, 2004). Data are needed on the catch value for each species/functional group and profitability for each gear (Table 11.2). All optimizations were run with the default discount rate of 0.04/year; also, the optimizations were set to the mode that allows the gears to operate under economic loss. The rationale is that although a gear can operate under unprofitable conditions, the sum of profits across all gears can compensate for those losses suffered by some gears (Christensen and Walters, 2004a).

Maximizing social benefits (employment)

EwE contains only simplified fishing fleet-dynamics, where the fishery yield is used as a proxy for employment. Under the social criterion, harvest benefits are assessed as the total number of jobs directly produced by the harvest plan, summed across each gear type and simulation year. The number of jobs is calculated as the sum product of catch value (calculated internally in Ecosim, Table 11.2) and jobs per-unit-catch-value (as input on the policy search form). In this study, Jobs-per-unit-catch-value for all gear types was assumed to equal 1, so that total employment was

Table 11.2: Landed value, total cost, and profitability of the 12 fishing gears in the Lake Victoria EwE model. These are estimated internally within EwE using input data on catch value for each species/functional group (US dollar/unit biomass, Supplementary Table S3) and the proportion of fixed and operational variable costs (Supplementary Table S4). Values in parentheses are used in the "penalty scenarios", where the cost of fishing using illegal gears is increased so that no profit is realised

Gear	Landed value (US$ thousand km^{-2})	Total cost (US$ thousand km^{-2})	Profitability (%)
Longline (motorised)	1.52	1.04	34.0
Longline (paddled)	0.28	0.19	31.0
Gillnet (motorised)	1.43	0.83	42.0
Gillnet (paddled)	0.35	0.28	19.5
Small seine (motorised)	2.22	1.35	40.0
Small seine (paddled)	0.88	0.50	43.0
Beach seine	2.52	1.01 (2.52)	60.0 (0.0)
Monofilament (motorised)	0.64	0.22 (0.64)	64.0 (0.0)
Monofilament (paddled)	1.57	0.85 (1.57)	45.6 (0.0)
Cast net	0.19	0.07 (0.19)	62.5 (0.0)
Hand line	0.24	0.12	50.6
Scoop net	0.12	0.08 (0.12)	31.5 (0.0)

proportional to catch value (Ainsworth and Pitcher, 2010; Christensen and Walters, 2004b).

Maximizing ecosystem structure

The objective function maximizes the overall biomass to production ratio (B/P) by summing B/P values across functional groups and simulation years throughout the model and is based on one of (Odum, 1969) measures of ecosystem maturity. Ratios of production to biomass (P/B = Z, /year) are available for all functional groupings as part of the standard Ecopath parameters (Supplementary Table S1). The inverse ratio, B/P, expresses average longevity (unit year) and is used as a biomass weighting factor for the optimization of "ecosystem structure". Increasing this index leads to an increase in the biomass of long-lived species; hence, index is used as a measure of ecosystem health and structure (Christensen, 1995).

Maximizing biomass diversity

The objective function maximizes the Q90 biodiversity index of Ainsworth and Pitcher (2006). Under this criterion, biodiversity refers to organismal diversity at the level of 'species' functional groups. The Q90 index is a variant on Kempton's Q index (Kempton and Tylor, 1976), and represents the interdecile slope of the cumulative species log-abundance curve (Equation 11.5). Each functional group in the EwE model represents one 'species', and the functional group biomass substitutes for abundance (i.e., biomass serves as a proxy for the number of individuals in that species). Q90 is calculates as

$$Q90 = \frac{0.8 \cdot S}{\log \frac{R_1}{R2}} \tag{11.5}$$

where, S is the total number of functional groups in the model, $R1$ and $R2$ are the representative biomass values of the 10^{th} and 90^{th} percentiles in the cumulative abundance distribution as shown in Equations 11.6 and 11.7, respectively.

$$\sum_{1}^{R_1-1} n_R < 0.1 \cdot S \leq \sum_{1}^{R_1} n_R \tag{11.6}$$

$$\sum_{1}^{R_2-1} n_R < 0.9 \cdot S \leq \sum_{1}^{R_2} n_R \tag{11.7}$$

where, nR is the total number of functional groups with abundance R.

Maximizing mixed objectives

The objective function maximizes, simultaneously, the weighted sum of NPV, catch value, B/P, and Q90 biodiversity index. Identifying ideal weights for a combined objective is not straight forward. Optimisations were first run by placing equal weights on all the objectives, i.e., "mixed objective with equal weights (1:1:1:1)" (Table 11.3). However, this criterion means that the relative improvement in harvest benefits over the baseline is equally weighted. Whereas this criterion can still give useful information on trade-off boundaries, there is no inherent comparability between the objectives (Christensen and Walters, 2004a). This weighting approach mostly affects the conservation criteria as it is easier to increase revenue or jobs than it is to restructure the ecosystem (Cameron Ainsworth, pers. com.). Therefore, in addition to the mixed objective with equal weights, other scenarios were included, testing, sequentially, the effect of higher weighting (in multiples of 10) on conservation objectives (B/P and Q90 index) (Table 11.3). This weighing approach on conservation objectives is comparable to those used in previous studies (Ainsworth et al., 2004; Ainsworth and Pitcher, 2010; Buchary et al., 2002; Mackinson, 2002; Zeller and Freire, 2002). Also, because of the relative importance of Lake Victoria fisheries to employment and livelihoods (Johnson and Bakaaki, 2016), the effect of higher weighting on social objectives (jobs) was tested using the same approach as conservation objectives, i.e., using weights 10x and 100x higher on catch value than other objectives (Table 11.3).

Table 11.3: Weighting criteria for different objectives used in the optimal policy search (OPS). Objectives are arranged as NPV:catch value:B/P:Q90.

Objective metric	Weighting criteria	Description
Net present value (NPV)	1:0:0:0	Single objective optimisation for economic value
Catch value (jobs)	0:1:0:0	Single objective optimization for social value
Biomass/Production (B/P)	0:0:1:0	Single objective optimization for ecosystem structure
Q90 index	0:0:0:1	Single objective optimization for biomass diversity
Mixed objective (NPV + B/P)	1:0:1:0	Combined optimization for economic value and ecosystem structure
Mixed objective (equal weighting)	1:1:1:1	Combined optimization for all objectives, weighted equally
Mixed objective (10·B/P+10·Q90)	1:1:10:10	Combined optimization for all objectives; weight on B/P and Q90 index 10x higher than others
Mixed objective (100·B/P+100·Q90)	1:1:100:100	Combined optimization for all objectives; weight on B/P and Q90 index 100x higher than others
Mixed objective (10·catch value)	1:10:1:1	Combined optimization for all objectives; weight on employment 10x higher than others
Mixed objective (100·catch value)	1:100:1:1	Combined optimization for all objectives; weight on employment 100x higher than others

11.2.6 Effect of illegal gears

Gears that are banned from the lake (for example, beach seine, monofilament gillnet, cast net) are the most profitable (Supplementary Table S4). These gears target high-value fisheries, mainly Nile perch and Nile tilapia (Luomba et al., 2018; Onyango, 2018). In the Kenyan part of the lake, for instance, the average catch per fisherman per day using beach seine is about 70kg (equivalent to KES 5,487,680 or US$ 54,800 per fisherman per year) compared to 42kg (equivalent to KES 1,394,722 or US$ 13,940 per fisherman per year) and 18kg (equivalent to KES 3,024,756 or US$ 30,247 per fisherman per year) using the allowed longlines and gillnets, respectively (Onyango, 2018). The cost of fishing (both fixed costs and operational variable costs) are also lowest for beach seines compared the other gears.

Christensen and Walters (2004b) showed that it may not be the most profitable gear or the gear with the highest landed value that has its fishing effort increased after optimization. However, results from most case studies (Araújo et al., 2008; Cheung and Sumaila, 2008; Heymans et al., 2009) show that the optimization always decreases fishing effort for costly gears and increases fishing effort for more profitable gears, especially those targeting high-value fisheries. In the case of Lake Victoria, the optimization with would likely increase the fishing effort of illegal gears (with profitability ranging between 50% and 65%) and decrease fishing effort for the right gears, where profitability is two times lower than the illegal gears (Supplementary Table S4). To test this, a penalty was added to all illegal gears by adjusting input data in Supplementary Table S4 such that the profitability of the illegal gears was zero. This scenario is analogous to fishing at a bioeconomic equilibrium (BE) point, where all the revenue is spent to cover the costs of fishing (Walters et al., 2005).

11.2.7 Simulation procedure and visualization of outputs

Non-linear optimization methods can converge to a local maximum (Fletcher, 1987). To avoid such solutions in non-linear optimizations, all optimizations began from a random location on the response surface, where fishing mortality exerted by each gear type is randomly set, and repeated the optimization for each objective ten times. Results are presented as mean change in harvest benefits from the baseline and standard deviations showing the range of all possible values.

After the OPS, both EwE and Atlantis were projected forward using fishing effort levels obtained for each objective (Supplementary Tables S5 and S6). Projections in Atlantis were conducted by changing the 2015 “end-state” fishing mortality (baseline) for each exploited fish group (Supplementary Tables S5 and S6) such that the relative change (either increase or decrease) in fishing effort from the 2015 baseline was proportional to the change in fishing effort for the same group in EwE after optimization.

EwE and Atlantis generate extensive outputs. Biomass predictions were aggregated into annual trends without spatial and size- and age-structure considerations to keep comparisons between models manageable. Changes in biomass of individual fish groups were analysed at the end of 20 years relative to the 2015 baseline values (Natugonza et al., 2019) according to the formula: (B_start/B_end)-1, where B_start and B_end are biomass values at the start and end of the projection, respectively. A value of zero indicated no change in biomass relative to baseline. The criteria used in the interpretation of results was similar to that in (Natugonza et al., 2019): predictions with the similar direction indicated consistent qualitative results, while those with similar direction and magnitude indicated consistent quantitative results.

11.3 Results

11.3.1 Objective optimisations

When optimizing for economic value alone, an improvement was observed in economic benefits and ecosystem structure only, in the order of 30-80%, and the benefits were seen to be higher when a penalty was applied to illegal gears compared to scenarios with no penalty on illegal gears (Figure

11.4). This objective showed that social benefits would reduce by 10-25% from the baseline; the reduction would be highest where illegal gears are penalised. This trend was the same across single objective optimization for ecosystem structure and biomass diversity (Figure 11.4c-d), and in all mixed objective optimisations, except where employment was given a higher weight than other objectives (Figure 11.4e-j).

Single-objective optimization for employment showed no change in all objective metrics, except for economic value, which slightly increased relative to the baseline (Figure 11.4b). The increase in economic value was also slightly higher under the penalty scenario compared to the no-penalty scenario. This trend was generally the same across mixed objective optimizations with a higher weight on social criterion (Figure 11.4i-j), except in the model run where the weight on the social objective was 10 times higher compared to other objectives. In this model run, results were comparable to those from single-objective optimization for economic value, except that there was no reduction in catch value from the baseline.

