IMPROVING FISHERIES MANAGEMENT STRATEGIES FOR LAKE VICTORIA BY MEANS OF ECOLOGICAL MODELLING OPTIMIZATION

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ABSTRACT

The ecosystem approach to management requires the status of individual species to be considered in a community context. Because single-species fisheries models do not accommodate the net effects of alternative fishing strategies on the ecosystem structure and functioning, as well as the effects on the biology and dynamics of the targeted stocks, they are limited in the scale and scope of management objectives and strategies that can be explored for future management. Here, a comprehensive mass balance model is implemented for the Lake Victoria ecosystem, using ECOPATH, to analyse the trophic structure, ecosystem attributes, and the role and impact of fisheries. The analysis shows an ecosystem with: heterogeneous groups (in terms of trophic levels), having moderate keystone properties, but without a distinct keystone in the food web; an advanced level of development nearing maturity (production-P: respiration-R ratio = 2.5); and high resilience capacity and able to recover quickly from perturbations (relative redundancy = 69.4%). Generally, the fishery is underexploited because the greatest biomass of highly productive species simply goes missing (i.e. lost to detritus). Contrastingly, the probability as to whether fishing is sustainable is zero. This is because human exploitation across trophic levels (TLs) is skewed to the low productive species at high TLs. As such, I recommend that balanced harvesting, an approach to fishing that distributes a moderate fishing mortality (e.g. $30\%P \leq F/Z \leq 40\%P$) across the widest possible range of species, stocks, and sizes in an ecosystem, in proportion to their natural productivity, so that the relative size and species composition is maintained, is incorporated in management of Lake Victoria. This means fisheries managers should shift from the archaic selective fishing philosophy, often augmented by gear size restrictions.

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1 INTRODUCTION

1.1 Background

Fisheries management efforts have largely failed given that at least 90% of the world's major fisheries resources are either fully exploited or overexploited, with clear signs of declines in catches (FAO, 2014). Improvement of fisheries management, therefore, requires new approaches and techniques. These approaches need to accommodate the net effects of alternative fishing strategies on the ecosystem as a whole, through taking into account the effects on ecosystem structure and functioning as well as the effects on the biology and dynamics of the targeted stocks. Single-species fisheries models are unable to capture interactions between species, especially trophic interactions, and do not accommodate spatial aspects of fish stocks and their prey and predators (Link, 2010). Thus, they are limited in the scale and scope of management objectives and strategies that can be explored for future management.

Following from the 2002 Johannesburg World Summit for Sustainable Development, the modern approach to fisheries management aims at, simultaneously, improving social welfare and equity, while maintaining ecological stability (FAO, 2003). The unequalled importance of this approach is that it balances diverse societal objectives, by taking into account the knowledge and uncertainties about biotic, abiotic, and human components of ecosystems and their interactions, and an integrated approach to fisheries within ecologically meaningful boundaries (Morishita, 2008). However, this approach adds another dilemma. How can management pursue multiple objectives, which may, in some instances, be in conflict with each other? For instance, how is it possible to create or maintain employment and generate increasing volumes of revenue, whilst sustaining stocks and biodiversity? A management routine that delivers these multiple objectives, especially with regard to Lake Victoria multi-species fisheries, would be ideal (Nunan, 2014). This, however, requires building an ecosystem model (Morishita, 2008).

Lake Victoria, the world's largest inland fishery, produces about one million tonnes (t) of fish per year, and provides livelihoods for about four million people (Mkumbo & Marshall, 2015). Lake Victoria, also, is surrounded by a dense and a fast growing human population of >30 million people (Kolding *et al*., 2014). Because of Lake Victoria's regional importance, optimal management to enhance its resilience is vital. Fish stocks of Lake Victoria, like in many parts of the world have changed, both in terms of the size of the fishable stock and also the mean fish length in catch. Between 1990 and 2009, Nile perch, *Lates niloticus* (Linnaeus, 1758), catches remained the same at about 230,000 t (Kolding *et al*., 2014), but the proportion of fish >50 cm total length in catches fell from >80% to <20% (Mkumbo & Marshall, 2015). Nile tilapia, *Oreochromis niloticus* (Linnaeus, 1758), also shows a similar trend, where the catches have not changed (Kolding *et al*., 2014), but the size structure contracted (Njiru *et al*., 2007). Monitoring of fish standing stock between August 1999 and September 2011 show a two-fold increase in the biomass (Taabu-Munyaho *et al*., 2014) and catches (Kolding *et al*., 2014) of the Silver cyprinid, *Rastreneobola argentea* (Pellegrin, 1904), known locally as dagaa, while the average has size decreased (Sharpe *et al*., 2012).

The claims that Lake Victoria is threatened by overexploitation (Mkumbo & Marshall, 2015), therefore, seem to be contradictory condiering that catches of the major fish groups have remained stable for more than two decades. Although the size structure has decreased among all the major fish groups, this may not necessarily be a consequence of of overfishing as claimed

by Njiru *et al*. (2007), Sharpe *et al*. (2012), and Mkumbo & Marshall (2015) but, instead, could reflect ecosystem effects of unbalanced harvesting, where fishing mortaliy is not distributed across a wide range of species and sizes in proportion to their abundance (Jacobsen, *et al*., 2014; Jacobsen, *et al*., 2015; Kolding *et al*., 2016). Therefore, it is imperative to understand whether fishing on Lake Victoria is sustainable, at ecosystem scale, where fishing distributes a moderate mortality across the widest possible range of species, stocks, and sizes, in proportion to their natural productivity (Garcia *et al*., 2012).

1.2   Statement of the problem

While management institutions are struggling to develop a fishery that can deliver ecosystem functions and services with no degradation beyond resilience capacity (Nunan, 2014), they lack an integrated ecological information framework to guide management decisions. The current single species models, from which management derive its decisions, provide biomass predictions of different fish species in the system as affected directly by fishing. Such analyses are unable to capture interactions between species, their prey, and predators (Link, 2010), and hence limited in the breadth and scope of management objectives and strategies that can be explored for future management.

1.3   Objectives of the study

The overall objective of this study was to investigate, by incorporating ecosystem processes and functions, the optimal fishing patterns for exploiting and conserving the fish stocks of Lake Victoria.

1.3.1   Specific objectives

  i. To develop a mass balance model for Lake Victoria that describes, quantitatively, the trophic flows, ecosystem attributes, and the role and impacts of fisheries.
 ii. To model the optimal harvesting patterns that can guarantee optimum fishing without degradation beyond resilience capacity.

1.4   Scope of the study

The study invokes, through mass balance modelling, trophic relationships and assesses the effect of changes in biomass of one group on the biomass of another 'trophically' dependent group. To achieve this, a most recent ECOPATH model that estimates energy fluxes through different functional groups within the lake food web is constructed. The model is optimised to estimate ecosystem attributes, such as system throughput, system omnivory, and system's organisation, which relate to ecosystem maturity and stability. From these indices, other ecosystem aspects, such as trophic level of the catch, fishing efficiency, and primary production required to sustain catches, all of which relate to fisheries management and sustainability within the boundaries of ecosystem structure and functioning, are estimated. Finally, the model, by adopting the concept of balanced harvesting (Garcia *et al*., 2012), is used to assess whether exploitation of fish in Lake Victoria is sustainable (fishing across a wider range of trophic levels-TLs) or unsustainable (fishing is skewed towards low productive species at high TLs).

1.5   Significance of the study

This study offers, quantitatively, a multivariate evaluation of fisheries management objectives, with in the tenets of ecosystem structure and functioning, which is better than the current one-sided analyses that focus only at fishing effort. It is anticipated, therefore, that this multivariate description and assessment of the whole system in terms of interaction between species, productivity, and major functional groups will offer management institutions a strong basis in the pursuit of modern management objectives, which, currently, are not considered in the single species fisheries models.

2   LITERATURE REVIEW

2.1   Lake Victoria fishery

Lake Victoria (0.5 º N–3 º S, 31.5–34.5 º E) is the world's second largest freshwater body and the largest tropical lake in terms of surface area (68,800 km^2), but it is shallow (maximum depth of 79 m, average depth of 40 m) relative to other Great Lakes in East Africa. Lake Victoria has an indented shoreline with numerous islands, bays, channels, and wetlands (Figure 1). A detailed description of the physical and hydrological characteristics of Lake Victoria is given in MacIntyre *et al*. (2014).

Figure 1. Lake Victoria with major riparian cities, major rivers (Kagera, Nzoia, Yala, Mara) and the indented shoreline with numerous islands, bays, channels, and wetlands.

Lake Victoria supports one of the world's biggest inland fisheries aimed at both domestic consumption and international export, with the annual landed fish catches >one million t (Marshall & Mkumbo, 2011). Before introduction of exotic species in Lake Victoria, the lake's fish community had > 300 species, mostly cichlids and cyprinids (Ogutu-Ohwayo, 1990). The most important commercial fisheries were two endemic tilapias; the Singida tilapia, *Oreochromis esculentus* (Graham, 1928), and Victoria tilapia, *Oreochromis variabilis*

(Boulenger, 1906). These fisheries, however, were fished down, especially in the Kenyan waters, where catch rates reported from the Winam gulf decreased from 25 fish net^{-1} in 1910 to around two fish net^{-1} in 1940 (Kolding *et al*., 2014). Four tilapia species, including Nile tilapia, Blue spotted tilapia, *Oreochromis leucostictus* (Trewavas, 1933), Redbreast tilapia, *Tilapia rendalii* (Boulenger, 1897), and Redbelly tilapia, *Tilapia zillii* (Gervais, 1848), were introduced in 1950s to boost the then declining endemic tilapia fishery. The introduced tilapias outcompeted the native species, which had actually not declined in the Ugandan and Tanzanian waters (Kolding *et al*., 2014). Nile perch was also introduced during the same period to convert the small bony *Haplochromis* spp. to fish flesh of commercial importance. Three decades later, a diverse and complex ecosystem was replaced by a system dominated by only four species; the native dagaa and atyid shrimp *Caridina nilotica* (Roux, 1833), and the introduced Nile perch and Nile tilapia (Goudswaard *et al*., 2008). Despite the diminished species diversity, the fishery grew spontaneously, with overall catches almost doubling every decade relative to the total number of fishers (Figure 2). Figure 2, also, shows that catches in Lake Victoria have never plummeted with increasing fishing effort, which further renders the claims of overfishing questionable.
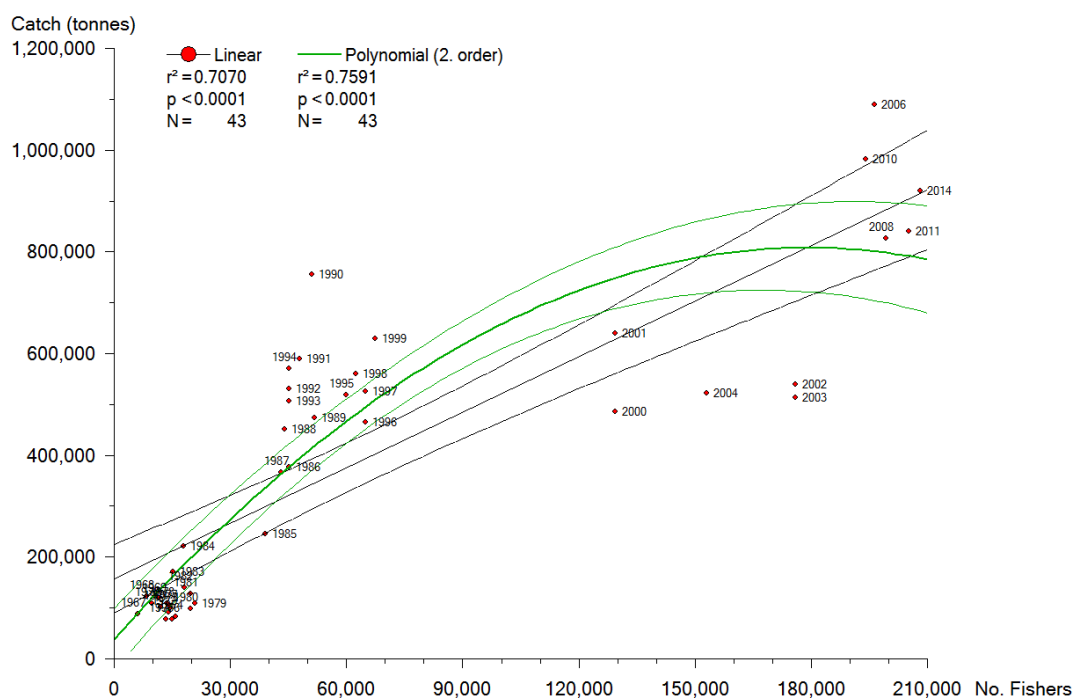
Figure 2. Total catch (tonnes) plotted versus total number of fishers in Lake Victoria (each point is a year of observation moving along the X-axis as effort has increased). Superimposed are a linear model and a polynomial curve (2. order) model with 95% confidence limits. Data from Kolding *et al*. (2014) supplemented by LVFO from 2010-2014.

