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. We 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). We compared model behaviour 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. We conclude 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.

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Introduction

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 (Pitcher et al., 2009; Essington and Punt, 2011). Several barriers have been identified as leading to the slow adoption of EBFM, including lack of inclusion of all stakeholders in the implementation process lead-

ing to misunderstandings about the approach (Patrick and Link, 2015; Trochta et al., 2018; Nielsen et al., 2019), conflicting nature of management objectives (Pope et al., 2019a), 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 are clearly understood: it enables evaluation of how fishing impacts entire ecosystem and fisheries, through alternative scenarios, which can be considered 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 ecosys-

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tem 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 (Lehuta et al., 2016; Grimm et al., 2017; DeAngelis and Gross, 2017). 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 rigor 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 also mean that it is risky to rely on a single ecosystem model to address all the questions under the EBFM framework (Fulton et al., 2011; Espinoza-Tenorio et al., 2012). Ecosystem models differ in detail of their biological processes and how they are represented, projection length and solution time steps (Plagányi, 2007). Even when the models are constructed based on the knowledge of the system (i.e., with minimal process uncertainty), and also utilizing the best available data, these are not adequate safeguards to the uncertainty that comes with modelling complex systems (McElhany et al., 2010). As model complexity increases, it becomes increasingly difficult to track 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. 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, 2004). However, for more complex, multidimensional ecosystem models with thousands of parameters, e.g., Atlantis (Fulton et al., 2011), full-scale sensitivity analysis is not feasible unless it is done for individual model components (e.g., 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 (Stow et al., 2009; Olsen et al., 2016). 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, 2004).

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

It is now widely recognised 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 can provide some form of "insurance" against the increased risk of uncertainty emanating from modelling complex systems (Espinoza-Tenorio et al., 2012; Collie et al., 2016; Bauer et al., 2019). An ensemble modelling approach is be 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). This is important for EBFM: convergence of model results increases confidence in the policy recommendations, while divergent results can 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).

Inter-comparisons of ecosystem models 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 (Fulton and Smith, 2004; Travers et al., 2010; Gårdmark et al., 2013; Smith et al., 2015; Forrest et al., 2015; Pope et al., 2019b; Bauer et al., 2019). 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, it is not clear whether consistency in multispecies interactions, including similar choice of functional groups and representation of feeding interactions, would minimise variations in predictions due to model structure and assumptions.

The structural and functional differences between multispecies models are huge. 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, 2004). 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, 2017b). 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 major insights into uncertainty around system structure and function.

