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Research

Coupled human and natural system dynamics as key to the sustainability of Lake Victoria's ecosystem services

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ABSTRACT. East Africa's Lake Victoria provides resources and services to millions of people on the lake's shores and abroad. In particular, the lake's fisheries are an important source of protein, employment, and international economic connections for the whole region. Nonetheless, stock dynamics are poorly understood and currently unpredictable. Furthermore, fishery dynamics are intricately connected to other supporting services of the lake as well as to lakeshore societies and economies. Much research has been carried out piecemeal on different aspects of Lake Victoria's system; e.g., societies, biodiversity, fisheries, and eutrophication. However, to disentangle drivers and dynamics of change in this complex system, we need to put these pieces together and analyze the system as a whole. We did so by first building a qualitative model of the lake's social-ecological system. We then investigated the model system through a qualitative loop analysis, and finally examined effects of changes on the system state and structure. The model and its contextual analysis allowed us to investigate system-wide chain reactions resulting from disturbances. Importantly, we built a tool that can be used to analyze the cascading effects of management options and establish the requirements for their success. We found that high connectedness of the system at the exploitation level, through fisheries having multiple target stocks, can increase the stocks' vulnerability to exploitation but reduce society's vulnerability to variability in individual stocks. We describe how there are multiple pathways to any change in the system, which makes it difficult to identify the root cause of changes but also broadens the management toolkit. Also, we illustrate how nutrient enrichment is not a self-regulating process, and that explicit management is necessary to halt or reverse eutrophication. This model is simple and usable to assess system-wide effects of management policies, and can serve as a paving stone for future quantitative analyses of system dynamics at local scales.

Key Words: *eutrophication; feedbacks; fisheries; Lake Victoria; model; multidisciplinary, social-ecological system; sustainability*

INTRODUCTION

Nile perch (*Lates niloticus*) was introduced to Lake Victoria in the 1950s and suddenly became dominant in the system in the 1980s (Goudswaard et al. 2008). Prior to this dramatic event, the ecosystem of Lake Victoria harbored a large diversity of haplochromine cichlids and a few native tilapia species destined for local and regional markets (Pringle 2005*a*). The Nile perch boom co-occurred with other major transformations to Lake Victoria's ecosystem, including a collapse of the native diversity of haplochromines and the eutrophication of the lake's waters (Witte et al. 2007*a*, Hecky et al. 2010).

Despite the dramatic diversity loss and catastrophic ecosystem changes that surrounded the Nile perch invasion, management currently aims to maintain the system in its Nile perch-dominated state, not to recover the former Nile perch-free, diverse ecosystem —should that even be possible. Indeed, Nile perch has become the product of an international export industry worth approximately US$250 million yearly (Pringle 2005*a*, Kayanda et

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al. 2009). Many people migrated to the lake's shores to benefit from the fisheries, a migration that has led to important transformations to the lake's societies. Currently, an estimated 30 million people live in the lake's basin and are shaping and being shaped by its ecology and economy (Awange and Ong'ang'a 2006).

Management measures on Lake Victoria have focused on fisheries and aim to manage a certain quality of catch (size structure of Nile perch) rather than total fishing effort or stock biomass (van der Knaap et al. 2002). Some of these methods are applied on the lake itself; e.g., banning beach seines and increasing the minimum mesh size of gillnets, or introducing fish slot sizes. In the case of Nile perch, measures exist at the processing output level, where there is a minimum length of fish that the factories are allowed to process. Approaches to managing the fisheries assume that the fisher communities, as well as fish stocks, are homogeneous (Muhoozi 2002). Management measures are difficult to implement and monitor given that Lake Victoria is the world's second largest freshwater lake by area (68,800 km^2), has a highly convoluted shoreline that is shared by three countries (Tanzania, Uganda, and Kenya), and the fisheries are open access. Also, the effectiveness of regulations is limited, in part because policies can be immediately detrimental to the filleting factories that process the fish for export markets (Johnson 2010). Resources available to implement or enforce policies are scarce, and enforcement can be subject to corruption.

Added to difficulties in choosing and implementing effective management measures, stakeholders and scientists disagree about the current state of the Nile perch fisheries and what the dominant threats to these fisheries are (Witte et al. 2007*a*). Indeed, owners of filleting factories complain that they are operating their factories at decreasing capacity, overlooking the fact that many of the factories were built at structural overcapacity (Abila and Jansen 1997, Johnson 2010). Some scientists read overfishing in the fishery survey data (Mkumbo et al. 2007, Mkumbo and Mlaponi 2007, Kayanda et al. 2009), while others see a total stock that fluctuates around a stable average despite increased fishing effort. The stable stock under increased pressure rests on the logic that increased productivity results from eutrophication (Kolding et al. 2008).

The cumulative pressures influencing Lake Victoria are multiple, intricately interconnected, and threatening to all its fisheries as well as to the lake's ability to carry out supporting services. Indeed, the whole ecosystem is influenced by climate change (Hecky et al. 2010, Cózar et al. 2012) and has been degraded through eutrophication (Dobiesz et al. 2010), which impoverishes the system by driving an irreversible decline in biodiversity (Seehausen et al. 1997*a*). Beyond a certain threshold, eutrophication threatens to cause a more general collapse of stocks, not only of Nile perch (Kolding et al. 2008). Additionally, Nile perch is not the only exploited fish. For example, the native pelagic cyprinid *Rastrineobola argentea* (known as dagaa in Tanzania, omena in Kenya, and mukene in Uganda; herein referred to as dagaa) has become an increasingly important product for local societies (Wanink 1999). Furthermore, since the explosion of Nile perch numbers in the lake, social and economic drivers of fishing effort have changed. Risks and opportunities that face fisher communities have evolved with increasing human population sizes and market value (Beuving 2013). Nile perch is destined predominantly to European markets that impose strict hygiene standards and influence fish prices. Market demand and processing costs influence factory owners, fish buyers, and trade middlemen, who in turn affect the organization of fishing and fisher communities and thus shape stock exploitation (Abila and Jansen 1997, Ponte 2007, van der Knaap and Ligtvoet 2010).

Two lake-wide organizations—the Lake Victoria Fisheries Organisation (LVFO) and the Lake Victoria Basin Commission (LVBC)—have played the most important roles in coordinating research on the lake's resources. While originally conceived as an instrument for holistic, ecosystem-based management, the LVFO has a much stronger fisheries perspective. The LVBC has the potential to address water quality and nonfisheries management issues through its Lake Victoria Environment Management Project Plan II (LVEMPII). So far, coordination of field efforts and data sharing between the two organizations are poor. Fishery science, and to some extent limnology, have undergone a measure of regional integration under LVEMP activities, but on the whole, an ecosystem's view is still distinctly lacking. Dissemination of results has also been limited at times, with LVFO investing greater effort in communications than the LVBC.