The expansion of the fishery in terms of total catches resulted into an unprecedented lucrative business, fetching around 500 million US$ annually for the riparian states, and has been the main source of income for ever-growing lakeside populations (Balirwa, 2007). The economic transformation of Lake Victoria fishery because of increased catches, especially during 1980s, coupled with the fast growing human population, however, instigated an increase in fishing pressure. The number of fishers and boats, for instance, increased threefold between 1990 and 2014 (Figure 3). Nonetheless, the catches, except for dagaa, which only increased after 2005, remained the same amidst increasing fishing effort (Figure 3). Why would catches remain constant amidst increasing fishing effort?
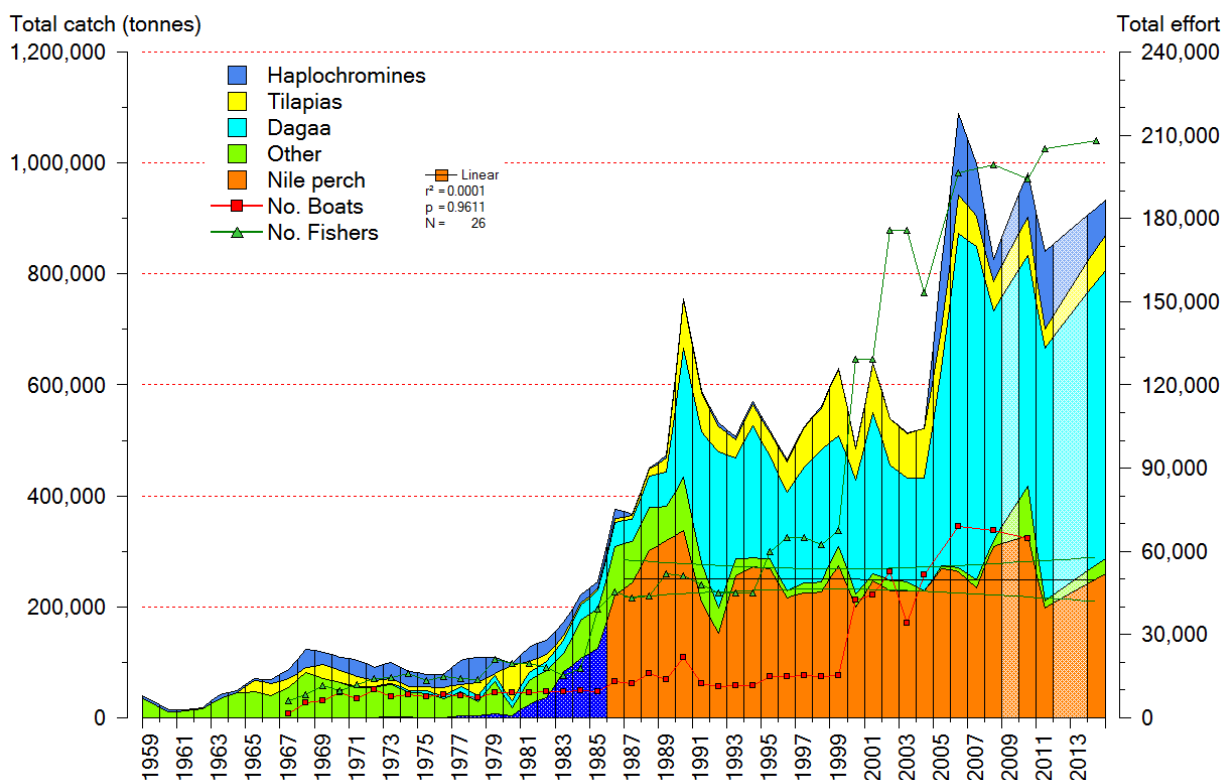
Figure 3. Total catch (tonnes) split into 4 major groups (Nile perch, Haplochromines, Tilapias, Dagaa, and 'others') and total effort (number of fishers and number of boats) in Lake Victoria 1959-2014. There has been no significant long-term change in the total Nile perch catches (mean ± SD = 247,000 ± 50,000 tonnes) since 1986 (r^2 = 0.001, p = 0.9611). There has been a significant linear increase of Dagaa catches of about 16,000 tonnes per year since 1985 (r^2 = 0.69, p < 0.001). Data from Kolding *et al.* (2014) supplemented by LVFO from 2011-2014. Data missing in 2009 and 2012-2013.

Jacobsen *et al.* (2014) showed that balanced fishing, where individuals are exploited in proportion to their productivity, produces a larger total maximum sustainable yield than the other exploitation patterns and, for a given yield, the least change in the relative biomass composition of the fish community. Because acoustic surveys conducted during 1999 –2002 and 2005–2011 show up to 30% decline in Nile Perch densities in the deep open water areas, and up to 65% reduction in the shallow inshore areas (Taabu-Munyaho *et al.*, 2014), followed by contraction of size structure (Mkumbo and Marshall, 2015) and constant fish catch (Figure 3), I hypothesise that fishing in Lake Victoria is not balanced (*sensu* Jacobsen *et al.*, 2014). This is also apparent where catch per unit effort (CPUE), expressed both in tones per boat per year and tones per fisher per year, decreased by >threefold between 1990 and 2014 (Figure 4). Contrary to claims by Mkumbo and Marshall (2015), the decrease in CPUE shows that fishing is taking place, and not necessarily overfishing.
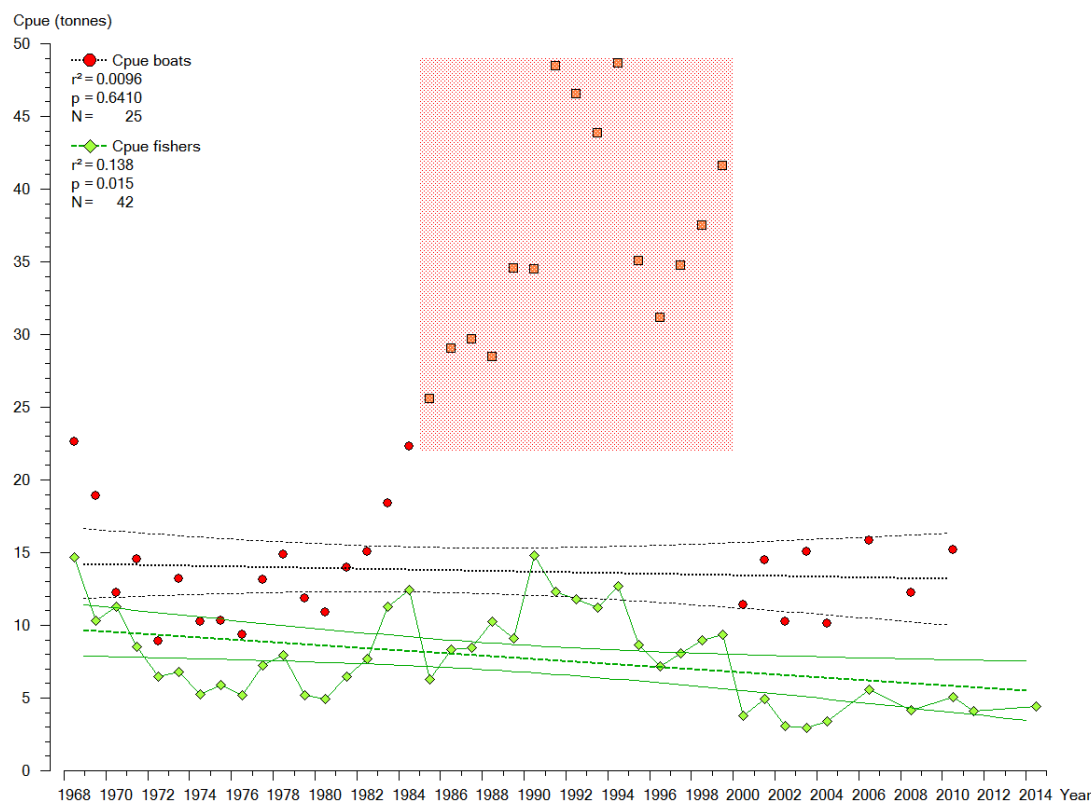
Figure 4. Catch (tonnes) per unit effort (fishers green diamonds, and boats red circles) in Lake Victoria 1968-2014. Linear trends are presented with 95% confidence limits. Total catch per fisher per year has decreased from around 10 tonnes to <5 tonnes, while catch per boat per year has decreased from about 50 tonnes to 10 tonnes between 1990 and 2014. Data from Kolding *et al*. (2014) supplemented by LVFO from 2011-2014.

2.2 Fisheries management around Lake Victoria

The first stock assessments in Lake Victoria was conducted in 1927-1928 by Graham (1929), and a follow up assessment in 1950s by Beverton (1959). All the recommendations from these studies pointed to gill net mesh size restrictions and protection of breeding sites. Between 1970 and 1990s, the monitoring surveys were uncoordinated, mostly done by independent states that share the lake. The comprehensive lake-wide surveys were done under the Lake Victoria Research Project (LVRP, 1999-2002) and Implementation of a Fisheries Management Plan (IFMP, 2005-2010) projects (Kayanda *et al*., 2009). Some major recommendations from these surveys included slot size landings regulation of $50 - 85$ cm TL aiming at protecting the juvenile and spawning stocks of Nile perch, minimum sizes for Tilapia to be landed of not less than 25 cm TL to protect juvenile stocks, minimum legal gillnet mesh size of 127 mm (5'') for Nile perch to protect juveniles fishes, and closed seasons and closed/protected areas in all three countries to protect spawning stocks and species diversity (LVFO/IFMP Technical Report, 2007 In: Kolding *et al.,* 2014*, appendix 2*). None of these measures either arrested the contraction of size structure of the major fish stocks (Njiru *et al*., 2007) or improved the catches.

Kolding *et al*., (2008) criticised management institutions around Lake Victoria for concentrating on controlling fishing effort, and yet the fisheries are not threatened by exploitation. The authors argued that the fisheries models used on the lake are already pre-ordained with fishery (top-bottom) drivers and, any outcome, therefore, would point to overexploitation. The authors, however, among other observations, noticed that even though

overexploitation was to be a threat, thus attracting such hyped attention, little attention has been paid to implications for fisheries management from the parallel ecological studies that have been conducted on the lake. Such omission constrains efforts for ecosystem approach to fisheries, which demand an information base that relates different ecosystem processes. One such approach, which captures ecosystem processes, that has received global popularity is mass balance modelling using ECOPATH (Christensen *et al*., 2014). This approach, despite its widely documented application in ecosystem modelling and management advice (Pitcher & Cochrane, 2002) has not been fully applied on Lake Victoria.

The first ECOPATH model on Lake Victoria was developed by Moreau (1995) for the Winam gulf, Kenya, and later updated by Villanueva and Moreau (2002). The only ecopath model that has been developed for the entire lake is that in Matsuishi *et al*. (2006). However, this model captured a simplified food-web, which ignored most of recovering haplochromine trophic groups, and does not report on the most important ecosystem attributes, such as trophic level of the catch, fishing efficiency, and primary production required to sustain the catches, all of which relate to fisheries sustainability and are important for fisheries management. Although the recovering groups were considered in Downing *et al*. (2012), the model was explicitly constructed for Mwanza gulf, Tanzania.

Additionally, the model in Downing *et al*., (2012) reports on ecosytem attributes that are theoretically doubtful. An example is the gross effeciency (GE), also called food conversion efficiency (FCE) in aquaculture, in other words, the physiological capacity to convert consumed food (Q) into tissue (P), of 66% for Nile tilapia and 61% for juenile Nile perch in 2005. Physiologically, FCE of 60% in fish is impossible. If both Nile perch and Nile tilapia were able to convert more than half of what they eat into tissue growth, then Lake Victoria, at present, would be the most energy efficient food web ever seen. The second dubious attribute is production to biomass (P/B) ratio of 12.5 year^{-1} for Nile tilapia. At steady states, P/B is equivalent to instantaneous rate of total annual mortality, Z (Allen, 1971). Although Nile tilapia is well known to be a super fish, it is theoretically imposible to reproduce own biomass 12 times per year, with a food conversion of 66%, on a diet dominated by phytoplankton. Thirdly, the authors reported a primary production to respiration ratio (PP/R) of 763 in 2005. The PP/R ratio is a measure of system maturity that is expected to approach 1.0 as the system matures. Values >1.0 reflect immature systems, while values <1.0 reflect eutrophication (Odum, 1969). Mwanza gulf is one of sections of Lake Victoria that are most burdened with large quantities of organic matter input from the heavily degraded watershed (Verschuren *et al*., 2002), which, in turn, has affected primary production because of light limitation and self-shading of large phytoplankton biomasses (Silsbe *et al*., 2006). Considering the eutrophication status of Mwanza gulf, and its ability to limit primary production (Silsbe *et al*., 2006; Kolding *et al*., 2008; Hecky *et al*., 2010), respiration is expected to either approach or supersede primary production. Innately, PP/R ratio should either approach 1.0, or become <1. In addition, the age of Lake Victoria, estimated at 250,000–750,000 years, although younger than the neighbouring Great Lakes, such as Tanganyika (9-13 million years) and Malawi (1-2 million years), is expected to show the characteristics of an ecosystem nearing maturity, although it has been heavily perturbed by species introductions, eutrophication, habitat degradation, and climate variability and change (Hecky *et al*., 2010). As a consequence, a new updated mass balance model for the entire lake is needed.

2.3   ECOPATH

ECOPATH is the most widely adopted tool for building models of marine and freshwater ecosystems (Christensen *et al*., 2014). This approach provides an ecological perspective for the assessment and management of multispecies and multigear fisheries. Using ECOPATH the system is partitioned into groups comprising species having a common physical habitat, similar diet, and life history characteristics (Christensen & Pauly, 1992). Unlike other ecosystem models, including the initial ecopath model developed by Polovina (1984), the current ECOPATH model (Christensen & Walters, 2004) does not entirely assume steady state conditions, but instead bases the parameterization on an assumption of mass balance over a defined period and, if the biomass at the beginning and the end of the modelled period is known, the rate of biomass increase or depletion is accounted for, thereby partly offsetting the risks of steady state assumption. A detailed description of ECOPATH mass balancing is in Christensen and Pauly (1992), Pauly *et al*. (2000), and Christensen and Walters (2004).

2.3.1   Model formulation

In a given ecosystem, the functional groups are regulated by gains (consumption, production, and immigration) and losses (mortality and emigration), and are linked to each other by predatory relationships (equation 1).

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

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, DC_{ji} is the fraction of prey i in the average diet of predator j, Y_i is the total fishery catch rate, E_i is the net migration rate (emigration – immigration), BA_i is the biomass accumulation rate, and EE_i is ecotrophic efficiency, which is the proportion of production that is utilised within the system either by predation or fishing.

Equation 1 suggests that that the net production of a functional group i equals the sum of (1) the total mass (or energy) 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.

