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

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ABSTRACT

Human and environmental factors have greatly challenged Lake Victoria ecosystem, especially in the last four decades. However, the lake continues to support the World's largest freshwater fishery, currently producing ca. one million tons of fish per year and directly supporting livelihoods of ca. four million people in three riparian countries. We used the Ecopath component of Ecopath with Ecosim modelling software to re-parameterise two existing mass balance models to reflect ecosystem state of Winam Gulf in 1971–1972 and 1985–1986, and construct a new model for the whole lake to reflect ecosystem state in 2014. The aim was to understand the structural and functional properties of Lake Victoria food web and the role of fisheries on the ecosystem. We found a decrease over time in productivity in relation with biomass and respiration, and food web connectivity, and an increase in biomass cycling. The total system throughput, decreased fivefold between 1971 and 1972 and 1985–1986, but was slightly higher in 2014 with a moderate shift from herbivory to detritivory. The implication of these changes on system maturity and resilience are discussed. The trophic level of catches increased between 1971 and 1972 and 1985–1986 due addition of high trophic level catches from the introduced piscivorous Nile perch (*Lates niloticus*) i.e. "fishing up". However, the decline in trophic level of catches between 1985 and 1986 and 2014 seems to have been due to sequential addition of low trophic level catches, especially from the native Silver cyprinid (*Rastrineobola argentea*), a phenomenon termed "fishing through", as opposed to a decline of high trophic level catches (or "fishing down"). Currently, exploitation is unbalanced and skewed to the least productive species at higher trophic level, with significantly less fishing occurring at the most productive species at lower trophic level, and the causes are discussed.

1. Introduction

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

Non-native invasive fish species (intentionally or accidentally introduced by humans) are increasingly recognized as a significant contributor to extinction threat in inland waters around the world by adding and/or worsening the threats associated with habitat loss and fragmentation, hydrologic alteration, climate change, overexploitation, and pollution (Dudgeon et al., 2006). While it is appreciated that non-native species can also have positive outcomes e.g. trophic subsidy, competitive release and predatory release (Rodriguez, 2006; Schlaepfer et al., 2010), many others, when they become invasive, exert negative ecological and evolutionary impacts, ranging from behavioural shifts of native species

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in the presence of invaders to the complete restructuring of food webs (see, for example, Witte et al., 1992).

Decline in aquatic biodiversity, but most importantly fish, is most felt by inland fisheries because of immense contribution of fisheries to livelihoods, where many people, largely from developing and underdeveloped nations, are poor and rely on fish as a food staple (Traoré et al., 2012). Inland fisheries contribute >6% of the world's annual animal protein supplies for humans and about 94% of all freshwater fisheries occur in developing and underdeveloped countries (FAO, 2009). In Africa, inland fisheries generate about US$4676 million from local, regional and international trade, employ >600,000 fishers (de Graaf and Garibaldi, 2014), and contribute at least 30% of total animal protein intake in most landlocked countries (FAO, 2009).

Africa's Lake Victoria supports one of the world's biggest inland fisheries, with the total landed fish catches of about one million tons per year (Mkumbo and Marshall, 2015). The fishery currently employs ca. one million people in fishing and other value-chain related activities; and when their dependants are included, supports livelihoods of about four million people. Traditional fisheries (before 1960s), however, harvested endemic tilapias e.g. Singida tilapia (*Oreochromis esculentus*), and Victoria tilapia *(Oreochromis variabilis*), and the small-bodied haplochromines. These harvests supported fisheries with only modest economic value. In an attempt to increase the economic value and use of fishes from the lake, the piscivorous Nile perch (*Lates niloticus*), was introduced in 1950s to convert the small bony haplochromine cichlids to fish flesh of commercial importance (Pringle, 2005). As intended, the Nile perch was a very successful predator, and populations boomed around 1980, and by 1990, the catch of this species had grown from almost nothing to 300,000 tons (making up 66% of the total catch), while the haplochromine fishery had virtually collapsed (Mkumbo and Marshall, 2015). The collapse of haplochromines due to Nile perch establishment (and hence predation) (e.g. Witte et al., 1992), however, is questioned in van Zwieten et al. (2016), who argue that effects of environmental changes, recruitment and predator-prey dynamics better explain the decline in haplochromines and increase in Nile perch in 1980s than other possible explanations. Nonetheless, after Nile perch establishment, the diverse fish community was reduced, leaving a system dominated by four species: the native Silver cyprinid *(Rastrineobola argentea*), locally known as dagaa, and the Atyid prawn (*Caradina nilotica*) as well as the introduced Nile perch and Nile tilapia (*Oreochromis niloticus*) (Goudswaard et al., 2008). The original complex food web was also simplified, where Nile perch, the top predator, fed mainly on the Atyid prawn (primary consumer), dagaa, and juvenile Nile perch (both secondary consumers) (Moreau et al., 1993).

Demographic changes in Nile perch population post 1990 contributed to the recovery of few haplochromines, notably zooplanktivores e.g. *Haplochromis pyrrhocephalus* and *H. laparogramma*, and detritivores e.g. *H.* 'paropius-like'„ *H.* 'cinctus-like', and *H. antleter* (Kishe-Machumu et al., 2015; Taabu-Munyaho et al., 2016). Through this recovery, a reorganisation of the food web (to some extent) was expected, and part of this was reported in Mwanza Gulf, Lake Victoria (Downing et al., 2012). However, the Ecopath models developed by Downing et al. (2012) used unconvincing parameter estimates (e.g. Production/Biomass = 12 year^{-1} and 1.6 year^{-1} for Nile tilapia and dagaa, respectively) that could have greatly influenced the results (Kolding, 2013). This also manifested in the model outputs (e.g. gross effeciency (GE) = 66 and 61% for Nile tilapia and juvenile Nile perch, respectively, and primary production to respiration ratio (PP/R) = 763) that deviate greatly from real-world ecosystems (Kolding, 2013). Here, we employ pre-balance (PREBAL) diagnostics (Link, 2010) to re-parameterise two existing mass balance Ecopath models for periods 1971–1972 and 1985–1986 for Winam Gulf, and construct a new model for the whole lake for the period 2014, in order to understand the structural and functional properties of Lake Victoria food web and the role of fisheries on the ecosystem.

2. Material and methods

2.1. Study area

Lake Victoria (Fig. 1) is the world's second largest freshwater body and the largest tropical lake in terms of surface area (68,800 km^2), but is shallow (maximum depth = 79 m and average depth = 40 m) relative to other East African Great Lakes. Lake Victoria has an indented shoreline with numerous islands, bays, channels, and wetlands. The lake has undergone dramatic trans-

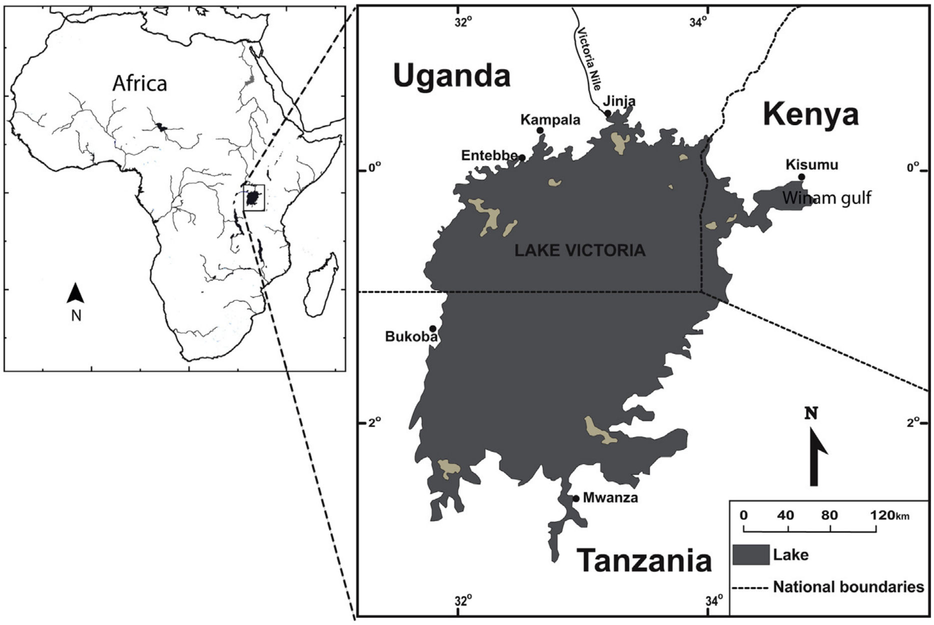

Fig. 1. Location of Lake Victoria, East Africa, and the Winam gulf.

formation, especially after 1970s, both in limnology and fisheries, including changes in trophic status, stratification pattern, water temperature, seasonality, and fish community, and these changes have been extensively discussed (e.g. Kolding et al., 2008, 2014; Hecky et al., 2010; MacIntyre 2012; MacIntyre et al., 2014; van Zwieten et al., 2016). Despite these changes, the lake continues to support the World's largest freshwater fishery, currently producing ca. one million tons of fish per year and directly supporting livelihoods of ca. four million people in three riparian countries (Mkumbo and Marshall, 2015). It is therefore important to understand the structural and functional properties of Lake Victoria food web and the role of fisheries on the ecosystem.

