ARTICLE IN PRESS

Journal of Great Lakes Research xxx (xxxx) xxx

Contents lists available at ScienceDirect

Journal of Great Lakes Research

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

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

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ARTICLE INFO

Article history:
Received 4 April 2019
Accepted 1 January 2020
Available online xxxx
Communicated by Craig Stow

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

ABSTRACT

Long-term time series data are not available for many of the African Great Lakes. This precludes fitting ecosystem model parameters to time series data, and we do not know how reliable non-fitted models are compared to fitted ones in terms of predicting consequences of alternative management strategies. To investigate this, we generate a historical Ecopath with Ecosim (EwE) model for Lake Victoria (East Africa), fitted to time series data (1980–2015), and a present-day EwE model (representing average conditions for the period 2010–2015). We do scenario simulations using the present-day model and the comparable 2015 end-state of the historical model, and test if incorporating information on short-term biomass trends by adjusting biomass accumulation (BA) parameter in the present-day model increases its reliability. We find that there are 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. We also compare the models with and without fitted vulnerability parameters. The models generally give comparable results for the dominant commercial fisheries at low fishing pressure; when fishing mortality is increased, the models give variable predictions. This study adds to the current understanding of the limitations of EwE models that are not challenged to reproduce long-term historical fishery responses to perturbations. We conclude that 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 first draft assumption in present-day models.

Introduction

The demand for ecosystem-based fisheries management (EBFM) in the recent years has spurred 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. 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 (Rose, 2012; Collie et al., 2016). At the heart of the EBFM discussions is the notion that well-fitted models that mimic true ecosystems are best suited for informing EBFM (Rose et al., 2015; Grüss et al., 2017). Consequently, model validation and skill assessment have become an important aspect of ecosystem modelling (Stow et al., 2009; Olsen et al., 2016).

Unlike single-species models, whose parameters can be estimated and statistically tested for their performance within the model, ecosystem models are multidimensional, generally with no computationally feasible means for estimating key model parameters internally. Instead, validation of ecosystem model parameters relies on fitting the model to time series data (calibration) until reasonable agreements between model predictions and observed long-term fishery dynamics are achieved (Heymans et al., 2016; Grüss et al., 2017). Unfortunately, model fitting is not possible in data-limited fisheries. This precludes fitting ecosystem

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https://doi.org/10.1016/j.jglr.2020.01.001

Please cite this article as: V. Natugonza, C. Ainsworth, E. Sturludóttir et al., Ecosystem modelling of data-limited fisheries: How reliable are Ecopath with Ecosim models without historical time series fitting?, Journal of Great Lakes Research, https://doi.org/10.1016/j.jglr.2020.01.001

model parameters to time series data, and we do 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 Walters, 2004) is the most widely used ecosystem modelling tool globally, with over 400 models (Colléter et al., 2016). It combines routines for ecosystem trophic mass balance analysis (Ecopath) with the dynamic and spatial modelling capabilities (Ecosim and Ecospace, respectively) to explore past and future impacts of fishing and the environment. Due to the relative paucity of fisheries data, less than 15% of the EwE models that exist globally are fitted to time series observational data (Heymans et al., 2014). The situation is worse for the inland fisheries, especially those 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 existing 20 models was fitted to time series data. The level of confidence that can be associated with predictions from these models is not known, which 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, 2004). 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, representing the degree of imbalance between production and losses, e.g., due to predation and fisheries) (Christensen et al., 2008). In Ecosim, vulnerability (i.e., 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), but 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, 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 affirmed by a combination of 'pretty fit' (the model's ability to reproduce long-term times series observations) as well as credible model behaviour (i.e., ecological accuracy of the parameters used) (Heymans et al., 2016). In cases where historical data are lacking (or for models of the present day which have no future observations), model validation is based on other criteria such as pre-balance (PREBAL) diagnostic checks (Link, 2010) and data quality appraisal using the "Pedigree" criteria (Christensen and Walters, 2004). Modellers of present-day models parameterize BA and the vulnerability matrix by simpler 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 heavy mortality due to predation and fisheries (Ainsworth and Walters, 2015), while the global vulnerability setting of 2 tends to ignore prior exploitation histories of predators (Plagányi and Butterworth, 2004) and may not be conservative enough to aid precautionary management (Bundy, 2004). Whereas most of the limitations underlying the use of default parameter settings have been discussed in the literature (e.g., 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.

The aim of this paper is 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 quality). To investigate this, we generate a historical model, fitted to time series data (1980–2015), and a present-day model (representing average conditions for the period 2010–2015). Then we do scenario simulations using the present-day model and the comparable 2015 end-state of the historical model. We test 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 they are sufficiently similar 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, we use Atlantis model of Lake Victoria (Nyamweya et al., 2016) as the reference historical ecosystem. 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., 2011). The confidence in the validity of the Atlantis model of Lake Victoria is derived from its ability to produce distributions of nutrients, primary production and major 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., 2016). Nevertheless, this is not to imply that Atlantis is a true reflection of the absolute biomass or catch amounts; therefore, we put more emphasis on fitting the trends rather than absolute values.