When optimizing for ecosystem structure, the addition of a penalty on illegal gears led to the most considerable reduction in economic value (Figure 11.4c). This scenario is associated with overfishing of the leading commercial fish species, Nile perch and silver cyprinid (see below), after the fishing effort of illegal gears is redistributed to short-lived species. However, the no-penalty scenarios led to a 20-30% improvement in both ecosystem structure and economic value. This trend was the same across mixed objective optimisations with a higher weight on ecosystem structure, except that the economic value decreased, while ecosystem structure improved, in both penalty and no-penalty scenarios (Figure 11.4g-h).

11.3.2 Gear configuration

Optimization for economic, social, or conservation objectives showed that the fishing gear would need restructuring to achieve a specific goal (Figure 11.5). Generally, the fishing effort would be increased in most gears to maximize social benefits, and reduced in most gears to maximize economic and conservation objectives. With a few exceptions, the fishing

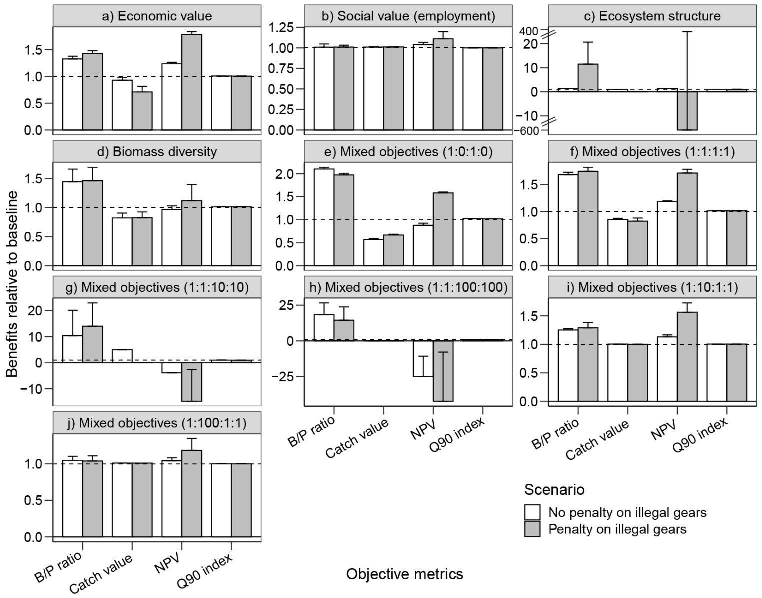

Figure 11.4: Results from single-objective optimizations for economic, social and conservation benefits. Values are expressed relative to baseline values from Ecopath model; values below and above the dotted lines show decrease and increase from the baseline, respectively. NPV stands for net present value, while B/P is biomass to production ratio.

effort increased in gears targeting high-value fisheries and decreased in gears either targeting low-value fishes (in terms of price per unit biomass) or where the operational costs (Supplementary Table S4) for using such gears were high. When optimizing for economic benefits, for instance, the fishing effort uniformly decreased in the small seine (motorised), scoop net, monofilament gillnet (both paddle and motorised), and multi-filament gillnet (paddle) (Figure 11.5a). Except for the latter gear, which targets high-value species (Nile perch and Nile tilapia), the rest of the gear categories, despite being profitable, are dominated by the catches of low-value species (for example, silver cyprinid and haplochromines). The reduction in fishing effort of multi-filament gillnet (paddle) is associated with the high operational costs; note that this the least profitable gears (Supplementary Table S4).

The influence of profitability on gear restructuring was apparent in the illegal gears when optimizing for economic benefits. The model showed an increase in the fishing effort of beach seine, cast net, and monofilament gillnet when operated without a penalty. However, the fishing effort decreased substantially (i.e., by 80-100% from the baseline) when a penalty was applied (Figure 11.5a). Although fishing effort decreased for the monofilament gillnet (paddle) and scoop nets, which are also an illegal gear, in both scenarios, the magnitude was two times higher when a penalty was applied compared to the scenario where no-penalty was applied.

Optimizations considering conservation benefits (ecosystem structure and biomass diversity) showed a reduction in fishing effort in most of the gears, especially when a penalty was applied to illegal gears (Figure 11.5c-d). Exceptions were beach seine, scoop net, small seine longline (motorised), whose effort increased when optimizing for ecosystem structure. The decrease in the fishing effort was more pronounced when optimising for ecosystem in combination with the economic objective (Figure 11.5e-f). Mixed optimisations with a higher weight on ecosystem structure and biomass diversity than other objectives led to mixed results, but generally, fishing effort increased in gear targeting the main commer-

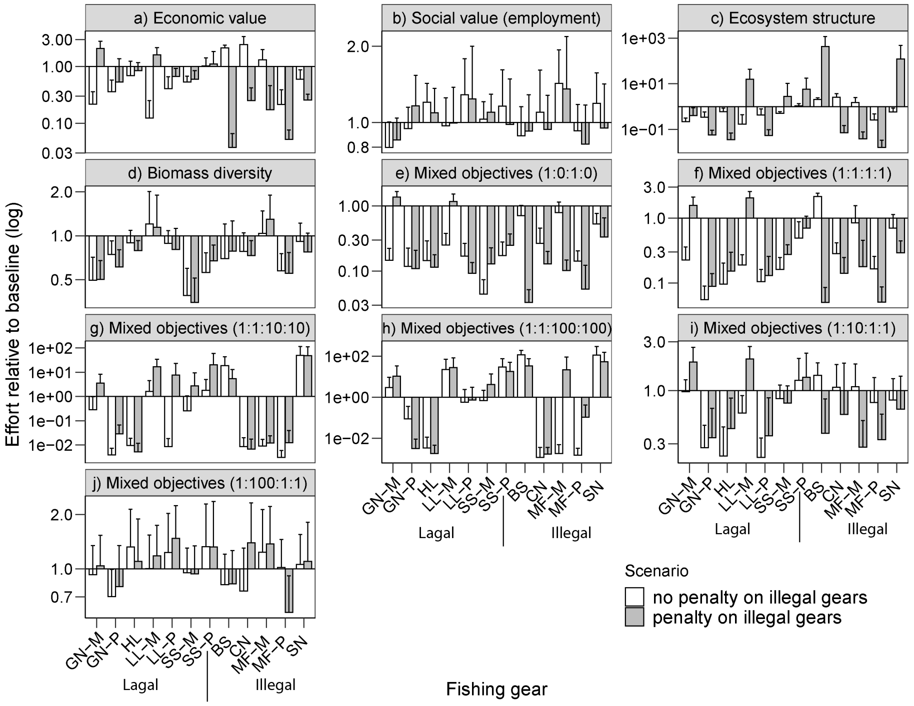

Figure 11.5: Gear effort configurations required to maximize economic, social and conservation benefits. All values are expressed relative to the Ecopath baseline run; values below and above 1 show decrease and increase in effort from the baseline, respectively. Error bars indicate the range of values obtained from 10 runs for each criterion.

cial fisheries, for example, gillnet, longline, and beach seine, which target Nile perch, and small seine, which target silver cyprinid (Figure 11.5g-h). Mixed objective optimisation with a slightly higher weight (ten) on social criterion produced results that were similar to the single-objective optimization for economic value, with fishing effort decreasing in most gear (Figure 11.5i). However, when the weight on social criterion was increased 100fold relative to other objectives, results were comparable to single-objective optimisation for social value, with fishing effort increasing in most gears, especially those targeting high-value fisheries (Figure 11.5j).

11.3.3 Species-level trade-offs

The two ecosystem models generally gave contrasting biomass predictions, mainly when no penalty was applied to the illegal gears (Figure 11.6). Exceptions were the species/groups with strong diet interactions (for example, Nile perch and haplochromines) and other demersal and benthopelagic groups (for example, North African catfish, semutundu, Ningu, other tilapias, Rippon barbel, silver catfish, and squeakers), where biomass trends (direction of change) were relatively consistent, despite the differences in the magnitude of predictions. For these demersal and benthopelagic groups, biomass decreased in most optimisations, but the decrease was more pronounced in EwE than in Atlantis. For Nile perch and haplochromines, single-objective optimizations resulted in about 25% increase and 25-50% reduction in biomass, respectively, in EwE, while Atlantis showed either small (<5%) or no change in biomass of these groups relative to the baseline (Figure 11.6). However, with a few exceptions, especially where a higher weight was added to the social criterion, mixed objective optimizations resulted in consistent biomass trends for Nile perch, which increased, and haplochromines, which decreased, across models. For example, mixed optimisations with a higher weight on economic and conservation objectives resulted in 1-2fold increase biomass of Nile perch, which ultimately collapsed the haplochromines. For the two other commercial fisheries (silver cyprinid and Nile tilapia), all the optimizations were associated with an increase in biomass in EwE and either a decrease (for silver cyprinid) or no change (for Nile tilapia) in Atlantis. Most of the native species in Atlantis were almost collapsed at the end of the historical reconstruction simulation, making them unresponsive to changes in fishing effort, except in scenarios where changes were substantially lower than baseline effort (Nyamweya et al., 2017).

When a penalty was applied to the illegal gears, biomass predictions for Nile perch and haplochromines were consistent across models even in single-objective optimisation (Figure 11.7). Both models showed that maximizing economic value would result in nearly 50% increase in the biomass of Nile perch relative to the baseline, which is two times higher

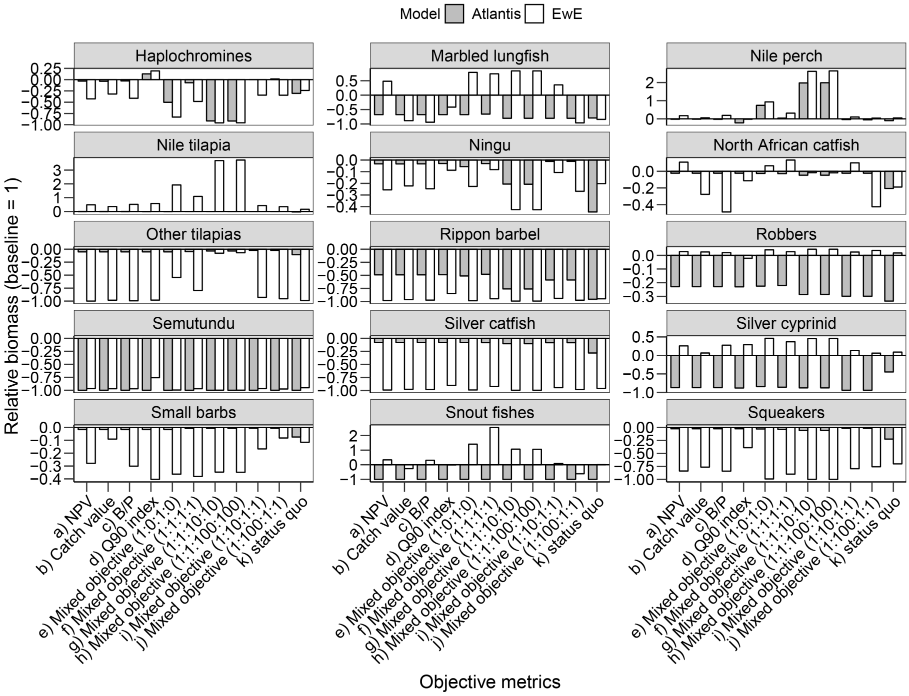

Figure 11.6: Biomass change (2034 relative to 2014 baseline) for the different functional groups as predicted by EwE and Atlantis when no penalty is applied to the illegal gears during the optimal fishing policy search. Bars below and above the zero line indicate decrease and increase in biomass from the baseline, respectively. Bars on the same side of the zero line (either positive or negative) indicate consistent qualitative results across models. Results of the 2015 status quo scenario are included for comparison because the ecosystem would be expected to change under any level of fishing, including the baseline fishing rates.