2.2. Model formulation

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

$$P_i = Y_i + B_i \cdot M2_i + E_i + BA_i + P_i \cdot (1 - EE_i) \qquad (1)$$

where, for each functional group (*i*), Y_i is the total fishery catch rate, B*i* stands for biomass per unit of habitat area, $M2_i$ is the total predation rate, E_i is the net migration rate (emigration–immigration), BA_i is the biomass accumulation rate, and EE_i is ecotrophic efficiency, the proportion of the production that is utilized in the system. The term $P_i \cdot (1 - EE_i)$ is an expression of 'other mortality', MO*i*, representing mortality other than that caused by predation and fishing.

Eq. (1) can be re-expressed as:

$$B_i \cdot \left(\frac{P}{B}\right)_i = \sum_{j=1}^{n} Bj \cdot \left(\frac{Q}{B}\right)_j \cdot DC_{ji} + B_i \cdot \left(\frac{P}{B}\right)_i \cdot (1 - EE_i) + Y_i + E_i + BA_i \qquad (2)$$

where, for each functional group (i), P/B stands for the production rate per unit of biomass, Q/B stands for the consumption rate per unit of biomass of predator *j*, and DCji is the fraction of prey *i* in the average diet of predator *j*.

Eq. (2) suggests that the net production of a functional group *i* equals the sum of (1) the total mass removed by predators and fishing, (2) the net biomass accumulation of the group, (3) the net migration of the group's biomass, and (4) the mass flowing to detritus. To achieve mass balances, the energy input and output of all biomass compartments must be balanced, such that:

$$\text{Consumption}\,(Q) = \text{production}\,(P) + \text{respiration}\,(R) + \text{unassimilated food}\,(U) \qquad (3)$$

Respiration is rarely measured in fisheries analysis, and is therefore estimated as the difference between consumption and production (plus unassimilated food), which are easily estimated.

2.3. Model groups

Table 1 shows a description of the different components of the functional groups used in the three mas-balanced models. Not all the functional groups were considered in the three models. For the existing models, for instance, Moreau et al. (1993) had not considered fish-eating birds. Also, Nile perch was not divided into adult and juvenile stages. The same approach was used in the re-parameterisation and the same functional groups were maintained, except that haplochromines were merged in the 1985 model as they had virtually disappeared. In the new model, however, Nile perch was separated into adult and juvenile groups to better account for the ontogenetic diet shifts between life stages (Kishe-Machumu et al., 2012; Nkalubo et al., 2014), while fish-eating birds were considered using data in Villanueva and Moreau (2002).

Table 1
Description of components of functional groups used in the Ecopath mass balance models parameterised to reflect ecosystem state in 1971–1972 and 1985–1986 for Winam gulf, and 2014 for the whole lake. 'Haps' refers to haplochromine fishes. The functional groups are based on the most abundant taxa captured during different research cruises in the lake, economic importance, and role in the food web.

No.	Group	Description
1	Birds	Fish–eating birds, including the Cormorants, African fish eagle, White–winged black tern, and Pied kingfisher
2	Adult Nile perch	Nile perch >40 cm total length. This is the minimum selected length of Nile perch by commercial fleet (Nyamweya, 2012)
3	Juvenile Nile perch	Nile perch <40 cm total length
4	Catfishes	*Bagrus* spp. and *Clarias* spp.
5	Marbled lungfish	The only lungfish representative in the lake
6	Snout fishes and squeakers	*Synodontis* spp. and family Momyridae
7	Zooplanktivorous 'Haps'	Includes *Haplochromis pyrrhocephalus* and *H. laparogramma*, which constitute about 71% of the recovering haplochromine standing stock (Kishe–Machumu et al., 2015)
8	Detritivorous 'Haps'	Includes *H.* 'paropius–like',, *H.* 'cinctus–like', *H. antleter*, which constitute 21% of the recovering haplochromine standing stock (Kishe–Machumu et al., 2015)
9	Other 'Haps'	Other trophic groups that constitute less than 10% of haplochromine biomass
10	Dagaa	Represents the only native pelagic fishery that persisted the ecosystem recession after species introductions in 1950s
11	Nile tilapia	Nile tilapia was known to be herbivorous fish, but has recently diversified its diet to include fish and invertebrates (Njiru et al., 2007)
12	Other tilapias and cyprinids	Red belly tilapia (*Tilapia zillii*) Red breast tilapia (*Tilapia rendalii*), Blue spotted tilapia (*Oreochromis leucostictus*) and *Barbus* spp.
13	Lake prawn	Atyd prawn, *Caridina nilotica*
14	Insects and Molluscs	Includes Diptera (especially the midge, *Chironomus*, and the phantom midge, *Chaoborus* larvae), Odonata and Ephemeroptera nymphs, bivalves, amphipods and gastropods.
15	Zooplankton	Copepoda, Ostracoda, Cladocera, and Rotifera
16	Phytoplankton	Major algae groups, including Cyanobacteria, diatoms, and Green algae
17	Benthic producers	Macrophytes, periphyton, epiphyton
18	Detritus	This is the cycling group composed of decaying organic matter

2.4. Model parameterisation

There are six key data requirements for parameterizing an Ecopath model i.e. Biomass (B), production/biomass (P/B), consumption/biomass (Q/B), other mortality, diets, and catches, but other supplementary parameters can be included such as discards, landings values, and fishing costs. A detailed explanation of these data requirements can be found in Pauly et al. (2000) and Christensen and Walters (2004).

2.4.1. Biomass (t/km^2/year)

In the two previous models by Moreau et al. (1993), biomasses were calculated by the model. Our contribution, except for the 1985–1986 model, aimed at entering biomasses of all fish groups as input to the models, ensuring that the models are well grounded in data. For the 1971–1972 model, biomasses for the fish groups were obtained from trawl surveys conducted between 1969 and 1971 (NaFIRRI unpublished data). All biomasses for the 1985–1986 model groups, however, were estimated by the model as there were no data available. Ecotrophic efficiencies were taken as 0.95 for all groups for which biomass data were not available, considering that 95% of the production is either consumed or exported from the system, as expected for groups with abundant consumers or fully exploited. For the 2014 model, biomasses of Nile perch, dagaa, and haplochromines from the lake-wide hydro-acoustic survey (LVFO, 2015) were used. According to this survey, <5% of the Nile perch from net hauls were >40 cm total length (the juvenile-adult threshold). We adjusted this proportion to 10% to account for any sampling deficiencies, and apportioned the Nile perch biomass into 90% juveniles and 10% adults. Separation of haplochromines into zooplanktivores and detritivores, which constitute >80% of the recovering haplochromine standing stock, and 'other' haplochromines was done using proportions in Kishe-Machumu et al. (2015). Biomasses of fish groups not capatured in the hydro-acoustic survey (e.g. catfishes and Marbled lungfish) were obtained from bottom trawl surveys conducted in 2008 during the Implementation of the Fisheries Management Plan (IFMP) project (NaFIRRI unpublished data). Biomass for Nile tilapia was calculated as a ratio of annual catch to annual fishing mortality. Fishing mortality of Nile tilapia was considered to be 1.32 year^{-1} (Njiru et al., 2007). Biomass of phytoplankton was obtained from Witte et al. (2012), while that of fish-eating birds from Villanueva and Moreau (2002). Biomasses of other lower trophic levels (TLs) were calculated by the model.

2.4.2. P/B ratio (per year)

At steady states, P/B is equivalent to instantaneous rate of total annual mortality (Z) (Allen, 1971). For the 1971–1972 and 1985–1986 models, P/B values for dagaa were increased from 1.8 and 2.2 per year to 3.9 and 4.0, respectively, basing on most realistic Z values in Wandera and Wanink (1995) and Njiru (1995). Basing on catch data of Marbled lungfish (0.42 t/km^2/year) in Moreau et al. (1993) and available biomass data from trawl survey for the same period (0.38 t/km^2), giving an average fishing mortality (F) of 1.1 per year, it appeared the P/B = Z of 0.3 per year for Marbled lungfish used in the 1971 model was underestimated. In the re-parameterised model, P/B of 1.7 was used. All other values of P/B in Moreau et al. (1993) were maintained. For the new (2014) model, Z values for fish groups were calculated as the sum of natural mortality (M) and F. The M was calculated using an empirical relationship (Pauly, 1980) linking M, two parameters of the von Bertalanffy Growth Function (VBGF), and mean environmental temperature (Eq. (4)).

$$M = K^{0.65} \cdot L_{\infty}^{-0.279} \cdot T^{0.463} \tag{4}$$

where L_{∞} is the asymptotic length, the mean length the individuals in the population would reach if they were to live and grow indefinitely (which is calculated from $\log L_{\infty} = 0.044 + 0.9841 \log \mathrm{L_{max}}$; where $\mathrm{L_{max}}$ = maximum length in the population (Froese and Binohlan, 2000)), K is the VBGF curvature parameter (expressing the rate at which L_{∞} is approached, and calculated using the empirical relationships in Froese and Pauly, 2016), and T is the mean environmental temperature (°C). An average temperature of 25.88 °C, adopted from Marshall et al. (2013), was used. Data on growth parameters used in calculation of M, and catches used in calculation of F, as well as their sources, are provided in Supplementary material. The P/B ratios for fish-eating birds and other low Trophic Level (TL) groups were taken from Villanueva and Moreau (2002).