In sum, changes in Lake Victoria are a complex product of social, economic, and ecological processes. To comprehend the dynamics of this complex system, to visualize the scenarios likely to result from alternative management measures, and to manage human activities that influence the lake in an intelligent and farsighted manner, the lake and lake basin ecosystem must be understood in their entirety. Many analyses of their parts—for example, water quality, diversity, or fisheries—have been conducted in isolation. Our aim is to connect the dots and study the interactions among the parts of Lake Victoria's system.

An important barrier to assembling the pieces of Lake Victoria lies in quantifying the ecosystem's components in a spatio-temporally representative way. As a first step in this direction, we employed a form of qualitative modeling called loop analysis (Levins 1974). We first built a feedback diagram of Lake Victoria's social-ecological system based on the components and interactions that compose it, matching the model to Lake Victoria's past trends and changes, and investigated the effects of quantitative and structural modifications to the system on its behavior.

SOCIAL-ECOLOGICAL SYSTEM REPRESENTATION

Qualitative models

We first created a feedback diagram containing three different types of objects: (1) the key elements of the system, (2) connections between interacting key elements, and (3) the sign of these interactions near equilibrium. If an increase in the value (biomass, concentration, or economic value) of an element causes an increase in a connected element, the sign is positive (+). If, on the other hand, an increase in one causes a decrease in the other, the sign is negative (-). We then carried out the loop analysis, where we identified the feedback loops in the system; i.e., the pathway of interactions that go from any element and back to it, through other elements in the defined system. We also identified whether these feedbacks are overall positive or negative by multiplying the

signs of the interactions along each pathway. A positive feedback loop reflects a "reinforcing" process, where an increase in one element causes it to increase further: positive feedback loops are therefore destabilizing. A negative feedback loop, on the other hand, is self-regulating: an increase in an element's value leads it to limit itself; a negative feedback loop is stabilizing. We obtained several outputs from this qualitative analysis: (a) a description of the system as a whole, (b) all the direct and indirect pathways connecting different parts of the system, (c) the effect—positive or negative—of the change in one element on its different connections; i.e., chain reactions across the system, (d) the multiple positive and negative controllers of each element, (e) stabilizing and destabilizing feedbacks, and (f) a view of key elements that can alter the sign of a feedback; i.e., those for which connection signs can be changed; e.g., policies.

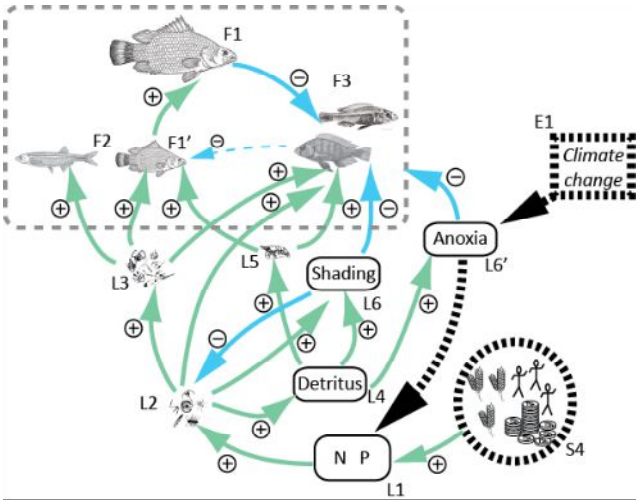
Determining which elements of a system are key is a subjective process. To reduce bias caused by the oriented knowledge of any single Lake Victoria scientist, scientists in the fields of aquatic ecology, fisheries sciences, and social sciences, as well as stakeholders, all with expertise in Lake Victoria's system, were brought together in a workshop in Dar es Salaam in May 2012. To make the process more manageable, we first built two separate diagrams: one for the ecological subsystem and one for the social subsystem, including fisheries. We then combined the two diagrams into a linked social-ecological system representation. Four groups of scientists and stakeholders with mixed expertise discussed and built the two subdiagrams. These groups thus determined the elements and the interactions to enter the model based on their understanding of underlying processes (e.g., eutrophication) and knowledge of the system (e.g., the types of fishes landed with different nets), and discussed them until the final diagrams satisfactorily represented the perspectives of the different topics (social sciences, water quality, and fisheries). The discussions continued online after the workshop and then included even more participants, who have in turn become the authors of this paper. In this way, the biases that remain are inherent to research conducted on Lake Victoria thus far. This is the first time such diverse perspectives on Lake Victoria's system have been assembled on an equal footing. Our representation of the system as we know it can further point out where ignorance remains.

To make the diagrams tractable, we excluded all self-effects and assumed density dependence to be negative, reflecting a stable system. Also, where interactions are known to be nonlinear, such as the effect of eutrophication on productivity, we cut the process down into its parts: the positive effect of eutrophication on growth, and the positive effect of eutrophication on anoxia and shading, which in turn is negative for growth. We emphasize that the model is not quantitative, and we do not include the weight of each interaction. In this way, our model can represent both locations or time periods where growth processes prevail over negative effects of deoxygenation, and vice versa, and thus represent the full system irrespective of its current state. To make our final linked diagram more parsimonious, we eliminated the elements flanked only by unidirectional positive interactions, as they add detail and complexity to the loops but do not alter their signs—and therefore, have no effect on the overall dynamics of the system.

Ecological subsystem

The nutrients of the system are represented in nitrogen (N) and phosphorus (P) (Fig. 1) that contribute to an increase in phytoplankton biomass, which is in turn consumed by zooplankton and fish (Fig. 1: phytoplankton --> zooplankton and haplochromines). The major source of nutrient input to the lake is through atmospheric deposition, resulting from intensive land use in the basin, through land clearing and burning (Tamatamah et al. 2005, Hecky et al. 2006) (Fig. 1: from the local and regional economy and society—herein abbreviated to Soc&econ—to N&P). An increase in nutrients has a nonlinear effect on the system. Indeed, while there is an initial phase of increase in phytoplankton biomass, as nutrient input continues increasing, phytoplankton biomass begins to limit light availability and eventually reaches an upper limit depending on light extinction and mixing depth (Silsbe et al. 2006). We try to account for this strong nonlinearity by adding phytoplankton's self-shading property and contribution to detritus (Fig. 1: phytoplankton --> shading and detritus). Detritus also increases shading and oxygen consumption, and exists as a trophic pathway for the shrimp *Caridina nilotica* (Fig. 1: detritus --> shading, anoxia, and *C. nilotica*).

Fig. 1. Ecological interactions. Green arrows represent growth processes (also identified by + sign); blue arrows represent mortality processes (associated with - signs); thick dotted lines and arrows represent complex systems/interactions not further developed. E refers to environmental variables, F to fish variables, L to limnological variables, and S to societal variables. E1 = climate change; F1 = large Nile perch; F1' = small Nile perch; F2 = *Rastrineobola argentea*; F3 = haplochromines; L1 = nitrogen and phosphorus; L2 = phytoplankton; L3 = zooplankton; L4 = detritus; L5 = *Caridina nilotica*; L6 = shading; L6' = anoxia; S4 = local and regional economy and society.