compared to the no-penalty scenario, and a decrease in the biomass of haplochromines. However, the magnitude of change in haplochromines was two times higher in EwE than Atlantis. Optimization for social benefits led to variable results, but generally, biomass decreased for most fish groups. Optimization for ecosystem structure led to the most significant change in the primary commercial fisheries, resulting in a collapse of Nile perch and silver cyprinid in both models. This objective was associated with the recovery of most demersal and benthopelagic groups (marbled lungfish, North African catfish, semutundu, Rippon barbell, silver catfish, Robbers, squeakers, and snout fishes), especially in EwE (Figure 11.7), majority of which were in a collapsed state at the start of the simulation (Natugonza et al., 2020). Optimization for biomass diversity also resulted in a consistent increase and decrease in the biomass of Nile perch and haplochromines, respectively, in both models. The trends for other major fisheries, such as silver cyprinid and Nile tilapia, however, were different, with biomass generally increasing in EwE and decreasing in Atlantis. Mixed objective optimization, especially those emphasizing economic value and ecosystem structure, resulted in biomass changes comparable to those from single-objective optimization for economic value.

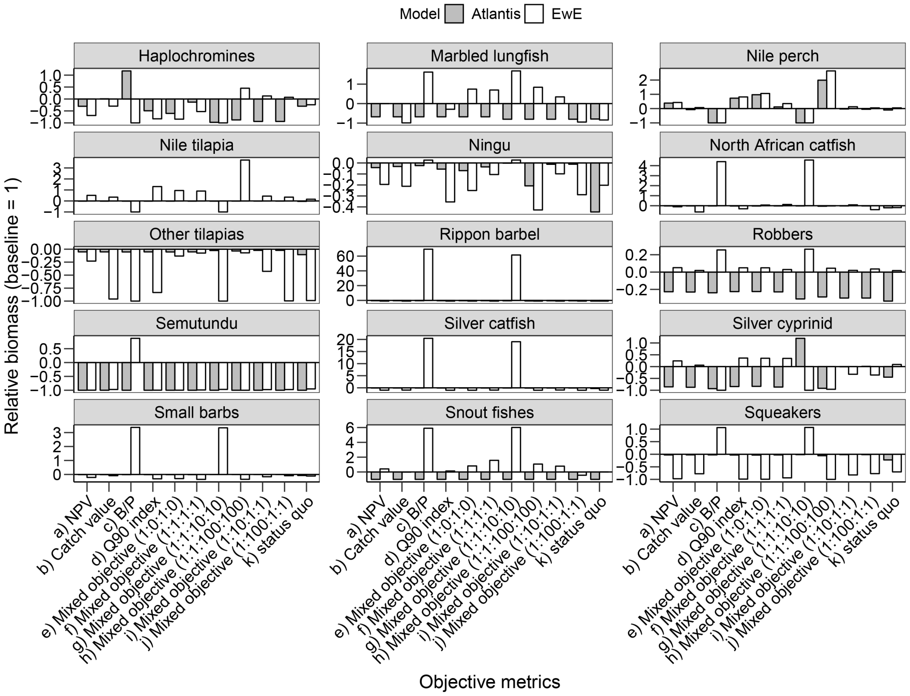

Figure 11.7: As for Figure 11.6, but a penalty is applied to the illegal gears during the optimal fishing policy search.

11.4 Discussion

This study analysed trade-offs between management objectives for a fishery with limited alternative livelihood options. The study involved the use of two structurally-distinct ecosystem modelling frameworks, EwE and Atlantis. Illegal gears were penalised in one of the scenarios by increasing fishing costs until fishing was no longer profitable. This scenario was based on the assumption that in the real world, managers can intensify enforcement and increase fines on the impounded illegal gear to a level where fishers make no profit from fishing illegal gears Mboya (2013). Results showed profit maximization to be more compatible with conservation objectives than is the maximization of catch value (or employment). Penalising illegal gears resulted in the highest economic benefits and biomass of main commercial fish species, but not when the objective was to maximize ecosystem structure exclusively. However, to maximize economic value and maintain ecosystem structure, fishing effort (and potential yield) would be reduced in almost every fishing sector/fleet. These findings are consistent with those from both empirical and modelling studies that have compared actual and potential outcomes of fisheries management objectives (Ainsworth and Pitcher, 2010; Andersen et al., 2015; Araújo et al., 2008; Cheung and Sumaila, 2008; Christensen and Walters, 2004b; Forrest et al., 2015; Heymans et al., 2009; Hilborn, 2007,1).

11.4.1 Trade-offs among objectives

Fisheries managers are more often interested in the stock status and fishing rates that can maintain harvested populations at or above target biomass levels while avoiding overfishing thresholds (Smith et al., 2007). However, the work presented here is also vital as it helps to gain valuable insight into the risks and benefits associated with alternative policies. This study revealed that trade-offs exist between socio-economic and conservation objectives and that the magnitude and severity of the trade-offs vary, depending on the weight given to each objective. For example, a higher weight on employment would possibly collapse the main commercial fish species in the long term due to the associated increase in fishing effort of most gears. A higher weight on the conservation objective would lead to little, more profitable catch, due to the reduction in fishing effort of most gears, but at the expense of livelihoods of riparian communities. These findings underscore the importance of i) identifying management objectives before choosing fleet capacity, ii) considering trade-offs when choosing between multiple ecosystem-level goals, and iii) stakeholder involvement in defining management objectives and evaluating trade-offs.

The benefits from conservation-oriented objectives are known: the risk of depletion is reduced, while biodiversity and ecosystem maturity are improved by protecting the intrinsically vulnerable ecological groups (Christensen, 1998). For Lake Victoria, model outputs show that achieving this objective would require a reduction in fishing effort of gears targeting mostly the demersal groups (marbled lungfish, Ningu, most catfishes and snout fish), especially when a penalty is applied to illegal gears. These fisheries are less dominant in catches, making up less than 15% of the total landings, and yet the objective still requires a reduction in catch. The trade-off here seems to emanate from the mixed nature of the fishery, where one single gear harvests more than one fish group. The gears that harvest the less productive demersal species (for example, gillnet, longline, and handline), for instance, are the same for the highly productive and high catch-value species (Nile perch and Nile tilapia). The catches of highly productive fisheries would, therefore, be sacrificed to protect the vulnerable groups, which has been a hindrance to single-stock MSY targets in multi-species fisheries (Walters et al., 2005).

The reduction in catches of Nile perch and Nile tilapia when maximizing conservation objectives, however, does not affect the net economic value. Instead, the two objectives (economic value and ecosystem structure) can be achieved concurrently by fishing less, similar to the concept of "pretty good yield" (Hilborn, 2010). In practice, however, fishing of haplochromines, the main prey for Nile perch, would need to be reduced to avoid drastic fluctuations when the fishing pressure on Nile perch is reduced (Natugonza et al., 2020; Nyamweya et al., 2017).

Nile perch supports largest commercial fishery in Lake Victoria in terms of catch value. By 2015, Nile perch catches constituted only 18% of the total annual fish landings (LVFO, 2016b). However, Nile perch landings were worth the US$ 307 million, i.e., 52% of the total revenues from the entire fishery, from direct sales at landing sites (LVFO, 2016b). This species is also a valuable export commodity, with exports mainly to Europe worth the US$ 300 million per year (LVFO, 2016a). The trade-off associated with maximizing ecosystem structure, involving the collapse of Nile perch stock, mainly when a penalty is applied to the illegal gears, seems to be severe and would have far-reaching socio-economic implications (Johnson and Bakaaki, 2016).

The current socio-economic set-up around Lake Victoria, where most fishers survive on daily fishing and regularly migrate to new fishing villages when catches decline (Johnson and Bakaaki, 2016; Nunan, 2014a), demand that employment creation is one of the objectives for management. Between 2000 and 2014, the total number of fishers increased from 60,000 to >210,000. The total number of fishing crafts using outboard engine increased from 4,000 to 21,600. While fishing crafts using paddles remained unchanged, the total number of gillnets doubled, and the number of longline hooks increased from 3.5 to 14 million (LVFO, 2016c). The increase in the use of outboard engines suggests that fishers are extending to deeper offshore waters. In reality, the social objective already has a higher weight. Although a higher weight on social criterion did not negatively affect economic value and ecosystem structure, the continuous increase in fishing capacity still poses a danger of overexploiting fisheries (Mangeni-Sande et al., 2018; Mkumbo and Marshall, 2015; Njiru et al., 2010). The observed decline in catch rates over the past decade may be an indication that fishing capacity has reached the upper limit (LVFO, 2016b).

Whereas economic and conservation objectives can be achieved concurrently, reducing fishing effort in a fishery with more than 200,000 fishers, along a 7,142 km shoreline, would not be straightforward. Several attempts have been made in the past, particularly the measures in the Regional Plan of Action on fishing capacity (RPOA-2), which was adopted in 2007 (LVFO, 2007a). However, these measures have not been successful as fishing capacity continued to soar (Mulanda et al., 2020). This continuous increase in fishing capacity has been attributed to the limited resources for effective policing (Mkumbo and Marshall, 2015; Mulanda et al., 2020), but this trend could also be related to the social cost of effectively curtailing fishing effort. On the Ugandan side of Lake Victoria, authorities have replaced beach management units (BMUs) with the military to restrict access and eliminate illegal gears (Glaser, 2018). The intervention seems to be working as seen from the improvement in harvested sizes of Nile perch (Anthony Taabu-Munyaho pers. comm.), but it could be short-lived. Elsewhere, studies have shown that a sole policing approach, without an alternative livelihood program, is never sufficient for fisheries that are already in a Malthusian overfishing state (Teh and Sumaila, 2007). Therefore, alternative livelihood plans are still needed for the affected fishers on Lake Victoria; otherwise, new versions of illegal fishing may emerge.