2.4.3. Q/B ratio (per year)

The Q/B ratio for each of the fish functional group, except Marbled lungfish whose aspect ratio (A) of the caudal fin could not be found, was estimated using an empirical formula (Palomares and Pauly, 1998) that relates Q/B with one parameter of the VBGF, habitat temperature, morphological variables, and food type (equation 5).

$$\log\left(\frac{Q}{B}\right) = 7.964 - 0.204 \log W\infty - 1.965T' + 0.083A + 0.532h + 0.398d \tag{5}$$

where W_{∞} is the asymptotic weight (g) that is analogous to asymptotic length, L_{∞}, (and calculated as $W_{\infty} = qL_{\infty}^{3}$, where q is the expression of condition factor in gram per cubic centimetre of fish (Sparre and Venema, 1998)), T' is an expression for the mean annual temperature of the water body, expressed using $T' = \frac{1000}{Kelvin}$ (where Kelvin = °C + 273.15), A is the aspect ratio of caudal fin (approximately equal to 1.32 and 1.9 for fish with round and forked tails, respectively (Froese and Pauly, 2016)), *h* is a dummy variable expressing food type (i.e. 1 for herbivores, and 0 for detritivores and carnivores), and *d* is a dummy variable also expressing food type (i.e. 1 for detritivores, and 0 for herbivores and carnivores). The W_{∞} data in Moreau et al. (1993) were used in calculation of Q/B for both 1971 and 1985 re-parameterised models. A mean annual temperature of 25 °C (Talling, 1987) was used in both cases. For the 2014 model, however, W_{∞} data used in calculation of Q/B, and their sources, are given in Supplementary material. An average temperature of 25.88 °C (Marshall et al., 2013) was used. For Marbled lungfish whose Q/B ratio could not be calculated from equation 4, an estimate of 4.3 per year in Villanueva and Moreau (2002) was used. The same source was used for Q/B ratios of non-fish groups.

2.4.4. Exports (catches, Y)

Data on catches for the re-parametrised models were maintained as those in Moreau et al. (1993). For the new model, however, data on catches for the whole lake were obtained from the regional catch assessment surveys conducted in April 2014 (LVFO, 2014) (suplementary material). We split the 2014 catch data according to fishing gear to permit identification of ecologically meaningful critical situations, especially when analysing mixed tropic impacts (MTI). Nile perch catches were also separated into juvenile and adult stages. According to Mkumbo and Marshall (2015), only 15% of the landed Nile perch were >50 cm total length. This value was doubled, assuming that Nile perch in the range of 41–49 cm total length account for not less than 15%. Accordingly, 30% of the Nile perch catches were classified as adult (>40 cm), while 70% as juvenile (<40 cm). Also, in the new model, we included Atyid prawn in exports because they are harvested as by-catch in small seines alongside dagaa and are not discarded into the lake. From the small seines that are used to harvest dagaa in the Tanzanian waters of Lake Victoria, approximately 10% of the total catch is Atyid prawn by-catch (Budeba and Cowx, 2007). In this study, we made a generalisation that ca. 10% of the fish caught in small seines in 2014 were Atyid prawn.

2.4.5. Diet composition (DC) and unassimilated food (U)

The diet composition matrices in the 1971–1972 and 1985–1986 models were maintained as those in Moreau et al. (1993). For the new model, diet compositions of both juvenile and adult Nile perch were obtained from stomach content analyses in Kishe-Machumu et al. (2012). The diet composition of Nile tilapia was obtained from Njiru et al. (2008). Diet composition for catfishes, dagaa, haplochromines, Atyid prawn, and zooplankton were obtained from Downing et al. (2012), while that of fish-eating birds, other tilapias and cyprinids, squeakers and snoutfishes, marbled lungfish, and insects and molluscs from Villanueva and Moreau (2002). The final diet matrices that achieved mass-balanced models are provided with suplemetary material. We used a default value of 0.2 in all models to represent the fraction of the food that is not assimilated for carnivorous groups, and 0.4 for herbivores (Christensen et al., 2008).

2.4.6. PREBAL diagnostics

Once all input parameters, as estimated from original data and literature, were entered into EwE software, we tested for underlying assumptions using PREBAL diagnostics (Link, 2010). A number of diagnostics were used in this study, including: assessing biomass across taxa/trophic levels (where biomass is expected to decrease with increasing trophic levels, reflecting lower abundance of larger-sized organisms at upper trophic levels); biomass ratios (where predators biomass should be less than that of 1 relative to their prey); and vital rates across taxa/trophic levels (should be a general decline with increasing trophic level).

2.4.7. Balancing Ecopath models

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

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

ii $0.1 \leq \text{GE} \leq 0.35$, except for fast growing groups with higher values, and top predators with lower values.

iii Net efficiency < 1.0 < Production/Consumption (P/Q) because net efficiency is the value for food conversion after accounting for U, and therefore cannot exceed GE.

iv Respiration/Assimilation (R/A) < 1.0 because the proportion of biomass lost through respiration should not exceed the biomass of food assimilated, and consistent with groups strategies for energy allocation i.e. R/A close to 1.0 for *K*-selected species and top predators, which invest more energy on growth and reproduction, and R/A«< 1.0 for *r*-selected species that invest less energy on reproduction.

v Respiration/Biomass ratio (R/B) i.e. the metabolic activity level of a group consistent with the group activities. Generally, R/B ratios are expected to be within 1–10 year^{-1} for fish and may be as high as 50–100 year^{-1} for groups with higher turnover such as zooplankton.

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

2.5. Assessing ecosystem indices that relate to maturity and stability

Various ecological attributes that are useful for analysing the ecological role of the different ecosystem components are incorporated in EwE. In this study, ecosystem metrics, including Total System Throughput (T) (the measure of the size of the entire system in terms of the summation of biomass flows from total consumption, respiration, export and flows to detritus), Total Primary Production (PP) (the summed primary production from all producers), Net System Production (NSP) (the difference between PP and total respiration), Primary Production/Respiration (PP/R) (the measure of system maturity that is expected to approach one as the system matures), Trophic transfer efficiency (TE) (the percentage of T entering a trophic level that is subsequently passed on to the next trophic level (or harvested)), Connectance Index (CI) (the ratio of the number of actual links to the number of possible links in the food web), System Omnivory Index (SOI) (the average omnivory index of all consumers weighted by the logarithm of each consumer's food intake), and Ascendency (A) (which quantifies both the level of activity and the degree of the organisation of the system) were compared with other systems in the region to understand the relative state of system development. The mathematical upper limit of A is the development capacity (DC), representing the scope of the system for further development, while the difference between the DC and A is the System Overhead (O), representing the ecosystem's potential for recovery. All the above indices, which are used to describe the relative impacts of different drivers of change, including fishing and environmental forcing, on system maturity, productivity, efficiency, and stability follow the theories in Odum (1969), Ulanowicz (1986), Ulanowicz and Puccia (1990), Christensen and Pauly (1992), Christensen (1995), Ulanowicz (2004), and Christensen et al. (2008).

In addition to the above indices, we assessed keystoneness to provide insight of the functional groups that are ecologically important in the food web. However, this was only done for the 2014 model as it the one that was parameterised to represent the whole lake, and not parts of the lake as in the 1971–1972 and 1985–1986 models. Keystone (species or groups of species) are ecologically important species, usually predators, in food webs, which have a disproportionately high trophic impact on their community, compared to their biomass (Valls et al., 2015). Thus, keystone species may allow for the management of a single focal species with the aim of maintaining the whole ecosystem. Three keystone (KS) indices exist in EwE, but we implemented only KS_3 (Valls et al., 2015), which balances contributions between trophic impact and biomass components in estimation of species keystoneness, without over-representing abundant or rare species, to identify keystone species.

2.6. Assessing the role of fisheries

We computed various indices to identify the current focus of fisheries.

i Mean trophic level of the catch (TL_C). This reflects the overall strategy of a fishery, and calculated by weighting the proportions of each fish/fish group from the catch by their respective TLs. The TL_C decreases as fishing impacts increase in the ecosystem since fishing tends to first remove the higher TL organisms.

ii Primary production required (PPR). The PP that is required to sustain the catches, and calculated from both primary producers and detritus in order to evaluate the sustainability of fisheries in terms of energy. It is calculated using an empirical formula

(Pauly and Christensen, 1995) linking PPR, fish catches, TE, and TL (equation 6).

$$PPR = \frac{1}{9} \cdot \sum_i Yi \cdot \left(\frac{1}{TE}\right)^{TLi-1} \tag{6}$$

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

Using catch and production data from the 2014 mass-balanced Ecopath model, we assessed whether the current fishing pattern is balanced i.e. fishing is done across the widest possible range of species in proportion to their natural productivity (Garcia et al., 2012) as well as fishing intensity. From the definition of Garcia et al. above, a balanced fishing pattern, also known as balanced harvesting, is achieved when all exploited fish groups have the same exploitation rates (E). To test this, we used a logarithmic plot of catches vs production because if all the fishes that are exploited through fishing have the same E, a linear regression of catches (Y) against production, (P) (both on logarithm scale) would have a slope of $b = 1$ and an intercept of $a = \log(E)$ (Kolding et al., 2015). Any deviations from a slope of 1 would show regular differences in E among fishes, and the magnitude of the difference from the slope of 1 would indicate how unbalanced the fishing pattern is; and, the higher the deviation around the slope, the more inconsistent (i.e. unbalanced) is the exploitation pattern. Also, because the intercept a of the linear regression on of Y against P (both on logarithm scale) represents the log average E, the closer the points lie to the Y = P line, in other words E = 1, the higher the fishing pressure and vice versa. The data used in this analysis are catches and annual production for each of the exploited functional groups. Annual production (P) for each functional group i, was calculated as $P_i = (P/B)_i \cdot B_i$. Both P/B and B are available in the 2014 mass-balanced model (see Table 2c) while data on catches for the same model period is provided in Supplementary material.