The shrimp *C. nilotica* is an important detritivore and became an important prey for juvenile Nile perch as well as for the mostly zooplanktivorous haplochromines that remained in the 1990s (Downing et al. 2012*a*) (Fig. 1: *C. nilotica* --> small Nile perch

and haplochromines). Recovering haplochromines have mostly reverted to feeding on zooplankton and other small invertebrates but they include shrimp and larger prey in their diets when these are abundant (Kishe-Machumu 2012, van Rijssel and Witte 2013). Light is of primary importance to haplochromines because they rely on color vision for successful breeding and efficient feeding (Seehausen et al. 1997*a*, Witte et al. 2013) (Fig.1: shading --o haplochromines). Poor light can also alter haplochromine species diversity by promoting hybridization (Seehausen et al. 1997*a*, Seehausen 2009).

We connected anoxia negatively to all fish since reduced oxygen is ultimately detrimental to them all, though usually through a complex nonlinear process (Fig. 1: anoxia --o all fish). In a first step, an anoxic deep water layer reduces the habitable part of the water column for sensitive species, and increases habitat overlap between species (Vonlanthen et al. 2012). Habitat overlap can result in increased predation rates of Nile perch on haplochromines, as well as hybridization rates between haplochromine species. In a later step, the seasonal upwelling of deep anoxic waters can lead to large fish kills (Ochumba 1990, Gophen et al. 1995). Reduced oxygen concentrations also have a chronic negative effect on species by influencing their metabolic processes and growth rates (Kolding 1993, Rutjes et al. 2007).

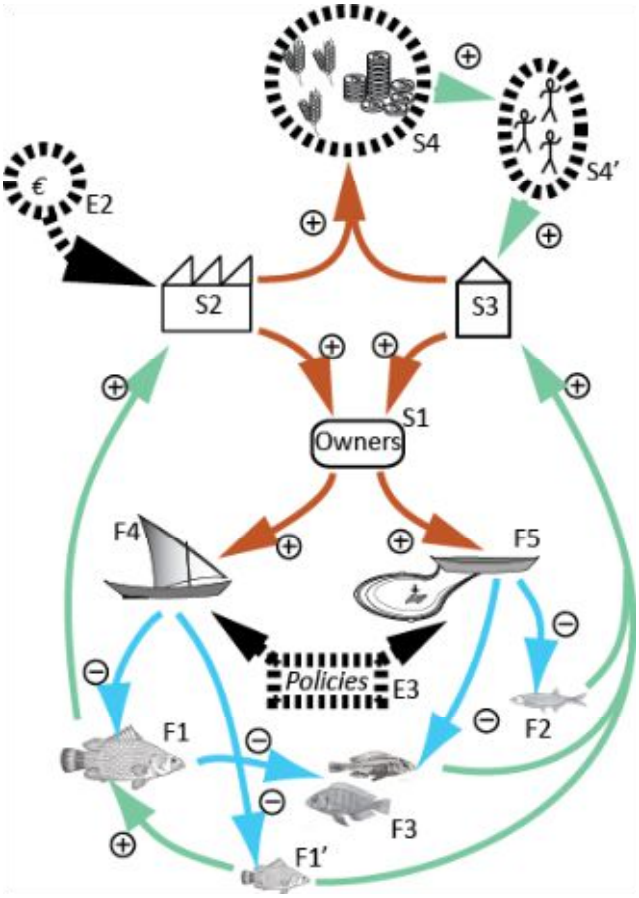
Additionally, oxygen plays a complex role in biogeochemical cycles: denitrification—a process that converts nitrate to dinitrogen gas (N_2)—takes place primarily in anoxic conditions, and these conditions also promote phosphorus release (Fig. 1: anoxia --> N&P). The effect of oxygen on biogeochemical cycles is temperature sensitive (Veraart et al. 2011), and both weather and temperature conditions influence the duration and extent of water stratification in the lake (Sitoki et al. 2010). These processes are thus likely to be greatly affected by climate change in complex and nonlinear ways (Fig. 1: dashed line from E1 --> anoxia --> N&P).

Besides the solid arrow indicating Nile perch predation on haplochromines, a dashed arrow was included to indicate the hypothesized negative effect of haplochromines on Nile perch recruitment. It has long been speculated that through either competition or predation, haplochromines have, or had, a negative influence on the growth of small Nile perch, in a process termed depensation (Fig. 1: haplochromines --o small Nile perch) (Walters et al. 1997, Walters and Kitchell 2001, Goudswaard et al. 2008, Downing et al. 2012*b*). However, a recent study suggests that such an interaction probably did not play a significant role at the scale of the whole lake (Downing et al. 2013*a*). Depensation should be included only in cases and areas where there is a demonstrated negative influence on the stock–recruitment relationship.

Society and fisheries

Catches of small Nile perch, dagaa, and haplochromines feed a regional market (in the lakeshore and neighboring countries) (Fig. 2: small Nile perch, dagaa, and haplochromines --> local and regional market; herein abbreviated as LocMar), and catches of large Nile perch go to a European export market (Fig. 2: Nile perch --> international market; herein abbreviated as IntMar). Markets convert catches into investment power, which allows the economy to grow, fuels further investment in alternative sources of income (such as agriculture and farming, or support businesses, including housing, transport, or entertainment), and stimulates human population growth. This growth feeds back into the regional market. The local and regional markets invest in boat or camp owners to ensure their supply of fish. Owners in turn convert their capital into effort, thus further increasing total catch (Fig. 2: IntMar and LocMar --> owners; IntMar and LocMar --> Soc&econ).

Fig. 2. Socio-economic interactions. Green arrows represent growth processes (also identified by + sign); blue arrows represent mortality processes (associated with - signs); rust arrows represent investment; thick dotted lines and arrows represent complex systems/interactions not further developed. E2 = international economy; E3 = policies; F1 = large Nile perch; F1′ = small Nile perch; F2 = *Rastrineobola argentea*; F3 = haplochromines; F4 = Nile perch fishing effort; F5 = *R. argentea* fishing effort; S1 = boat and camp owners; S2 = international market; S3 = local and regional market; S4 = local and regional economy; S4' = local society.



By separating camp and boat owners from the rest of society, we have the means to reflect social, political, and economic disparity. Owners are entrepreneurs, drawing either on their own funds and

profits or on investments by industries, and they themselves can invest in further effort and gain. Labor, however, is cheap, always abundant enough, and plays a role in every industry: we therefore neglected its impact on owners. Owners can switch between the international Nile perch fishery and regional fisheries or be part of both (Fig. 2: owners --> Nile perch and dagaa fishing effort), depending on the status of the owners and the benefits each fishery yields.

We added two exogenous processes to this diagram that influence the cost-benefits that in turn regulate where owners focus their investments: the international economy and policies (Fig. 2). The international economy, driven by many more products, trends, and fashions than the resources of Lake Victoria, can influence the price Nile perch fetches, as well as quality requirements of the Nile perch destined for export (Kambewa 2007, Ponte 2007, Johnson 2010) (Box 1). This international influence is in large part independent of conditions in the lake but nonetheless defines many of the costs in the Nile perch industry (e.g., installing and maintaining storage and hygiene facilities, or higher investment in societies through eco-labeling requirements) and therefore shapes the catch level necessary to offset costs and reap a benefit (van der Knaap et al. 2002, van der Knaap and Ligtvoet 2010).