Material and methods

Study area

This study focused on Lake Victoria, East Africa (Fig. 1). Lake Victoria is world's second largest freshwater lake in terms of surface area (68,800 km^2). The lake shoreline, which extends about 7142 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 relatively 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, Lake Victoria has endured multiple stresses, including new species introductions, intensive fishing, habitat degradation, invasive weeds, and climate variability (Hecky et al., 2010). These have been accompanied by changes in lake size, limnological conditions, and fish species composition (Hecky et al., 2010; Awange et al., 2019; Taabu-Munyaho et al., 2016). The original fishery (i.e., 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*) (Ogutu-Ohwyo, 1990a; Table 1). 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, 2016a). Haplochromines have been slowly recovering following a drastic decline in the mid-1980s (Witte et al., 2007), and constitute the

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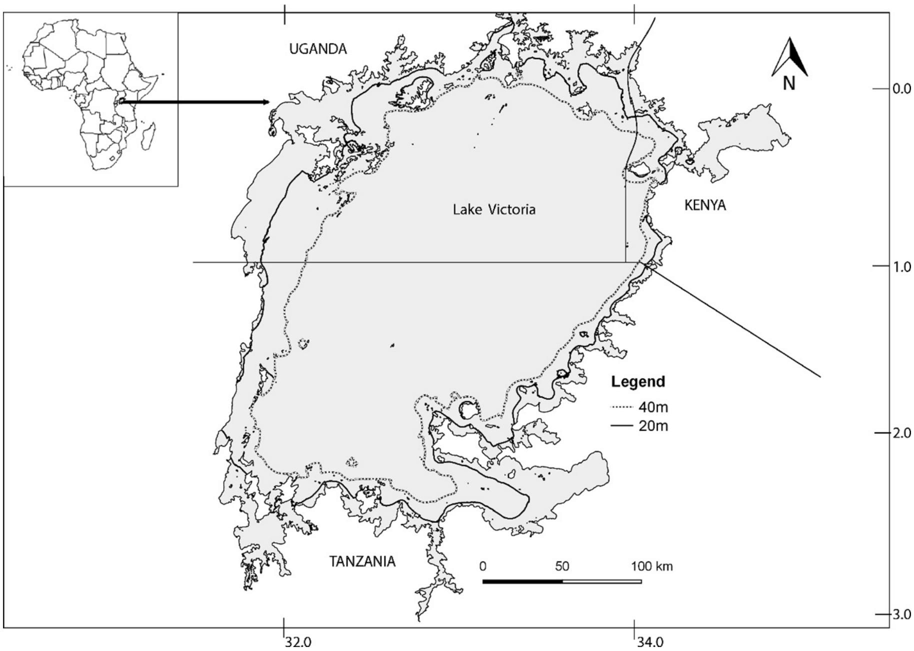

Fig. 1. Lake Victoria in East Africa (extent of the modelled area). Depth contours show inshore (<20 m), coastal (20–40 m) and deep (>40 m) areas.

Table 1
Functional groups in the historical and present-day EwE models. For the fish groups, information on common and scientific names, occurrence, habitat, and feeding mode is based on FishBase (Froese and Pauly, 2018).

Group code	Species/taxa included	Common name	Occurrence	Habitat	Feeding mode
BD	*Haliaeetus vocifer, Ceryle rudis,* Cormorants	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, Gnathonemus longibarbis*	Snout fishes	Native	Demersal	Insectivore
SC	*Schilbe intermedius*	Silver catfish	Native	Pelagic	Piscivore
RB	*Labeobarbus altianalis*	Ripon barbel	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, Bivalvia	Insects and molluscs		Domain	Detritivore
ZP	Copepoda, Ostracoda, Cladocera, and 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).

major prey for the introduced Nile perch (Kishe-Machumu et al., 2012). However, the rest of the native species have never recovered, and their commercial importance for the fisheries in the lake is considered negligible (Goudswaard and Witte, 1997).

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, 2004). 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 immigration) and losses (mortality and emigration), through predator-prey relationships (Eq. (1)).

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

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,

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consumption rate must equal the sum of production rate, unassimilated food (*UA*) and respiration *(R)* (Eq. (2)).

$$B_i \cdot \left(\frac{Q}{B}\right)_i = B_i \cdot \left(\frac{P}{B}\right)_i + R_i + UA_i \tag{2}$$

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 (Eq. (3)).

$$\frac{dB_i}{dt} = g_i \cdot \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - B_i \cdot (MO_i + F_i + e_i) \tag{3}$$

where, for each functional group i, $\frac{dB}{dt}$ is the rate of change in biomass, g is the net growth efficiency (i.e., 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_{ij}, are calculated based on the 'foraging arena' concept (Ahrens et al., 2012), where the biomasses of prey species, B_i's, are divided into vulnerable and invulnerable pools. Consumption is computed as

$$Q_{ij} = \frac{v_{ij} \cdot a_{ij} \cdot B_i \cdot B_j \cdot T_i \cdot T_j \cdot S_{ij} \cdot M_{ij}/D_j}{v_{ij} + v_{ij} \cdot T_i \cdot M_{ij} + a_{ij} \cdot M_{ij} \cdot B_j \cdot S_j \cdot T_j/D_j} \tag{4}$$

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. 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.

Model domain and functional groups

The historical and present-day EwE models are 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 multi-species groups depending on habitat, feeding behaviour, economic importance or availability of data. These included: 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 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 only four fishing gears that are commonly used on the lake: gillnets, targeting most species except small fishes such as silver cyprinid; longlines, targeting Nile perch and other demersal and benthopelagic species (Table 1); small seines, targeting silver cyprinid, with freshwater shrimp (*Caridina nilotica*) and haplochromines as by-catch; and 'others', an aggregation of gears (e.g. beach seines, cast nets, traps) targeting a variety of fish species from shallow inshore regions.