Applying a penalty to the illegal gears also has trade-offs, both positive and negative. The model showed that net economic benefits would be higher when a penalty is applied to illegal gear than a scenario where the profitability of illegal gears is unchecked. The assumption is that fishers do not continue fishing at a bioeconomic equilibrium point. The increase in net economic value is associated with the reduction in effort of beach seine, monofilament gillnets (motorised) and cast net, which releases pressure on Nile perch and its prey (haplochromines) and Nile tilapia. However, when the objective is set to maximize ecosystem structure, the penalty on illegal gears leads to the most considerable reduction in net economic and social benefits. The penalty causes the effort of longline (motorised) and beach seine (both targeting Nile perch) and small seine (targeting silver cyprinid) to be increased, while attempting to maximize biomass of long-lived species, which drives the two groups to extinction. The implications of the outcome for management are twofold. First, the effort of illegal gear may grow out of proportion, when a penalty is introduced to limit their profitability, since fishers may not be willing to work with less profit. Second, if management succeeds in eliminating illegal gears, the fishing effort should not necessarily be redirected to the right gears as this can cause overfishing of the new target fishery. Because the primary target species differ in each gear, an unplanned increase in effort of the right gears could also lead to overfishing of the target species. The current enforcement on the Ugandan side of the lake seems to be focusing more on undersized gears, and not on the excess numbers of the large gear. This strategy needs to be reconsidered because the life-history changes that may arise as evolutionary responses to intensive, size-selective fishing could rapidly and continuously destabilize and degrade the ecosystem (Kuparinen et al., 2016).

Application of these findings in a management context should take cognisance of the assumptions underlying the OPS in EwE as well as study-specific assumptions. First, the formulation of the multi-criterion objective function in EwE requires that all fishing sectors/gears cooperate to maximize the overall benefits of the fisheries (Christensen and Walters, 2004a). In some instances, however, the benefits of some fishing gears can be maximized at the expense of other gears, thereby affecting the resulting fleet-effort configuration, although the overall trade-off relationships are expected to remain valid. Second, when maximizing the social criterion, the assumption was that jobs-per-unit-catch-value for all gear types in the model were to equal 1, so that total employment was proportional to catch value. EwE coarsely handles employment estimates and provides only a rough estimate of employment benefits. Future investigations should consider using better estimates of employment rates per gear type, which may require surveys and interviews to consider both fisheries and other supporting sectors. Third, in the mixed objective optimisations, a simple benchmark was used by assigning relative weights to the objective metrics; in one scenario, for example, a weight of 1 was assigned to each of the economic, social, and ecological objectives. This weighting scheme, however, means that a scenario that doubles NPV, for example, would be worth the same to the overall objective score as a scenario that doubles the number of jobs or doubles the B/P ratio of the ecosystem. Yet, the units used to express benefits are different, and there is no inherent comparability between NPV, catch value and ecosystem maturity index. For example, a doubling of the B/P ratio would represent a dramatic change in ecosystem structure, whereas doubling NPV might be as simple as redistributing fishing effort to more profitable gear. To ensure an "even" mix between these objectives, optimisations were also ran using higher weights on ecological and social objectives. However, the choice of the weights was random, and a large part of trade-off space remains unexplored. In a management context, the parameter space will need to be fully explored, and the ideal weightings to use on these objectives is a matter of societal values.

11.4.2 Model comparisons

The structural and functional differences between EwE and Atlantis are enormous. The models differ in their degree of complexity, incorporation of heterogeneity in lake habitats, physics (temperature, depth, light), and algorithms of biomass elaboration and feeding (Audzijonyte et al., 2017a; Christensen and Walters, 2004a). The calibration process also differs between the models; Atlantis tracks the age structure and weight-at-age of fish groups, whereas calibration in EwE is mainly achieved through adjustment of foraging arena parameters. Nonetheless, these modelling frameworks have been shown to give consistent qualitative policy evaluations (Forrest et al., 2015; Natugonza et al., 2019; Pope et al., 2019a). This study has further shown that structurally-distinct ecosystem models can provide consistent qualitative advice for strategic management, which underscores the importance of structured modelling in addressing uncertainty in complex ecosystem models (Espinoza-Tenorio et al., 2012). The observed differences in qualitative results can be attributed to the modelling approach, where the optimal fishing effort resulting from EwE's OPS may not necessarily be optimal in Atlantis.

While the predicted biomass trends were relatively comparable across models, quantitative results differed substantially (Figure 11.6 and 11.7). These differences can be attributed to both model structure and biases in individual models by the modeller. For example, Forrest et al. (2015) found the dynamics of several functional groups in Atlantis to be more influenced by bottom-up processes (fluctuations in primary production, driven by the oceanographic components in the physical sub-model) than in EwE, where there were no explicit primary productivity drivers, which contributed to large deviations in the magnitude of predictions between the models. This study also used the EwE model of Lake Victoria in its simplest, non-spatial, form, which could also be the main reason for the differences in the magnitude of predictions. Both empirical and modelling studies have shown seasonal variation in Lake Victoria's physical processes and spatial heterogeneity in nutrient concentrations, which are all positively correlated with fish species abundance (Hecky et al., 2010; Nyamweya et al., 2016b). Future studies may need to compare the models that are standardised as much as possible. Environmental and non-fishing anthropogenic factors can be incorporated in the EwE model using appropriate forcing functions (Christensen et al., 2008), while spatial effects may be considered using the Ecospace routine of EwE (Christensen and Walters, 2004a).

11.4.3 Conclusions

This paper analysed socio-ecological trade-offs between management objectives for Lake Victoria. The OPS routine of EwE was used to search for the long-term, gear-specific, fishing effort (optimal fishing effort) that can maximize benefits from a defined management objective. The optimal fishing effort was then used in both EwE and Atlantis models to predict future changes in the biomass of exploited fish groups. Results showed that economic benefits could be optimised while maintaining ecosystem structure, but the fishing effort (and potential yield) would be reduced in almost every fishing sector/fleet. This trade-off seemed to be severe for a fishery with limited alternative livelihood options. The current socio-economic set-up around Lake Victoria, where approximately 1000 new fishers enter the fishery per year (LVFO, 2016c), demands that employment creation is one of the priorities for management. However, since the lake is already in a state characteristic of “Malthusian overfishing”, where reduction of fishing effort is inevitable, planning and developing alternative livelihoods for the fishery-dependent communities will be necessary.

The importance of this study is in weighing the relative risks against the benefits of different management objectives, which will enable stakeholders and the public to conduct informed discussions on future management policies. The study particularly underscores the importance of developing clear policy objectives in consultation with different fishery stakeholders. Stakeholders must decide which of the objectives to prioritize and what they would be prepared to sacrifice to achieve the desired goal. This study only showed the trade-off boundaries. However, it is unlikely that stakeholders will choose an extreme end that favours, for instance, the ecosystem. More likely, it will be some combination of weights, not necessarily the combinations that have been tested in this study. Part of the stakeholder consultation process should involve sampling the whole trade-off space to understand not only the potential costs and benefits, but the nature of the different strategies employed with regards to what fishing sectors are favoured, and what functional groups bear the highest levels of exploitation.

The optimal fishing effort may vary with different parameter combinations in Ecopath, but the extent of variation has not been determined in this study. The results described in this paper may be interpreted and applied in qualitative terms, i.e., as an aid to discussions on long-term strategic management policies. The EwE and Atlantis models of Lake Victoria were parameterised and calibrated independently, but rigorously using the best available data and following the best practices documented in the literature. The differences in predictions across models do not mean that the models are faulty. Instead, the findings point to areas where different model considerations lead to varying predictions. This modelling approach is necessary as inconsistencies can be incorporated in the policy recommendations.

11.4.4 Acknowledgement

Special thanks to Villy Christensen for the advice on the implementation of optimal policy search in EwE. Elizabeth Fulton and Rebecca Gorton offered us support with the Atlantis code. This work was done as part of the PhD research by the lead author, which is funded by the United Nations University-Fisheries Training Program (UNU-FTP), Reykjavík, Iceland.

11.5 Supplementary data

Supplementary data to this paper can be found at `https://www.dropbox.com/s/vua42wb6uqptv0d/SUPPLEMENTARY_MATERIAL_FISH9693.docx?dl=0`

12

Paper VI

Spatiotemporal variation in fishing patterns and fishing pressure in Lake Victoria (East Africa) in relation to balanced harvest

Vianny Natugonza, Erla Sturludóttir, Laban Musinguzi, Richard Ogutu-Ohwayo, Sam Bassa, Tumi Tomasson, Chrispine Nyamweya, Gunnar Stefansson

Abstract

Balanced harvest (BH) refers to applying moderate fishing pressure across a broad range of species, trophic levels (TL), stocks, or sizes in an ecosystem in proportion to biological production (the total cumulated biomass over a given period) instead of putting pressure on particular, selected taxa, or sizes. Modelling and empirical studies show that BH can lead to higher fish yield than selective fishing, with minimal changes to ecosystem structure and function. However, few investigations have been done on the distribution of fishing patterns and fishing pressure in relation to BH, especially for inland fisheries. This paper uses data on yield and production from eight Ecopath models, covering the period 1970-2014, to explore whether fishing on Lake Victoria (East Africa) is consistent with BH strategy and to identify ecological groups (taxa) that might be heavily exploited and those that are underexploited relative to each taxa's production. Results show that high TL groups are exploited harder than low TL groups, with the overall fishing pattern inconsistent with BH strategy. Exploitation rates above 50% of annual production ("overexploitation") are observed for large (the adult sizes) of Nile perch (*Lates niloticus*), Nile tilapia (*Oreochromis niloticus*), and other less productive demersal groups (for example, catfishes, squeakers, and marbled lungfish). This fishing pattern is consistent with the collapse and failure of these demersal groups to recover, and the reduction in body size and size at maturity of main commercial fish species (Nile perch and Nile tilapia). The possible drivers of this fishing pattern and the likely outcomes from maintaining a *status quo* are discussed.