Ecosystem models of Lake Victoria

Lake Victoria, East Africa (Fig. 1), supports a lucrative fishery with annual total fishery production approaching one million tonnes which is worth US $600–900 million for the direct sale of fish at landing sites (LVFO, 2016a). 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 1950 s and 1960 s. Before the introduction, there were 500 + species of haplochromines in the lake (Witte et al., 2007). Predation by the introduced Nile Perch, after successful establishment during the mid-1980 s, 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 (Table 1) also declined/collapsed either directly from Nile perch predation or indirectly through competition for haplochromine prey (Ogutu-Ohwyo, 1990). However, demographic changes in Nile perch stock during the 1990 s, attributed to intensive fishing, led to the resurgence of haplochromines (Witte et al., 2007). 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 Witte, 1997). Landings are presently dominated by the introduced Nile perch and Nile tilapia and the native silver cyprinid (*Rastrineobola argentea*) and haplochromines (LVFO 2016a). The silver cyprinid constitutes the bulk of the catch (50%), followed by Nile perch (24%) and haplochromines (10%) (LVFO, 2016b). This pattern 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/
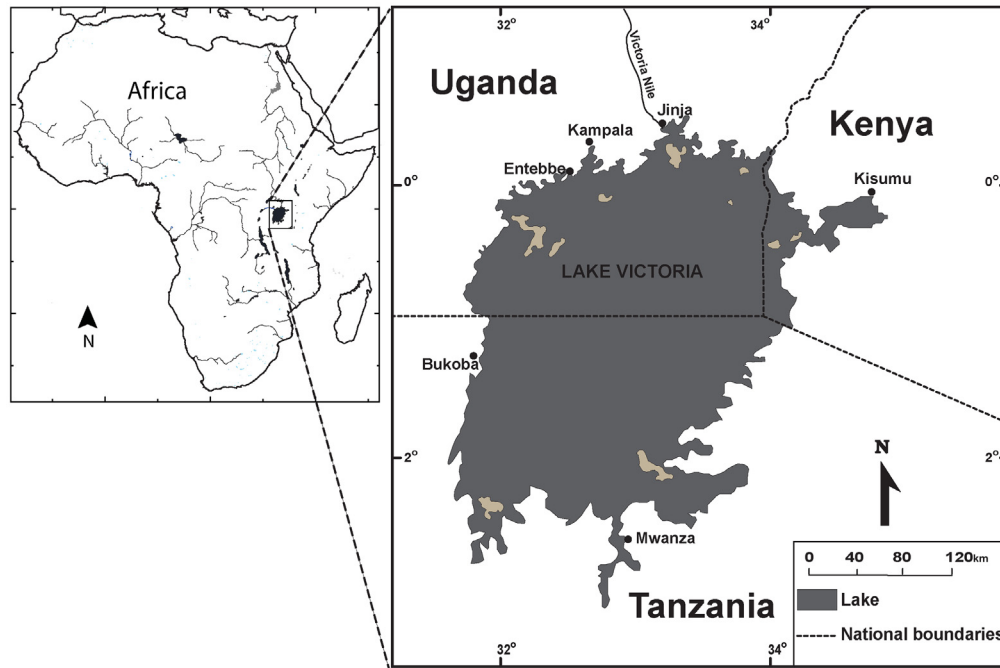
Fig. 1. Location of Lake Victoria in East Africa.

Table 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	Phytoplantivore	Yes	Yes	No	No	No
Haplochromis spp. (Phytoplanktivorous, Benthivorus, and Piscivorous *haplochromis*)	Haplochromines	Native	Benthopelagic	Variable[a]	3 groups	1 group	Yes	Yes	No
Rastrineobola argentea	Silver cyprinid	Native	Pelagic (schooling)	zooplantivore	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, Benthic filter feeder, Shallow filter feeder, Deep filter feeder Microphtybenthos	Insects and molluscs		Water surface or demersal	Detritivore	5 groups	1 group			
Microzooplankton, Mesozooplankton,	Zooplankton		Pelagic	Phytoplantivore	2 groups	1 group			
Macroalgae, Large phytoplankton, Dinoflagellates, Pico-phytoplankton	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).

outboard engine-propelled Sesse boats in coastal and deep areas (greater than 20 m) (LVFO 2016b).

Considerable attempts have been made towards modelling these 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 (Fulton et al., 2011; Colléter et al., 2016). Most of the historical EwE models for Lake Victoria either considered short time periods, e.g. one year, or were developed for a specific section of the lake (Musinguzi et al., 2017). However, a new calibrated 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. (2016): the historical simulation period in both models is the same; both models are based on existing knowledge of the system and follow rigorous parameterisation with the best available data; the choice of most vertebrate groups and representation of feeding interactions are comparable; both models use similar forcing data (annual landings). These models are, therefore, good candidates for testing the effects the sensitivity of alternative fishing scenarios to model choice.

The overall aim of this study is to compare the behaviour of EwE and Atlantis models, which differ in structure and assumptions, using fishing scenarios. We wish to compare models 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. Rather, 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. To keep comparisons between models manageable, biomass and catch predictions are aggregated into annual trends without spatial and size- and age-structure considerations.