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; Electronic Supplementary Material (ESM) Fig. 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 taken from another model (i.e., Atlantis, Nyamweya et al., 2016). 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., 2016). 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 (ESM Table S1). Diet composition for fish groups (except for haplochromines) was based on information from literature (Corbet, 1961; Ogutu-Ohwayo, 1990; 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. (2016). 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). To balance the Ecopath model, other parameters such as E and BA were maintained at default Ecopath values (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 major changes to the existing 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, Ripon barbel (*Labeobarbus altianalis*), small barbs (*Enteromius* spp.), 'robbers' (*Brycinus* spp.), and 'other tilapias' (see Table 1 for example species); merging of three haplochromine groups into one group; merging of the juvenile and adult Nile perch groups into one group. This was aimed at ensuring 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 hydro-acoustic surveys (LVFO, 2015, 2018; ESM Fig. S1). Biomass data for other fish groups were based on experimental bottom trawl surveys conducted only on the Ugandan side of the lake (NaFIRRI unpublished data; ESM Fig. S1). Data on catches for the main commercial fisheries (Nile perch, silver cyprinid, Nile tilapia, and haplochromines) were based on catch assessment surveys (LVFO, 2016a), and these were apportioned to different gears using information from the frame survey conducted in 2014 (LVFO, 2014). Because the landings of other groups, which constitute less than 5%, are often merged and not reported at species/genus level, we used data simulated by another model (Nyamweya et al., 2016) to represent their catches.

We used the 'pedigree' routine of EwE (Christensen and Walters, 2004) to assess the overall quality 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 arising from 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). In addition, the pedigree information is used to determine low quality parameters, which can be modified during the balancing procedure (Christensen and Walters 2004). Once the Ecopath data and parameters were entered into the software, we recorded the origin and the perceived quality of the data, and assigned to each input a data pedi-

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gree 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 ESM Table S2. We also checked the model's consistency with the physiological constraints, such as the general decline in biomass and vital rates with increasing TL, using the PREBAL approach (Link, 2010).

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. We adjusted mostly P/B values upwards for these groups because of their low pedigree values until all EEs were less than 1. 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., 2012), we increased P/B for haplochromines and biomass for the freshwater shrimp. For the demersal groups, we also adjusted biomass upwards since pedigree index values were suggestive of low quality data.

Assessing ecosystem indices

We compared indices from Ecopath mass balances in the historical and present-day models to get insight into changes in system maturity, productivity, and stability over time. These indices are based on works of Odum, (1969), Ulanowicz and Puccia (1990); Pauly and Christensen (1995), Pauly et al. (1998), and Libralato et al. (2006) and are listed as follows. (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): this is also a measure of system maturity, and decreases as the system matures. (3) Mean trophic level of the catch (TL_C): 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

Ecosystem dynamics (Ecosim)

The historical EwE model was fitted to Atlantis-simulated biomasses and observed landings (Nyamweya et al., 2016) for the period 1980–2015. The use of complex models such as Atlantis to test parameters in a simpler models is relatively new, but has already shown promising results (Weijerman et al., 2017; Sturludottir 2017). 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 variation in reported catch per unit effort (CPUE) and landings, respectively, and all the metrics used in skill assessment (e.g., 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 we encourage readers to see Nyamweya et al. (2016) for details about set-up, parameterisation and calibration.

In Ecosim, we used fishing mortality (F) time series generated from annual landings and Atlantis-simulated biomasses (F = catch/biomass) as a driver. Model fitting followed an iterative, stepwise procedure involving: (i) reading the time series data file from an Excel csv file and storing it in the EwE database; (ii) projecting the model 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) searching for the sensitivity of sum of squares (SS) to vulnerability parameters using prey-predator pairs; (iv) searching for vulnerabilities that minimize SS of differences between model predictions and observations; (v) iteratively adjusting BA rates for the introduced fish groups and silver cyprinid (whose fisheries expanded by more than 200-fold during the initial 10 years of the historical simulation period) and searching for vulnerabilities again until the SS were lowest; (v) manually adjusting the diet matrix 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.

Skill assessment

We conducted skill assessment to measure how well the model fits to the reference data. A number of metrics have been proposed to evaluate model skill, measuring either scale mismatch or correlation between predictions and reference data (Stow et al., 2009). Olsen et al. (2016) suggests that multiple metrics should be used to evaluate model skill. In this study we chose to use three metrics that demonstrate in different ways how the model fits to reference data: modelling efficiency (MEF, Eq. (5)), reliability index (RI, Eq. (6)), and Pearson correlation (r, Eq. (7)).

$$MEF = \frac{\left(\sum_{i=1}^{n}\left(O_i - \bar{O}\right)^2 - \sum_{i=1}^{n}\left(P_i - O_i\right)^2\right)}{\sum_{i=1}^{n}\left(O_i - \bar{O}\right)^2} \tag{5}$$

$$RI = exp\sqrt{\frac{1}{n}\sum_{i=1}^{n}\left(log\,\frac{O_i}{P_i}\right)^2} \tag{6}$$

$$r = \frac{\sum_{i=1}^{n}\left(O_i - \bar{O}\right)\left(P_i - P'\right)}{\sqrt{\sum_{i=1}^{n}\left(O_i - \bar{O}\right)^2 \cdot \sum_{i=1}^{n}\left(P_i - P'\right)^2}} \tag{7}$$

where O_i and P_i are the i^{th} of n observations and predictions, respectively, and the $\bar{O}$ and $\acute{P}$ are the corresponding averages. MEF measures how well the model fits to the data compared to the average. A value 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 that is worse than simply using the average of the data in terms of providing direct biomass estimates. However, negative a 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 correlation is positive (i.e., has the same trend as the data). RI measures how far on average the predictions

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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 would indicate, for instance, 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 perfect 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, it is important to note that this metric can be 1 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, we also tested model validity by comparing the simulated diet composition and ecosystem metrics (such as TL of catch, total system biomass and catch) with those estimated directly from recent data.