2.3.2   Parameterization

ECOPATH sets up a system with as many linear equations, of form 1, as there are functional groups in a system, and it solves the set for one of the following parameters for each group, biomass, P/B ratio, Q/B ratio, or EE. In addition to these input parameters, mandatory data, for every defined functional group, are required for exports (usually catches), net migration rate, biomass accumulation rate, food assimilation rate, and diet composition. ECOPATH does not rely on solving a full set of linear equations, since there may be less equations than there are groups in the system. Instead, during the parameterization algorithm, ECOPATH estimates, iteratively, as many missing parameters as possible before setting up the set of linear equations. The values of EE vary between 0 and 1, and usually approach 1 for groups with considerable predation or fishing pressure. Therefore, 1-EE is everything that cannot be explained by the model, in simple terms, the biomass that simply goes missing (into detritus). Because EE is hard to estimate directly, it is desirable that all other parameters, including B, P/B, and Q/B are given so that EE (equation 2) is the only parameter to be estimated by the program.

$$EE = \frac{E_i + Y_i + BA_i + B_i + M2_i}{P_i} \qquad (2)$$

where M2 is predation mortality, estimated from $\quad M2_i = \sum_{j=1}^{n}(Qj \cdot DC_{ji})/B_i \qquad (3)$

During the parameterisation algorithm, FCE, which is expressed in terms of both production (P) and consumption (Q) per unit of biomass (B), for each functional group (i), is estimated as

$$FCE_i = \frac{\left(\frac{P}{B}\right)_i}{\left(\frac{Q}{B}\right)_i} \qquad (4)$$

2.3.3 Balancing the model

The energy balance within each group *i* is ensured when consumption by *i* equals the sum of production by *i*, respiration by *i*, and food that is unassimilated by *i*. To balance the model, all input parameters are optimized so that EE is ≤1 for every group. This is done by adjusting input parameters and/or data. If automatic balancing routine is used, the danger is that, while searching for optimal convergence, input parameters with well-known values (with narrow confidence intervals) may be greatly perturbed, leading to dubious estimates. A mitigation approach, which includes the simulated annealing algorithm, has been incorporated in the new version of ECOPATH (Christensen & Walters, 2004) in order to constrain how far the balancing routine can perturb parameters from their original values.

3 MATERIAL AND METHODS

3.1 Defining functional groups

Several studies have reported about the recovery of *Haplochromis* spp., following an unpresented decline in 1980s because of introduced Nile perch, and an overall recovery and reorganisation of the food web, although biodiversity is still lower than pre-1980 period (e.g. Downing *et al*., 2012). In this study, 18 functional groups were modelled (Table 1). Nile perch was separated into adult and juvenile groups to better account for the ontogenic diet shifts between life stages (see Kishe-Machumu *et al*., 2012; Nkalubo *et al*., 2014). The species that are important to fisheries, both at commercial and subsistence scales, and for which data were available, formed individual groups in order to accurately represent their roles in the trophic mass balance.

3.2 Model parameterisation

Three out of the four parameters, including biomass (t/km^2), P/B ratio (year^{-1}), Q/B ratio (year^{-1}) and EE, for every defined functional group, are required to initialise the ECOPATH mass balance model. In addition, mandatory data are required on exports (usually catches, t/km^2), diet composition (% volume), proportion of unassimilated food, biomass accumulation, and net migration rates (year^{-1}). These input parameters and data were estimated as follows.

Table 1. Description of components in functional groups used in the present Lake Victoria mass balance model.

No.	Group	Description of groups/species considered in a group
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 modelled minimum length of Nile perch available for selection by commercial fleet (Nyamweya, 2012)
3	Juvenile Nile perch	Nile perch < 40 cm total length
4	Catfishes	*Bagrus* spp. and *Clarias* spp.
5	Lungfish	The species used here is the Marbled lungfish, *Protopterus aethipicus*
6	Snout fishes and squeakers	*Synodontis* spp. and Momyridae
7	Zooplanktivorous dwarf breams	Considered only *Haplochromis pyrrhocephalus* Witte and Witte-Maas, 1987, and *H. laparogramma* Greenwood and Gee 1969, which account for 71% of the current *Haplochromis* spp.standing stock (Kishe-Machumu *et al.*, 2015)
8	Detrivorous dwarf breams	Considered *H*. 'paropius-like', *H*. 'straight head dusky', *H*. 'cinctus-like', *H. antleter* Mietes and Witte 2010, which currently constitute 21% of the *Haplochromis* spp. standing stock (Kishe-Machumu *et al.*, 2015)
9	Other dwarf breams	This group constitutes mostly large predatory *Haplochromis* spp, but these are very rare
10	Dagaa	Represents the only group of pelagic fishes that persisted the ecosystem downturn after various 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, Red breast tilapia, Blue spotted tilapia, and *Barbus* species
13	Lake prawn	Atyd prawn (*Caridina nilotica*)
14	Insects and Molluscs	Diptera (especially the midge, Chironomid, and the phantom-midge, *Chaoborus* larvae), Odononata 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	Marcrophytes, periphyton, epiphyton
18	Detritus	This is the cycling group composed of decaying organic matter

3.2.1 Biomass (B)

Biomass estimate for fish eating birds was taken from Villanueva and Moreau (2002), assuming they have not changed significantly. Biomass for juvenile and adult Nile perch groups, Nile tilapia, and other tilapias were calculated as $B = \dfrac{\text{Yield}}{\text{Fishing mortality}}$ (Haddon, 2011). Fishing mortality (F) for both juvenile and adult Nile perch was considered to be 0.53 year^{-1} (Nyamweya, 2012), and that of Nile tilapia and other tilapias at 1.32 year^{-1} (Njiru et al., 2007). Biomasses of dagaa and *Haplochromis* spp. were obtained from Taabu-Munyaho *et al.,* (2014). Separation of *Haplochromis* spp. biomass into zooplanktivores and detrivores, which account for account for >80% of the *Haplochromis* spp. stock, and other *Haplochromis* spp.was done using proportions in Kishe-Machumu *et al*. (2015). Biomasses of other fish groups (e.g. catfishes, marbled lungfish, snout fishes and squeakers) were obtained from lake-wide trawl surveys carried out in 2008. Because of absence of new estimates for lower trophic levels (groups 13-18, Table 1), biomass estimates in Villanueva and Moreau (2002) were considerd, except for phytoplanton whose latest biomass was obtained from Witte *et al.*, (2012).

3.2.2 P/B ratio

The P/B ratio for fish eating birds was taken from Villanueva and Moreau (2002), as there were no new data. The P/B ratio for each of the fish functional group was assumed to be equivalent to instantaneous rate of total annual mortality (Z) (Allen, 1971). The Z value for each fish group was calculated as the sum of natural mortality (M) and fishing mortality (F). The F, with exception of Nile perch (both juvenile and adult), Nile tilapia, and other tilapias, whose F values were available from literature (Njiru *et al.,* 2007; Nyamweya, 2012), was estimated directly from $F = \frac{Yield}{Biomass}$. 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 (equation 6).

$$M = K^{0.65} \cdot L_\infty^{-0.279} \cdot T^{0.463} \qquad (6)$$

where L_∞ is the asymptotic length, i.e., the mean length the individuals in the population would reach if they were to live and grow indefinitely (which, also, in this study, was calculated from $\log L_\infty = 0.044 + 0.9841 \log L_{max}$; where L_{max} = maximum length in the population; Froese & Binohlan, 2000), K is the VBGF curvature parameter (expressing the rate at which L_∞ is approached and, here, calculated using the empirical relationships in Froese & Pauly, 2015), and T is the mean environmental temperature (°C). An average temperature value of 25.88 °C, adopted from Marshall *et al*. (2013), was used.

The Z values for the lower trophic levels were assumed to be the same as those in Villanueva and Moreau (2002).

3.2.3 Q/B ratio

The Q/B ratio for fish eating birds was taken from Villanueva and Moreau (2002). The Q/B ratio for each of the fish functional group was estimated using an empirical formula (Palomares & Pauly, 1998) that relates Q/B with one parameter of the VBGF, habitat temperature, morphological variables, and food type (equation 7).

$$\log\left(\frac{Q}{B}\right) = 5.847 + 0.28 \log Z - 0.152 \log W\infty - 1.36 T' + 0.062 A + 0.510 h + 0.390 d \quad (7)$$

where W_∞ is the asymptotic weight (g) that is analogous to L_∞ (and calculated, for this study, as $W_\infty = qL_\infty^3$, where q is the expression of condition factor in gram per cubic centimetre of fish; Sparre & 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 & Pauly, 2015), *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).

For the lungfish group, whose Q/B ratio could not be calculated from equation 10 because of lack of realistic information on the aspect ratio of the caudal fin, an estimate of 4.3 year^{-1} in Villanueva and Moreau (2002) was used. The same source was used for Q/B ratios on non-fish groups.

3.2.4 Exports (catches)

Energy in the harvested fish is not used within the system, and is often termed as exported energy (Christensen *et al*., 2008). For those groups exploited commercially, data on catches for the whole lake were obtained from the regional catch assessment surveys conducted in April 2014 (LVFO, 2015). The catch data were split according to fishing gear (Table 2) for convenience during evaluation of mixed trophic impacts (MTI) in ECOPATH. Disaggregated data, also, permit the identification of ecologically meaningful critical situations, when MTI are considered, and, also avoid masking (averaging) the effects and accounts for differential development and adaptability of different gear (Moutopoulos *et al*., 2014).

Nile perch catches had to be split into juvenile and adult Nile perch. According to Mkumbo and Marshall (2015), only 15% of the landed Nile perch are >50 cm TL. This value was doubled, assuming that Nile perch in the range of 41-49 cm TL account for not less than 15%. Accordingly, 30% of the Nile perch catches were classified as adult (>40 cm TL), while 70% as juvenile (<40 cm TL). Lake prawn are always harvested as by-catch in small seines alongside dagaa, but are not discarded in the lake and, hence, their energy is also exported. 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 & Cowx, 2007). In this study, a generalisation was made, therefore, that 10% of the fish caugh in small seines in 2014 were atyid prawn.

3.2.5 Diet composition and unassimilated food

For both juvenile and adult Nile perch, the diet composition was obtained from stomach content analyses in Kishe-Machumu *et al*., (2012). The diet composition of Nile tilapia was obtained from Njiru *et al*., (2008). For catfishes, dagaa, *Haplochromis* spp., lake prawn, and zooplankton, diet composition were estimated as mid-points of ranges published in Downing *et al*. (2012). The diet composition of fish eating birds, other tilapias and cyprinids, squeakers and snoutfishes, marbeled lungfish, and insects and molluscs were based on estimates in Villanueva and Moreau (2002). These values, which were used to perfom the firt model run, but not used in the final balanced model, are shown in Appendix 1.

In ECOPATH sofware, if values of unassimilated food are not available, a default value of 0.2 is suggested for carnivorous fish groups to represent the fraction of the food that is not assimilated (Christensen *et al*., 2008). For herbivores, however, the proportion not assimilated can be up to 0.4. In this study, therefore, Nile tilapia, other tilapias, and zooplankton groups, whose diet is mainly composed of phytoplankton, the proportion of unassimlated food was set at 0.4. The other groups were left at the default value of 0.2.

Table 2. Total landed catches (t/km^2/year) for Lake Victoria, derived from the regional catch assessment surveys (LVFO, 2015). Values in both the rows and columns may not exactly add to the totals because they have been truncated for clarity. No truncation of data was done in ECOPATH.

Group name	Small seine	Castnet	Gillnet	Handline	Trap	Beach seine	Longline	Scoopnet	Others	Total
Adult Nile perch	0.0006	0.002	0.448	0.051	0.0008	0.120	0.446		0.023	1.094
Juvenile Nile perch	0.001	0.005	1.047	0.119	0.001	0.281	1.041		0.055	2.55
Catfishes		0.0002	0.017	0.003	0.0005	0.0004	0.030		0.002	0.056
Marbled lungfish		0.0004	0.034	0.005	0.002	0.005	0.013			0.062
Squeakers and snoutfishes		9.40E-05	0.241		0.004	0.0003	0.0002			0.246
Zooplanktivorous dwarf breams	0.562	0.013	0.063	0.007		0.031				0.678
Detrivorus dwarf breams	0.166	0.004	0.018	0.002		0.009				0.2
Other dwarf breams	0.063	0.001	0.007	0.0008		0.003				0.07
Dagaa	6.43		0.023					0.934		7.395
Nile tilapia	8.64E-05	0.098	0.236	0.036	0.021	0.025	0.002		0.273	0.694
Other tilapias	2.16E-05	0.024	0.059	0.009	0.005	0.006	0.0007		0.068	0.173
Lake prawn	0.493									0.493
Total	7.724	0.151	2.199	0.235	0.037	0.484	1.535	0.934	0.424	13.72

3.2.6 Net migration and biomass accumulation rates

The model was constructed to capture trophic interactions for the whole lake, which was considered to be a closed system. As a result, net migration rate was assumed to be zero. In addition, the parameterisation procedure was based on the principle of mass balance for a period of one year (2014) and, hence, biomass accumulation for every group was assumed to be zero.

3.2.7 Ecotrophic efficiency (EE)

Once all the above parameters and data have been estimated and entered, ECOPATH software, through a system of linear equations, of form 1, as there are functional groups in a system, automatically solves for EE using equation 2. In this study, all parameter estimates and input data for the defined functional groups were entered, and allowed ECOPATH to estimate their EEs.

3.2.8 Model balancing and diagnostics

When all input parameters and data, as estimated from original data and literature, were entered into ECOPATH software, the model was balanced such that energy fluxes in and out of the model were equal. The model was considered mass balanced when all the following physiological constraints (Heymans *et al*., 2016) were simultaneously met i.e.

i. EE ≤ 1 for every group (i.e., biomass utilization of the group being lower or equal to biomass production of that group). The value for EE should never exceed 1.0 because it is not possible for more production to be passed on to the next trophic level than was originally produced. An EE value near to 1.0 is expected when the main part of production is consumed by predators or taken by fishing. A value near to 0.0 is expected for a group, such as an apex predator, which suffers no predation and is not exploited by a fishery.
ii. Values of gross food conversion efficiency (production/consumption ratios, P/Q, or FCE) for functional groups varying between 0.1 and 0.35, except for fast growing groups with higher values, and top predators with lower values;
iii. Net Efficiency $< 1.0 <$ P/Q. Net Efficiency is the value for food conversion after accounting for unassimilated food for which the ECOPATH default value is 20%. Therefore, net efficiency should never exceed gross food conversion efficiency.
iv. Respiration/Assimilation (R/A) < 1.0. The proportion of biomass lost through respiration should not exceed the biomass of food assimilated. For *K*-selected species and top predators, which are expected to invest more energy on growth and reproduction are expected to have R/A ratios close to 1.0. In contrast, *r*-selected species are more likely to invest less energy on growth and reproduction resulting in an R/A ratio $\ll 1.0$.
v. Values of respiration/biomass ratios (R/B) consistent with the group's activities. The R/B indicates the metabolic activity level of a group. Intuitively, R/B should be high for small organisms, with rapid turnover, as well as top predators. Generally, RA/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.