Material and methods

The models

Ecopath with Ecosim (EwE)

EwE is a biomass model that is widely used in modelling food-web dynamics (Christensen and Walters, 2004). 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 estimated outside 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 on the basis of 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 parametrisation is tested using fishery drivers (e.g. 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 Fig. 2. The model can be accessed from https://doi.org/10.6084/m9.figshare.7306820.v4. Parameterisation and calibration of the model follow best practices documented in the literature (Heymans et al., 2016); thermodynamic inconsistencies are 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.

The EwE model of Lake Victoria covers an area of approximately 68,800 km^2 (3.05°S to 0.55°N and 31.5° to 34.88°E) 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, organised either in single species or multispecies groups depending on habitat, feeding, economic importance or availability of data. The functional groups include 15 fish groups, 1 fish-eating birds group, 1 reptile group, 3 invertebrate groups, 2 primary producers (phytoplankton and macrophytes), and 1 detritus group (Table 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 major prey for piscivores (Table 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., 2012). Size-related dietary shifts are modelled implicitly by including all possible prey for juvenile and adult Nile perch in the same diet matrix.

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 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).
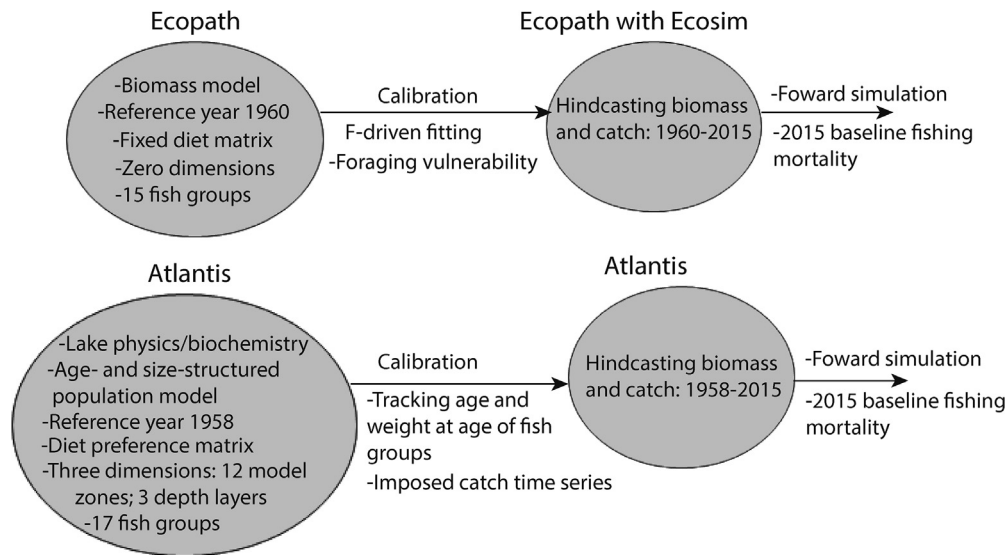
Fig. 2. Schematic diagram showing the major features of EwE and Atlantis models for Lake Victoria. F stands for fishing mortality.

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., 2011). A summary of the Atlantis modelling framework is included here, but a detailed description of the setup, process equations, parameterisation and calibration procedures can be found elsewhere (e.g., Audzijonyte et al., 2017a, 2017b). 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 on the basis of 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. 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. (2016) and a summary of features applicable to this study is shown in Fig. 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 (greater than 40 m). The initial conditions represent 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., 2016). The biological model has 36 functional groups: 1 fish-eating birds group, 1 reptile group, 17 fish groups, 9 invertebrate groups, 4 primary producers, 2 bacteria and 2 detritus groups (Table 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; long-line, mainly targeting Nile perch and other demersal and benthopelagic fishes; small-seine, mainly 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 correlation 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.

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, 2016c). These groups are of great economic 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. We assumed that the representation of these groups in both models is fairly grounded in data, and therefore, their projections are less likely to suffer from the effects of data uncertainty compared to less-studied groups.