Box 1: Influence of the international market

European markets set regulations on the quality of the fish they imported, which created a need for filleting factories to invest in technologies such as freezers and insulated trucks to obtain quality certifications (Johnson 2010) (Fig. 3: international economy(+) --> IntMar --> owners --o Nile perch fishing effort…). European regulations caused import bans several times in the late 1990s because of poor hygiene. During these periods, Nile perch was exported to alternative markets, such as Japan, though at lower prices, and fishing effort was temporarily reduced (Fig. 3: international economy(-) --o IntMar --o Nile perch fishing effort --> Nile perch…) (van der Knaap et al. 2002). Such sanctions or a collapse in the international market can close up the pathways that promote investment in fishing by owners. Such effects could percolate down to show a positive effect on stocks (e.g., Fig. 3: international economy(-) --> IntMar --> owners --> Nile perch fishing effort and dagaa fishing effort --o Nile perch, dagaa, and haplochromines). However, this depends on the importance or adaptability of the local market relative to the international one, as a collapse of the international economy could simply shift dynamics toward the local and regional market, if the local market has a substantial income-source independent of fisheries.

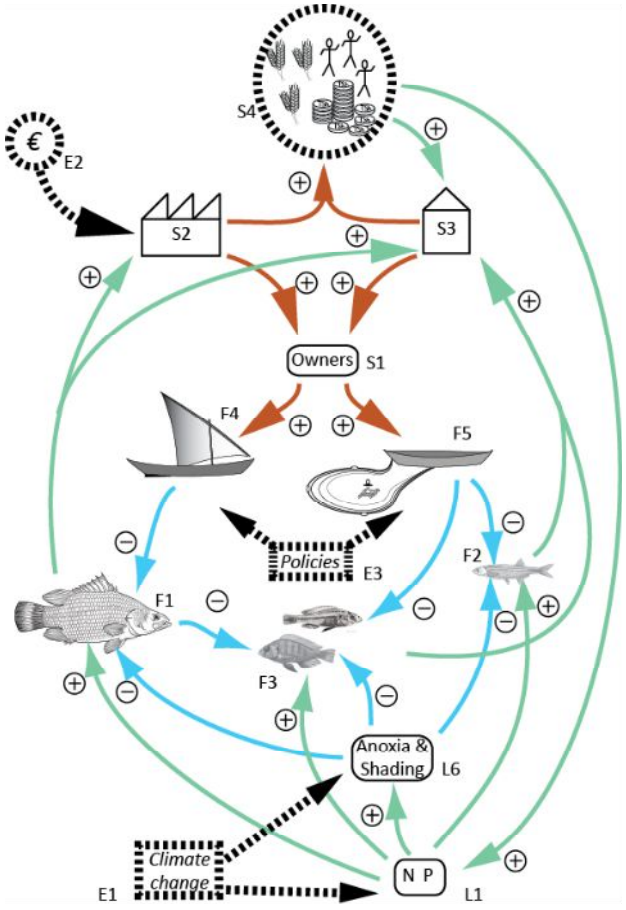
The social-ecological system

We combined both diagrams and simplified the model to make it manageable. We summarized the positive interactions that dominate the ecological perspective into two main processes: the positive effects of nutrient input that promote growth in fish species (Fig. 3: N&P --> Nile perch, dagaa, and haplochromines), and the negative effects that come from enrichment but are represented by anoxia and shading (Fig. 3: N&P --> shading --> Nile perch, dagaa, and haplochromines).

We removed small Nile perch from the fish groups. Instead, Nile perch as a whole contribute to both the regional and international markets (Fig. 3: Nile perch --> IntMar and LocMar). The population size structure of Nile perch has changed since its first introduction, though trends in these changes vary spatially (Kolding et al. 2008) and are likely a response to both the environment—through diet changes—and to size-selective fishing (Downing et al. 2013*c*).

We merged society and the economy into one since they are connected with positive interactions. Here, they directly contribute to nutrient enrichment (Fig. 3: Soc&econ --> N&P).

Fig. 3. Social-ecological system interactions. Green arrows represent growth processes (also identified by + sign); blue arrows represent mortality processes (associated with - signs); rust arrows represent investment; thick dotted lines and arrows represent complex systems/interactions not further developed. E1 = climate change; E2 = international economy; E3 = policies; F1 = Nile perch; F2 = *Rastrineobola argentea*; F3 = haplochromines; F4 = Nile perch fishing effort; F5 = *R. argentea* fishing effort; L1 = nitrogen and phosphorus; L6 = anoxia and shading; S1 = boat and camp owners; S2 = international market; S3 = local and regional market; S4 = local and regional economy and society.



Loop analysis

Our social-ecological system diagram has 25 loops. We excluded the direct feedback between local market and society from our analysis since it holds no emergent information. Among the remaining 24 loops, we separated nutrient-driven processes, including nine "enrichment" loops (Table 1), in which nutrients lead to stock growth, increased fishing, and economic and population growth, and thus more enrichment, and nine "eutrophication" loops (Table 2), where stronger nutrient input leads to anoxia and shading, influences stock growth as well as economic and population expansion, and thus controls nutrient input. Additionally, we have six "exploitation" loops (Table 3) that describe dynamics from the different stocks through to the markets and back.

Table 1. Enrichment loops and their signs. N;P = nitrogen and phosphorus; Np = Nile perch; IntMar = international market; Soc&econ = society and economy; LocMar = local and regional market; Haplo = haplochromines; Dagaa = *Rastrineobola argentea*; --> = positive interaction; --o = negative interaction.

Loop	Sign
1. N;P-->Np-->IntMar-->Soc&econ-->N;P	+
2. N;P-->Np-->LocMar-->Soc&econ-->N;P	+
3. N;P-->Haplo-->LocMar-->Soc&econ-->N;P	+
4. N;P-->Dagaa-->LocMar-->Soc&econ-->N;P	+
5. N;P-->Np--oHaplo-->LocMar-->Soc&econ-->N;P	-
6. N;P-->Np-->IntMar-->owners-->Dagaa effort--oHaplo--> LocMar-->Soc&econ-->N;P	-
7. N;P-->Np-->IntMar-->owners-->Dagaa effort--oDagaa--> LocMar-->Soc&econ-->N;P	-
8. N;P-->Haplo-->LocMar-->owners-->Np effort--oNp--> IntMar-->Soc&econ-->N;P	-
9. N;P-->Dagaa-->LocMar-->owners-->Np effort--oNp--> IntMar-->Soc&econ-->N;P	-

Positive enrichment loops go from nutrients promoting the growth of stocks, through their positive effect on markets, then society, and back to nutrient input (Table 1). Negative eutrophication feedback loops follow the link between nutrients and anoxia and shading. Anoxia and shading are the drivers on stocks whose negative effects cascade to markets and society, and thus lead to reduced nutrient input (Table 2). In the case of negative exploitation loops, they link each stock, through to the market it trades to, back to owners, increased effort, and thus a reduction in stock (Table 3), which is ultimately self-regulating.