3. Results

3.1. PREBAL and mass balances

The re-parameterised models and the new model were evaluated against PREBAL diagnostic checks, assessing biomass, biomass ratios, and vital rates across trophic levels. Generally, biomass was found to decline with increasing trophic level, although the new model exhibited 'Middle-Heavy' and moderate 'Top-Heavy' biomass decomposition. We did not modify the biomass data for the new model that tended to violate this rule of thumb (Link, 2010), because (1) most of middle TL groups comprised of potentially recovering haplochromine biomass, (2) the high TL groups constitute the introduced (and well-known) invasive predatory fish, the Nile perch, and (3) most of the data on these pelagic species were obtained from a reliable source, including a hydro-acoustic survey carried out in 2014 (LVFO, 2015). All the vital rates, however, including P/B, Q/B, and R/B, were largely found to decline with increasing TL. Excepting the 1985–1986 model, where EE values were pre-defined, biomass utilization for every taxa was lower than biomass production of that taxa, and EE consistent with group's mortality rate. For instance, fish-eating birds, the top predators, are neither harvested nor consumed in the system; hence, their EE was zero. In addition, total human removals were less than total production, suggesting that general ecological and fishery principles were met, thus requiring no further modifications. The resulting mass balance food web models are presented in Fig. 2, and the model parameters in Table 2.

The modelling procedure assigns a TL of 1 to primary producers and detritus, and a TL of 1+ (weighted average of the preys' TL) to consumers, resulting in TLs that are not necessarily integers (*sensu* Odum, 1969). The highest TL in the lake was occupied by Nile perch, except where fish-eating birds were included, while Nile tilapia, other tilapias, detritivorous and planktivorous haplochromines, and zooplankton occupied the lowest TLs among the consumers, except in the new model where Nile tilapia occupied a higher trophic level (Table 2). The trophic omnivory of Nile perch decreased significantly between 1971 and 1972 and 1985–1986, as showed by a sharp decrease in OI, while the opposite was true for Nile tilapia, which exhibited the greatest shift in feeding spectrum, with an increase in OI from 0.06 and 0.08 in the 1971–1972 and 1985–1986 models, respectively, to 0.5 in the 2014 model.

Fig. 3 shows the Lindeman spines for the three models (excluding TLs > IV). The main flows, including detritus, occurred within TLI and TLII, generating 90–93% of T. Although the amount of total net PP consumed by herbivores increased from 85% in 1971–1972 to 92% in 1985–1986, and decreased slightly to 90% in 2014, with the remaining portion of PP, respectively, flowing to the detritus compartment, the detritivory/herbivory ratio doubled from 12 to 14% in the 1971–1972 and 1985–1986 models to 27% in the 2014 model (Fig. 3). Transfer efficiencies (TEs), which tend to decrease as one ascends the trophic pyramid (Christensen and Pauly, 1993), increased along each successive TL in the 1985 model, resulting into mean TE of 13.74% that deviated from the 10% Lindeman rule of trophic transfer efficiency.

3.2. Ecosystem indices

Table 3 shows the summary statistics of energy flows and biomasses in Lake Victoria over time, compared with other lakes in the region. Total production, consumption, exports, respiratory flows and flows to detritus decreased more than sevenfold between 1971 and 1972 and 1985–1986, and either increased slightly (e.g. consumption, exports, and respiratory flows) or decreased further (e.g. flows to detritus) between 1985 and 1986 and 2014. The total system throughput (T) (i.e. the sum of all flows) decreased fivefold between 1971 and 1972 and 1985–1986, and increased slightly between 1985 and 1986 and 2014, and is currently comparable to Lakes Kivu, Tana, and Ébrié. During the three time periods, 1971–1972, 1985–1986, and 2014, the proportion of T, respectively, consumed by predation increased from 40.9 to 43.5 to 49.1%; that dissipated by respiration increased from 20.7 to 22.3 to 24.1%; that exported (through catches) decreased from 16.8 to 14.2 to 8%; and the flows to detritus decreased from 21.4 to 19.7 to 18.6%. All the synthetic indicators used to assess the ecosystem status, including PP/R, PP/B, B/T, CI, Finn's cycling index, and Finn's path length, showed a system that is maturing, with relatively high productivity in relation with the total biomass and respiration, despite having low biomass in relation to the total flows of energy, and low connectivity within the food web. Table 3 shows that there has been a decrease in productivity in relation with biomass and respiration, a decrease in food web connectivity (as shown by decrease in CI and SOI), and an increase in biomass cycling (with a reduction in number of groups that a flow passes through as shown by Finn's cycling index and Finn's path length, respectively). Concerning the food web organisation descriptors, both system's A and O decreased fivefold between 1971 and 1972 and 1985–1986, and increased slightly between 1985 and 1986 and 2014. However, the system's redundancy (O/DC) fluctuated between 66 and 70%.

Fig. 4 shows keystone index and relative total impact of the different functional groups considered in the 2014 Ecopath model.

Table 2
Parameter estimates and other outputs (e.g. production/consumption (P/Q), net efficiency (NE), and omnivory index (OI)) for the three models on Lake Victoria. Parameters in italics were estimated by EwE software to balance the model. Values of Ecotrophic efficiency (EE) in parentheses were pre-set to balance the model where biomass data were not available. Flows to detritus are expressed in t/km^2/year. B stands for biomass, P/B is production/biomass, and Q/B is consumption/biomass. 'Haps' refer to haplochromine fishes.

1971–1972 model (re-parameterised)									
Group name	Trophic level	B (t/km^2)	P/B (/year)	Q/B (/year)	EE	P/Q	Flow to detritus	NE	OI
Nile perch	4.09	0.26	0.39	2.52	*0.07*	0.15	0.22	0.19	0.408
Catfishes	3.48	1.41	0.79	6.74	*0.79*	0.11	2.12	0.14	0.23
Marbled lungfish	3.18	0.38	*1.75*	4.8	(0.98)	0.36	0.37	0.45	0.28
Snout fishes and squeakers	3.39	0.3	1	9.96	*0.99*	0.10	0.59	0.12	0.17
Other 'Haps'	3.68	5.21	1.4	10.73	*0.90*	0.13	11.89	0.16	0.21
Planktivorous 'Haps'	2.04	5.21	2.5	52	*0.56*	0.04	59.91	0.06	0.05
Benthivorous 'Haps'	3.10	15.65	2.5	37.4	*0.31*	0.06	143.75	0.08	0.14
Dagaa	2.61	*6.95*	3.9	23.5	(0.95)	0.16	34.05	0.20	0.313
Nile tilapia	2.058	0.06	0.65	22.95	*0.68*	0.02	0.56	0.047	0.06
Other tilapias	2.05	1.88	1	29.9	*0.73*	0.03	22.97	0.05	0.06
Lake prawn	2.48	*12.13*	14	64	(0.7)	0.21	206.2	0.27	0.28
Macrozoobenthos	2.24	*183.8*	5	25	(0.95)	0.2	965.14	0.25	0.22
Zooplankton	2.052	*59.04*	33.5	140	(0.7)	0.23	3899.9	0.39	0.052
Phytoplankton	1	*27.01*	365		(0.85)		1478.8		
Benthic producers	1	*113.04*	25		(0.85)		423.9		
Detritus	1	10			*0.21*				0.28
b) 1985–1986 model (re-parameterised)									
Nile perch	3.51	*12.58*	0.98	2.4	(0.95)	0.40	6.65	0.51	0.09
Catfishes	3.34	*0.69*	0.85	6.74	(0.95)	0.12	0.96	0.15	0.16
Marbled lungfish	3.16	*0.83*	0.3	4.8	(0.95)	0.06	0.81	0.07	0.20
Squeakers and snoutfishes	3.20	*0.27*	0.9	9.96	(0.95)	0.09	0.56	0.11	0.13
Haplochromines	3.10	*0.13*	2.83	33.37	(0.95)	0.08	0.91	0.105	0.14
Dagaa	2.61	*2.10*	4	23.5	(0.95)	0.17	10.33	0.21	0.31
Nile tilapia	2.06	*5.67*	0.82	22.95	(0.95)	0.03	52.36	0.059	0.08
Other tilapias	2.06	*0.516*	1.2	29.9	(0.95)	0.04	6.20	0.06	0.07
Lake prawn	2.48	*2.61*	16	64	(0.95)	0.25	35.58	0.31	0.28
Macrozoobenthos	2.24	*43.48*	5	25	(0.6)	0.2	304.41	0.25	0.22
Zooplankton	2.05	*10.26*	33.5	140	(0.8)	0.23	643.53	0.39	0.05
Phytoplankton	1	*4.53*	365		(0.95)		82.70		
Benthic producers	1	*25.66*	25		(0.85)		96.23		
Detritus	1	10			0.29				0.18
b) 2014 model (new)									
Fish-eating birds	3.897	0.005	0.3	60	*0.0*	0.005	0.06	0.006	0.142
Adult Nile perch	3.837	1.82	0.922	4.811	*0.65*	0.19	2.33	0.239	0.20
Juvenile Nile perch	3.335	16.2	3.5	11.73	*0.17*	0.29	84.51	0.372	0.12
Catfishes	3.206	0.093	0.991	6.009	*0.99*	0.16	0.11	0.20	0.09
Lungfish	3.242	0.076	1.12	4.3	*0.79*	0.26	0.082	0.326	0.243
Squeakers and snout fishes	3.061	*0.276*	1	8.76	(0.95)	0.11	0.49	0.14	0.13
Zooplanktivorous 'Haps'	3.040	9	2.7	21.58	*0.981*	0.12	39.32	0.15	0.002
Detritivorus 'Haps'	2	2.438	2.53	47.96	*0.83*	0.05	24.40	0.06	
Other 'Haps'	3.463	0.928	1.83	13.45	*0.86*	0.13	2.72	0.17	0.16
Dagaa	2.56	19.1	3.93	30.79	*0.82*	0.12	131.04	0.159744	0.25
Nile tilapia	2.568	0.624	2.02	19.6	*0.91*	0.10	5.00	0.172109	0.50
Other tilapias and cyprinids	2.052	*0.232*	2.37	33.42	(0.95)	0.07	3.12	0.118189	0.051
Lake prawn	2.1	*13.75*	16	64	(0.98)	0.25	180.4	0.3125	0.09
Insects and molluscs	2.106	*17.47*	5	25	(0.8)	0.2	104.8	0.25	0.101
Zooplankton	2	*15.24*	34	140	(0.95)	0.24	879.56	0.404762	
Phytoplankton	1	7.1	*373.45*		(0.95)		132.5		
Benthic producers	1	13.40	25		*0.57*		142.9		
Detritus	1	10			*0.57*				0.30