We tested four fishing scenarios, which were defined as follows: *NP: 0.6F*, where Nile perch fishing mortality was reduced by 40% from the baseline level; *NP: 1.4F*, where Nile perch fishing mortality was increased by 40% from the baseline level; *HP: 0.0F*, where fishing mortality for haplochromines (the major prey for Nile perch, Fig. 3) was reduced to zero; and status quo (SQ), where 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 (i.e. 2015). Table 2 shows key 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 sce-

nario 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 2, Electronic Supplementary Material (ESM) Table S1).

Ecosystem indicators for comparison

Ecosystem indicators spanning a wide range of processes and biological groups have been used previously to detect a range of impacts from fishing (e.g. Fulton et al., 2005; Smith et al., 2015; Forrest et al., 2015). Indicators can be evaluated at a functional group level, e.g., biomass or catch of individual species, and at a community level, e.g. relative abundance of key functional groups (piscivores vs. planktivores, pelagic vs. demersal), mean TL of 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:

$$MTL_{biomass} = \sum_i TL_i \times \frac{B_i}{B} \qquad (1)$$
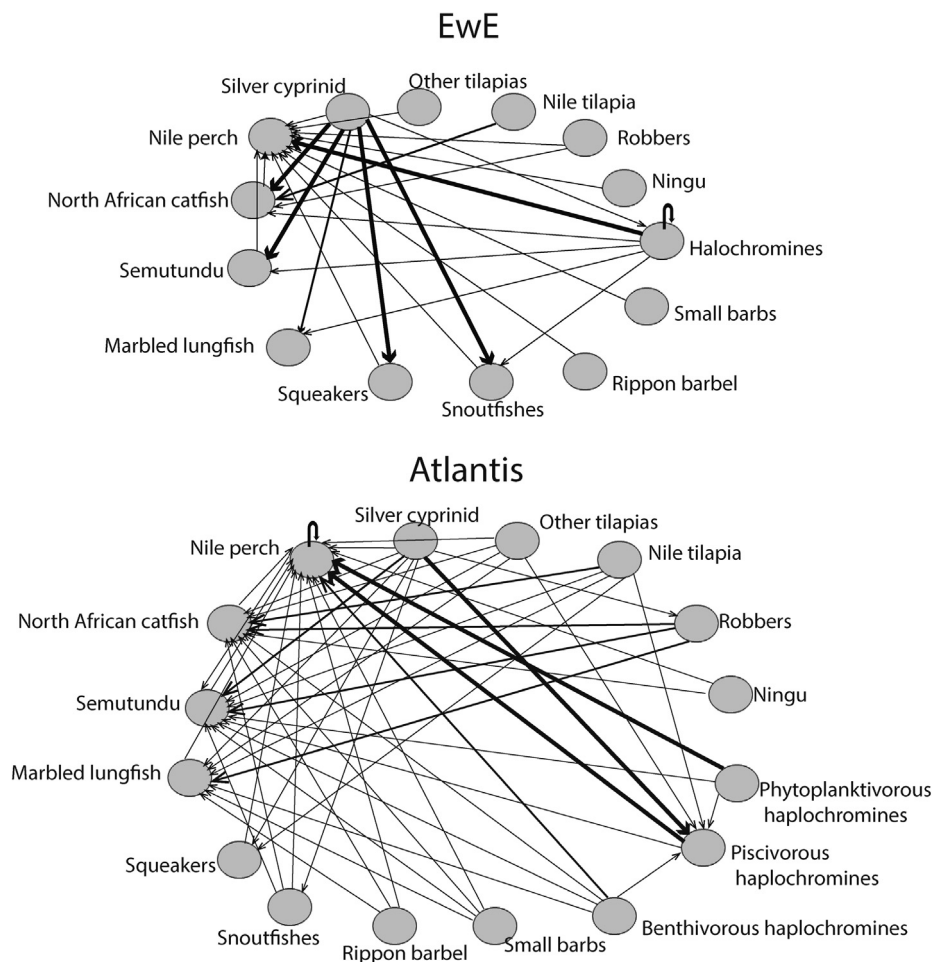
Fig. 3. Schematic representation of predation interactions in EwE and Atlantis models of Lake Victoria. Model groups shown here are only for fish species, which are represented in both models, to ease comparisons. Note that arrows move towards the predators and arrow thickness is consistent with the contribution of prey to the predator's diet. Thick and black arrows indicate that the prey species 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.