Keywords: Balanced harvest; Ecopath; Lake Victoria; productivity; overexploitation

12.1 Introduction

Ecosystem approach to fisheries (EAF) has become a popular tool in fisheries management in recent years (Garcia et al., 2003; Patrick and Link, 2015). The fundamental objectives of the EAF are to maintain ecosystem structure and functioning and to avoid overfishing (Garcia et al., 2003). Balanced harvest (BH), a fishing strategy that considers moderate fishing pressure across a broad range of species, trophic levels (TLs), stocks, or sizes in an ecosystem in proportion natural production (the total cumulated new biomass produced from an ecological group during a given period), is viewed as a holistic fishing strategy that can achieve both objectives of EAF (Zhou et al., 2019). Studies have shown that BH can minimize the adverse fishing impact on the relative size and species composition of aquatic ecosystems, and increase or maintain sustainable yield from such ecosystems (Jacobsen et al., 2013; Kolding et al., 2016c; Law et al., 2014; Zhou et al., 2015). This new concept has attracted wide interest and discussion in the management of fisheries (Burgess et al., 2015; Froese et al., 2016; Kolding et al., 2016b; Reid et al., 2016; Zhou et al., 2019). While investigations on the broader distribution of fishing patterns and fishing pressure across different ecosystems in relation to each taxa's production have been conducted for marine systems (Kolding et al., 2016a), similar investigations are limited for the inland fisheries. This gap precludes the understanding of ecological groups that could be heavily exploited and those that may be underexploited, leading to inefficient utilization of the fishery in terms of food energy value (Kolding et al., 2016a).

Previous investigations into the distribution of fisheries exploitation patterns across stocks and species show exploitation to be skewed towards high TL species, with significantly lower fishing pressure on low TL, highly productive groups (Kolding et al., 2016a). In large scale marine fisheries, where most of these investigations have been conducted, this exploitation pattern is expected because of the market preference for large fishes (Charles et al., 2015; Sethi et al., 2010). Similar investigations are needed for small scale fisheries, where food provisioning and nutritional security, i.e., from maximizing biomass catch of small and low-value fishes, are as crucial as profit maximization from large, high-value fisheries (Kolding et al., 2018).

Lake Victoria (Figure 12.1) is the world's second-largest freshwater body and the largest tropical lake, in terms of surface area (68,800 km^2), with annual fish landings approximately equal to one million tonnes (Taabu-Munyaho et al., 2016). Over the past five decades, the lake has undergone considerable changes, both in limnology and fisheries, aided by new species introductions, intensive fishing, habitat degradation, invasive weeds, and climate variability (Hecky et al., 2010). However, the sustainability of the fisheries amid increasing fishing pressure has been a central focus of discussion by scientists and managers, although no consensus has been reached to date. Some authors have suggested that the levels of exploitation are not sustainable and that fisheries are exhibiting signs of overfishing, as seen from the reduction in catch rates (catch per unit effort (CPUE)) and size structure of main commercial fish species, Nile perch (*Lates niloticus*) and Nile tilapia (*Oreochromis niloticus*) (Matsuishi et al., 2006; Mkumbo and Marshall, 2015; Njiru et al., 2006; Pitcher and Bundy, 1995). However, other authors are strongly opposed to this view (Kolding et al., 2008; Kolding et al., 2014). These authors argue that the overall landings have not plummeted, despite the continuous increase in fishing effort, and that the reduction in CPUE, biomass, and size structure of primary commercial fisheries is a normal response to fishing.

The disagreements partly emanate from the mixed nature of the fishery, which makes it challenging to assess fishing effort on individual fish species and to estimate catch rates precisely. The CPUE is mainly approximated using indirect methods, for example, from the combined catches and either the total number of fishers or fishing crafts (Kolding et al., 2014). While this approach may help to give a general picture of the fishery, it has shortcomings, arising from lack of separation of catches and fishing effort. Consequently, a different method is needed to assess the status of the fisheries at the functional group level. One potential approach is by examining how fishing pressure is distributed across the broader trophic spectrum in relation to the biological productivity of an individual group or TL (i.e., balanced harvest), similar to the one used by Kolding et al. (2016a). This approach would help in identifying species that are overexploited, relative to biological production, and those that are sustainably exploited.

The specific objectives of this paper are threefold. First, to explore whether fishing on Lake Victoria (in space or time) is consistent with the BH strategy. Second, to identify ecological groups (taxa) that are likely overexploited, where exploitation rate (E, the ratio of yield to production) is consistently above 50% (Alverson and Pereyra, 2001), and those that are least exploited relative to each taxa's production, where E is less than 40% (Patterson, 1992; Pikitch et al., 2012). Third, to explore the relationship between the historical changes in body sizes and size at first maturity, especially the high-value species (Nile perch and Nile tilapia), and the observed fishing pattern. Because of the current size-selective regulations on the lake, for example, the minimum mesh size policy, and the emphasis by governments on maximizing revenue from high-value fisheries (Johnson and Bakaaki, 2016; LVFO, 2016a), one would expect higher-TL species to be exploited harder than lower-TL groups, resulting in a fishing pattern that is inconsistent with the BH strategy.

12.2 Material and methods

12.2.1 Study area

The study was conducted on Lake Victoria (Figure 12.1), given its direct contribution to the livelihoods of more than 4 million people (Mkumbo and Marshall, 2015). The fisheries of Lake Victoria have evolved in three major phases. Before 1980s, the fishery was dominated by haplochromines, the catfishes (for example, *Clarias gariepinus*, *Synodontis* spp., *Bagrus docmak*, and *Schilbe intermedius*), marbled lungfish (*Protopterus aethiopicus*), and cyprinids (particularly *Labeo victorianus*). During the mid-1980s and 1990s, fisheries were dominated by introduced

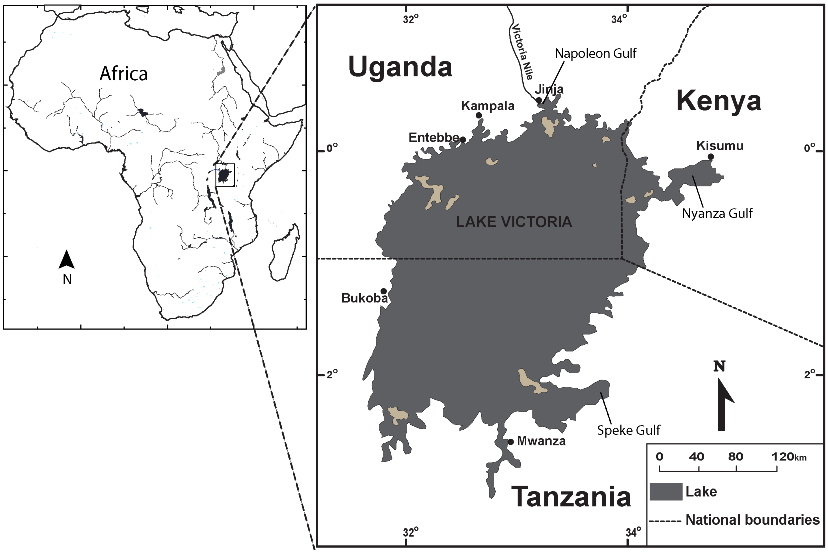

Figure 12.1: Location of Lake Victoria in East Africa.

species (Nile perch and Nile tilapia). Beginning from the mid-2000s, the fishery was dominated by the native silver cyprinid (*Rastrineobola argentea*), locally known as dagaa, the introduced Nile perch and some recovering haplochromines (Taabu-Munyaho et al., 2016).

The shifts in major fisheries have also been accompanied by changes in fishing effort, fishing methods and overall catches. Before the 1970s, the number of fishers was less than 20,000, and the overall annual landings were approximately 100,000 tonnes (Kolding et al., 2014). Between 1985 and 2000, there were approximately 60,000 fishers, landing (on average) 500,000 tonnes per year (Kolding et al., 2014). Afterwards, the fishing effort increased rapidly: the number of fishers increasing fivefold; the number of gillnets and hooks increased 3-4 times; the overall annual landings reached approximately one million tonnes by 2014 (LVFO, 2016b).

12.2.2 Data and sources

Assessing fishing patterns and fishing pressure in relation to BH requires data on yield and production across all exploited species in an ecosystem, either by TL or size. These data are readily available in standardized formats in Ecopath models by species or functional groups and TL (Christensen and Pauly, 1992).

Ecopath with Ecosim (Christensen and Walters, 2004a, EwE,) is the most widely used tool for building models of marine and freshwater ecosystems, with over 400 models (Colleter et al., 2015). The EwE modelling suite provides an ecological perspective for the assessment and management of multispecies and multi-gear fisheries (Christensen and Walters, 2004a). Using Ecopath, an ecosystem is partitioned into functional groups comprising individual species or species groups that perform a similar function in the ecosystem, i.e., have the same physical habitat, diet, growth rates, consumption rates, and predators (Christensen and Pauly, 1992). This modelling approach follows that, for the period of the model, biomass flows in an ecosystem are regulated by gains (consumption, production, and immigration) and losses (mortality and emigration), through predatory relationships, and no more is used than can be produced. The net production of a TL group equals the sum of (1) the total mass removed by predators and fishing, (2) the net biomass accumulation of the group, (3) the net migration of the group's biomass, and (4) the mass flowing to detritus (Christensen and Walters, 2004a). This way, Ecopath provides a standardized representation of an ecosystem and its fisheries, from which estimates of production, exploitation rate, TL of functional groups can be derived.

Eight published Ecopath models on Lake Victoria covering the period 1970-2014 were used in this analysis, including three models representing the Kenyan waters for the periods 1971-1972, 1985-1986, and 1995 (Moreau et al., 1993a; Natugonza et al., 2016; Villanueva and Moreau, 2002), four models representing different parts of the lake (Uganda, Kenya and Tanzania waters and the whole lake) for the year 2000 (Matsuishi et al., 2006), and one model representing the whole lake for the year 2014

(Natugonza et al., 2016). The three models of Mwanza gulf representing food web status in 1977, 1987, and 2005 (Downing et al., 2012) were not included in this analysis because of the limitations in model parameters (Kolding, 2013).

After accessing these models, estimates of production (P) for each functional group i, P_i, were derived from two Ecopath input parameters: production per unit of biomass (P/B = total mortality, Z (/year)) and biomass per unit of habitat area (B, ton/year) as shown in Equation 12.1.

$$P_i = \frac{P_i}{B_i} \cdot B_i \tag{12.1}$$

The catch, which is an input parameter in Ecopath, was used to represent biological yield (Y) for each functional group i. These data on production and yield can be found at `https://doi.org/10.6084/m9.figshare.10266464.v1`.

12.2.3 Data analysis, visualization and interpretation

This study relies on both the graphical method, showing the relationship between yield and production (Kolding et al., 2016a), and exploitation indicators, i.e., trophic balance index (TBI) and exploitation index (EI), showing the variability of exploitation across ecosystem-specific TLs (Bundy et al., 2005). By definition, the ratio of yield to production is equivalent to E, i.e., E = Y/P (Patterson, 1992). Therefore,

$$\log Y = \log P + \log E \tag{12.2}$$

A linear regression of log(Y) against log(P) would give a slope of $b = 1$ and an intercept of $a = log(E)$ as shown in Equation 12.3.

$$\log Y = b \log P + a \tag{12.3}$$

The graphical method follows that if all the exploited fishes have the same E (i.e., exploitation is consistent with BH strategy), they should be on a straight line with a slope $b = 1$. Deviations from the slope of 1 would show systematic differences in E among fishes. The slope $b < 1$ specifically shows that fishes with low P are heavily exploited compared to fishes with high P. The magnitude of the difference from the slope of 1 would indicate how unbalanced fishing is, i.e., the higher the deviation around the slope, the more unbalanced is the exploitation pattern. The same intuition is used to analyze fishing pressure. Because the intercept a of the linear regression of log(Y) against log(P) represents the log average E, *log(E)*, the closer the points lie to the $Y = P$ line (i.e., E = 1), the higher the fishing pressure and vice versa.