Despite the fact that the original input parameters and data were obtained from the best available information, the model could not balance on the first run. The EE for squeakers and snoutfishes, zooplanktivorous and detrivorus dwarf breams, other tilapias and cyprinids, lake prawn, and zooplankton were >1. This implied that demands on these groups were too high to be reasonable

and, hence, certain thermodynamic constraints were violated. Because parameter estimates, especially for the fish groups, were obtained from known narrow ranges, only diet compositions were modified to achive a mass balanced model. However, modification of diet composition was done pragmatically so that the final diet composition matrix (Table 3), which achieved a mass balanced model, was still in the same range as that reported from most stomach content analyses on the lake, and summarised in Downing *et al*., (2012).

When no further adjustment of diet could be done, and yet the EE for squeakers and snoutfishes, zooplanktivorous dwarf breams, and other tilapias were still >1, a value of 0.95, which was derived as the average EE for these groups in models previously published by Moreau (1995), Villanueva & Moreau (2002), and Matsuishi *et al*., (2006), was fixed as their EE and let ECOPATH software determine their realistic biomasses. At this stage, all other mass balance and physiological contsraints, as outlined above, had been met.

Table 3. Diet composition (proportion) of groups in Lake Victoria after adjustment to achieve a mass balanced model, but whose values are still in the range reported in literature (Villanueva & Moreau 2002; Njiru *et al.* 2008, Kishe-Machumu *et al.* 2012, Downing *et al.* 2012).

No.	Prey \ predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	Fish eating birds															
2	Adult Nile perch															
3	Juvenile Nile perch	0.15	0.28	0.023	0.04	0.05										
4	Catfishes	0.01				0.05	0.007									
5	Marbled lungfish	0.01					0.001									
6	Squeakers and snoutfishes					0.05										
7	Zooplanktivorous dwarf breams	0.15	0.3	0.2	0.002	0.001	0.001			0.05		0.07				
8	Detrivorus dwarf breams		0.06	0.022	0.002	0.003	0.003					0.02				
9	Other dwarf breams	0.15	0.005	0.003	0.001	0.001	0.001			0.05						
10	Dagaa	0.53	0.2	0.243	0.1	0.05	0.05			0.4		0.09				
11	Nile tilapia		0.037		0.04	0.02	0.04									
12	Other tilapias and cyprinids		0.037		0.005	0.005	0.005									
13	Lake prawn			0.437	0.15	0.1	0.05	0.35		0.05	0.1				0.01	
14	Insects and molluscs		0.078	0.043	0.62	0.570	0.71	0.05		0.4		0.24	0.02	0	0.05	
15	Zooplankton			0.027	0.03	0.05	0.05	0.6			0.45		0.03	0.1	0.04	
16	Phytoplankton										0.3	0.57	0.45	0.2	0.05	1.0
17	Benthic producers				0.01						0.1		0.3		0.3	
18	Detritus					0.05	0.082		1.0		0.05	0.01	0.2	0.7	0.55	
	Import															

3.3   Assessment of ecosystem attributes that relate to maturity and stability

After balancing the model, it was possible to estimate various indices, by functional group, which are useful for analysing the ecological role of the different ecosystem components. These indices describe the relative impacts of different drivers of change, including fishing and environmental forcing, on system maturity, productivity, efficiency, and stability. These indices follow the theories expounded in Odum (1969), Ulanowicz (1986), Ulanowicz & Puccia (1990), Christensen and Pauly (1992), Christensen (1995), Ulanowicz (2004), Christensen *et al*., (2005), and Christensen *et al*., (2008). A comprehensive trophic description, in this study, therefore, was accomplished by computing:

i. Total system throughput (TST) - the sum of all flows (consumption, respiration, detritus and export) in a system (t km^{-2} year^{-1}) and is a measure of the size of the entire system in terms of biomass flows. Ecosystem growth translates into an increase in the T.

ii. Total Primary Production (TPP) - calculated as the summed primary production from all producers, and net system production (NSP) as the difference between TPP and total respiration. NSP is large in immature systems and close to zero in mature ones.

iii. Primary production to respiration ratio - measure of system maturity that is expected to approach 1 as the system matures. Values >1.0 reflect immature system, while <1.0 reflects eutrophication.

iv. Primary production to biomass ratio - also a measure of maturity that is expected to decrease as a system matures

v. The trophic transfer efficiency (TE) - percentage of throughput entering a trophic level that is subsequently passed on to the next trophic level (or harvested), and is estimated to give an indication of all the inefficiencies of the food web (due to respiration, excretion, egestion, and natural mortality). The TE was calculated between successive discrete trophic levels as the ratio between sum of the exports from a given trophic level and the flow from that trophic level to the next, and the throughput on the trophic level.

vi. Connectance index (CI) - ratio of the number of actual links to the number of possible links in the food web. CI correlated with system maturity, since the food chain is expected to change from linear to web-like as the system matures.

vii. System omnivory index (SOI) - the average omnivory index of all consumers weighted by the logarithm of each consumer's food intake. This index characterizes the extent to which an ecosystem exhibit web-like features, and is also an attribute of ecosystem maturity.

viii. Niche overlap - an index based on Lotka-Voltera competition coefficients (Pianka, 1973), which describes the measure of resource partitioning in the food web. Theoretically, an index value close to 0 indicates that two groups have a low resemblance in terms of food consumed and vice versa for a value close to 1.

ix. Cycling index (CI) - the fraction of TST that is recycled in the system and is correlated with maturity, resilience, and stability.

x. Ascendency (A) - quantifies both the level of activity and the degree of the organization of the system. It accounts for both import, internal flows, export, and respiration. The mathematical upper limit of A is the development capacity (DC), representing the scope of the system for further development. In addition, the system Overhead (O) (the difference between the DC and A) was also estimated, representing the amount by which DC exceeds A. It represents the ecosystem potential for recovery (resilience).

xi. Mixed trophic impacts (MTI) - quantifies the trophic impact that a hypothetical insignificant change in the biomass of a group (or fishing fleet) would have on each of the other functional groups (or fleets). The interaction between the impacting group j

and the impacted group i, MTIj,i = DCj,i – FCj,i; where DCj,i, is the diet composition term expressing how much (i) contributes to the diet of (j), and FCj,i, is a host composition term giving the proportion of the predation on (i) that is due to (j) as a predator. Fishing fleets are included as 'predators' in determining host composition.

xii. Keystone (species or groups of species, KS) - low biomass biotic components with a structuring role in their food webs, and calculated following Libralato *et al*., (2006) as KS=log[ε_i(1-p_i)]; where p_i is the contribution of the group (i) to the total biomass of the food web and ε_i is the overall effect. This index is high when functional groups have both low relative biomass and strong overall effects. In general, species/groups with KS values higher than zero (or close to zero) can be considered keystones.

3.4 Assessment of ecosystem-based reference framework for fisheries management

i. Mean trophic level of the catch (TL$_C$) - reflects the overall strategy of a fishery, and was calculated by weighting the proportions of each type of organisms from the catch by their respective trophic levels. The TL$_C$ decreases as fishing impacts increase in the ecosystem since fishing tends to first remove the high trophic level organisms.

ii. Gross fishing effeciency (GFE) - computed as the sum of all fisheries catches divided by total primary production. 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.

iii. Primary production required (PPR) - primary production 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 was calculated using an empirical formula (Pauly & Christensen, 1995) linking PPR, fish catches, transfer efficiency, and trophic level (equation 8).

$$PPR = \frac{1}{9} \cdot \sum_i Yi \cdot \left(\frac{1}{TE}\right)^{TLi-1} \tag{8}$$

where where Yi is the catch of a given group i, TE is the mean transfer efficiency, TLi is the trophic level of a group i, and factor 1/9 is the average conversion coefficient from wet weight to gC.

iv. L index - quantifies the loss in secondary production due to fishing, and was calculated using an empirical formula (Libralato *et al*., 2008) linking L index, primary production (PP), TE, TL$_C$, and PPR (equation 9). Equation 9 shows that for equivalent amount of catches expressed in PPR units, the relative loss in secondary production increases when TL$_C$ decreases since TE is always <1. Hence L index increases with fishing impact, and intensifies when fishing quickly depleted higher TLs. This is in accordance with the negative effects of fishing down the food web (Pauly *et al*., 1998).

$$L_{index} = -\frac{PPR \cdot TE^{TLc-1}}{PP.lnTE} \tag{9}$$

Following from the above index, the probability of an ecosystem being sustainably exploited (P$_{sust}$) was estimated for the lake using the L index classifcation models in Libralato *et al*. (2008) for over exploited and sustainably utilised fisheries.

4   RESULTS

4.1   Mass balances

A balanced model was successfully constructed for the Lake Victoria ecosystem with 18 functional groups. In general, EE values were high, as expected, for the fish groups, except for Nile perch (both juvenile and adult) and dagaa (Table 4), implying that 'other mortality' rates, $M0_i = P_i \cdot (1 - EE_i)$, which can neither be attributed to predators nor fishing activities, were higher for Nile perch and dagaa compared to other fish groups. Fish eating birds, the top predators, are neither harvested nor consumed in the system and, hence, the EE was zero. The low EE for benthic producers, phytoplankton, insects and molluscs, and detritus indicate that only a small proportion of their production, with respect to biomass, is grazed in the water column, a large biomass flows towards detritus (Table 5).

Table 4. Parameter estimates for the final mass balanced model. Italics and/or bold: Parameters estimated by ECOPATH software to balance the model.

Group name	Biomass (t/km²)	P/B (/year)	Q/B (/year)	EE	P/Q
Fish eating birds	0.005	0.300	60.000	*0.000*	*0.005*
Adult Nile perch	2.070	0.831	3.728	*0.637*	*0.223*
Juvenile Nile perch	4.819	3.997	12.065	*0.332*	*0.331*
Catfishes	0.093	0.991	6.009	*0.998*	*0.165*
Marbled lungfish	0.076	1.123	4.300	*0.798*	*0.261*
Squeakers and snoutfishes	***0.276***	1.000	8.763	0.950	*0.114*
Zooplanktivorous dwarf breams	***6.515***	2.513	21.589	0.950	*0.116*
Detrivorus dwarf breams	0.894	2.534	47.965	*0.944*	*0.053*
Other dwarf breams	0.341	1.832	13.459	*0.963*	*0.136*
Dagaa	15.800	3.936	30.798	*0.420*	*0.128*
Nile tilapia	0.624	2.024	15.030	*0.881*	*0.135*
Other tilapias and cyprinids	***0.215***	2.370	33.420	0.950	*0.071*
Lake prawn	8.000	16.000	64.000	*0.990*	*0.250*
Insects and molluscs	10.000	10.000	25.000	*0.292*	*0.400*
Zooplankton	11.000	34.000	140.000	*0.980*	*0.243*
Phytoplankton	7.100	365.000		*0.698*	
Benthic producers	13.407	25.000		*0.375*	
Detritus	10.000			*0.276*	

The gross food conversion efficiencies (GE or FCE) were within the expected range of 0.1-0.35, except for fish eating birds, which had lower P/Q (<<0.1), and insects and molluscs, which had higher P/Q (0.4), and the reasons for this are discussed.

The modelling procedure assigns a trophic level (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). Subsequently, the highest fractional TLs in the lake were occupied by fish eating birds and adult Nile perch, while other tilapias and cyprinids, detrivorous dwarf breams, and zooplankton occupied the lowest TLs among the consumers (Table 5).

Table 5. Fractional trophic level (TL) and biomass flows to detritus for different groups in the Lake Victoria food web.

Group name	TL	Flow to detritus (t/km^2/year)	Net efficiency	Omnivory index (OI)
Fish eating birds	3.912	0.061	0.006	0.157
Adult Nile perch	3.864	2.168	0.279	0.238
Juvenile Nile perch	3.431	24.500	0.414	0.167
Catfishes	3.211	0.112	0.206	0.105
Marbled lungfish	3.248	0.082	0.326	0.253
Squeakers and snoutfishes	3.062	0.498	0.143	0.130
Zooplanktivorous dwarf breams	3.040	28.950	0.146	0.002
Detrivorus dwarf breams	2.000	8.702	0.066	
Other dwarf breams	3.469	0.940	0.170	0.175
Dagaa	2.560	133.400	0.160	0.257
Nile tilapia	2.569	3.901	0.224	0.501
Other tilapias and cyprinids	2.052	2.894	0.118	0.051
Lake prawn	2.100	103.600	0.313	0.090
Insects and molluscs	2.106	120.800	0.500	0.102
Zooplankton	2.000	623.500	0.405	
Phytoplankton	1.000	782.000		
Benthic producers	1.000	209.400		
Detritus	1.000			0.391

Adult Nile perch, marbled lungfish, dagaa, and Nile tilapia had lower trophic specialisation, with individual OI >0.2, compared to other consumer groups. Nile tilapia, however, had the greatest feeding spectrum, with OI that was two folds higher than its generalist counterparts (Table 5). The OIs of detrivorus dwarf breams and zooplankton were zero as they feed exclusively on prey from first trophic level. Among the fish groups, zooplanktivorous dwarf breams, and other tilapias and cyprinids showed lowest degree of trophic plasticity as shown by OI<<0.1 (Table 5).