Table 2

Baseline (2015) fisheries conditions in the Atlantis and EwE model used in the forward simulations. Biomass and catch values are presented in t/km². F is fishing mortality approximated as catch/biomass.

Model	Atlantis			EwE		
Functional group	Baseline biomass	Baseline catch	F	Baseline biomass	Baseline catch	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

where TL_i and B_i are 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 (equation (2)).

$$MTL_{catch} = \sum_i TL_i \times \frac{B_{Ci}}{B_C} \qquad (2)$$

where B_{Ci} is the biomass of catch of model group i and B_C 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).

To assess the changes that may occur in response to each fishing scenario, each indicator was analysed at the end of the projection relative to baseline values according to the formula:

$$100 \cdot \left(\frac{IV_{end}}{IV_{start}} - 1 \right) \qquad (3)$$

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 prescribed indicator was the same (either increase or decrease relative to baseline values), while consistent quantitative results were indicated by predictions with similar direction and magnitude.

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, we compared the direction and strength of the association between EwE- and Atlantis-simulated biomasses using Spearman rank correlation (r). We calculated r 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).

Results

Species-level indicators

Comparison of EwE and Atlantis models in both the historical reconstruction simulations (Fig. 4) and forward simulations under alternative fishing scenarios (Table 3, ESM Fig. 