The TBI, on the other hand, gives a measure of the variability of exploitation across ecosystem-specific TLs, also showing whether exploitation is balanced or not. The TBI is calculated as the coefficient of variation of E, as shown in Equation 12.4.

$$TBI = \frac{S_E}{\bar{E}} \tag{12.4}$$

where, S_E and $\bar{E}$ are standard deviation and mean of group-level exploitation rates, respectively (E is calculated for each harvested groups as Y/P). Interpretation of results follows that when E is the even across all TL groups (i.e., BH), S_E is zero and so is TBI; exploitation is unbalanced if TBI is further away from zero (Bundy et al., 2005).

Also, the EI gives a measure of E but integrated over TLs. The index represents the overall flow of biomass out of the system as a result of fishing and is calculated by dividing the total yield with total production for all exploited TL groups as shown in Equation 12.5.

$$EI = \frac{\sum_{i:TL_i \geq 2} Y_i}{\sum_{i:TL_i \geq 2} P_i} \tag{12.5}$$

An increase in EI results in changes in life-history variables of individual species, such as reduced age at maturity or smaller length-at-age, with consequences for the size spectrum of prey, and effects on fish community structure and function (Bundy et al., 2005).

12.3 Results

Figure 12.2 shows the relationship between productivity, production, and biomass with TL. Results show a decrease in productivity, production, and biomass with TL, suggesting that TL may be appropriate to use as a proxy trait for fish size in the interpretation of BH (Kolding et al., 2016a). However, the decrease, especially in biomass, with increasing TL is not as steep as expected from ecological studies (for example, Link, 2010)), which may be due to the high productivity of the mid-TL juvenile Nile perch (an introduced species) and the silver cyprinid (*Rastrineobola argentea*), commonly known as dagaa.

Figure 12.3 shows the relationship between yield and production; each point represents a functional group in the respective TL as calculated by Ecopath. In all the 8 models, the slopes the linear regression between yield and production are different from 1, implying that exploitation is not evenly distributed across TLs for the period covered in the analysis. Generally, groups with low production were exploited harder than groups with high production, except during the 1980s and 1990s. Even when groups with high production were generally exploited more than groups with low production during the 1980s and 1990s, exploitation was still uneven. The slope of the linear catch regressions on production during the period 1971-1972 is nearly flat and is not significantly different from zero. The most recent models (especially those of 2000) appear close to the balance, having a smaller deviation around the slope compared to other models. Nevertheless, all slopes are still significantly different from 1, indicating that exploitation across the targeted species is not consistent with the BH strategy.

Exploitation was concentrated on the large demersal fishes, for example, adult Nile perch, catfishes, mormyrids and squeakers, and marbled lungfish, with the E exceeding 50% of group's annual production, except during the 1980s and 1990s (Figure 12.3). The small pelagic groups (for example, juvenile Nile perch, dagaa, and haplochromines) were least exploited, considering their production, except during 2000, where exploitation rate for dagaa increased substantially (approaching 50% of

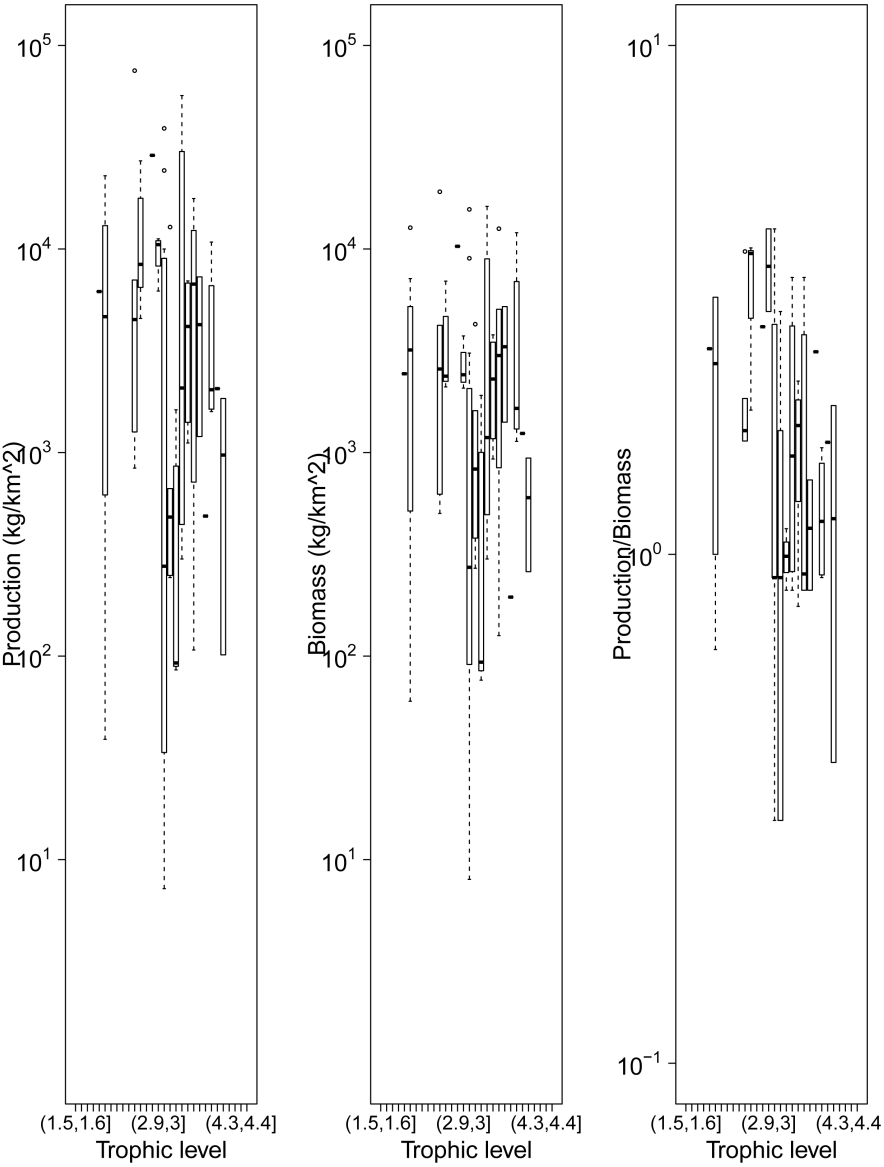

Figure 12.2: Relationships between production to biomass ratio (P/B, /year), production (kg/km^2/year), and biomass (kg/km^2/year) (on logarithm scale) with TL in binned in 0.1 intervals of different functional species groups eight Ecopath models.

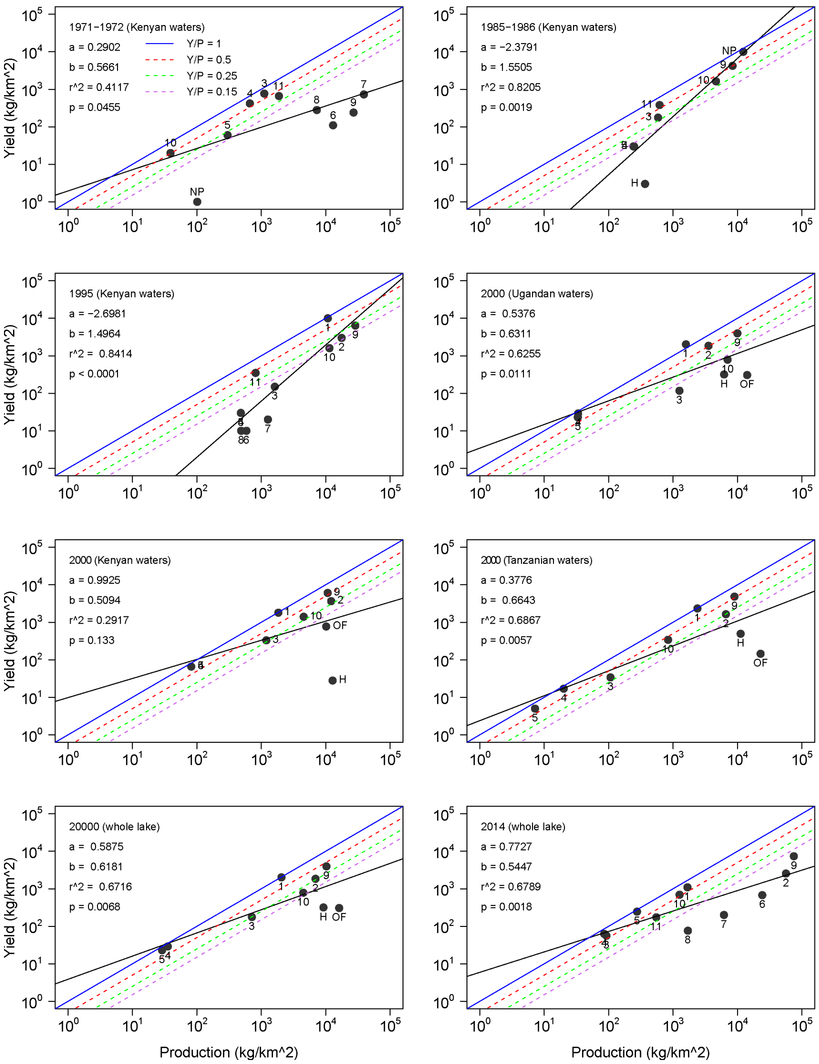

Figure 12.3: Harvest relative to production (on logarithm scales) for species harvested in Lake Victoria over time. The more the slope deviates from the 1:1 line between yield and production (i.e., F/Z = Y/P = 1), the more "unbalanced" (*sensu* Garcia et al. (2012)) exploitation is. Exploitation rates equivalent to 15, 25, and 50% of production are given as dotted parallel lines. p-values give the test of slope $\neq 1$. Numbers/letters represent species/functional groups: adult Nile perch (1), juvenile Nile perch (2), catfishes (3), marbled lungfish (4), squeakers and snout fishes (5), zooplanktivorous haplochromines (6), Detritivorous haplochromines (7), other haplochromines (8), dagaa (9), Nile tilapia (10), other tilapias (11), other fishes (OF), unseparated haplochromines (H), unseparated Nile perch (NP).

Table 12.1: Fishing indicators from eight ecopath models representing Lake Victoria ecosystem for the period 1971-2014. TBI = Trophic Balance Index, and EI = Exploitation Index.

