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

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ABSTRACT

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

1. Introduction

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

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

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

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

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

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

2. Material and methods

2.1. Study area

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

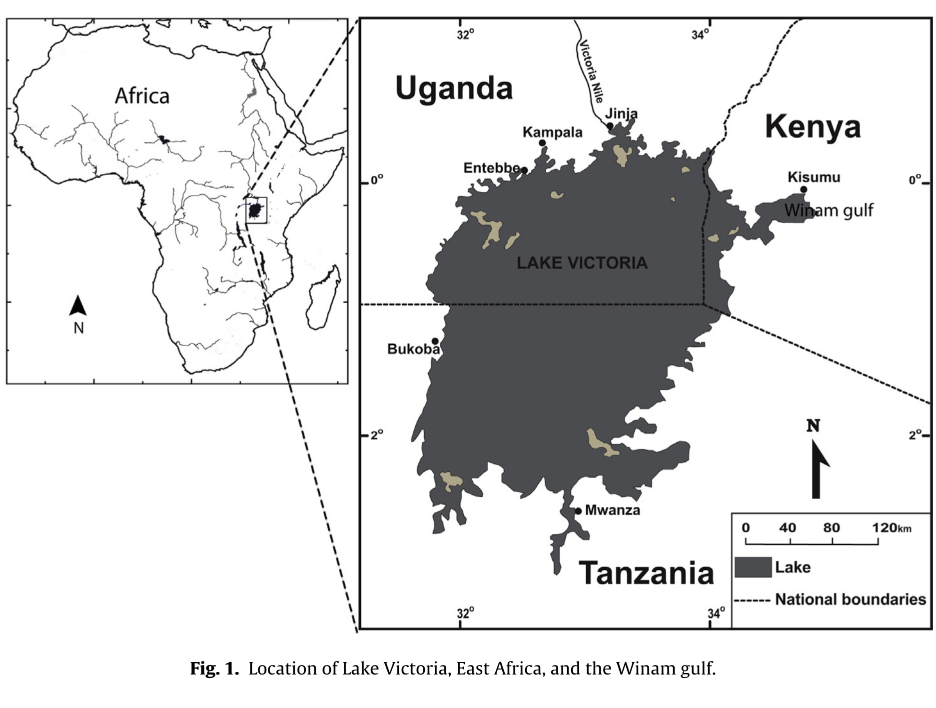

Fig. 1. Location of Lake Victoria, East Africa, and the Winam gulf.