Keystone indices were high for adult Nile perch, phytoplankton, and Lake prawn, but only adult Nile perch had low biomass and highest relative trophic impact.

3.3. *The focus of fisheries*

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

The TLc increased from 2.9 to 3.1 between 1971 and 1972 and 1985–1986, but declined thereafter, and by 2014, it had dropped to 2.8. The initial increase in TLc coincided with the Nile perch (an introduced high TL invasive species) explosion during 1980s (Fig. 5). We therefore examined the trends in catches of two predominant fisheries, a high TL species, Nile perch, and a low TL species, dagaa, to assess whether the decline in TLc was either due to the decline in catches of the high TL (predatory) fish(es) (in line with 'fishing down' the food web e.g. Pauly et al., 1998; Stergiou and Tsikliras, 2011) or progressive increase in catches of low TL

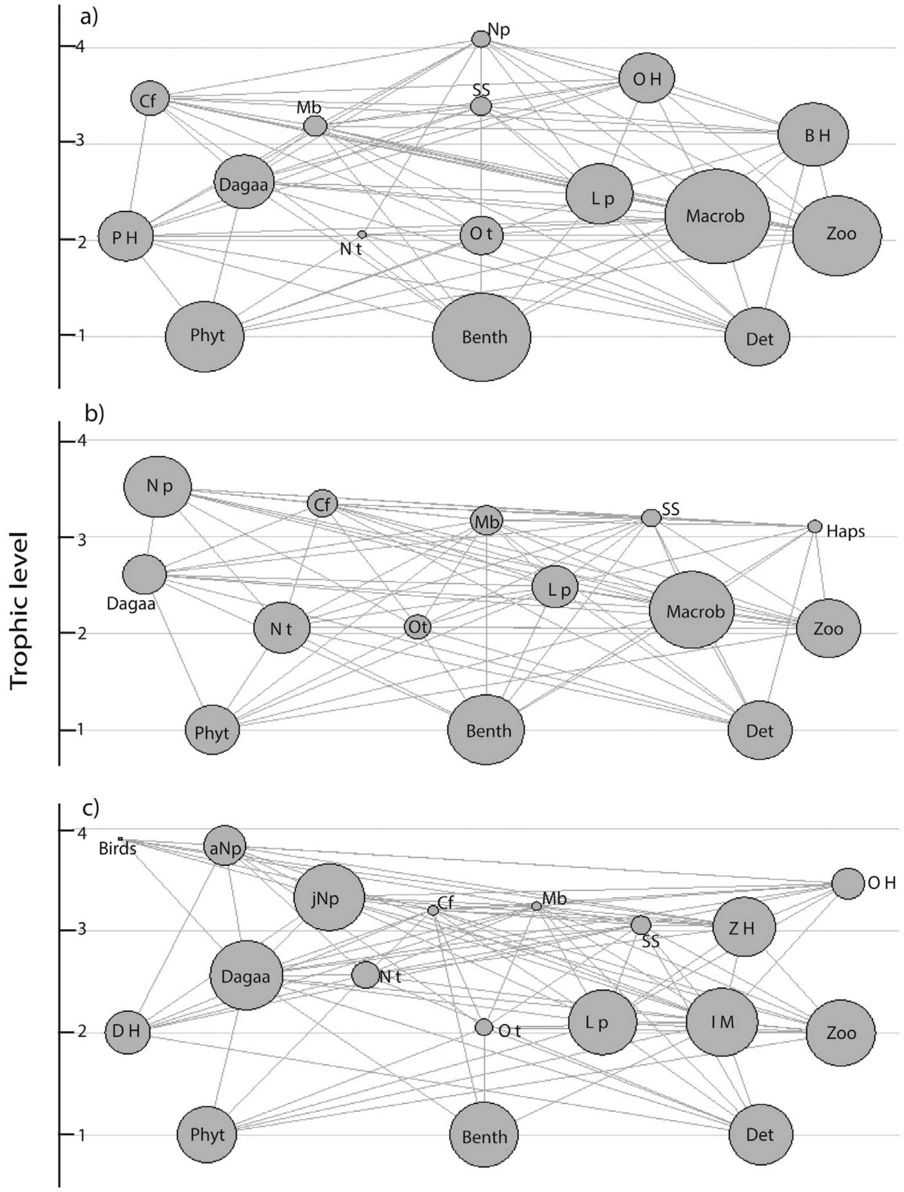

Fig. 2. Flow diagrams of the Lake Victoria ecosystem models for three periods: a) 1971–1972, b) 1985–1986, and c) 2014, organized by compartments at different trophic levels. Circles are proportional to the magnitude of biomass. Abbreviations stand for Phytoplankton (Phyt), Benthic producers (Benth), Detritus (Det), Zooplankton (Zoo), Detritivorous haplochromines (DH), Lake prawn (Lp), Insects and Molluscs (IM), Other tilapias (Ot), Nile tilapia (Nt), Nile perch (Np), juvenile Nile perch (jNp), adult Nile perch (aNp), Other haplochromines (OH), Planktivorous haplochromines (PH), Haplochromines (Haps), Catfishes (cf), Marbled lungfish (Mb), and Snoutfishes and Squeakers (SS).

fishes (in line with fishing through the food web e.g. Essington et al., 2006). We found that the decline in TLc coincided with a significant increase in catches of dagaa, a small pelagic species that occupies TL of 2.56, with no indication of change in Nile perch catches (Fig. 5).

Fig. 6 shows the fishing pattern in Lake Victoria, expressed as yield (kg/km^2) vs. production (both on logarithm scale) from an Ecopath model parameterised to reflect ecosystem status in 2014. The small pelagic groups (e.g. juvenile Nile perch, dagaa, and haplochromines) were exploited at <15% of their total annual production. However, large pelagic groups (e.g. adult Nile perch and Nile tilapia) and demersal fishes (e.g. catfishes, momyrids and squeakers, and Marbled lungfish) sustained excessive exploitation rates (>50%) relative to production. From a balanced fishing perspective, if all the fished groups have the same exploitation rate, they should be on a straight line with a slope $b = 1$, and with the intercept $a = \log$ (F/Z) representing average fishing pressure (Kolding et al., 2015). Fig. 6 shows that the ratio of slope between yield and production was significantly different from 1, implying that fishing mortality was not equally distributed across a wider range of TLs, and exploitation is not in balance.

Fig. 7 shows the fishing intensity in Lake Victoria, expressed as average exploitation rate (E) per 0.4 TL intervals, compared with the total average production (kg/km^2) (on logarithm scale) from an ecopath model parameterised to reflect ecosystem status in 2014. Exploitation was skewed to the least productive species/groups at higher TLs, and significantly less fishing (F/Z < 15%) occurs at the highly productive species/groups at lower TL. This analysis, however, only includes species or groups (above TL = 2) that are exploitable, and therefore does not include all functional groups in the ecosystem.