Model period/location	TBI	EI
1971-1972 (Kenyan waters)	1.03	0.03
1985-1986 (Kenyan waters)	0.77	0.60
1995 (Kenyan waters)	1.38	0.28
2000 (Ugandan waters)	0.96	0.21
2000 (Kenyan waters)	0.75	0.26
2000 (Tanzanian waters)	0.75	0.18
2000 (whole lake)	0.97	0.18
2014 (whole lake)	0.99	0.07

production) in the Kenyan and Tanzanian waters. However, by 2014, the E for dagaa, averaged for the whole lake, was less than 10% of total production (Figure 12.3).

Results from the logarithmic Y/P plots were consistent with those derived from the fishing indicators (Table 12.1). The TBI was much higher than zero for all the areas and periods covered in the analysis, indicating uneven exploitation pattern across TLs.

EI ranged between 4 and 60% (Table 12.1). Both the highest and lowest values were recorded in the Kenyan waters, but generally, EI declined since the 1990s and was less than 10% by 2014.

Figure 12.4 shows overall fishing pressure, expressed as E for each TL compared with production (kg/km^2/year). In a fishery where exploitation is balanced, E would systematically decrease with production and the trend line for exploitation would be parallel to that of production (Kolding et al., 2016a). However, Figure 12.4 shows that production decreases, but E instead increases with TL. Higher values of E (>40% of production) were dominated by adult Nile perch and most demersal fishes (with low production) and tilapias.

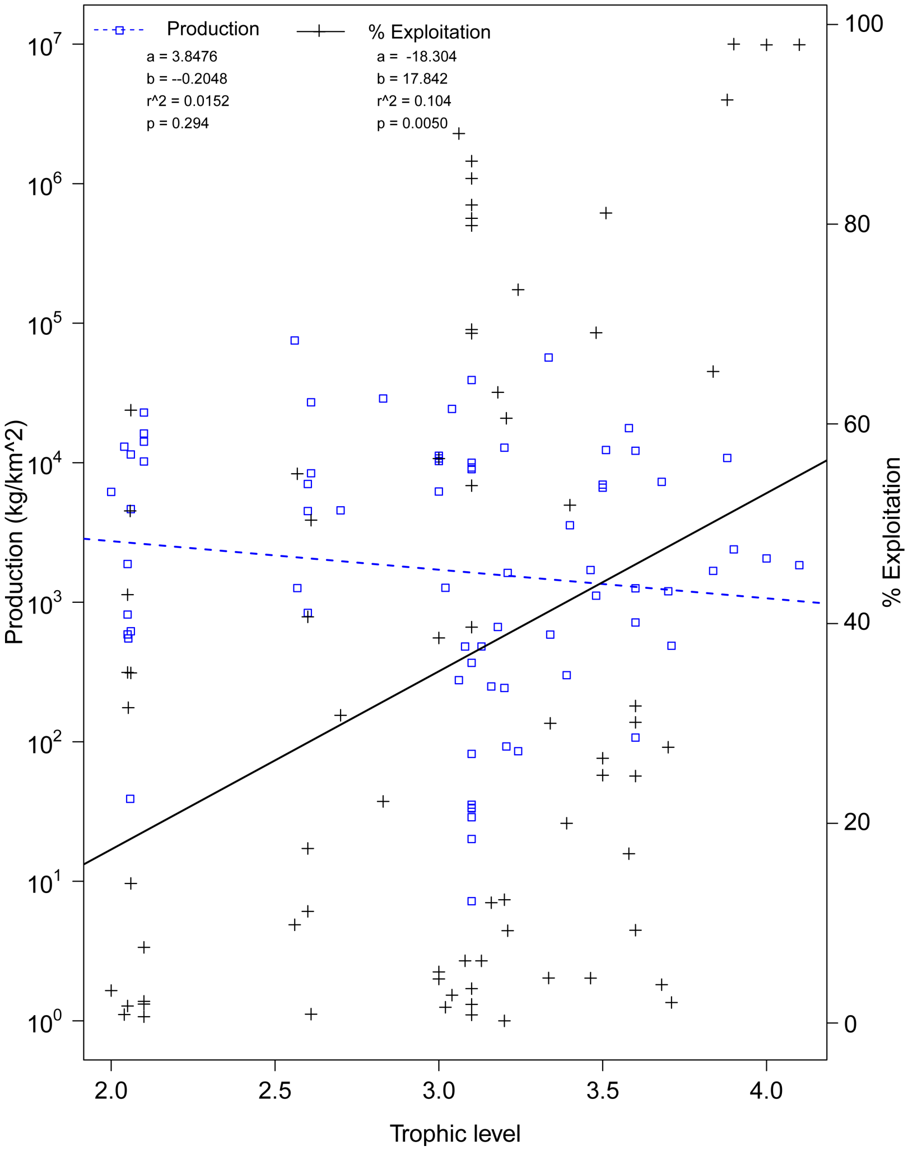

Figure 12.4: Production (kg/km^2/year) (on logarithm scale) and exploitation rate (%) per Trophic level. Filled square blue = production and plus = exploitation rate. Superimposed are linear trends for exploitation (ascending black line) and production (descending blue dotted line).

12.4 Discussion

This study used data on yield and production from Ecopath models to explore fishing patterns and fishing pressure on Lake Victoria in relation to the proposed BH strategy. Two complementary approaches: the logarithmic Y/P plots (Kolding et al., 2016a) and fishing indicators (TBI and EI; Bundy et al., 2005) were used. Whereas the two approaches are structurally and constructively different, results are in agreement that fishing on Lake Victoria is not consistent with the BH strategy. Heavy fishing selects large and high TL species. This exploitation pattern is expected and generally consistent with global fishing patterns, where high E is exerted on most profitable fishes at higher TL, and significantly less E is exerted on lower TL groups (Kolding et al., 2016a; Sethi et al., 2010).

The BH strategy aims to distribute fishing pressure across TLs in proportion to productivity (Garcia et al., 2012). Figure 12.2 shows that low production occurs at higher TLs due to the 90% loss of energy between each integer level, and hence higher exploitation is expected at lower TLs than higher TLs to achieve BH. However, during the 1970s, E was higher for less productive groups (catfishes, marbled lungfish and other tilapias) compared to more productive groups (haplochromines and dagaa). During the 1980s and 1990s, exploitation was close to balance, being higher for more productive species, except that E for Nile perch and other tilapias was exceedingly high (above 0.8; Figure 12.3). Most of the Nile perch harvested during the 1990s were destined for factory processing and export (Pitcher and Bundy, 1995), and this may explain the higher selection for large Nile perch (with E exceeding 80% of production) compared to the smaller-sized Nile perch. After 2000, exploitation was still inconsistent with balanced harvest (i.e., skewed to high TL groups–adult Nile perch, squeakers and marbled lungfish); however, unlike in the previous years, exploitation pressure was substantially low ($E < 0.1$) for the most productive groups in the system (small-sized Nile perch, dagaa and haplochromines). From a BH point of view, this exploitation pattern suggests an inefficient utilization of the food energy value of the system (Kolding et al., 2016a). It could partly explain the changes in species composition, catch rates, and other biological attributes observed in Lake Victoria, especially for the dominant commercial fisheries (Nile perch and Nile tilapia, see below).

12.4.1 Effect of selective fishing on fish species composition and yield

Patterson (1992) and Pikitch et al. (2012) suggest that the E should not exceed 0.4 for fishing to be sustainable and that values greater than 0.6 are associated with 80-100% likelihood of stock decrease, with no chance for the affected stock to recover. Other researchers put the maximum E at 0.5, where fishing mortality (F) equals to natural mortality (M) (e.g. Alverson and Pereyra, 2001). This study shows that the E for most demersal fishes, particularly catfishes, marbled lungfish, and *Synodontis* spp. were above 0.5, especially during the 1970s. This high exploitation explains why these groups eventually collapsed during the late 1970s and early 1980s in terms of their contribution to commercial fisheries and never recovered (Goudswaard and Hecky, 1997). Since the 1980s, E has also been exceedingly high (i.e., above 50% of production) for large Nile perch (adult stock) and Nile tilapia. The high fishing pressure on these high-value fisheries may explain the reduction in their catch rates (LVFO, 2016b; Mkumbo and Marshall, 2015). A more balanced harvest regime, perhaps, would increase yields (Jacobsen et al., 2013; Kolding et al., 2016c; Law et al., 2013; Zhou et al., 2015), but this would require decreasing fishing pressure on and rebuilding and protecting the adult Nile perch stock, Nile tilapia, and other low productive large predators (catfishes and marbled lungfish).

Some researchers caution that fishing too many small fish (forage fishes) would endanger the higher TLs and that a reduction in exploitation of low TLs is required to sustain forage fishes as well as rebuild stocks of high-value fishes at higher TLs (Essington et al., 2015; Pikitch et al., 2012; Smith et al., 2011). This view is also supported by findings from ecosystem-level analyses: Nilsen (2018) used the Atlantis modelling framework (Fulton et al., 2011a) to test the effect of BH on yield in the

Nordic and Barent Seas. Whereas a BH returned marginal increase in yield compared to the conventional selective fishing, inclusion of low TLs caused drastic changes to the ecosystem in the form of stock collapses or by severely changing biomass levels at the ecosystem level. The lower TL groups generally have higher natural mortality applied than commercially harvested species, implying that BH can also be unsustainable, except where additional fishing on these groups helps to reduce competition among forage fishes that depend on the same prey (Law et al., 2013).

The latter case is important for Lake Victoria. Haplochromines and dagaa are the main prey for the high TL fishes and, therefore, fit in the classification of “forage fishes”. Both groups are zooplanktivorous and their biomass has been expanding recently. Dagaa is exclusively zooplanktivorous; its fishery expanded after the initial collapse of haplochromines, apparently due competitive release (Wanink and Witte, 2000; Witte et al., 2007). Haplochromines have also started recovering, and these are dominated by zooplanktivores (Kishe-Machumu et al., 2015; Witte et al., 2007). This recovery of zooplanktivorus haplochromines could increase competition again and ultimately endanger the large predators. If so, under-exploitation of dagaa and haplochromines (as seen in the 2014 data, 12.3), might be counter-productive; perhaps, a more BH regime would reduce competition and benefit all fishery groups (Garcia et al., 2015; Law et al., 2013).

12.4.2 Effect of selective fishing on size structure

Fished stocks can show decreasing sizes-at-age or size-at-maturity due to several factors. (i) Direct removals of oldest and largest individuals through size-selective harvesting. (ii) Contemporary evolution towards smaller size-at-age owing to selective harvesting of fast-growing individuals or climate change. (iii) Contemporary evolution towards increased/earlier energy allocation to reproduction, and consequently smaller realized size-at-age owing to high fishing mortality. (iv) Physiological declines in growth rates owing to increasing temperatures and decreasing oxygen concentration (Cheung et al., 2013; Pauli et al., 2017). Separating these drivers is not straightforward. However, notable declines in size structure have been associated with selective removal of large-sized individuals as well as high fishing mortality on a given stock (Kuparinen et al., 2016).