Besides these expected loops, we obtained a few inverse loops, where enrichment is self-regulating, while eutrophication and exploitation are self-reinforcing (negative loops in Tables 1 and 3; positive loops in Table 2). These inverted-sign loops describe longer—and presumably weaker through their indirectness—chain reactions stemming from the presence of alternative sources of income for society.

Exploitation loops are mostly self-regulating, implying that as a stock dwindles, its exploitation costs increase and it invites less fishing effort (Table 3: negative loops). However, here we see that exploitation loops can connect two fisheries either directly (Table 3: loops 3 and 5) or indirectly through owners or the local market. These stocks are thus not independent in the eyes of exploitation. For example, pelagic, zooplankton-eating haplochromines can make up a large fraction of the dagaa bycatch. This could compensate for dwindling dagaa stocks since there is no barrier to continuing exploitation in similar ways if, for a time at least, the fish initially targeted is easily replaced (Box 2). In the same way, local and international markets provide outlets for small and large Nile perch, respectively. Therefore, if a size class becomes less available, fishing camp owners would not necessarily see diminishing returns immediately (Table 3: loops 1 and 2). The exact dynamics would of course depend on the price that different fish and fish-size classes fetch, and the fact that these prices are subject to demand-driven fluctuations. In the short term, this might be perceived as evidence of functional complementarity, a benefit of diversity. However, it also signifies a dampening of the self-regulating nature of the negative feedback.

Table 2. Eutrophication loops and their signs. N;P = nitrogen and phosphorus; Anox&Shade = anoxia and shading; Np = Nile perch; IntMar = international market; Soc&econ = society and economy; LocMar = local and regional market; Haplo = haplochromines; Dagaa = *Rastrineobola argentea*; --> = positive interaction; --o = negative interaction.

Loop	Sign
1. N;P-->Anox&Shade--oNp-->IntMar-->Soc&econ-->N;P	-
2. N;P-->Anox&Shade--oNp-->LocMar-->Soc&econ-->N;P	-
3. N;P-->Anox&Shade--oHaplo-->LocMar-->Soc&econ-->N;P	-
4. N;P-->Anox&Shade--oDagaa-->LocMar-->Soc&econ-->N;P	-
5. N;P-->Anox&Shade--oNp--oHaplo-->LocMar-->Soc&econ--> N;P	+
6. N;P-->Anox&Shade--oNp-->IntMar-->owners-->Dagaa effort--oHaplo-->LocMar-->Soc&econ-->N;P	+
7. N;P-->Anox&Shade--oNp-->IntMar-->owners-->Dagaa effort--oDagaa-->LocMar-->Soc&econ-->N;P	+
8. N;P-->Anox&Shade--oHaplo-->LocMar-->owners-->Np effort--oNp-->IntMar-->Soc&econ-->N;P	+
9. N;P-->Anox&Shade--oDagaa-->LocMar-->owners-->Np effort--oNp-->IntMar-->Soc&econ-->N;P	+

Table 3. Exploitation loops and their signs. Np = Nile perch; IntMar = international market; Soc&econ = society and economy; LocMar = local and regional market; Haplo = haplochromines; Dagaa = *Rastrineobola argentea*; --> = positive interaction; --o = negative interaction.

Loop	Sign
1 Np-->IntMar-->owners-->Np effort--oNp	-
2 Np-->LocMar-->owners-->Np effort--oNp	-
3 Haplo-->LocMar-->owners-->Dagaa effort--oHaplo	-
4 Dagaa-->LocMar-->owners-->Dagaa effort--oDagaa	-
5 Np--oHaplo-->LocMar-->owners-->Np effort--oNp	+
6 Np-->IntMar-->Soc&econ-->LocMar-->owners-->Np effort--oNp	-

Box 2: Connectedness of the fisheries

Haplochromine populations in the offshore and pelagic waters were on a steep decline from the late 1970s and collapsed to low levels in the wake of the Nile perch boom (Witte et al. 1992). Surprisingly, haplochromine biomass started recovering in the early 1990s (Seehausen et al. 1997*b*) and quickly achieved precollapse pelagic stock biomass (Witte et al. 2007*b*). Haplochromines now represent up to 80% of the pelagic fish biomass, and together with dagaa, they constitute more than 50% of the lake's total fish biomass (Tumwebaze 1997, Wanink 1999, Kayanda et al. 2009). In Tanzania, since their resurgence, haplochromines have shifted from being an important bycatch of the dagaa fishery (sometimes constituting 50–90% of the catch) (Witte et al. 2000) to becoming a target that is sold to regional markets or is used as bait in the Nile perch fishery (Ngupula and Mlaponi 2010). Indeed, since the mid-1990s, the dagaa fishery has harvested an increasing amount of zooplanktivorous (genus *Yssichromis*), benthivorous, and detritivorous haplochromines (*Haplochromis* "paropius-like," also referred to as *Haplochromis* "broken bar" in Seehausen et al. [1997*b*]) (van Rijssel, *personal observation*), indicating that benthic species migrate up at night (Kishe-Machumu 2012), and that the dagaa nets—extending 10 m deep—can influence benthic populations. The relative abundance of dagaa and haplochromines in catches is site- and season-specific, suggesting that the dagaa–haplochromine interaction hides multiple underlying drivers. While fishers and markets in Tanzania have adapted and now specifically target haplochromines, in Uganda and Kenya, haplochromines are still only bycatch, though they are sold on local markets. The scale of haplochromine bycatch is clearly indicative that dagaa fishing methods are not selective enough, which is important because haplochromines have slower growth rates than dagaa, are more sensitive to eutrophication, and can therefore not sustain the same levels of fishing mortality. Furthermore, since both dagaa and haplochromines can be sold in multiple forms (bait, fodder, human consumption), the actual taxonomic content of the dagaa catch has little effect on fishers. Therefore, since the resurgence of haplochromines, the dagaa and haplochromine fisheries and stocks have become tightly connected, which reduces the strength of negative feedbacks and the self-regulating ability of the system (Fig. 3: dagaa fishing effort --o haplochromines versus dagaa fishing effort --o dagaa; haplochromines and dagaa --> LocMar). Indeed, if a reduced stock does not lead to a reduced catch (e.g., should dagaa replace haplochromines, or vice versa), the negative feedback of a dwindling stock on fishers and markets is reduced. This conclusion contrasts the view that selective fisheries—as opposed to balanced harvesting (Garcia et al. 2012)—are detrimental to the ecosystem as a whole. In this particular instance, the lack of selectivity does not equate to a balanced harvesting methodology since it is not adapted to the habitats, life histories, and growth rates of dagaa and haplochromines.