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 (Fig. 4), but the forward simulations showed opposite trends in most of the scenarios (Table 3). Also, under the SQ scenario, Atlantis predicted an increase for Nile perch, but EwE instead predicted a decrease (ESM Fig. S1). We observed very strong disagreements between models (i.e., opposite trends in biomass predictions) in the historical simulation for Nile tilapia, other tilapias, Ripon barbell, , silver catfish, and small barbs (Fig. 4). However, foward 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 3). Interestingly, even when these groups showed weak or negative correlations for the entire simulation time series (Table 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 (Fig. 5). This 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 (ESM Fig. 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 (Fig. 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 and small barbs was less than 2% in each model, while the
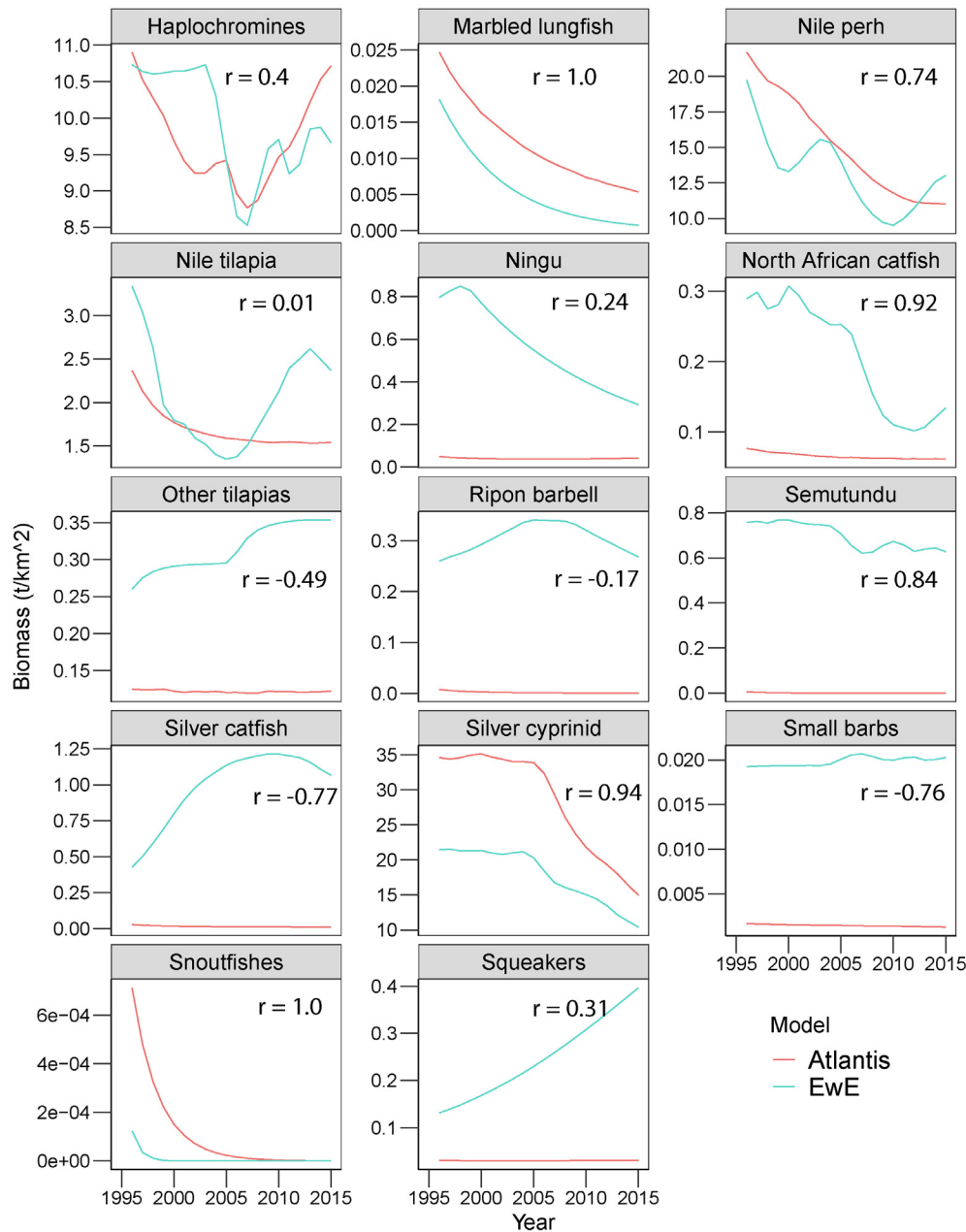
Fig. 4. Biomass of fish groups simulated by EwE and Atlantis models of Lake Victoria in the historical reconstruction simulation (1996–2015). Trends are presented with values of Spearman rank correlation coefficient (*r*), showing the level of consistency between EwE and Atlantis predictions in the hindcast.

snout fishes collapsed in each model before the end of the projection (Fig. 5).

Community-level indicators

Changes in community-level indicators with respect to alternative fishing scenarios are shown in Fig. 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 feed-

ing and habitat guilds, i.e., planktivorous/piscivorous and pelagic/demersal ratios, respectively, under the *NP: 1.4F* scenario; 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 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 is 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

Fig. 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.