Model comparison

We compared two model types, the historical model end-state (A) and the present day model representing average conditions for the period 2010–2015 (B). First, we compared the simulated biomasses, diet composition, TL of catch, 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. Correlation of diet matrices was used to compare diet compositions in model A (ESM Table S3) and model B (ESM Table S4). Second, we performed forward simulations 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 Ecosim 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, 2018). For the rest of the fish groups, biomass estimates were derived from another model (Nyamweya et al., 2016). 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 (e.g., 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 greatest ecological and economic importance in the system, i.e., Nile perch (high TL piscivore; high economic value) and haplochromines (mid-TL forage fish). The scenarios were as follows: reducing Nile perch 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 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 scenario on species biomass was assessed by calculating the change in biomass for each scenario relative to the baseline according to the formula:

$$\left(\frac{B_{end}}{B_{start}} - 1\right) \quad (8)$$

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 value 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.

Results

The historical model

The initial conditions of the Ecopath model were balanced with key parameters shown in Table 2. The underlying mass balance assumptions and thermodynamic rules were checked using key indices (EE, P/Q, PP/R, respiration/assimilation (R/A)), and were found to be in the range described in literature (e.g., 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. Also, fish-eating birds had exceptionally high Q/B value considering the trophic position of the group. The overall Ecopath pedigree index was 0.53.

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 2). The silver cyprinid and haplochromines were an exception with exceptionally 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 substantial 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 catches dominated by native tilapias, Ningu, and catfishes) to about one million tonnes at the end of the simulation (with catches 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 hypothesised 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).

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Table 2

Input parameters and some of the 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 biomass accumulation for the groups), production/consumption (P/Q), fishing mortality /total mortality (F/Z = exploitation rate). 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
Ripon barbel	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

Generally, most of the groups had their biomass decrease substantially either immediately at the start of the simulation (e.g., all native fisheries, except silver cyprinid) or towards the end of the model run (for the case of introduced species) (Fig. 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 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 declined beginning from the 1990s when fishing intensified (Fig. 2). However, BA rate for these groups was positive at the end of the simulation (Table 2).

The simulated biomass trajectories of 14 functional groups were compared with reference data, and showed reasonable agreements for most groups (Fig. 2). Table 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 the poorest fit to reference data for the 'robbers', with both MEF and *r* being negative 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, which was better than several groups with positive values of MEF and *r* (e.g., semutundu, marbled lungfish, Ripon barbel, and Ningu) (Table 3). It is important to note that RI is very sensitive if there are few years where the magnitude is incorrect. This was the case for some native groups, e.g., semutundu, marbled lungfish, and Ripon barbel) where the biomass and landings were very low. Here, the total difference in tons was not high (Fig. 2), but because of the low numbers, the difference in magnitude could be large. This 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 (Fig. 3). All groups had positive MEF except silver cyprinid and other tilapias. The magnitude of the simulated landings was also close to reference data for most groups; RI values suggest 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. 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.

The present-day model

The parameters and selected outputs of the balanced Ecopath model are shown in Table 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 increased because of the low abundance reflected in surveys. The vital rates were fairly consistent with the PREBAL rules, and generally increased 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 the introduced Nile perch to have a negative impact on most fish groups except

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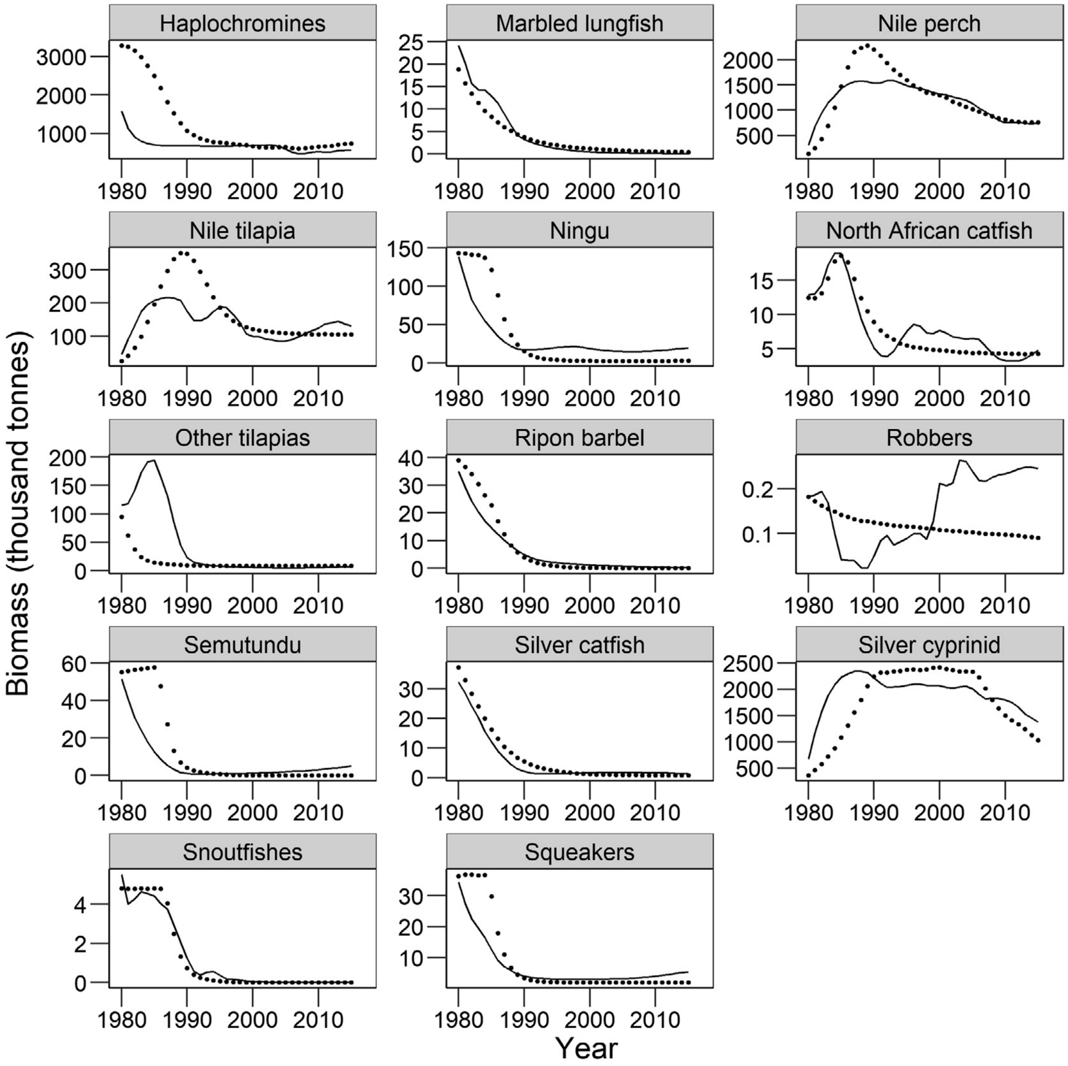