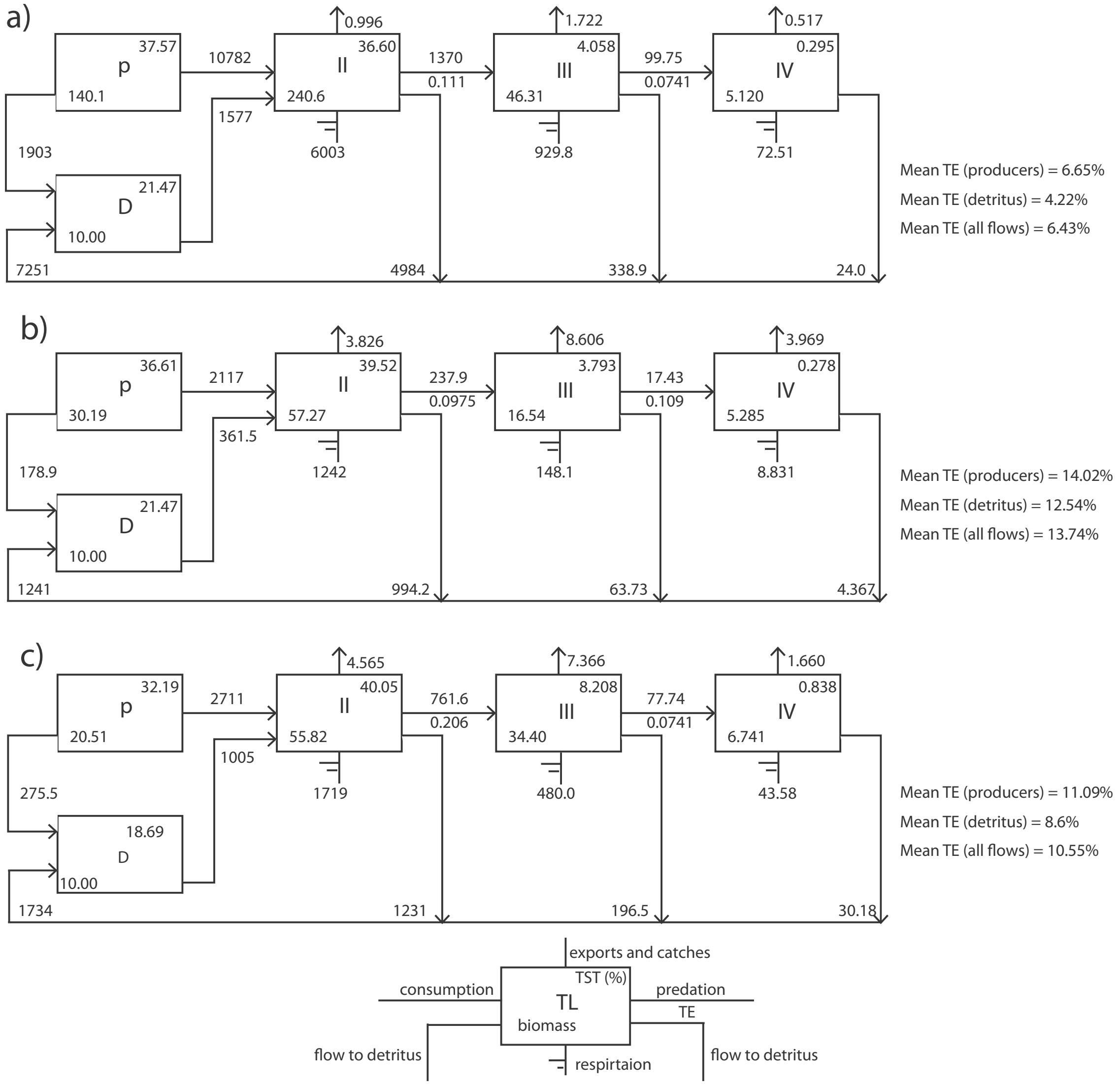

Fig. 3. Lindeman spine Lake Victoria during a) 1971–1972, b) 1985–1986, and c) 2014, with discrete trophic levels (TLs), showing flows and biomasses. All flows and biomasses are expressed in t/km^2/year. P stands for producers, D for detritus, and TE for trophic transfer efficiency.

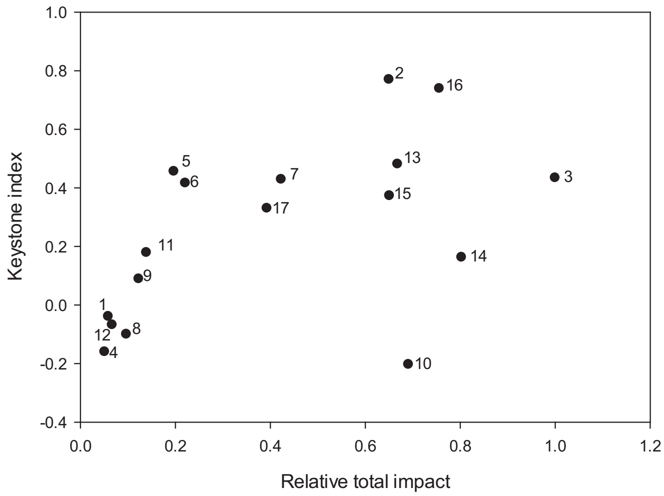

Fig. 4. Keystone index and relative overall effect of each functional group from the mass balance Ecopath model of the Lake Victoria parameterised to represent ecosystem status in 2014. The numbers identify the functional groups of the Ecopath model (Table 1).

4. Discussion

4.1. Caveats

Ecopath, like any model, has shortfalls and limitations. These limitations are discussed in Christensen and Walters (2004). Perhaps the most outstanding limitation of any ecosystem model is the quantity and quality of data available to feed the model. We attempted to minimize this shortfall by using data collected at the model location to calculate input parameters. However, not all functional groups are measured during surveys with equal intensity and precision. In Lake Victoria, commercially important species, Nile perch, Tilapias, and dagaa, are measured more often and more accurately than other groups. The approach of providing records of only commercially important species, and condensing >10 ‘trophically’ distinct functional groups into ‘others’ encumbers ecosystem modelling efforts, and could have (to some extent) affected the quality of both the new and re-parameterised models.

To ensure confidence and quality in model design, parameterization, and implementation, however, we checked for a set of pre-balance (PREBAL) diagnostics, including checking the biomass decomposition and vital rates across trophic levels (Link, 2010).

Table 3
Summary of ecosystem attribute statistics related to biomass flows and systems organisation for Lake Victoria, comparing with other lake ecosystems in the region. Ecosystem statistics in the shaded columns have been adapted for Lakes Kivu (Villanueva et al., 2008), Awassa (Fetahi and Mengistou, 2007), Tana (Wondie et al., 2012), and Ébrié and Nokoué (Villanueva et al., 2008). Most flows for Lake Awassa have been omitted because of different units used.

Parameter/Lake	Victoria			Kivu	Awassa	Tana	Ébrié	Nokoué	
	1971	1985	2014						units
Sum of all production	15842.6	2926.2	3980.4	3040			2902	19595	t/km^2/year
Sum of all consumption	14787	2933.1	4585.6	2190		760.7	1207.6	25731.4	t/km^2/year
Sum of all exports	5677.2	896.2	742.6	1499.8		2530.2	2119.7	1327.4	t/km^2/year
Sum of all respiratory flows	7007.6	1399.3	2243.9	1233.9		498.9	510.9	10498.5	t/km^2/year
Sum of all flows into detritus	7250.5	1241.3	1733.6	1762.1		2657	2402.9	20410	t/km^2/year
Total system throughput (T)	34723.2	6469.9	9305.8	6686		6447	6240	57967	t/km^2/year
Total net primary production	12684.8	2295.5	2986.7	2733.8		3028.9	2629.9	11826	t/km^2/year
Total primary production/total respiration (PP/R)	1.81	1.64	1.33	2.21	5.83	6.07	5.15	1.126	
Net system production (NSP)	5677.2	896.3	742.7	1499.5		2530.1	2119	1327.4	t/km^2/year
Total primary production/total biomass (PP/B)	29.3	20.9	25.3	52.22	28.6	39.8	41.6	23.7	
Total biomass/total throughput (B/T)	0.012	0.016	0.012	0.008	0.016	0.012	0.01	0.009	year^{-1}
Total biomass (excluding detritus)	432.4	109.4	117.7	52.2		76.04	63.3	497.1	t/km^2
Connectance Index (CI)	0.41	0.49	0.32	0.396			0.191	0.266	
Finn's cycling index	4.33	5.84	4.75				2.57	34	%TST
Finn's path length	2.74	2.82	3.12				2.37	4.9	
System Omnivory Index (SOI)	0.17	0.16	0.12	0.148			0.145	0.156	
Ascendency (A)	44502	8310	12110				7656.1	47224	Flowbits
Overhead (O)	88200	17174	28189				3876.7	186154.3	Flowbits

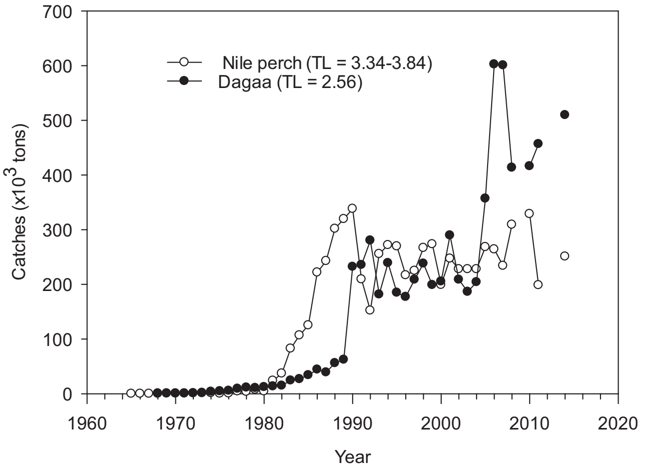

Fig. 5. Total catch (tons) of two predominant fisheries, Nile perch and dagaa, plotted versus years in Lake Victoria. Data from Kolding et al., (2014) supplemented by LVFO (2014) from 2010 to 2014.