A certain level of nutrient input can increase productivity for one species (enrichment) but represent reduced fitness or increased mortality (eutrophication) for another. Haplochromine species, for example, are particularly sensitive to low light (Seehausen et al. 1997*a*), whereas dagaa is probably relatively more sensitive to deoxygenation than is Nile perch (Wanink et al. 2001). Without explicit management, nutrient enrichment would most likely always lead to further enrichment—i.e., it is not intrinsically self-limiting or regulating. Enrichment would, however, translate only to increased stock growth until the negative consequences of eutrophication start taking effect and while fishing effort does not cause mortality rates that exceed growth rates (i.e., stock collapse). Ultimately, sustainability of stocks is a function of the relative strength of fishing-induced mortality versus a stock's response in growth through feeding. Since enrichment and eutrophication alter growth rates, sustainable fishing mortality rates must be variable, not constant. Also, although eutrophication affects the whole lake, the distribution and effect of nutrients on the biochemistry of the lake is spatially heterogeneous (Box 3, Table 4). Therefore, the processes that drive growth of stocks—and thus dictate levels of sustainable harvesting—are site-specific and not generalizable across the whole lake at any one time.

Box 3: Spatial heterogeneity of the lake

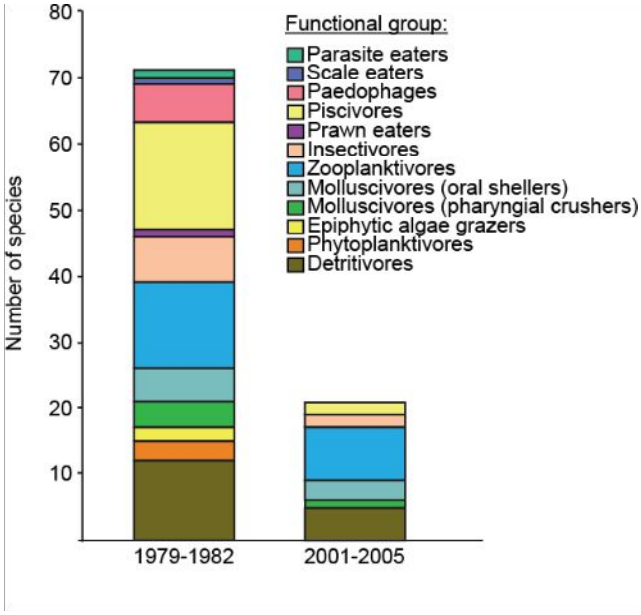
In inshore areas, terrestrial runoff and detritus are primary sources of light limitation, whereas further offshore it is algal biomass that induces light limitation, and thus restricts photosynthesis to a narrower surface layer. Eutrophication affects the whole lake, as half the total phosphorus input to the lake is from atmospheric deposition (Tamatamah et al. 2005), though there is a lot of spatial heterogeneity in its effects—not only in an inshore-offshore gradient, but also between bays around the lake (Silsbe et al. 2006, Loiselle et al. 2008, Cornelissen et al. 2013). Total nitrogen concentrations have increased since the 1960s, primarily through cyanobacteria fixation, and nitrogen generally follows a decreasing concentration pattern from the coast to offshore waters (Hecky et al. 2010). While nutrient loading has created the light-limited conditions of the lake, seasonal and interannual variations in primary productivity are now driven primarily by climate (Silsbe et al. 2006, Cózar et al. 2012). This is of particular relevance since it highlights an important characteristic of qualitative models such as the one we use: they do not account for time or effect lags (Justus 2005). The synergistic and cumulative effects of warming and eutrophication on phytoplankton and the food web will probably delay the effects of eutrophication management (Schindler 2006).

Increases in nutrients no longer lead to increased phytoplankton primary production in the northern Murchison Bay and Napoleon Gulf of Lake Victoria, indicating that these areas are phosphorus saturated (Silsbe et al. 2006) (Fig. 3: N&P --> shading). However, recent experiments conducted on samples from the Mwanza Gulf in southern Lake Victoria show that the increase in primary productivity with further nutrient enrichment can still take place (Cornelissen et al. 2013). Effects of further nutrient enrichment are therefore likely to be area- and season-specific. Over the years, chlorophyll *a* measurements have shown a great degree of variability (Table 4). Even though differences in sampling frequency and measurement methods, as well as in location, depth, and timing of sampling make it impossible to draw accurate trends from these data, it appears that chlorophyll concentrations in the northern parts of the lake are higher than in the south (Table 4).

Table 4. Variability in chlorophyll *a* (Chl) concentrations in the lake, as found in the literature. Seasons: DS = (dry season): June–August; SR = (short rains): September–December, LR = (long rains): January–May. SD = standard deviation. N = number of measures. LVRO = Lake Victoria Fisheries Organisation.

Source	Location	Year	Season	Depth (m)	Chl (µg/l)	SD	N
Acoustic survey LVFO	Murchinson Bay	2005	DS	< 20	44.6		1
	Mwanza Gulf	2005	LR	< 20	18.43		1
	Nyanza Gulf	2005	DS	< 20	11.29	8.19	2
	Nyanza Gulf	2006	LR	< 20	8.91	2.97	4
	Speke Gulf	2005	LR	< 20	20.76	9.18	9
Akiyama et al. (1977)	Mwanza Gulf	1973–1974	DS	8	4.35	1.60	6
	Mwanza Gulf	1973–1974	LR	8	5.1	2.01	6
	Mwanza Gulf	1973–1974	SR	8	3.7	1.10	8
Cózar et al. (2007)	Murchinson	2003	DS	< 20	80.92	13.73	13
Gikuma-Njuru (2008)	Nyanza Gulf	2005–2006	All year	< 20	17.57	3.60	7
Haande et al. (2011)	Murchison Bay	2003–2004	DS	< 11	21.43	6.63	14
	Murchison Bay	2003–2004	LR	< 11	31.4	10.41	20
	Murchison Bay	2003–2004	SR	< 11	24.06	6.54	16
Lehman and Branstrator (1993)	Napoleon Gulf	1992	SR	< 10	48		
Lung'Ayia et al. (2000)	Nyanza Gulf	1994–1995	SR	< 10.5	20.77	7.48	11
	Nyanza Gulf	1994–1996	LR	< 10.5	13.45	2.77	11
Mugidde (2001)	Napoleon Gulf	1994–1998	All year	< 20	71	100.4	47
	Napoleon Gulf	1994–1999	LR	< 20	38.11	20.33	9
	Napoleon Gulf	1994–2000	DS	< 20	27.5	18.37	6
	Napoleon Gulf	1994–2001	SR	< 20	82.5	79.94	10
Ngupula et al. (2011)	Tanzania	2005–2007	All year	< 10	16	6	10
	Tanzania	2005–2007	All year	10–20	22.5	8.5	11
	Tanzania	2005–2007	All year	20–30	11	5	9
North et al. (2008)	Jinja	2001–2002–2004	SR	< 26	52.9	10.60	12
Okello et al. (2009)	Bunjako (Uganda)	2004	DS	< 5	9	1.41	2
	Murchinson Bay	2004	DS	< 5	18	7.07	2
	Napoleon Gulf	2004	DS	< 20	10.5	0.71	2
Shayo et al. (2011)	Kayenze (Speke Gulf)	2005	DS	< 20	14.67	7.58	6
	Kayenze (Speke Gulf)	2005	LR	< 20	18.17	3.76	6
	Kayenze (Speke Gulf)	2005	SR	< 20	13.67	6.46	9
	Magu (Speke Gulf)	2005	DS	< 20	20	10.12	6
	Magu (Speke Gulf)	2005	LR	< 20	18.17	12.19	6
	Magu (Speke Gulf)	2005	SR	< 20	17.56	7.21	9
	Mwanza Gulf	2005	DS	< 20	9.83	2.79	6
	Mwanza Gulf	2005	LR	< 20	13.67	4.72	6
	Mwanza Gulf	2005	SR	< 20	17.56	6.17	9
Silsbe et al. (2006)	Fielding	2001–2002	DS/SR	< 10	42	23.06	?
	Murchison Bay	2001–2002	DS/SR	< 8	69.5	24.33	?
	Napoleon Gulf	2001–2003	DS/SR	< 14	26	6.292	?
Sitoki et al. (2010)	Whole lake	2000	DS	< 20	12.8	11.3	?
	Whole lake	2000	LR	< 20	13.2	4.4	?
	Whole lake	2001	DS	< 20	10.9	7	?
	Whole lake	2001	LR	< 20	10.8	6.7	?
	Whole lake	2006	DS	< 20	16.2	8	?
	Whole lake	2006	LR	< 20	14.8	10.9	?
	Whole lake	2007	DS	< 20	14.4	8.4	?
	Whole lake	2007	LR	< 20	15.7	8.5	?
	Whole lake	2008	DS	< 20	14.5	11.2	?
	Whole lake	2008	LR	< 20	16.8	8.6	?
	Whole lake	2009	DS	< 20	14.8	6.1	?
	Whole lake	2009	LR	< 20	12.7	12.5	?
Yasindi and Taylor (2003)	Napoleon Gulf	1998	SR	< 15	34		
Cornelissen et al. (2013)	Mwanza Gulf	2009–2011	DS	< 25	13.24	4.71	68
	Mwanza Gulf	2009–2011	LR	< 25	14.96	8.05	73
	Mwanza Gulf	2009–2011	SR	< 25	13.45	4.60	72