Fig. 2. Simulated biomass from the historical EwE model (lines) compared to reference biomass estimates from the Atlantis model of Lake Victoria (dots) for 14 fish groups.

Table 3
Skill assessment for predicted biomass and observed landings. The metrics used are modelling efficiency (MEF), reliability index (RI), and Pearson correlation (r) (see equations 5–7).

Group	Biomass			Landings		
	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
Ripon barbel	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

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 (ESM Table S5). Other native fisheries constituted less than 5% of the landings; however, the exploitation rate (F/Z) for these groups, with the exception of semutundu and snout fishes, was substantially high (i.e., above 0.5). BA for most native groups was also negative, except for the squeakers, Ningu, and other tilapias (Table 4).

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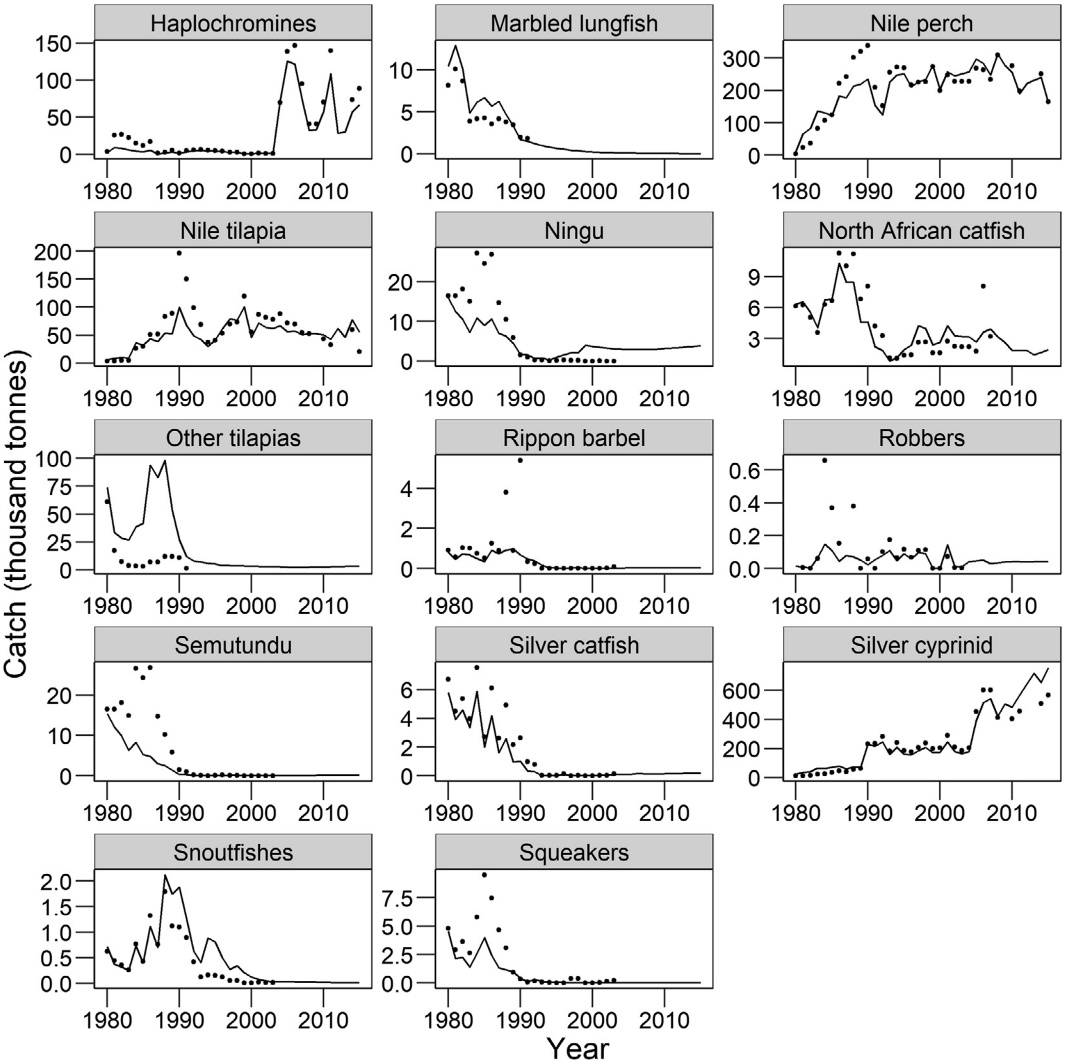

Fig. 3. Simulated landings from the historical EwE model (lines) compared to landings data (dots) for 14 fish groups.

Table 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
Ripon barbel	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		

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Model comparison

Comparison of the historical model end-state (model A, ESM Table S5) with the present-day model (model B, Table 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 TL_C 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 (ESM 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 2 vs. Table 4). Whereas BA rates for most native groups were negative in both models, 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, BA was negative in model A and positive in model B.