After PREBAL diagnostic checks and subsequent fine tuning of the models, most metrics showed the fulfilment of principle ecological and physiological rules i.e. biomass utilization for every group lower or equal to biomass production of that group; gross GE vary-

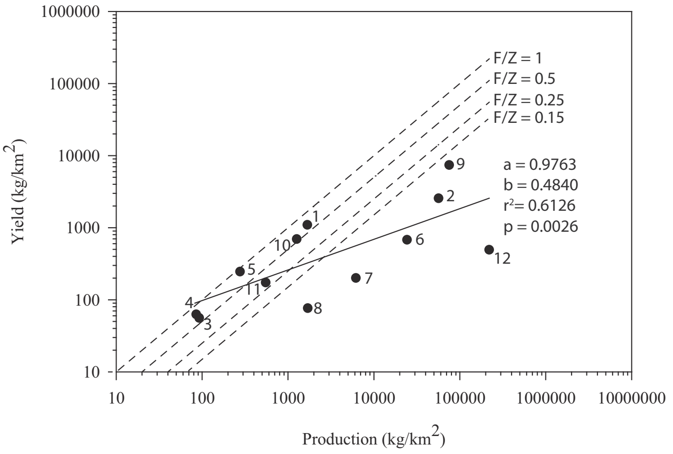

Fig. 6. Harvest relative to production (on logarithm scales) for stocks or groups harvested in Lake Victoria using data extracted from an Ecopath model (see Table 2c) parameterized to reflect ecosystem state and fisheries in year 2014. The more the slope deviates from the 1:1 line between yield and production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

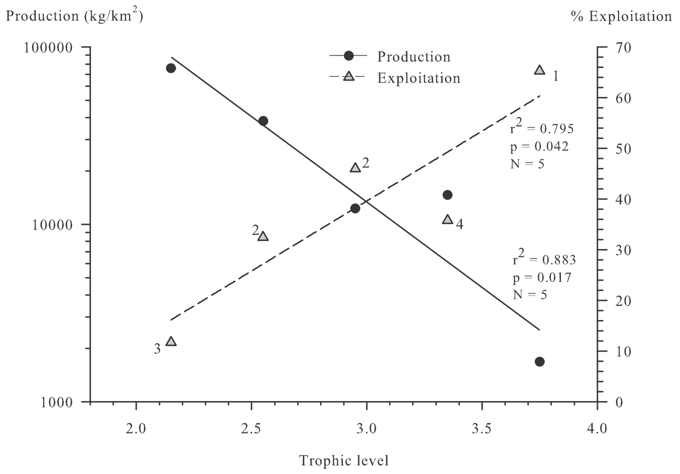

Fig. 7. Production (kg/km^2) (on logarithm scale) and exploitation rate (%) per Trophic level (binned in 0.4 TL intervals). Numbers represent the total number of exploited trophic groups in each interval. Black circles = production and grey triangles = exploitation rate. Superimposed are linear trends for exploitation (ascending black line) and production (descending black line).

ing between 0.1 and 0.4, R/B higher for small organisms and top predators compared to lower trophic levels; R/A <1, and high for top predators; and net efficiency <1 (Christensen et al., 2008; Heymans et al., 2016).

4.2. Mass balances

The lower gross growth efficiencies (GEs), also called food conversion efficiency (FCE) in aquaculture i.e. the physiological capacity to convert consumed food (Q) into tissue (P), than the average 10%, the proportion of food consumed that is expected to be converted into tissue in finfish (Christensen et al., 2008), for planktivorous and benthivorous/detritivorous haplochromines, and other tilapias can be attributed to the inclusion low quality food, majorly detritus and phytoplankton, in their diet. Nile tilapia, which depended on similar phytoplankton-based diet in 1970s and 1980s had similar low GE values (2 and 3% in the 1971–1972 and 1985–1986 models, respectively), but increased to 10% in the 2014 model, coinciding with a shift in diet from exclusive phytoplankton to more diversified diet, including insects and fish, in 1990s and 2000s (Njiru et al., 2007). This is also shown by an upward shift in omnivory index from 0.06–0.08 during 1971–1972 and 1985–1986 to 0.5 in 2014 (Table 2).

The GEs in our models sharply contrast with those in previous models for the same lake e.g. Downing et al. (2012), although the model localities are different. In Downing et al., GE values of 66% for Nile tilapia and 61% for juvenile Nile perch, for instance, were reported in the 2005 model parameterised for Mwanza gulf, Lake Victoria, but these are likely to have overestimated (Kolding, 2013). These results implied a highly efficient food web, where both Nile perch and Nile tilapia were able to convert more than half of what they eat into tissue growth. Even if Nile tilapia was a carnivore, and feedingly exclusively on protein-rich animal material, which is not the case, its GE would not exceed 35%. The high GE of 66% could therefore have been due to overestimation of production. The authors used a very high P/B ratio of 12 per year during parameterisation, which implied that Nile tilapia would reproduce its own biomass 12 times per year, a trait is biologically less likely. These examples are not a critique of previous works by Downing et al., but they are mentioned here to emphasize the importance of conducting PREBAL diagnostic checks before balancing the models (Link, 2010; Heymans et al., 2016).

4.3. Ecosystem development and stability

Ecosystem development or succession is the process by which an ecosystem progresses towards a mature state, and involves a directional, orderly, and predictable process that results in a biomass maximum and optimization of energy (Odum, 1969). We used network analysis to characterise the Lake Victoria ecosystem status, and compared it with other lakes in the region. We found a decrease over time in productivity in relation with biomass and respiration, a decrease in food web connectivity, and an increase in biomass cycling. All these are indicators suggest that the system is still maturing; however, the system is in advanced stages of development compared to other systems in the region, such as Lakes Kivu, Awassa, Tana, and Ébrié, except Nokoué, which is basically mature (Table 3).

The connectance of a food web is the number of connections in the ecosystem as a proportion of the total possible trophic connections (Ulanowicz, 1986), and trophic connections are expected to evolve from linear to web-like structure as the system matures (Odum, 1969). implying low CI and high biomass cycling as the system progresses to maturity. The attributes of food web connectance, such as Finn's cycling index and Finn's path length have increased, while CI has decreased especially between 1985 and 1986 and 2014. Despite the changes in species composition, it appears that Lake Victoria is stable, with some signals indicating a maturing system. Finn's mean path length is also related to the recovery time of the ecosystem (Vasconcellos et al., 1997). Therefore, the high Finn's mean path length in the 2014 model, suggests that the current ecosystem would likely recover more quickly than the 1970s or 1980s. The current level of food web connectivity is also comparable with other maturing ecosystem in the region, including Lakes Kivu, Ébrié, and Nokoué (Table 3). However, anthropogenic and natural stressors can limit the maturity level an ecosystem can reach (e.g. Christensen, 1995). Lake Victoria has endured multiple stressors, including exotic species introductions, habitat degradation, pollution, and eutrophication, since 1970s (Hecky et al., 2010). These stressors, will be compounded by climate variability and change, and these could undermine the level of maturity the system would reach.

Before the introduction of an invasive fish predator, Nile perch, into Lake Victoria, a diverse fish community dominated by >500 haplochromine cichlids, which formed more than 80% of the fish biomass, was eminent (Seehausen, 1996; Kaufman et al., 1997). According to Moreau (1995) the major food chains that formed key functional groups in Lake Victoria were: via zooplankton to herbivorous (haplochromines and dagaa) to the top predators (catfishes and piscivorous haplochromines); via zooplankton, insect larvae, and molluscs to zoophagous fish taxa (Haplochromines, Mormyridae, *Barbus* spp., *Alestes* spp., *Synodontis* spp.) and Marbled lungfish to top predators; and a direct flow to several herbivorous *Tilapia* spp. and haplochromines. After the Nile perch establishment in 1980s, the complex food web (whose all biomass flows = T totalled 34723.2 t/km^2/year) was simplified, reducing T by fivefold, where the fish community was dominated by only four major species, the two introduced Nile perch and Nile tilapia and two native dagaa and Lake prawn. After the resurgence of some haplochromine species, especially in the southern parts of the lake, a recovery in the original trophic structure and seemingly a re-organisation of the food web reported (Downing et al., 2012). Although this was specifically for Mwanza gulf, and not the entire lake, our results showed that the food web is still simple and less diversified, with few groups that flows pass through as well as high biomass cycling.