Variations in quantive results for the rest of the groups (e.g., 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 differencies in mechanisms governing predation in ecah model outweighing the direct effects from fishing. in EwE, predation mortality is governed by the foraging arena theory, mainly through the vulnerability parameter (Walters et al., 1997; Ahrens et al., 2012), 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 (Christensen and Walters, 2004; Ainsworth and Walters, 2015). 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 main predator) are all less than 2, and this 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 understimation of extinction risk (Christensen and Walters, 2004). This is clearly seen under the *NP:0.6F* scenario (Fig. 5): when Nile perch biomass increases by 25% in Atlantis due to reduced fishing pressure, the biomass of haplochromines (the main prey) decreases by 50%; however, in EwE, a 50% increase in Nile perch biomass under the same scenario is accompaigned by 10% decrease in haplochromine biomass. Sub-
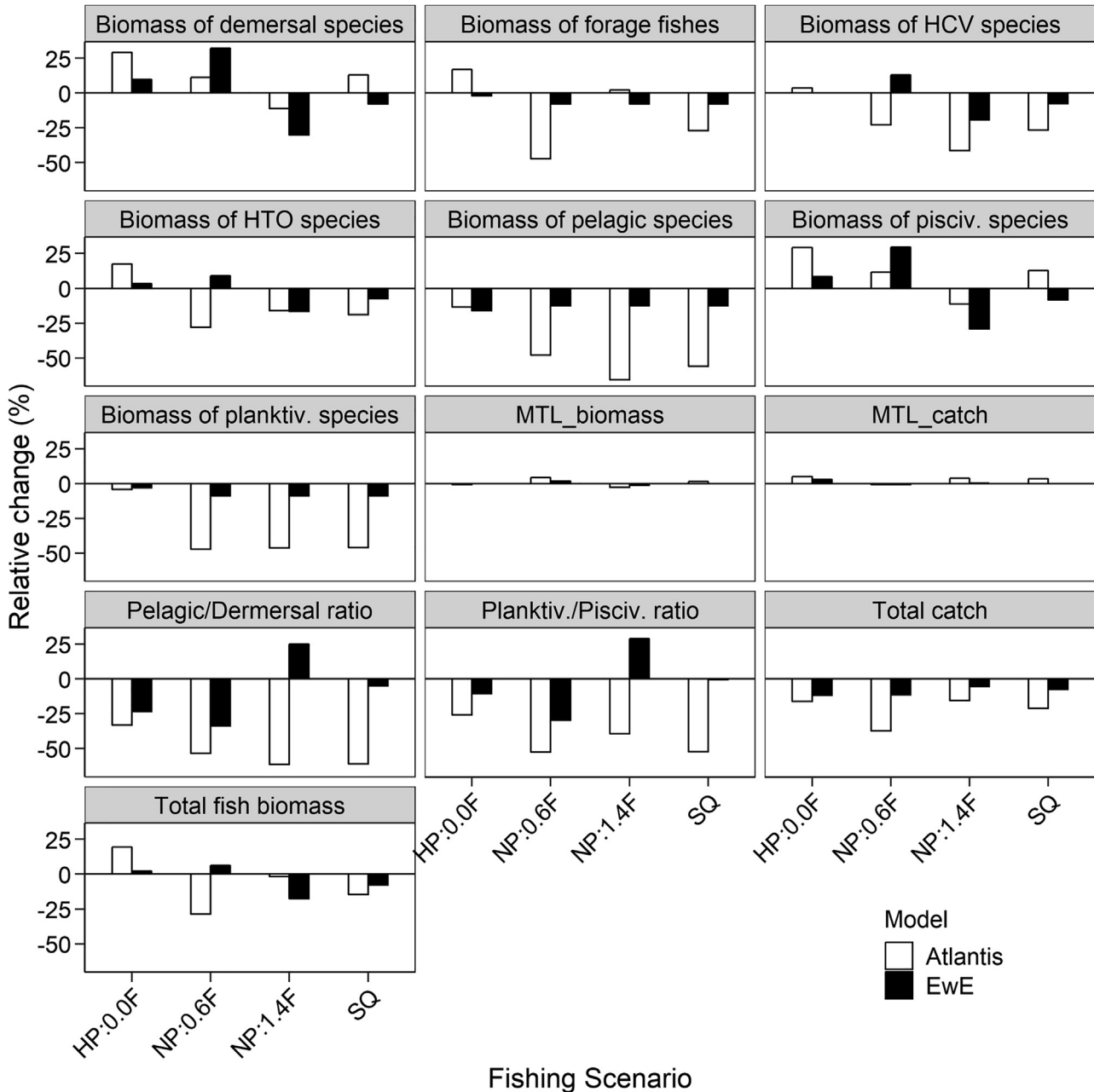
Fig. 6. Indicators based on biomass and catch of fish groups as predicted by EwE and Atlantis. Values represent 2035 value of indicator under each fishing scenario relative to 2015 baseline value. Zero indicates no change. Abbreviations stand for piscivorous (pisciv.), planktivorous (planktiv.), high commercial value (HCV).