Fig. 4. Species and functional diversity loss in the soft-bottom fish community of Lake Victoria. The bars represent the number of haplochromine species per functional group collected in the sublittoral waters (6–14 m) of the northern part of the Mwanza Gulf, over soft bottom, in 1979–1982 and 2001–2005. Between 1979–1982 and 2001–2005, 65–70% of species and 50% of functional groups were irreversibly lost. One unclassified species is omitted here. Data from Witte et al. (2013). Not only does the number of functional group decrease, but the degree of specialization within trophic groups also decreases: e.g., former zooplanktivores have broader diets in 2001–2005 than in 1979–1982 (Kishe-Machumu 2012, van Rijssel and Witte 2013).



When using the diagrams, it is important to account for underlying assumptions, and to look at different feedback loops in concert. As an example, if nutrient enrichment leads to higher Nile perch stocks (Table 1, row 7), this promotes investment from the international market, which can drive owners to invest effort in alternative stocks, such as dagaa, which would then reduce dagaa stocks. This would thus negatively influence the local and regional market and lead to a decrease in human population growth, which would lead to a decrease in nutrient input. Taken in isolation, such a scenario would be based on questionable assumptions: it would assume that nutrient enrichment has a positive effect only on Nile perch, not on dagaa. It would also assume a single fishery target with no alternative stimuli for the regional market, and that this dynamic is the major determinant of human population growth. This type of loop would represent a case where international economic input does not lead to social and economic growth in the region, and thus does not lead to increased nutrient input to the lake. The diagrams presented here are tools that can enhance understanding and map multiple system variables simultaneously, but even though they are simple tools, their interpretation should not be oversimplified.

Our combined social-ecological diagram allows us to see the effects of change in a broader context, but it has a limited predictive value: indeed, it cannot account for adaptation in either human or fish populations to declines in stock or in environmental conditions. However, with a limited time frame in mind, the diagram can give an idea of the far-reaching effects of any single action on the whole system. We indicated three exogenous stressors: climate change, the international economy, and regional policies. More might exist, and they could have broader effects than illustrated here. These stressors are dubbed exogenous because they are not solely or directly influenced by Lake Victoria's system. Exogenous stressors are important in that they could shift the sign of loops in the feedback diagrams or change the relative importance of any given interaction or loop and thus alter system dynamics.

SYSTEM TRENDS AND CHANGES MATCHED TO THE MODEL

Here we look into Lake Victoria's past to contextualize the model and identify how its elements and interactions illustrate trends that have shaped the dynamics of the social-ecological system. Through this juxtaposition of model and trends, we can identify the model's scope and limitations and indicate its best uses. Furthermore, it allows us to explore how weights of different interactions might have changed over time.

In the beginning…

Before the introduction of Nile perch, Lake Victoria harbored a small though diverse, multispecies artisanal fishery. Fishing, along with agriculture and livestock herding, constituted the economic foundations of lakeshore societies. The main fishing targets were the native tilapia *Oreochromis esculentus* and *O. variabilis* (Balirwa et al. 2003, Pringle 2005*b*). Fish were initially sold by number rather than weight, which invited catches of small fish (Beverton 1959, Balirwa 1998). The introduction of gillnets in the 1920s as a new tool quadrupled fishing efficiency, and the fishery became commercial—a process further helped by urban infrastructure development (including road and rail) around the lake (Balirwa 1998) (Fig. 3, development of local/regional market: dagaa and haplochromines --> LocMar --> owners and Soc&econ…).

Since the 1960s, effects of eutrophication—driven by human population growth around the lake and subsequent changes in land use (Verschuren et al. 2002, Hecky et al. 2010)—became apparent. The phytoplankton community underwent a transition from a diatom-dominated community to one increasingly dominated by nitrogen-fixing cyanobacteria, and primary production increased. In turn, the zooplankton community shifted to be dominated by small species (Mwebaza-Ndawula 1994, Gophen et al. 1995, Wanink et al. 2002). The dominance shift in the phytoplankton community has been hypothesized to be a cause in the zooplankton shift (Wanink et al. 2002) (Fig. 1: change in relative importance of phytoplankton --> zooplankton versus phytoplankton --> detritus and anoxia & shading).

Introduced species, changed ecosystem

As native stocks were declining from exploitation, eutrophication, and habitat destruction, Nile tilapia (*Oreochromis niloticus*) and other tilapiine species were introduced. Simultaneously (between 1954 and 1964), Nile perch were introduced to boost the

productivity of the fisheries and convert the native diversity of haplochromines into a more desirable fishery product (Kudhongania and Chitamwebwa 1995, Pringle 2005*b*). From 1965, Nile tilapia gradually replaced native tilapia, became a major commercial catch (Balirwa 1998), and is currently an important product for local and regional markets (Njiru et al. 2008). Tilapia does not figure explicitly in our diagrams because it appears to interact little with other stocks (Downing 2012, Downing et al. 2013*b*). It is, however, of course also influenced by enrichment, eutrophication, and exploitation processes, and contributes to the regional market, and can therefore be read in the system in a similar way to haplochromines or dagaa, but with tilapia-specific sensitivities to the different driving processes.