A simplified food web was further evident when analysing the relation between ascendency, overhead, and development capacity (Table 3). A system with high ascendency is normally developed, and much diversified. Conversely, a system with high overhead is more resilient and has strength in reserve (Christensen, 1995). The system's ascendency and overhead decreased ca. fivefold between 1971 and 1985, and increased only slightly between 1985 and 2014. By definition of ascendency and overhead, the 1971 ecosystem was more diversified and resilient than 1985 and 2014 ecosystems. However, the relative redundancy (O/DC), which is also used to measure system's strength to meet unexpected perturbations (Christensen, 1995), has fluctuated between 66 and 70%. This suggests that the even if the modelled system is not yet in an ecological climax state, the system's reserved strength, from which it can draw to meet unexpected perturbations, is high and the system has been resilient.

In immature systems, primary production is expected to greatly exceed respiration (Odum, 1969). The PP/R ratio is related to community energetics and is expected to decrease as a system matures due to the accumulation of biomass in mature systems, and the commonly observed range is 0.8–3.2 (Christensen and Pauly, 1993). When analysing trends in system maturity of Mwanza gulf, Lake Victoria, using ecopath, Downing et al., (2012) reported PP/R ratios that were approximately 800fold higher than the expected range. This, in addition to other ecosystem metrics, particularly GE, could have been due to use of parameters outside realistic ranges (Kolding, 2013). In this study, we observed a declining trend in productivity in relation with respiration, with values of PP/R ranging between 1.33–1.81 suggesting that the system is that is not yet mature, although there has been an increase in detritivory over time (Fig. 3), which is indicative of maturing systems (Odum, 1969; Christensen, 1995).

The of ability of a predator with low biomass to disproportionately influence the food web structure of its community was high for only adult Nile perch. This group had disproportionately high trophic impact compared to its biomass, and could possibly, by definition (e.g. Valls et al., 2015), be a keystone. Keystone properties were also exhibited by low TL groups, such as phytoplankton (Fig. 4), and this heterogeneity in terms of TLs is suggestive of mixed control by top-bottom and bottom-up mechanisms in the food web, where a core set of ecosystem components has a predominant role on the control of biotic interactions exerted by both top-down (e.g. Nile perch) and bottom-up (phytoplankton) mechanisms (see Libralato et al., 2006). The aspect of mixed control mechanisms was also observed in mixed trophic impacts. Majority of the fish groups had minimal or no impact on the other groups, except Nile perch, especially juvenile, which exerted negative impact on all groups, and lower TL groups e.g. phytoplankton, which exerted a positive impact on majority of the groups. An increase in biomass of adult Nile perch, for instance, could destabilise the whole ecosystem, as seen from the ecosystem down-turn in 1980s after its successful establishment (e.g. Witte et al., 1992), and a bit of species recovery from 1990s onwards following intensive fishing of Nile perch (Taabu-Munyaho et al., 2016).

4.4. The focus and impact of fisheries

The higher percentage of total PPR for the fishery in the 1985–1986 and 2014 models reflects the higher landings (13.7–16.4 tons km^{-2} per year) compared to 1971–1972 (3.3 tons km^{-2}). In particular, the PPR to sustain Nile perch was higher during the 1985–1986 and 2014 model periods because their abundance was much higher relative to that of their prey compared to the 1971–1972 model period. The lower PPR to sustain Nile perch fishery in 1985–1986 compared with 2014 is because (1) Nile perch fed at lower trophic levels during that time (when it shifted its diet from haplochromines to Lake prawn after disappearance of the former) (Moreau et al., 1993) and (2) the increase in TE (leading to energy optimization) probably compensated for the exploitation of fish at high trophic levels. Exploitation of fish at lower trophic levels can compensate for the inefficient transfer of energy from one trophic level to the next and make the fishery ecologically less expensive (Jarre-Teichmann, 1998). This can also explain the lowest fraction of PPR to sustain the fishery in the 1971–1972 model, even when TE was the lower than the commonly referred Lindeman's 10%, and the lower the fraction of PPR to sustain dagaa fishery (which constituted >50% of the total catches) compared to the adult Nile perch fishery (which constituted only 8% of the total catches) in the 2014 model.

The mean TLc, which has remained one of the most widely used indices for testing fishing down (Pauly, 2010; Stergiou and Tsikliras, 2011; Stergiou and Christensen, 2011) despite contestation from other researchers (e.g. Branch et al., 2010; Branch, 2010), who have persistently questioned (or rather rejected) its usefulness in describing the status of marine and freshwater fisheries, was used to assess the focus of Lake Victoria fisheries. By 2014, the total landed catches from Lake Victoria were about 919,310 tons out of which, Nile perch, a high TL species, and dagaa, a low TL species, contributed 82.7% (LVFO, 2014). Since 1990, the catches of Nile perch (TL = 3.3–3.9) have remained stable, while the catches of dagaa (TL = 2.56) have increased almost threefold. This is consistent with findings of Essington et al. (2006) who described a decline in mean TLc as due to the sequential addition of low TL catches rather than a decline of high TL ones using the term "fishing through". The increase in catches of dagaa, especially after 2005 coincided with an abrupt shift in fish populations, where the biomass of dagaa doubled between 1999 and 2002 and 2008–2011 (Taabu-Munyaho et al., 2014); and in fact, the biomass of dagaa has continued to increase in the last four years where, in certain areas of the lake, the standing stock densities reach 40 tons/km^2 (LVFO, 2015). Interestingly, the biomass of Nile perch has also consistently increased since 2007 (LVFO, 2015). The decrease in mean TLc in Lake Victoria, therefore, may not be a consequence of depleting Nile perch (because its population has remained relatively stable); but rather, is due to increasing abundance of low TL species as well as shift in targeting patterns.

With regard to fishing patterns, exploitation is unbalanced and skewed to the least productive species/groups at higher TLs, with significantly less fishing occurring at the highly productive species/groups at lower TL. This unbalanced fishing can be attributed to the selective management architype. For instance, the innovation of slot size of 50–85 cm as well as the minimum mesh size of gillnets of 5″ for Nile perch aimed at harvesting only large and mature individuals (Kayanda et al., 2009). Fishing lower size class (<50 cm total length), which currently constitutes >95% of the total Nile perch biomass (LVFO, 2015) and >80% to total landed Nile perch catches (Mkumbo and Marshall, 2015) is regarded illegal. This management framework has recentlyfaced criticism as hindering rather than helping achieve the goals of Ecosystem Based Fisheries Management (EBFM), with recommendations to shift to unselective fisheries strategies (Zhou et al., 2010, 2015), which automatically lead to balanced fishing especially in small-scale fisheries (Plank et al., 2016).

Fishing effort that is distributed equally across the widest possible range of species, stocks, and sizes in proportion to productivity produces a larger total yield than the selective patterns and, for a given yield, the least change in the relative biomass composition of the fish community (Jacobsen et al., 2014; Kolding et al., 2016). However, questions still linger on how and whether it is possible (or even economical) to implement balanced fishing (Froese et al., 2016; Reid et al., 2016; Howell et al., 2016). On the other hand, Plank et al. (2016) showed that balanced fishing in small-scale fisheries may emerge by individual decisions of fishers who are allowed to operate without size-based regulation, implying that the cost of management would also be low, while acknowledging the need for controls to avoid overfishing. Although our study only assesses the current fishing pattern, and not specifically the potential of (and benefits from) balanced fishing on Lake Victoria, it is an approach that should inform discourses on the future sustainability of the fishery. For instance, despite the minimum mesh size policy as well as punitive actions in response to non-compliance, fishers on Lake Victoria have continued to use gillnets with mesh size <5″ (see LVFO, 2013) as well as catching Nile perch <50 cm total length (Mkumbo and Marshall, 2015). Interestingly, although our results showed unbalanced exploitation across TLs, the magnitude of the deviation from balanced fishing line was smaller compared to those seen in efficiently managed marine systems (see Kolding et al., 2015). This is suggestive of a fishery that could be potentially, but illegally, moving toward balanced fishing; and the outcomes, which normally include low-value catches (Sethi et al., 2010), may benefit small-scale fishers as well as riparian communities where poverty and malnutrition are high because here provision of biomass for food is more important than the market value of the catch.

5. Conclusion

Lake Victoria's food web is still simple, with low connectivity, and the re-organisation of the food web after recession in 1980s, despite the recovery of some haplochromines, is not apparent. Although there has been an increase in detritivory over time, the ecosystem is still phytoplankton-based, with efficient utilization of primary productivity. The large biomass flowing into detritus at consumer level suggest that the groups are less exploited by fisheries. Although Lake Victoria is not mature, optimization of energy as seen by high TE, and biomass accumulation as seen by decrease over time in productivity in relation with biomass and an increase in biomass cycling, suggests the ecosystem is in advanced stages of development. Similarly, the high relative redundancy suggests that the system is stable and has enough strength in reserve to meet with unexpected perturbations.

We tested the fishing pattern, which is currently not in balance, with exploitation skewed to the low productive species at high TLs. Specifically, the most productive juvenile Nile perch, dagaa, and all haplochromines groups are underexploited, while adult Nile perch, Nile tilapia, catfishes and Marbled lungfish are exploited beyond sustainable threshold. This imbalance, with particular reference to the Nile perch, is abetted by selective fisheries management models, which have not been successful in most small-scale open access fisheries all over the World.

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