Niche overlap series showed that catfishes and marbelled lungfish, and catfishes and squeakers and snoutfishes had the highest prey overlap (Figure 5). Other groups with relatively high overlap included detrivorous dwarf breams and lake prawn. Among the fish groups, detrivorous dwarf breams, and other tilapias and cyprinids had the most divergent preferences in terms of resources consumed.
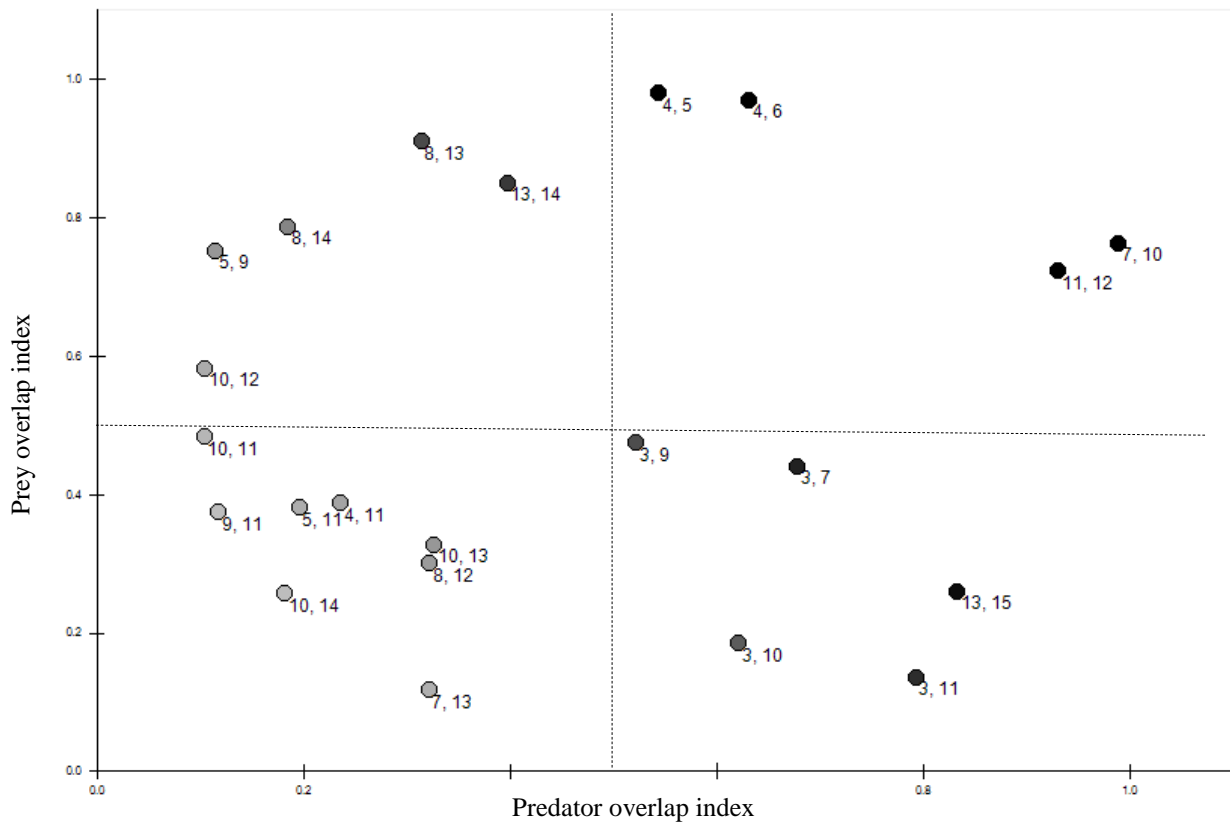
Figure 5. Prey vs. predator niche overlap plot. Symbol colors are scaled to the extent of overlap (light shade = least overlap, and black shade = highest overlap). Numbers 3-15 represent functional groups as exactly defined in Table 1.

Table 6 shows the summary statistics of energy flows and biomasses. The total system throughput (TST) (i.e., the sum of all flows) was 8035.5 t/km^2/year. Of this, 38% was consumed by predation, 17.8% was dissipated by respiration, 18.5% was exported (through catches), and 25.4% were flows to detritus.

By aggregating the Lake Victoria food web into discrete trophic levels *sensu* Lindeman (1942), seven discrete TLs (7th TL not shown in the Lindeman spine) were observed, although main flows, including detritus, occurred within TLI and TLII, generating 93% of TST (Figure 6). About 66% of the total primary production was consumed by herbivores, while the remaining 34% flowed to the detritus compartment. Figure 6, also, shows that trophic flow originating from primary producers to consumers was three folds higher than that from detritus, resulting in a detritivory/herbivory ratio of 0.29, and an average trophic transfer efficiency of 11.9%.

Table 6. Summary of ecosystem attribute statistics related to flows and biomasses.

parameter	value	units
Sum of all production	3633.3	t/km^2/year
Sum of all consumption	3062.7	t/km^2/year
Sum of all exports	1494.4	t/km^2/year
Sum of all respiratory flows	1432.2	t/km^2/year
Sum of all flows into detritus	2045.5	t/km^2/year
Total system throughput (TST)	8035.0	t/km^2/year
Total net primary production	2926.6	t/km^2/year
Total primary production/total respiration (PP/R)	2.5	
Net system production (NSP)	1494.4	t/km^2/year
Total primary production/total biomass (PP/B)	36.0	
Total biomass/total throughput (B/T)	0.01	year^{-1}
Total biomass (excluding detritus)	81.2	t/km^2
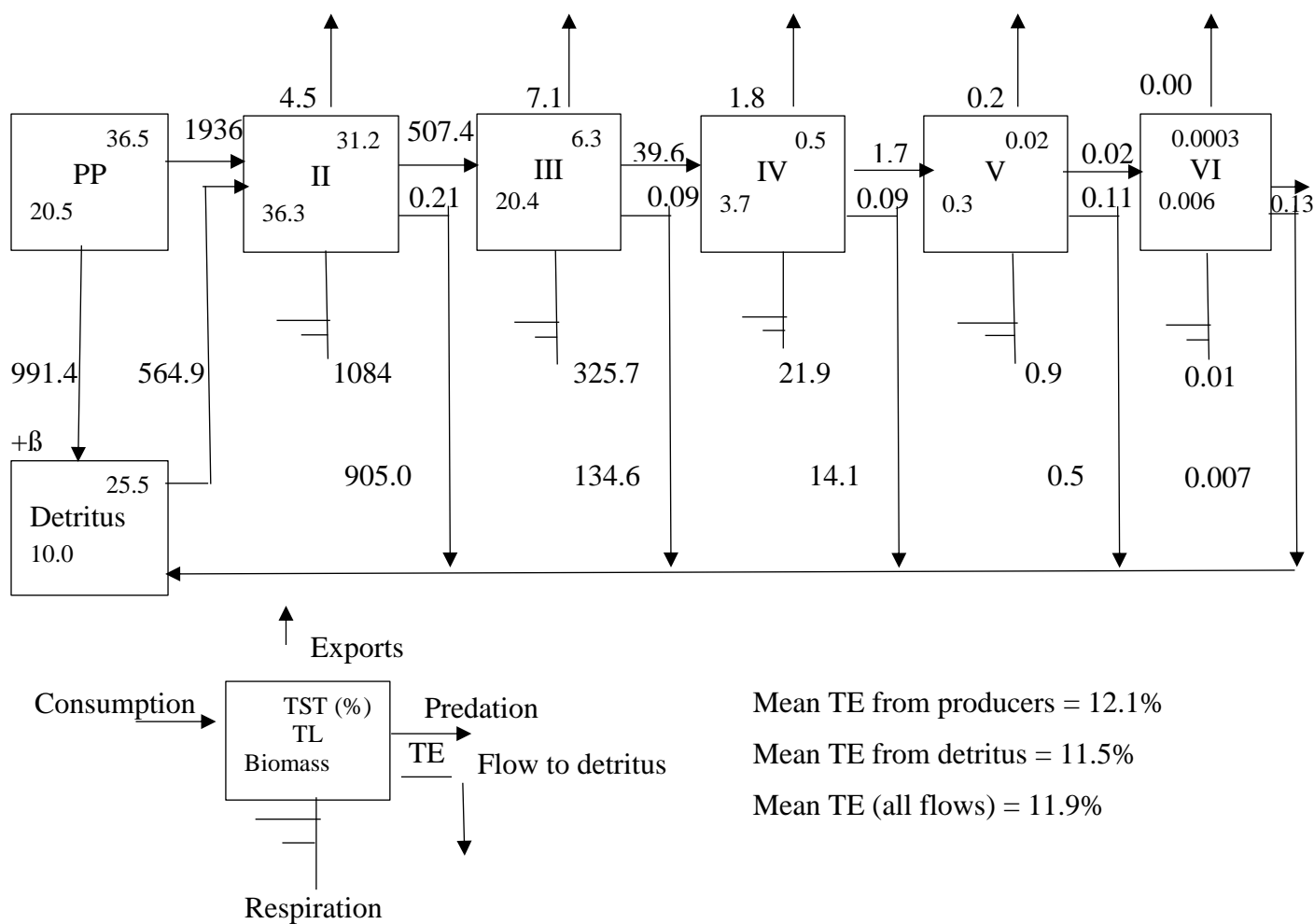
Figure 6. Food web of Lake Victoria, condensed into discrete trophic levels (TL), showing flows and biomasses. All flows and biomasses are expressed in t/km2/year

4.2   Ecosystem development and maturity

The ratios used to assess the ecosystem status, including PP/R, PP/B, and B/T showed a maturing system with relatively high productivity in relation with the total biomass and respiration, despite having low biomass in relation to the total flows of energy. On comparative basis, however, the TST was lower for Lake Victoria compared to other lakes in the region, including Lakes Kivu (Villanueva *et al.*, 2008), Awasa (Fetahi & Mengistou, 2007), and Malawi (Darwall *et al.*, 2010). Connectance index (CI) showed that 33% of the possible links occurred in the food web, while the SIO (0.12) reflected a rather low degree of connectivity among groups (Table 7). The cycling index showed that 244.8 t/km^2 of throughput (including detritus) is recycled within the system per year, with the path length, which is the average number of groups that a flow passes through, of 2.75. Concerning the food web organisation descriptors, system's A reached 30.6% of the DC, leaving an overhead, which is the measure of system's strength in reserve to meet unexpected perturbations (resilience), of 69.4% (Table 7).

Table 7. Summary of ecosystem attribute statistics related to network flow and information.

Index	value	units
Connectance Index (CI)	0.33	
Finn's cycling index	3.05	%TST
Finn's path length	2.75	
System Omnivory Index (SOI)	0.12	
Ascendency (A)	10,001.9	Flowbits
Overhead (O)	22,666.8	Flowbits

The keystone series presented the highest index as well as relative impact for the Nile perch, lake prawn, insects and molluscs, zooplankton, and phytoplankton (Figure 7). However, no distinct keystone(s) could be discerned in the Lake Victoria food. Nonetheless, the trophic cascades, herein presented as MTI, showed majority of the fish groups with minimal or no impact on the other groups, except Nile perch, which exerted negative impact on most fish groups (Figure 8). Figure 8 also shows the importance of detritus and phytoplankton in supporting the higher trophic levels as they had positive impact on majority of the groups.

1. Fish eating birds
2. Adult Nile perch
3. Juvenile Nile perch
4. Catfishes
5. Marbled lungfish
6. Squeakers and snoutfishes
7. Zooplanktivorous dwarf breams
8. Detrivorus dwarf breams
9. Other dwarf breams
10. Dagaa
11. Nile tilapia
12. Other tilapias and cyprinids
13. Lake prawn
14. Insects and molluscs
15. Zooplankton
16. Phytoplankton
17. Benthic producers

Figure 6. Keystone index and relative overall effect of each functional group from the ecological model of the Lake Victoria ecosystem.

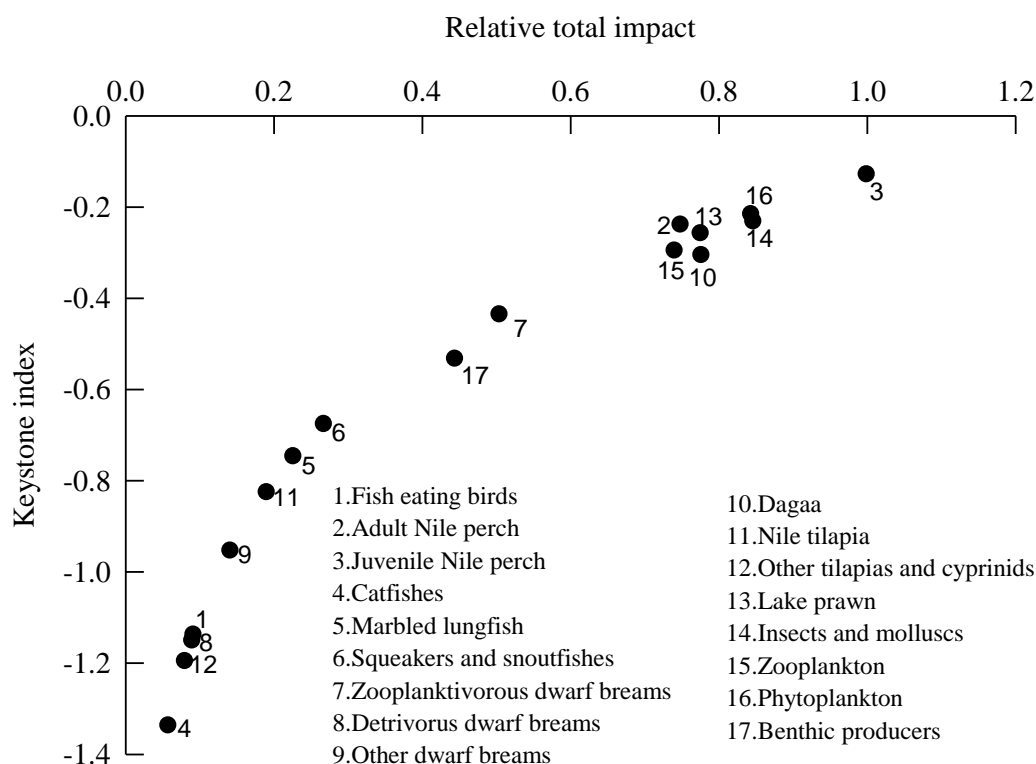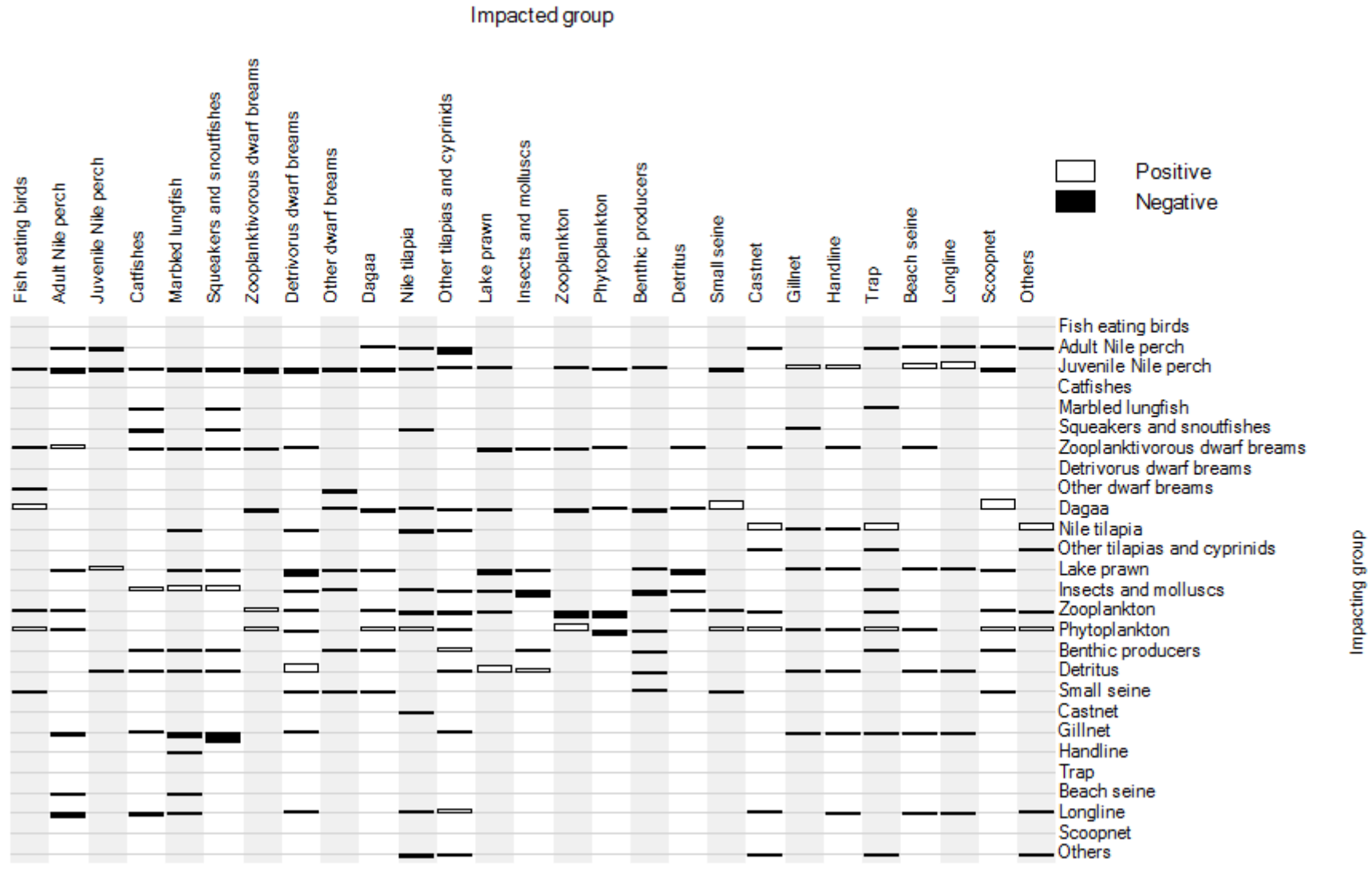Figure 7. Mixed trophic impacts in Lake Victoria ecosystem showing, on a relative scale, the combined direct and indirect impacts of a change in the biomass of each group on the other groups. The fishing gear are included because they are considered 'predators' when determining host compositions.