The changes in size structure of Nile perch and Nile tilapia observed in Lake Victoria can, therefore, be attributed to a selective fishing pattern (high fishing pressure on large-sized fishes). Table 12.2 shows some growth parameters of Nile perch from Lake Victoria over time, including length at 50% maturity as well as the mean length of catch. Between 1980 and 2015, both length at 50% maturity (L_50) and asymptotic length (L_∞) halved, although the changes became more pronounced after 2000, consistent with the high fishing pressure on adult sizes (Figure 12.3). The growth rate (as seen from the VBGF growth curvature, K) has increased (Table 12.2), concurrent with reduced lifespan (Njiru et al., 2006). Length frequency distributions from experimental bottom trawl survey data collected between 1997 and 2015 also show that size structure has shrunk (Figure 12.5). Until the early 2000s, Nile perch exhibited distinct year classes, although the sizes were already diminished compared to the 1980s and early 1990s (Table 12.2). After 2007, the majority of the Nile perch remained small in size, i.e., less than 50 cm in total length (Figure 12.5). These changes are now reflected in catches, where the proportion of Nile perch $>$50 cm in total length has plummeted from around 80% during 1980-2000 to $<$5% by 2011 (Mkumbo and Marshall, 2015).

Nile tilapia has experienced similar changes (Figure 12.6). Distinct size classes are apparent until 2008, after which the distributions become skewed toward smaller sizes. This trend is consistent with other biological parameters estimated from gillnet survey data, especially in the Kenya waters. For instance, during the mid-1980s, L50 (unsexed) for fishes from Nyanza Gulf was 35 cm total length (Getabu, 1992). During 1998-2000, L_50 had not changed for males but was 25 cm total length for females, and by 2004-2005, the L_50 had decreased to 22 cm total length for females and 25 cm total length for males (Njiru et al., 2006). These changes have

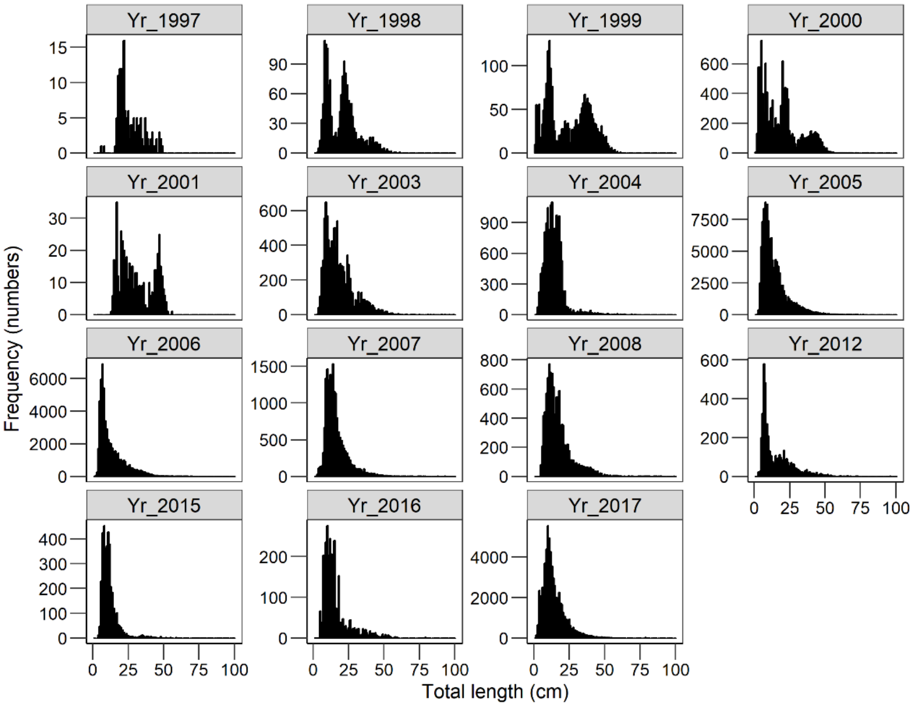

Figure 12.5: Length frequency distribution (by numbers) of Nile perch over time. Data are from bottom trawl surveys conducted in the Ugandan part of Lake Victoria between 1997 and 2017.

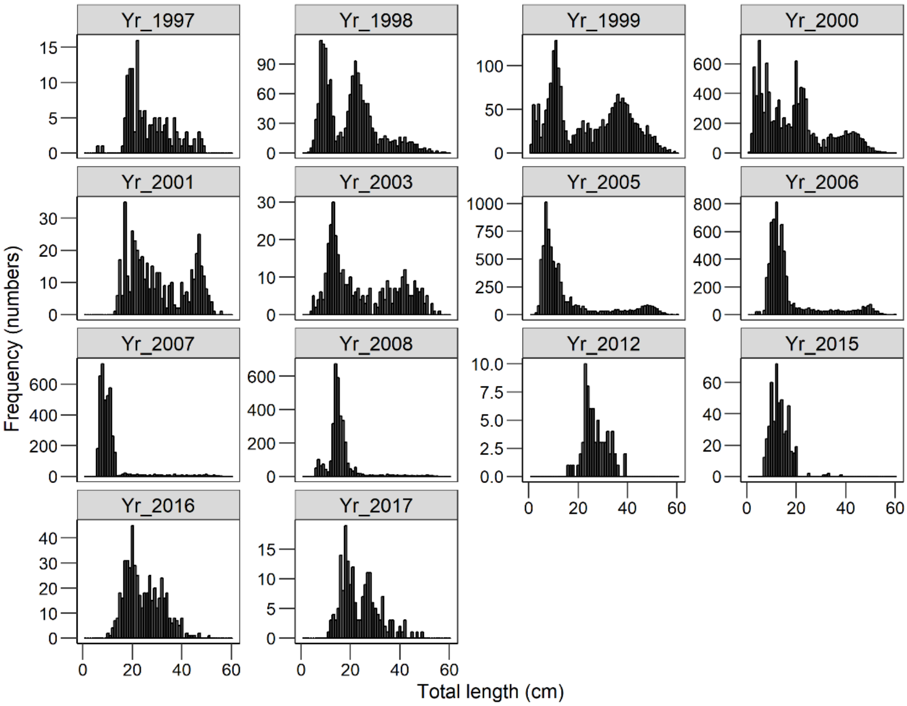

Figure 12.6: Length frequency distribution (by numbers) of Nile tilapia over time. Data are from bottom trawl surveys conducted in the Ugandan part of Lake Victoria between 1997 and 2017.

previously been attributed to intensive fishing (Njiru et al., 2006), which is also consistent with our findings on TL-specific fishing pressure.

Table 12.2: Some parameters related to growth of Nile perch (Female, F, and Male, M) in Lake Victoria over time. L_∞ (cm total length) represents the asymptotic length, and K (/year) is the VBGF curvature parameter expressing the rate at which L_∞ is approached. U stands for Ugandan side of Lake Victoria; NG is Nyanza Gulf (Kenyan side of Lake Victoria); SG is Speke Gulf (Tanzanian side of Lake Victoria); T stands for Tanzanian part of Lake Victoria.

Period	L_{50} (F)	L_{50} (M)	Source	K	L_∞	Source
1978-1984 (NG)	105	74	Asila and Ogari (1988)	0.19	205	Asila and Ogari (1988)
1982 (U)	93	43	Ogutu-ohwayo (2004)			
1983 (NG)	80-85	50-55	Hughes (1992)			
1987-1988 (SG)	100	60	Ligtvoet and Mkumbo (1990)	0.17	185	Ligtvoet and Mkumbo (1990)
1988-1992 (U)	90-99	50–54	Ogutu-ohwayo (2004)			
1991 (NG)				0.185	230	Rabour et al. (2003)
1998-2000 (T)				0.19	2016	UNECIA (2002)
1998-2000 (NG)	76	60	Njiru et al. (2006)	0.21	204	Njiru et al. (2006)
1998-2000 (U)				0.29	256	UNECIA (2002)
2000 (U)				0.17	221	Muhoozi (2002)
2004-2005 (NG)	62	54	Njiru et al. (2006)	0.25	133	Njiru et al (2007)
2006-2007 (U)	50	45	Nkalubo (2012)			
2015 (U)	47	38	Trawl survey (unpublished)	0.25	78	Trawl survey (unpublished)

In response to these changes, fishers have progressively shifted to smaller-sized gears, especially after 2000 (LVFO, 2016c). The fishers response may account for the higher overall catch of the small-sized Nile perch compared to adult Nile perch by 2014, although the E for the former group is still substantially low (i.e., less than 10%, Figure 12.3). This scenario could be attributed to the current slot size regulation that bars fishers from harvesting Nile perch less than 50 cm total length (LVFO, 2016a). Balancing exploitation across a broader range of TLs or sizes has the potential not only to increase overall catches significantly (Jacobsen et al., 2013; Kolding et al., 2016c; Zhou et al., 2015), but also to maintain the size structure of harvested stocks (Law et al., 2014). However, in Lake Victoria, a shift to more balanced harvest would require a review of the minimum size regulations (LVFO, 2016a).

12.4.3 Caveats

The data used in this analysis were derived from Ecopath models. The ‘snapshot’ nature of these models, usually representing ecosystem status for one year, could be a limitation to this study. However, this limitation is common of most ecological data and the absence of long term data does not mean Ecopath models are flawed. Although most of the models used in this analysis were specific to the periods being modelled, usually one year, some of the parameters used are averages based on several years of field data collection from the system, and hence represent average states. Besides, each decade was represented by at least one model, and regardless of model complexity, the results were consistent for the whole period under consideration.

12.5 Conclusions

This study aimed at exploring fishing patterns and fishing pressure in Lake Victoria in relation to BH. Results showed fishing (both in time and space) to be skewed to the low productive groups at high TLs, and hence inconsistent with the BH strategy. This exploitation pattern suggests that the fishery is inefficiently utilized in terms of food energy value. From a BH point of view, adult Nile perch, Nile tilapia, and other demersal groups (catfishes, speakers, and marbled lungfish) are overexploited. This selective fishing could be responsible for the body size truncation in Nile perch and Nile tilapia, and the collapse of the rest of demersal fisheries. A shift to a more BH regime could increase yields and maintain ecosystem structure (Jacobsen et al., 2013; Kolding et al., 2016c), but this requires further investigations. Studies on the African small scale inland fisheries have shown that BH may emerge as a result of individual fishers' decisions to maximize their biomass catch, without externally imposed restrictions (Plank et al., 2016). A similar strategy would be worth exploring on Lake Victoria, given that consumption of small fish food has recently increased, and fishers are progressively shifting effort and gear sizes to target small pelagic fisheries (Kolding et al., 2014, 2018).

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