Fig. 4 shows 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 direction of change) for the direct fishing-induced effects on target species, but the consequent effects of changes in target groups on their respective prey/predators groups ("indirect trophic effects") were variable, depending 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*, we observed a uniform increase and decrease in haplochromine biomass, respectively, accompanied by an increase and decrease in the biomass of its main predator (Nile perch). Similar responses were observed 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 largely different, especially 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 e.g., marbled lungfish, ningu, Ripon barbel, silver catfish and snout fishes (Fig. 4).

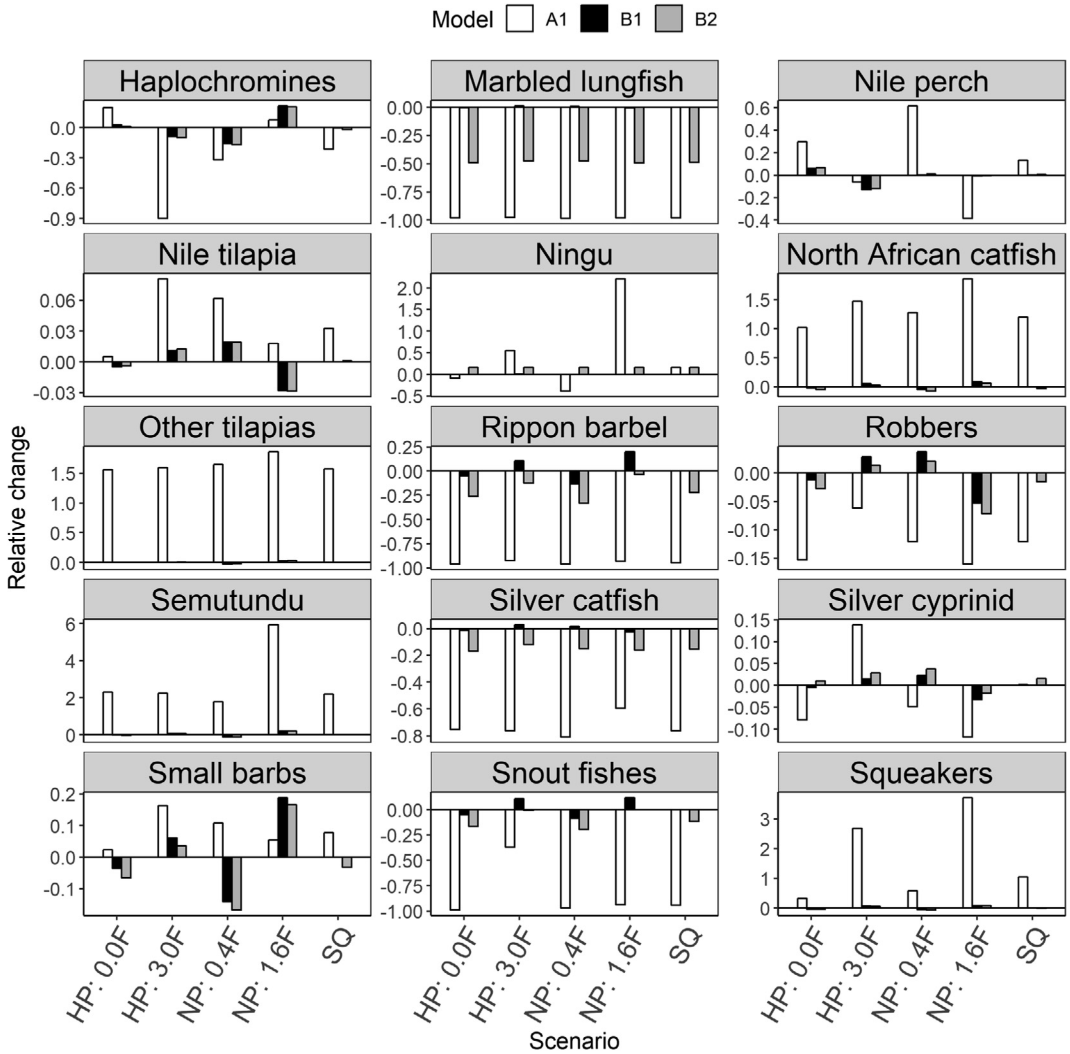

Fig. 4. Percentage change (2035 relative to 2015) in biomass of functional groups as predicted by the historical model end-state (A1) and present-day models: B1 (using default biomass acummulation) and B2 (using empirically-derived biomass accumulation rates). Bars on the same side of zero line (either positive or negative) indicate qualitative agreements between models.

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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 (Fig. 4), largely emanating from the differences in BA rates and vulnerabilities. The BA rates were substantially 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 B2). For haplochromines, the higher response (i.e., relative change in biomass) in model A1 than models B1 and B2 is expected as both fishing (i.e., scenarios *HP: 0.0F* and *HP: 3.0F*) and predation by Nile perch (i.e., 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 ESM 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, vulnerability was observed to exert strong influence, especially for the groups with strong diet interactions (e.g., Nile perch and haplochromines) at high fishing pressure (Fig. 5). At low fishing pressure (e.g., in the *NP: 0.4F* and *HP: 0.0F* scenarios), the response of both Nile perch and haplochromines in models A1 and A2 was largely the same, except that haplochromines responded in different direction when fishing was halted. At high fishing pressure (i.e., in the *NP: 1.6F* scenario), biomass change for Nile perch and its major immediate prey (haplochromines) was about three times higher in A2 compared to A1. However, under the *HP: 3.0F* scenario, the relative changes in 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.