4.3 Ecosystem productivity

4.3.1 The focus of fisheries

Total fish biomass of Lake Victoria is about 32 t/km^2, with the yield estimated at 13.7 t/km^2/year. The catches were concentrated in TLII and TLIII (Figure 9), and the primary production that is required to sustain these catches was estimated at 1016.2 t/km^2/year. This is equivalent to 20.44% of the total system primary production (excluding detritus). When expressed relative to the total flow from TL1, the PPR used in ECOPATH corresponds to the ecological footprint (EF). For the catch (C), EF, the size of the area in km^2 that is needed to sustain 1 t of fish, equals PPR/PP×C. Resultantly, EF of the fishery was found to be 0.01km^2, with the GFE of 0.0046.
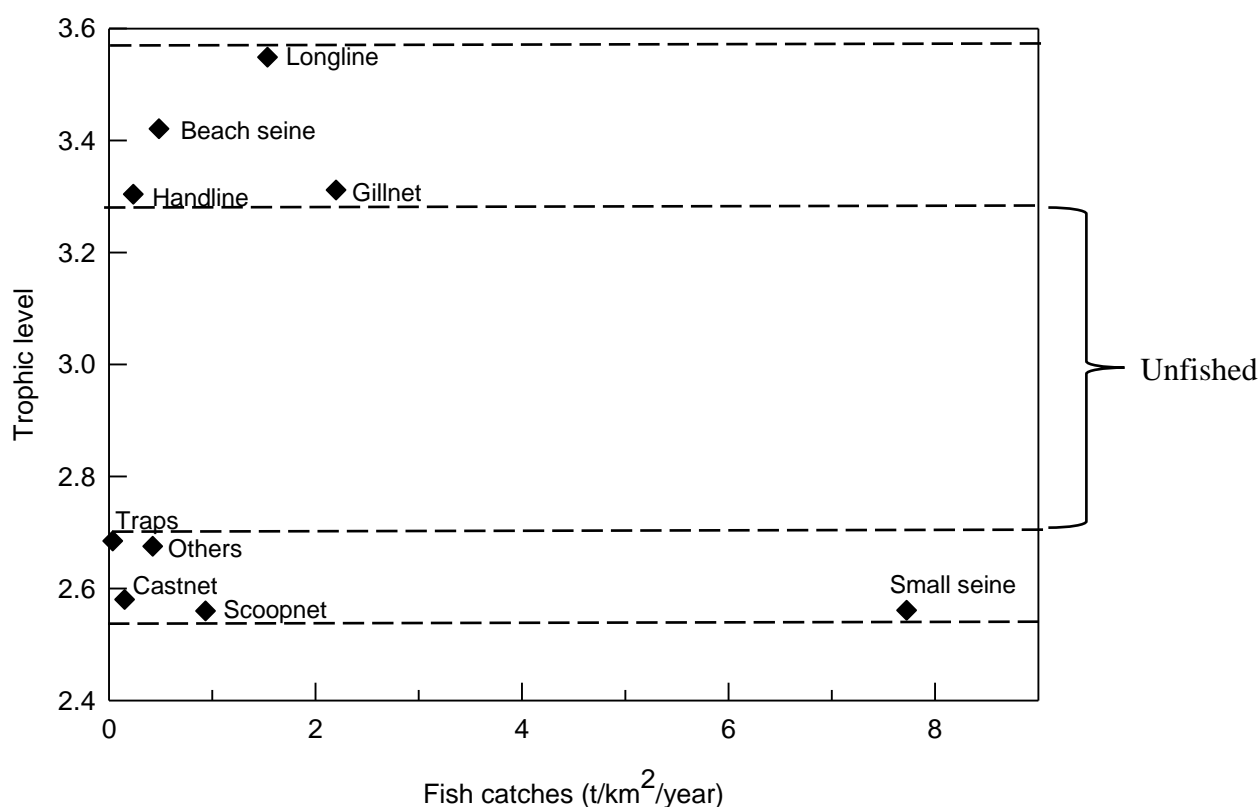
Figure 8. Trophic level (TL) of the catch per fishing gear in the Lake Victoria mass balance model, 2014. This is the first indication of unbalanced harvesting where fishing is concentrated only at TL 2.5-2.7 and TL 3.3-3.5.

The role of commercial fisheries during the study period was equivalent to a predator occupying a mean trophic level of 2.84. This was lower compared to TL$_C$ previously published e.g. 3.1 (2005) and 3.5 (1987) for Mwanza gulf (Downing *et al.*, 2012), and 3.18 (1995-1996) for Winam gulf (Villanueva & Moreau 2002). Although fishing tends to first remove the high trophic level fishes (see fishing down the food web by Pauly *et al.*, 1998), such a linear decrease in TL$_C$ could also reflect a shift to fisheries at lower TLs. Nonetheless, I tested whether the current fishing is sustainable or not using two approaches. First, I tested whether there is balanced harvesting on Lake Victoria. Balanced harvesting is an approach to fishing that distributes a moderate fishing mortality across the widest possible range of species, stocks, and sizes in an ecosystem, in proportion to their natural productivity, so that the relative size and species composition is maintained (Garcia *et al.*, 2012). The plot of log$_{10}$ yield (kg/km^2/year)

vs. log$_{10}$ production (same units) showed that 50% of the total number of exploited species/groups are harvested at a rate <15% of their production, and the reminder at a rate ≥50% of their production (Figure 10).
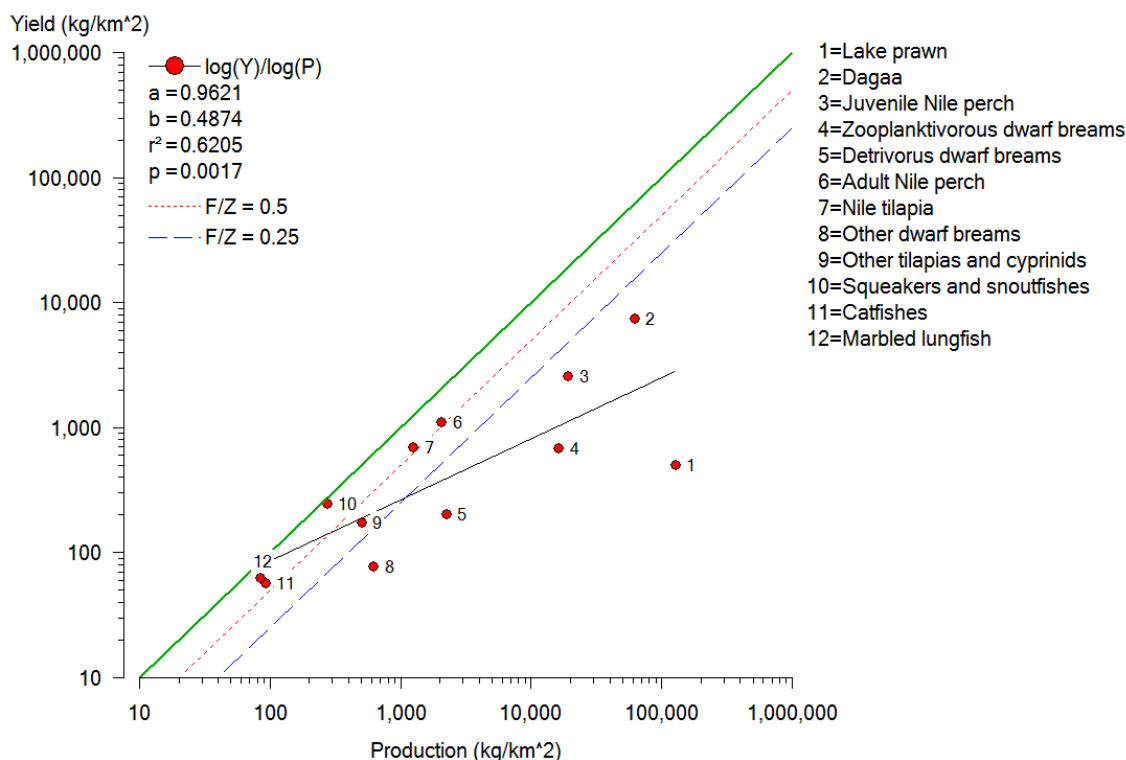
Figure 9. Average fishing pattern in Lake Victoria as of 2014, expressed as log$_{10}$ yield (kg/km^2/year) vs. log$_{10}$ production (same units). Production = Z*B. The more the slope deviates from the 1:1 line (green) between yield and production, the more "unbalanced" (*sensu* Garcia et al., 2012) the fishery is. Fishing pressure or exploitation rate (E) is inversely correlated with orthogonal distance from the 1:1 line where yield = production. Exploitation rates equivalent to 25 and 50% of production are given as red and blue parallel lines, respectively. p-value gives the test of slope ≠1. The ratio of slopes was significantly different from 1, implying that fishing mortality is not fairly distributed across a wider range of trophic levels, hence unbalanced.

Additional evidence of unbalanced harvesting was obtained from the inverted food pyramid. A representation of both production and exploitation as a function of fractional TLs (Figure 11) showed that exploitation is skewed to the least productive species/groups at higher TLs, and significantly less fishing (F/Z < 15%) occurs at the highly productive species/groups, most of which reproduce their own biomass four times a year, at lower TLs.
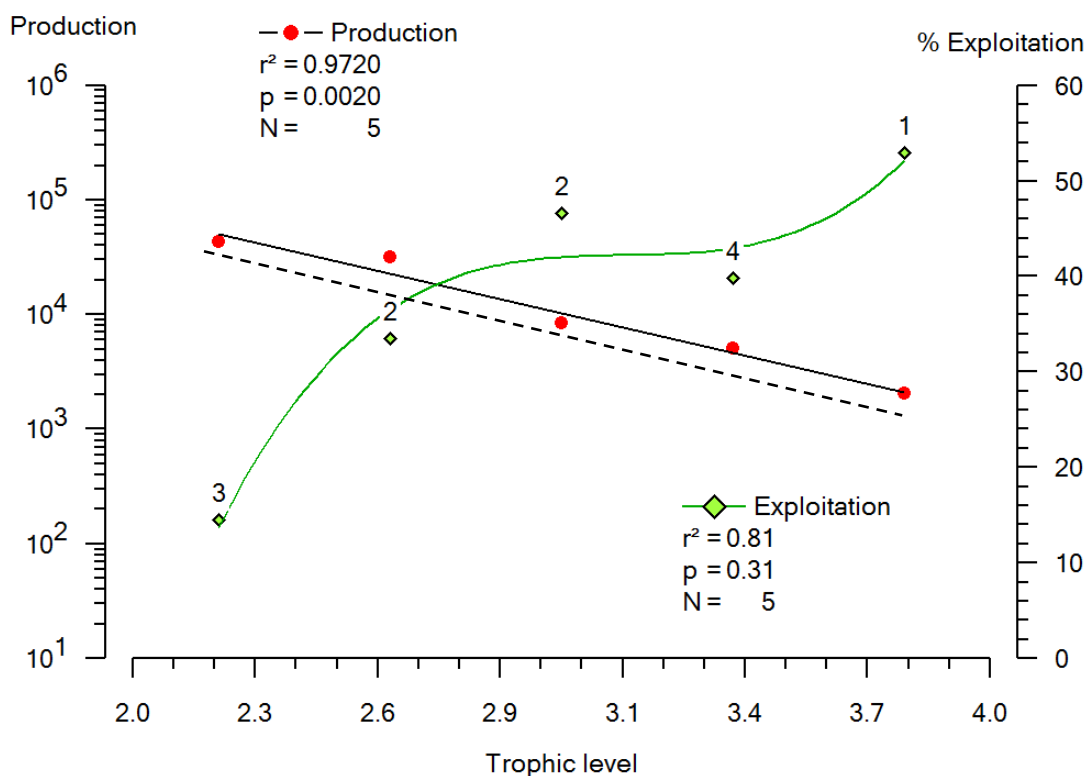
Figure 10. Production and exploitation level (%) per trophic level (in 0.4 TL intervals). The numbers represent the number of exploited trophic groups in each interval. Here, production is inversely proportional exploitation rate i.e. the lower trophic groups (5) have the highest production, but with least exploitation rate. This is highly unbalanced fishing and non-ideal. The black dotted line shows hypothetical ideal fishing pattern where fishing mortality is distributed across a wide range of TL in proportion to their production.