sequent improvements to the EwE model of Lake Victoria may need to rexamine the vulnerability matrix and ensure that the fitted vulnerabilities donot 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 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 (e.g., Smith et al., 2011; Kaplan et al., 2013; Forrest et al., 2015), which has been attributed to the "delaying" features incorporated in the Atlantis modelling framework, e.g., 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 (e.g., Smith et al., 2015) found Atlantis to be more responsive than EwE, even when the former 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 that there may be no 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. This underpins the importance of ensemble modelling approach to help identify such areas before the models are used in management, but more importantly, it highlights the risk of relying on one ecosystem model to inform management decisions.

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 (e.g., nutrient inputs), which may have an effect on Lake Victoria's ecosystem functioning (Hecky et al., 2010; Downing et al., 2014). 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 there were no explicit primary productivity drivers, and this contributed to major deviations between model predictions. This could also be contributing to the differences observed in this study. At the core of Lake Victoria's Atlantis model is a ROMS model, which provides hydrodynamic input (Nyamweya et al., 2016). 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., 2016). In contrast, the EwE model is used in its simplest, non-spatial form. This may be a shortcoming to this study, i.e., contrasting a 3-dimensional Atlantis model with a zero-dimensional EwE model; however, comparisons are made between biomass and catch predictions that are 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, 2004), and evaluate alternative scenarios using the two models at habitat level (inshore vs. coastal vs. deep open waters).

Effect of species aggregation on model sensitivity

Our study shows $MTL_{biomass}$ to increase under the *NP: 0.6F* scenario and decrease under the *NP: 1.4F* scenario in both models. This is expected given the TL 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, and the reverse occurs when fishing pressure on the predator is intensified under *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 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, this 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. In addition, the increase in catches of the predator in the short-term can increase TL of the catch and this 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 vs. 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 MTL_{biomas} and MTL_{catch} was less than 1% and about 1.5%, respectively, while in OSMOSE, MTL_{biomas} 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 $MTL_{biomass}$ and 3% for MTL_{catch}, with EwE predicting the least change in all cases. It is not clear whether such changes can be detected in real-world fisheries amidst multiple stressors (Branch et al., 2010).

By examining the feeding guilds, we expected to observe a fishing-driven decline in the piscivore guild under the scenario of increased fishing pressure on Nile perch (*NP: 1.4F*). In turn, we expected this to cause an increase in forage fishes, which are major prey for the piscivore guild. Whereas results of Atlantis were somewhat 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*), we also expected planktivore to piscivore ratio to increase following a fishing-driven decline in Nile perch. However, results show that this indicator only increased in EwE, but decreased in Atlantis. The decline in Atlantis can be attributed to a strong reduction (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 strong decline in silver cyprinid cancels out the effect of a decline in Nile perch on piscivore 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.

Conclusion

The question that motivated this work was: can EwE and Atlantis give similar policy evaluations? While there were large quantitative differences in model predictions for individual species/groups, the models generaly gave similar qualitative results for the major groups that are targeted by fisheries. This illustrates the capacity of EwE and Atlantis models, which differ in structure and biological processes included in the models, to provide consistent 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, even for similar ecosystems, are constructed by independent research groups; practically, this will always be the case. Model inter-comparisons, therefore, should be emphasised as these play a major role in highlighting scenarios that are less sensitive to model choice and for which sim-

pler models (e.g., EwE) could still provide reliable advice for EBFM. Although there are multiple drivers that can influence the simulated fishery responses between structurally-distinct models, we suggest that minimizing the differences in the trophic linkages between the models, i.e., by using similar functional groupings and feeding interactions, may help to minimise variations in fishery responses due to model structure. This also implies that 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 true 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, it is easier to track backwards and identify which key ecological processes cause disparities in simulated responses to alternative scenarios, as seen in the case of Nile perch in the present study.

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Appendix A. Supplementary data

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

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