Discussion

The aim of this study was to test ecosystem model skill and the influence of parameter quality on model projections in data-poor situations. To achieve this, we developed and compared a present-day model and the comparable 2015 end-state of the historical model, and tested if incorporating information on short-

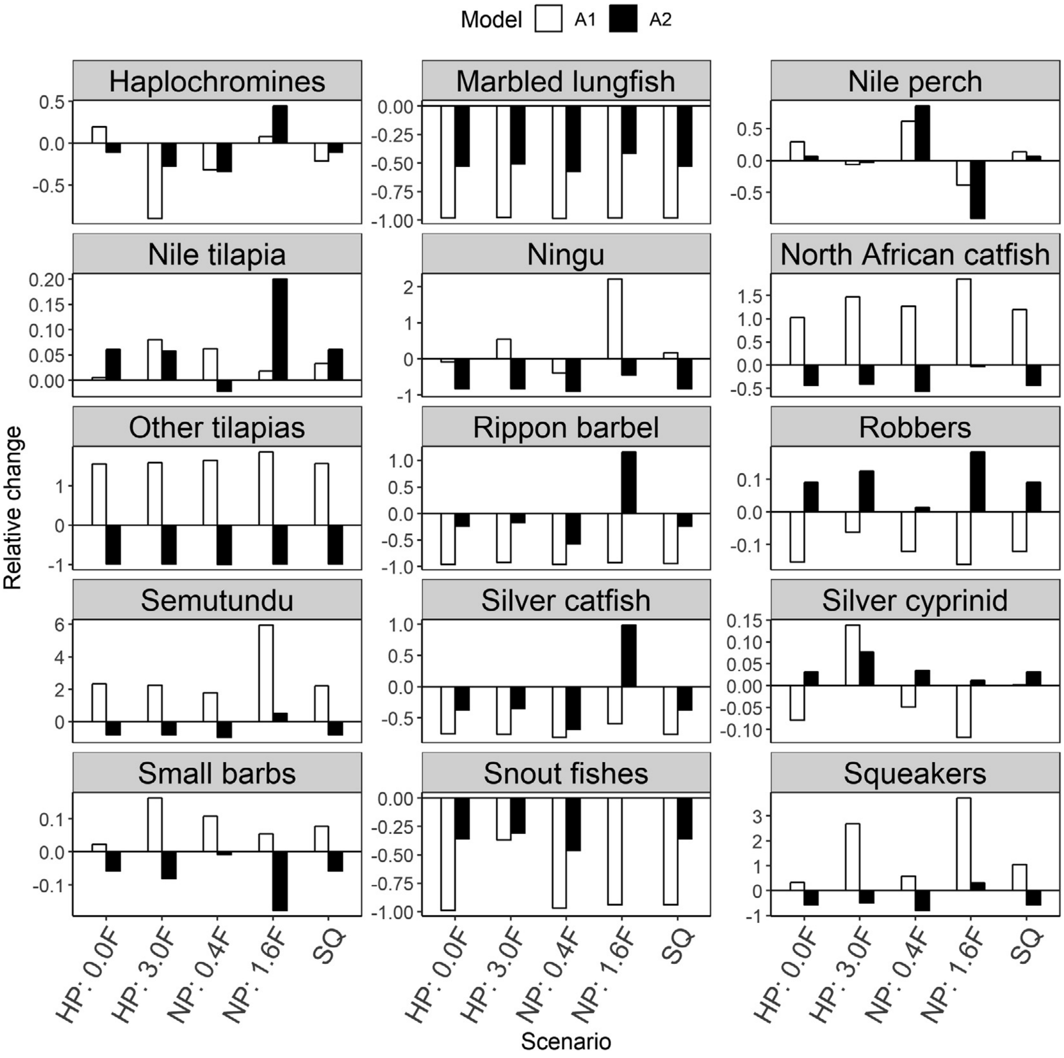

Fig. 5. Percentage change (2035 relative to 2015) in biomass of functional groups as predicted under default (A1) and fitted vulnerabilities (A2). Qualitative similarities between models are indicated by bars on the same side of zero line.

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term biomass trends by adjusting BA parameters in the present-day model increases its reliability. We found 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. We also compared the models with and without fitted vulnerability parameters. We found that vulnerability exerted a stronger influence on model predictions at high fishing pressure than at low fishing pressure, especially for groups with strong diet interactions. We also found that low vulnerabilities were associated with low model responsiveness especially for the key prey groups. These findings are generally consistent with those reported in literature (e.g., Mackinson et al., 2003; Heymans et al., 2011; Ainsworth and Walters, 2015; Heymans et al., 2016) and have important implication on ecosystem modelling in data-limited situations.

Data pedigree

We used the pedigree criteria to assess the quality 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, 2004). 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 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 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 present-day model. This may be attributed to the lopsided research in the recent years, largely focusing on commercially important species, e.g., 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, Trewavas, 1983, Ogutu-Ohwayo, 1990b). There are no studies of comparable magnitude that have been conducted recently, yet the diet is one of the major components in food web models and has been observed to change over the years (e.g., Njiru et al., 2010). Even where limited data on diet are available, they are opportunistically collected based on frequency of occurrence that express diet composition on the basis of dominant prey items, which may not be directly used in EwE. The groups that are considered to be of less commercial value are part of the ecosystem, forming an important 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 experimental bottom trawl surveys. Although these could have been efficient for the demersal and benthopelagic groups, which were the dominant fisheries, they likely underestimate fish biomass in the non-trawlable inshore areas, which are inhabited by majority of these groups. During Ecopath model balancing, biomass estimates for these groups were always 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 (e.g., silver cyprinid and haplochromines) were based on sound survey data, there are still gaps associated with separating species as well as underrepresentation of inshore areas during hydro-acoustic surveys. With regards to harvests, recent data on annual landings are only disaggregated to species/genus level for Nile perch, Nile tilapia, silver cyprinid and haplochromines. The rest of the fish groups are reported as "others" (LVFO, 2016a). For these groups, we chose to use landings simulated by another model (Atlantis, Nyamweya et al., 2016), which could have also contributed to the low pedigree index for the present-day model.