4.3.2   What is the implication of this unbalanced harvesting for sustainability?

I tested the rate at which secondary production is depleted by fishing activities using L index that relates %PPR, TE, and TL_C (Libralato *et al*., 2008). The value of L index was found to be 0.191. Using the published models of both sustainably and unsustainably exploited fisheries (Libralato *et al*., 2008), the corresponding probability as to whether the lake is sustainably exploited by fishing (P_{sust}), considering the current catch of 13.7 t/km^2/year, ranged between zero and 10% (Figure 12). This was expected because it has been demonstrated that unbalanced harvesting can lower maximum sustainable yield (MSY) as well as fishing that produces MSY, F_{MSY} (Jacobsen et al., 2014). Because L-index increases with fishing impact (Libralato *et al*., 2008), and resultantly reducing sustainability, Figure 12 shows that the current harvesting pattern in Lake Victoria is putting fishers at a very big disadvantage, yet the fishery could sustain more effort if fishing was distributed across a wide range of TLs in proportion to their natural productivity.
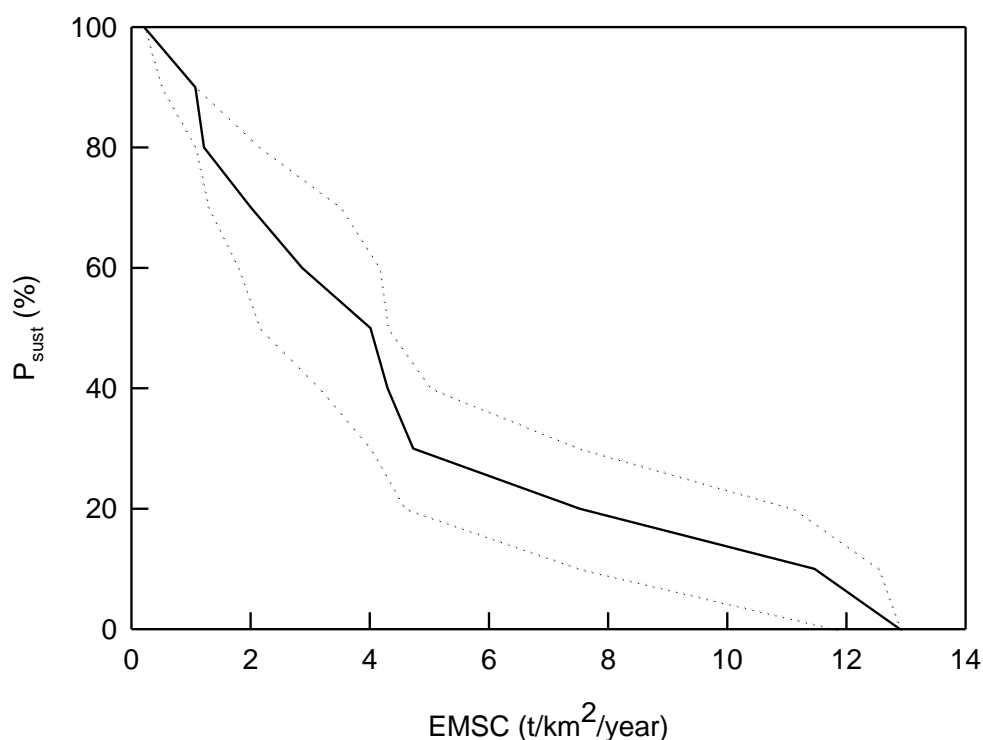
Figure 11. Ecosystem-based maximum sustainable catches (EMSC) for Lake Victoria under different management objectives (defined by p_{sust}). The dotted lines represent the 95% confidence interval. Data on L-index corresponding to p_{sust}, and from which EMSCs were calculated, were obtained from Libralato *et al*., (2008).

5   DISCUSSION

This study reports the implementation of a comprehensive model of the Lake Victoria ecosystem analysing the trophic structure, ecosystem attributes, and showing the role and impacts of the fisheries. The model was mainly based on local data collected from the studied area during 2014, although a fraction of input information was acquired from the literature sources. The model diagnostic test conducted during the mass balancing 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 food conversion efficiency varying between 0.1 and 0.35, except for fast growing groups with higher values, and top predators with lower values; 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).

5.1   Mass balances

The high EE values of phytoplankton and zooplankton were expected, and this accentuates the importance of these groups in supporting higher trophic levels (Heymans *et al*., 2016). However, EE was very low (<0.7) for several consumer groups, including juvenile Nile perch, dagaa, and insects and molluscs. This implies low utilization of these groups in the system, with large biomass being wasted to detritus. Either the 'other mortality' rate (M0), which is neither

attributable to predators nor fishing activities, is higher for juvenile Nile perch, dagaa, and insects and molluscs compared to other groups or both predation and fishing mortality rates are significantly low relative to production. All these possibilities imply that these huge resources are a 'sink' rather than a 'link' to higher trophic level (through predation) and direct utilization by fisheries. This is the first indication that these two fisheries are underexploited. For instance, only 2.5 and 7.4 t/km^2 of juvenile Nile perch and dagaa, respectively, are harvested per year (Table 2), and yet 29 and 133 t/km^2 for the two respective groups disappear or flow to detritus per year (Table 6). Because these two consumer groups reproduce ~four times their biomass per year, such low exploitation rate can cause an imbalance within the ecosystem since fishing would be the only way to reduce competition, predation, and cannibalism within the community (Jacobsen *et al*., 2014). The effects of such imbalances can cascade to other trophic levels, theirby lowering fishing mortality that produces maximum sustainble yield, and make the whole fishery inneficient and less productive (Pikitch *et al*., 2014; Jacobsen *et al*., 2014; Kolding *et al*., 2016;). This could explain why researchers have insisted that Lake Victoria is overfished (Mkumbo and Marshall, 2015), and yet data do not show such effects of overfishing (Figures 2 & 3).

The 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), unexpectedly, were lower than 10% (minimum proportion of food consumed that is expected to be converted into tissue in finfish, Winberg, 1956), for detrivorus dwarf breams and other tilapia and cyprinids. This, however, can be attributed to the inclusion low quality food (i.e. detritus and phytoplankton, respectively, in their diet (Table 3; Christensen *et al*., 2008). Nile tilapia exhibits similar characteristics, but its GE (13.5%) was relatively higher and within the expected range of 10-30% for finfish (Winberg, 1956; Christensen *et al*., 2008) because the fish has (recently) diversified its diet to include protein-rich animal material, although phytoplankton is still a major component of their (Njiru *et al*., 2007). But, the current GE of Nile tilapia sharply contrasts with GE of 66% in 2005 (Downing *et al*., 2012). Even if Nile tilapia was a carnivore, feedingly exclusively on protein-rich animal material, its GE would never exceed 30% because the fish reproduces only two times its biomas per year (Table 5). The high GE of 66% in Downing *et al*. (2012) could have been due to overestimation of production relative to biomass (equivalent to instantantneous rate to total annual mortality, Z, at steady state), which was estimated at 12.5 year^{-1} compared to 2.0 year^{-1} for this study. In this study, also, the GEs for juvenile Nile perch (carnivore) and insects and molluscs (zooplanktivores) were 33 and 40%, respectively, because these groups are numerous (have high production relative to biomass, Table 5) and consume less food relative to their weight (Palomares & Pauly, 1998). Such diagnostic attributes, also, highlight the robustness of the present model, with ability to reproduce realistic biological parameters (Heymans *et al*., 2016).

5.2 Ecosystem development and stability

The SOI (0.12) for the Lake Victoria is low, but is consistent with low individual OI (Table 6) and less prey overlap for most groups (Figure 2, Appendix 3). Both aspects indicate a simple food web, with most functional groups exhibiting a certain degree of diet specialization. One limitation of ECOPATH, however, is that the diet matrix is fixed and does not explicitly accommodate ontogenetic diet shift, unless a multi-stanza modelling approach is used (Christensen & Pauly, 2004). In this study, only Nile perch was separated into juvenile and adult because of well-studied ontogenetic diet shift during its life history and, also, because of availability of data. The exclusion of other groups which do not necessarily show diet shifts but can change diet depending on availability (Köster & Möllmann, 2000), from multi-stanza

approach could have led to underestimation of trophic omnivory and resource overlap. Nonetheless, the calculated CI of 0.33 is comparable to the theoretical value (0.317) computed using the regression model for maturing systems (Christensen & Pauly 1992). Also, the SOI and CI values are comparable to those computed for other systems in the region, notably Lake Kivu (Villanueva *et al*., 2008) and can, in addition to trophic specialisation, suggest the co-existence of both weak and strong interactions observed among groups as expressed by the various EE values (Table 5). Because trophic connections are expected to evolve from linear to web-like structure as the system matures (Odum, 1969), and thereby expecting CI and SOI to be positively correlated with system maturity, the values obtained for Lake Victoria denote a system whose maturity could be undermined by system perturbations (see Christensen, 1995). This is apparent because the lake has endured multiple stresses, including exotic species introductions, unbalanced harvesting, habitat degradation, pollution, eutrophication, and climate variability and change, since 1970s (Hecky *et al*., 2010).

Before establishment, in the 1980s, of the introduced Nile perch, the major food chains that formed key functional groups in Lake Victoria (Moreau, 1995) were: via zooplankton to herbivorous *Haplochromis* spp. and dagaa to the top predators (catfishes and piscivorous *Haplochromis* spp.); via zooplankton and insect larvae to zoophagous fish taxa (*Haplochromis* spp., Mormyridae, *Barbus* spp., *Alestes* spp., *Synodontis* spp. and *Protopterus*) to top predators; and a direct flow to several herbivorous *Tilapia* and *Haplochromis* spp. After the Nile perch boom in 1980s, the complex food web was simplified to four functional groups in which Nile perch, the top predator, fed mainly on the atyid prawn (primary consumer), dagaa, and juvenile Nile perch (both secondary consumers). Although a resurgence of *Haplochromis* spp. has been reported in certain areas of the lake, notably the zooplanktivorous *H. pyrrhocephalus* and *H. laparogramma* (Witte *et al*., 2007; Kishe-Machumu *et al*., 2015), the reorganisation of the food web and recovery of original trophic structure claimed by Downing *et al*. (2012) is unfounded and highly speculative because the system still exhibits minimal biomass cycling, where only 3.05% of TST is cycled, and this another characteristic of underdeveloped systems (Odum, 1969; Christensen, 1995).

However, when analysing the relation between Ascendency (A), Overhead (O), and Development Capacity (DC) (Table 9), an intermediate situation is observed. The relative redundancy (O/DC), which is the measure of system's strength in reserve to meet unexpected perturbations (Christensen, 1995), of 69.4% suggests that the even if the modelled system is not yet in an ecological climax state, it is in advanced stages of development and is resilient. This conclusion is reinforced by the low PP/R that is close to 1 (for a fully mature system *sensu* Odum, 1969; Table 7). Considering the ongoing eutrophication threat on Lake Victora (Kolding *et al*., 2008; Hecky *et al*., 2010), the system may not attain full maturity.

In the previous models, when analysing system maturity, an unrealistic PP/R ratio that is approximately 800fold the expected ratio of one, for a mature system, was reported for Mwanza gulf, Lake Victoria (Downing *et al*., 2012). First, Mwanza gulf is one of areas that are burdened with large quantities of organic matter from the heavily degraded watershed (Verschuren *et al*., 2002), and this can limit primary productivity because of light limitation and self-shading of algae (Silsbe *et al*., 2006). Innately, considering such eutrophication status, respiration is expected to supersede production, and the PP/R should be <1. This could have been due to overestimation of production, and the example is that of Nile tilapia (P/B≈12.5 year^{-1}) that falls short of biological realism. In this study, a low ratio between production and respiration (2.5) for the whole lake is noted. Such value, which is also comparable to other tropical lakes e.g. Lakes Kivu (Villanueva *et al*., 2008) and Malawi (Darwall *et al.,* 2010), further shows a system

that is still maturing. Because the ecosystem is phytoplankton-based i.e. 77.4% of the total flow originating from TL1 comes from primary producers while only 22.6% originates from detritus (Figure 6), the production of some groups that is not fully utilised (groups with low EE e.g. juvenile Nile perch, dagaa, insects and molluscs) is lost to the anoxic bottom sediment because of low detrivory, and this could be contributing more to eutrophication and hindering system maturity.

Nile perch, lake prawn, insects and molluscs, zooplankton, and phytoplankton exhibited high keystone index, as well as relative impact close to 1 (Figure 7). Such groups showed some level of keystoneness, although no distinct keystones were identified in the food web. The groups that showed keystone properties, however, showed remarkably heterogeneous TLs, where Nile perch (both juvenile and adult) represented top predators, while phytoplankton and zooplankton represented low TLs. This suggests mixed control by top-bottom and bottom-up mechanisms in Lake Victoria, where a core set of ecosystem components has a predominant role on the control of biotic interactions exerted by both top–down (Nile perch) and bottom–up (phytoplankton) mechanisms (Libralato et al., 2006).

The aspect of mixed top and bottom control mechanism was also apparent in MTIs. The trophic cascades showed majority of the fish groups with minimal or no impact on the other groups, except Nile perch, which exerted negative impact on all fish groups (Figure 8), and lower TLs e.g. phytoplankton, which exerted a positive impact on majority of the groups. This suggests that an infinitesimal increase in biomass of Nile perch, especially sub-adults, can destabilise the whole ecosystem and sufficiently lower the MSY as well as F_{MSY} (Jacobsen et al., 2015; Kolding et al., 2016). The effects can be exacerbated when such young life history stages are not fished, owing size selective fisheries that is often augmented by mesh and gear restrictions. This has been demonstrated in the man-made Lake Kariba (Kolding et al., 2016) and could also be possible for Lake Victoria.