There are still major gaps in data that need to be filled to promote ecosystem modelling on Lake Victoria. The historical model presented here represents the first attempt to fit 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 model fitting approach, where the EwE model is fitted to data simulated by the Atlantis modelling framework. This approach is relatively new, but is equally robust given that the true ecosystem is never really known but only the data from those systems. Some studies has have shown that complex end-to-end models such as Atlantis can be used to test parameters in other, simpler, ecosystem models (Weijerman et al., 2017; Sturludottir 2017) and this study is one 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.

Model validation

Fitting ecosystem models to time series data is a critical step in development of credible models for policy analysis as it shows how best the model can reproduce observed historical responses to disturbances such as fishing (Rose et al., 2015; Heymans et al., 2016; Grüss et al., 2017). 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., 2016; Olsen et al., 2016; Ortega-Cisneros et al., 2017; Sturludottir et al., 2018). These authors have reported correlation higher than 0.5 and positive MEF (using either biomasses or landings or both) for most groups, similar to what we have obtained in the present model (Table 3). While we included metrics that measure scale mismatch (ME and RI), we focused more on emulating trends rather than the absolute values in reference time series. The values of correlation obtained in this study suggest that model performed well in emulating historical trends in fisheries. Nevertheless, ecosystem models need constant improvement as new data become available, and so 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 is able to reproduce major historical events documented in literature, including: (1) the establishment of introduced species in the 1980s; (2) the decline/collapse of most native species/groups during the 1980s; (3) the decline of haplochromines following the establishment of Nile perch; (4) the decline of introduced species during the 1990s due to intensive fishing, and stability at low numbers starting from 2000; (5) the resurgence of haplochromines starting from late 1990s through 2000s following the decline in Nile perch (Taabu-Munyaho et al., 2016; Marshall, 2018; ESM Fig. S1).

Several studies have attributed the decline/collapse of most native fishes to intensive fishing and predation from the introduced Nile perch (Ogutu-Ohwyo, 1990a). For the native tilapias (referred to as "other tilapias" in our models), it is also suggested that competition from the introduced Nile tilapia further

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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 2). The decline of haplochromines due to Nile perch predation could also have narrowed their prey base and further suppressed the stocks (Goudswaard and Witte, 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, we chose to initialize the model using the upper limit of the biomass estimates from the trawl surveys conducted at the beginning of the 1980s (ESM Fig. S1) and not the reference data from Atlantis. The trend for haplochromines observed in Fig. 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. In addition, the model fails to emulate the trend 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.

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 (e.g., 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 opposite direction. Multispecies models are strategic decision support tools, therefore, qualitative results (showing the direction of change in target and non-target species) are important (Fulton et al., 2011). 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, there are lessons from this study that can improve predictions from present-day models where time series data are completely lacking to fit the model parameters. This study shows that the major differences in model outputs emanate from the parameterisation 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; Eq. (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 declining trends in every fishing scenario during forward projections. It is therefore not surprising that two models give opposite results for most of the groups when the steady-state assumption (BA = 0) is used, but give consistent qualitative results when short-term BA rates (also depicting a decline) are used. Nonetheless, there are still major quantitative differences in the latter case because of the differences in magnitude of BA values derived from long-term trends (historical model: Table 2) and short-trends (present-day model: Table 4). This may explain 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). This has an important implication in models that assume zero BA, which is the common practice in Ecopath models. We suggest that if a group is less productive, and is heavily fished or predated upon, it may be safer to assume negative BA as a first draft assumption than assuming steady state conditions. For the high productivity groups or groups that are not heavily predated upon, negative BA is unlikely; for these groups, assuming 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 (Christensen, 1998; Shannon et al., 2000; Mackinson et al., 2003; Neira et al., 2014). Vulnerability sets the maximum predation mortality in Ecosim, and its value ranges from one to infinity (Christensen and Walters, 2004). It is a common practice for modellers to assume low vulnerabilities in present-day models 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). Our results 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 major prey may be used cautiously to avoid over constraining 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 tested 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. In this study, we did not test the full range of vulnerability values, which range from one to infinity. There is still need to examine a larger vulnerability space and also test the effects of other Ecosim parameters on system dynamics. In addition, there are other important parameters in Ecosim that can influence the model results, e.g., foraging time, predator effect on feeding time (Mackinson et al., 2003), but these were all kept at default Ecosim values in the present study, but may need to be explored in future.

Conclusion

In this study, we 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. Several EwE models exist on Lake Victoria, but none of these has been validated by fitting to historical dynamics and tested for predictive skill. We have constructed a historical EwE model for Lake Victoria that is 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 in order 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. We suggest that the fitted model in this study should be interpreted as the best working hypothesis rather than a definitive

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representation of the Lake Victoria ecosystem. The model is open to further improvements; in particular, sensitivity analysis of EwE outputs to different input combinations is needed.

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 quality 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. We have learned that if there is no long-term time series data 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 initialisation year, especially for the less productive groups and those that suffer heavy mortality (either due to predation or fisheries). For such groups, it may be appropriate to use negative BA as first draft assumption in present-day models.

Acknowledgement

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.

Appendix A. Supplementary data

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

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Please cite this article as: V. Natugonza, C. Ainsworth, E. Sturludóttir et al., Ecosystem modelling of data-limited fisheries: How reliable are Ecopath with Ecosim models without historical time series fitting?, Journal of Great Lakes Research, https://doi.org/10.1016/j.jglr.2020.01.001