5.3 The role and impact of fisheries on the ecosystem, and implications for management

5.3.1 Diagnosing claims of overfishing

The claims of overfishing on Lake Victoria, which started in 1920s after Graham's work, have persisted for close to a century (Graham, 1929; Beverton, 1959; Pitcher & Bundy, 1995; Schindler et al. (1998), Mkumbo et al. (2002), Getabu et al., 2003; Matsuishi et al., 2006; Nyamweya, 2012; Mkumbo & marshall, 2015). Indeed, when analysing some indicators, in this study, such as the TL_C, %PPR, and the L index, the results suggested an ecosystem that is not sustainably utilised (Figure 12). This, however, is not because of overfishing but, instead, a decline in TL_C over the years, whose application in the model without considering the history of the fishery can be highly misleading. The role of commercial fisheries in this study was equivalent to a predator occupying a mean trophic level of 2.84. This was lower compared to TL_C previously published e.g. 3.1 (2005) and 3.5 (1987) for Mwanza gulf (Downing et al., 2012), and 3.18 (1995-1996) for Winam gulf (Villanueva & Moreau 2002). Once the history of the fishery is not put into consideration, one such outrageous claim would be that the decrease in TL_C is a consequence of fishing down the food web (Pauly et al., 1998). The TL_C in Lake Victoria decreased because dagga, which occupies a lower TL (2.56), abruptly increased after 2005 (Taabu-Munyaho et al., 2014 where biomass doubled between 1999-2002 and 2008-2011), and currently constitutes >50% of the total harvest (Figure 3). In addition, the decrease in TL_C cannot be due to overfishing because catches of the major exploited groups, especially

Nile perch and Tilapias, in Lake Victoria have never plummeted despite a threefold increase in fishing effort (Figure 2).

Generally, the claims that the fisheries of Lake Victoria are overexploited are unfounded by this study. There are three grounds in support of this deviation. First, the largest proportion of production of Nile perch sub-adults and dagga, the two major fisheries in terms of quantities landed (Table 2), is not utilised within the system, as denoted by their low EE values (Table 4). This production that cannot be accounted for by either predation or fishing simply goes missing (i.e. disappears into detritus). Second, biological overfishing happens when catches, and not biomass or CPUE, decrease as a function of effort. The catches in Lake Victoria have increased steadily and significantly (see both linear and polynomial 2.order models-Figure 2) over the last three decades, although Nile perch and Tilapias stabilized after 1995 (Figure 3). Some of the claims of overfishing on Lake Victoria have been as a result of deliberate exclusion of detail in interpretation of data. For instance, Mkumbo and Marshall (2015) compared catches of only three years (1990, 2005, and 2011), in a span of two decades, and concluded that Nile perch stock is exhibiting problems of overfishing because the catches in 2011 were lower than catches in 1990. And, yet the analysis of long-term data reveals no significant change in catches of Nile perch (Figure 3). Because CPUE is a measure of abundance, and inversely proportional to fishing mortality, the decrease (Figure 4) only shows that fishing is taking place, and this has nothing to do with overfishing. Besides, the current average CPUE of about five tonnes/per fisher/year for Lake Victoria is higher than other African lakes, where the average is three tonnes/per fisher/year (Kolding & Zwieten, 2011; 2012). Third, the species/groups, especially Nile perch sub-adults and dagaa, which reproduce their own biomass ~four times per year (P/B≈4), and Haplochromines (P/B≈2.5) are exploited at a rate <15% of their production (Figure 10). This is four times lower than the upper limit of exploitation (50% of production) for forage fishes (Pikitch *et al*., 2012; Pikitch *et al*., 2014; Kolding *et al*., 2015), and would therefore not be regarded as excess exploitation rate.

5.3.2   *Where the problem and what is the solution?*

Management institutions on Lake Victoria, like many other open access fisheries across the globe, are still stuck with the old selective fishing beliefs, often abetted by mesh and gear regulations (see recommendations of LVFO/IFMP technical report, 2007). The decrease in average size of Nile perch (Mkumbo & Marshall, 2015), Nile tilapia (Njiru *et al*., 2007), and dagga (Sharpe *et al*., 2012) in Lake Victoria, therefore, is not because of overfishing but, instead, is due to selectively harvesting larger individuals with total disregard of their natural productivity. Because competition, cannibalism, and predation are highest in highly productive groups, as well as young life history stages that are also small in size, the current fishing pattern in Lake Victoria depicts a situation where management institutions have preferred to replace fishing mortality by natural mortality. This has a negative implication for F_{MSY}, as it will always be lower than when natural mortality, especially in young life history and small sizes, is substituted by fishing mortality (Gislason, 1999; Jacobsen *et al*., 2014). The current management strategy is therefore counterproductive and will never work in a generation with rapidly increasing human population, and demanding for jobs as well as fish protein.

To avert this, balanced harvesting, an approach to fishing that distributes a moderate fishing mortality across the widest possible range of species, stocks, and sizes in an ecosystem, in proportion to their natural productivity, so that the relative size and species composition is maintained (Garcia *et al*., 2012), could be incorporated in the management strategy of Lake Victoria. This concept, although relatively new, is inspired by the fact that in nature, changes

in the abundance at higher trophic levels affect the productivity of lower trophic levels. Therefore, removing fish relative to their natural productivity can increase MSY as well as F_{MSY}, and thereby offsetting the impact of increasing number of fishers (Jacobsen *et al.*, 2014; Garcia *et al.*, 2015; Kolding *et al.*, 2016). In this study, I have showed that the opposite, with regard to balanced harvesting and its benefits, is happening in Lake Victoria. First, fishing is concentrated only at TL 2.5-2.7 and TL 3.3-3.5 (Figure 9), and the highly selective gears, including gillnet and longline, are concentrated at species/groups at higher TL, which are always larger in size but less productive compared to those at lower TL. This can explain the continuous contraction of size structure of major stocks. Second, the species/groups at the lower TLs, which have the highest production, have least exploitation rate and vice versa (Figure 11).

Because % PPR and L-index determine how much of the secondary production should be removed without causing negative ecological consequences, fish production in Lake Victoria could also be limited by system's basal production. Then, what role does eutrophication play? Kolding *et al.* (2008) indicated that the nutrient enrichment in Lake Victoria was a potential threat to fish production, and not overfishing. This view was strongly opposed by Sitoki *et al.* (2010) and Mkumbo and Marshall (2015), who suggested that the severity of eutrophication for fish production in Kolding *et al.* was overstated, but could not show evidence of overfishing either. This study indicates combined threats from unbalanced harvesting, whose effect on F_{MSY} is discussed, and eutrophication (see %PPR). Nutrient enrichment reduces primary production through light limitation, and subsequent self shading of algae (Silsbe *et al.* 2006) and, at higher levels can reduce fish production. Sitoki *et al.* (2010), however, suggested that such effect would be mitigated by efficient utilisation of primary productivity by consumers at lower TLs. This view seems incorrect as the present analysis showed a large flow (77.4%) to TLII originating from primary producers, low detrivory/herbivory ratio (0.29), and high TE efficiency (21.2%) between producers and primary consumers (Figure 6). This suggests that primary production is efficiently utilised, and hence reduced primary productivity due to eutrophication still poses a big threat. Thus, much of the carbon needs to be removed from the system through balanced harvesting in order to reduce any risks that nutrient enrichment, sometimes exacerbated by under exploitation, would pose.

6   CONCLUSIONS

Lake Victoria has heterogeneous groups i.e. Nile perch (top predator) and phytoplankton (primary producer) with keystone properties. Although no distinct keystone could be discerned in the food web, which is also characteristic of food webs that lack resolution (Libralato *et al.*, 2006), the heterogeneity of groups with moderate keystone properties shows an ecosystem with mixed control (both bottom-up and top-down) mechanisms. The ecosystem is phytoplankton-based and primary productivity is fairly utilized (high TE), with less flows to detritus. However, at consumer level, mass balances show underutilization of highly productive groups (Nile perch sub-adults and dagaa, which reproduce their own biomass ~four times per year), with largest biomass disappearing into detritus. These groups, therefore, are underexploited by fisheries. Continued under exploitation of these highly productive groups has potential to destabilise the ecosystem, as well as fisheries, where, for instance, infinitesimal increase in biomass of Nile perch sub-adults can negatively impact all other trophic groups (see mixed trophic impacts, Figure 8). In addition, the flow of such large biomass to detritus has negative implication for eutrophication and system maturity.

The effect of eutrophication on system maturity has been demonstrated. Lake Victoria is an underdeveloped system. Nonetheless, the high relative redundancy suggests that the even if the modelled system is not yet in an ecological climax state (PP/R>1), it is in advanced stages of development and is highly resilient. The high resilience capacity of Lake Victoria can also be noticed from the history of the lake, where the lake has been able to withstand and/or recover from a wide range of stressors, including species introductions, eutrophication, unbalanced fishing, invasive aquatic weeds, pollution, climate variability and change (Hecky *et al.*, 2010). Considering that many of these stressors are at still present, Lake Victoria is not likely to reach full maturity in the near future.

The fisheries of Lake Victoria are not overexploited because catches have never plummeted as a function of fishing effort. The decrease in CPUE, which is a measure of abundance, only shows that fishing is taking place, while the contraction of size structure of all exploited groups confirms unbalanced and size selective harvesting, all of which do not relate to overfishing. In fact, the fisheries of Lake Victoria are currently underexploited, considering that the greatest biomass of highly productive species simply goes missing (i.e. lost to detritus). Specifically, the most productive juvenile Nile perch, dagaa, and all Haplochromine groups are underexploited, while Adult Nile perch and Nile tilapia are at the limit of full exploitation. This means human exploitation across trophic levels (TLs) is skewed to the low productive species at high TLs. This has made the current fishing unsustainable. It is important that balanced harvesting, where a moderate fishing mortality ($30\%P \leq F/Z \leq 40\%P$, Pikitch *et al.*, 2012) across the widest possible range of species, stocks, and sizes in an ecosystem, in proportion to their natural productivity, so that the relative size and species composition is maintained, is incorporated in management of Lake Victoria. This means fisheries managers should shift from the archaic selective fishing philosophy, often augmented by gear size restrictions.

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ACKNOWLEDGMENTS

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Appendix 1. Original diet composition (proportion) of the various groups in Lake Victoria as obtained from literature (sources cited in subsection 3.2.5). The values in the columns that do not add to one have been truncated for clarity. No truncation of data was done in ECOPATH.

Group	Prey \ predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	Fish eating birds															
2	Adult Nile perch															
3	Juvenile Nile perch		0.156	0.023	0.04	0.05										
4	Catfishes				0.01	0.05	0.05									
5	Marbled lungfish				0.005		0.05									
6	Squeakers and snoutfishes				0.005	0.02										
7	Zooplanktivorous dwarf breams	0.15	0.439	0.307	0.002	0.003	0.003			0.1		0.07				
8	Detrivorus dwarf breams	0.15	0.06	0.046	0.002	0.001	0.001			0.1		0.02				
9	Other dwarf breams	0.2	0.005	0.003	0.001	0.001	0.001				0.05					
10	Dagaa	0.5	0.185	0.110	0.1	0.05	0.05			0.4		0.09				
11	Nile tilapia		0.037		0.04	0.02	0.02									
12	Other tilapias		0.037		0.005	0.005	0.005									
13	Lake prawn			0.437	0.2	0.15	0.05	0.25		0.05	0.2				0.01	
14	Insects and molluscs		0.078	0.043	0.5	0.55	0.65			0.3		0.24	0.02		0.05	
15	Zooplankton			0.027	0.03	0.05	0.05	0.75			0.6		0.03	0.4	0.04	0.05
16	Phytoplankton										0.2	0.57	0.45	0.1	0.05	0.95
17	Benthic producers				0.01		0.02						0.3		0.3	
18	Detritus				0.05	0.05	0.05		1.0			0.01	0.2	0.5	0.55	
	Import															

Appendix 2. Estimates of mortality rates for the different functional groups in the Lake Victoria food web.

Group name	Fishing mortality (/year)	Predation mortality (/year)	Other mortality (/year)	Exploitation rate
Fish eating birds			0.3	0
Adult Nile perch	0.52		0.30	0.63
Juvenile Nile perch	0.52	0.79	2.66	0.13
Catfishes	0.60	0.38	0.001	0.60
Marbled lungfish	0.82	0.07	0.22	0.73
Squeakers and snoutfishes	0.89	0.05	0.05	0.89
Zooplanktivorous dwarf breams	0.10	2.28	0.12	0.04
Detrivorus dwarf breams	0.22	2.18	0.12	0.08
Other dwarf breams	0.22	1.54	0.06	0.12
Dagaa	0.46	1.18	2.28	0.11
Nile tilapia	1.01	0.611	0.28	0.53
Other tilapias and cyprinids	0.78	1.39	0.11	0.34
Lake prawn	0.06	15.80	0.13	0.003
Insects and molluscs		2.93	7.06	
Zooplankton		33.34	0.65	
Phytoplankton		254.92	110.07	
Benthic producers		9.39	15.60	

Appendix 3. Prey overlap indices for the different functional groups within the Lake Victoria food web. The values range from 0 to 1, with values close to 0 indicating high diet specialisation and values close to 1 indicating high niche overlap (Christensen *et al*., 2008).

	Group name	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	Fish eating birds	1																
2	Adult Nile perch	0.68	1															
3	Juvenile Nile perch	0.50	0.46	1														
4	Catfishes	0.15	0.25	0.33	1													
5	Marbled lungfish	0.09	0.24	0.25	0.97	1												
6	Squeakers and snoutfishes	0.06	0.18	0.16	0.96	0.96	1											
7	Zooplanktivorous dwarf breams		0.01	0.44	0.22	0.22	0.16	1										
8	Detrivorus dwarf breams					0.07	0.10	0	1									
9	Other dwarf breams	0.69	0.51	0.47	0.79	0.75	0.72	0.09	0	1								
10	Dagaa			0.18	0.08	0.10	0.07	0.76	0.07	0.01	1							
11	Nile tilapia	0.15	0.19	0.13	0.38	0.38	0.38	0.02	0.01	0.37	0.48	1						
12	Other tilapias and cyprinids	0	0.01	0.01	0.04	0.06	0.07	0.04	0.29	0.02	0.58	0.72	1					
13	Lake prawn			0.01	0.01	0.08	0.11	0.11	0.90		0.32	0.25	0.53	1				
14	Insects and molluscs		0.01	0.02	0.08	0.15	0.18	0.06	0.78	0.05	0.25	0.11	0.61	0.84	1			
15	Zooplankton										0.45	0.81	0.67	0.25	0.07	1		
16	Phytoplankton																	
17	Benthic producers																	