While the Nile perch introductions had little immediate effect, in the 1980s many changes occurred quite rapidly. Nile perch suddenly became dominant in the whole lake, and—in concert with increased hypoxic and anoxic conditions—contributed to the collapse of haplochromine stocks and mass disappearance or extinction of native fish species (Witte et al. 1992, Hecky et al. 1994, 2010, Verschuren et al. 2002, Goudswaard et al. 2008). The high abundance of haplochromines proved to be favorable for Nile perch as growth estimates in both the Tanzanian and Kenyan waters through the end of the 1980s—covering the time when Nile perch were still feeding heavily on haplochromines—showed that Nile perch grew at least twice as fast as in haplochromine-poor lakes (e.g., Lake Chad, Lake Turkana, Lake Albert, Lake Nasser) (Ligtvoet and Mkumbo 1990) (Fig. 3: Nile perch --o haplochromines). Ecological opportunities afforded by the vanishing haplochromines were exploited in short succession by two native species, first the detritivorous shrimp *C. nilotica* (Goudswaard et al. 2006) and then the zooplanktivorous cyprinid dagaa (*R. argentea*) (Wanink et al. 2002).

Since the 1990s, effects of eutrophication and fishing have become more apparent, and Lake Victoria's ecosystem is still undergoing many changes. The water hyacinth (*Eichhornia crassipes*), which first appeared in the lake in 1989 (Chapman et al. 2008), had produced large mats by 1995. These mats severely interfered with fishing operations, with important social-economic consequences (Opande et al. 2004), and altered the bio-physico-chemical environment of the water under them (Masifwa et al. 2001, Kateregga and Sterner 2008). This event supports the notion that water quality influences stocks and catches, and importantly, that when the lake's environment is compromised in such a way, neither international nor regional markets can act as backups, and society has little (perhaps only agriculture) left to rest on (Fig. 3: N&P and anoxia & shading --> Nile perch, dagaa, and haplochromines --> IntMar and LocMar --> Soc&econ). The hyacinth invasion was in large part managed between 1997 and 1999 through manual removal and the introduction of a weevil (*Neochetina eichhorniae*). The effects of these management procedures were probably enhanced by an El Niño episode (1997–1998), during which elevated water levels broke off large hyacinth stands, and where low light conditions (clouds) and rain reduced hyacinth growth (Njiru et al. 2002, Williams et al. 2005, 2007, Wilson et al. 2007). Even though the hyacinth bloom was probably triggered by eutrophication, its decline is not a reaction to improved water quality: there are multiple pathways to any single phenomenon.

Dominance of cyanobacteria in the phytoplankton community has led to an increase in concentrations of toxins produced by cyanobacteria (e.g., microcystin). Higher trophic levels—including humans—are increasingly exposed to such toxins, both directly through water and through their accumulation in fish tissues (Poste et al. 2011). Low fish quality would probably reduce fish prices on (or even access to) the international market, but decreased wellbeing or increased illness in lakeshore societies would probably have more complex and further reaching consequences. At this point, however, the extent to which cyanotoxins affect human health around Lake Victoria is unknown, though it is important to keep toxicity in mind as a process in eutrophication.

Societal adaptations

The advent of the Nile perch boom in the 1980s changed societies dramatically (Fig. 3: IntMar --> owners and Soc&econ versus LocMar --> owners and Soc&econ). People migrated to the lakeside to enter the fisheries, which accelerated human population growth and altered the kinship relations that had existed previously. Human populations around the lake continue to grow at a higher rate than the African average (Odada et al. 2009).

Filleting factories were constructed around the lake, and the fish were exported to Europe (Pringle 2005*a*, Johnson 2010). The major filleting factories were built to process up to 25 tons of Nile perch each, per day, but would break-even on costs when operating at about 30% capacity (Johnson 2010). Nile perch catches reached a peak in 1990, but effort has continued to increase since.

Changes in dagaa, haplochromines, and the regional market

Although dagaa is native to Lake Victoria, a directed fishery for it first developed only in the 1960s. The stocks of dagaa rapidly increased after the Nile perch boom and haplochromine collapse. Dagaa became the lake's second most important fishery by the 1990s (Wanink 1999), when landing sites started organizing themselves into camps, also presenting a strong social structure, from trader to owner, through camp supervisors and laborers, with women drying the fish. Dagaa is currently a dominant commercial fishery of the lake in terms of biomass (Tumwebaze et al. 2007), and it trades on domestic and regional markets (Gibbon 1997). Catch that is successfully dried and cleaned of sand is destined for human consumption as it serves as a cheap source of protein for the poor and middle class (Medard 2012), and the rest sells as animal feed: chicken fodder, for example. Traders play an important role, checking the quality of the product as well as establishing its price (Gibbon 1997). Despite no apparent decrease in its stock size, dagaa has undergone behavioral, morphological, and life history changes in some regions of the lake, which may reflect local adaptive response to predation by Nile perch, fishing pressure, and/or eutrophication and associated hypoxia (Wanink 1999, Wanink and Witte 2000, Manyala and Ojuok 2007, Sharpe et al. 2012). Fishing effort has been on a steady increase (Mkumbo et al. 2007), at least until 2006, from where data suggest a stabilization in effort (Kolding et al. 2014) (Fig. 3: N&P --> dagaa versus dagga fishing effort --o dagaa). Dagaa remains a product destined mostly for a local and regional market, and is, therefore, less well monitored, regulated, and studied than Nile perch (Medard 2012).

SOCIAL-ECOLOGICAL CHANGE SEEN IN MODEL STRUCTURE

The single diagram we developed to represent Lake Victoria's social-ecological system can be used to analyze and represent a whole variety of dynamics. This is necessary because system dynamics have seen both short- and long-term dynamics. Seasons influence light, temperature, weather, and wind conditions, which influence the growth of organisms as well as access to different areas of the lake. Dynamics also have a heterogeneous spatial distribution, considering, for example, the different nutrient environments in the north and south of the lake (Box 3, Table 4), or the atmosphere of conflict in contested Ugandan—Kenyan fish camps (Box 4), or differences in fishing practices (Beuving 2014). All of these factors imply that a quantitative model of Lake Victoria's social-ecological dynamics ought to be set in a clearly defined spatio-temporal setting. Meanwhile, this purely qualitative model allows us to analyze three types of structural changes to the system and their influence on dynamics and role in the effectiveness of policies and regulations: (1) a change in the relative weight of different interactions, (2) the change in the sign of interactions or loops, and (3) the addition or removal of interactions. Here, we analyze—through examples of past changes and hypothetical management policies—the effects of these three types of changes on the dynamics on Lake Victoria's social-ecological system.

Box 4: Societal reorganization and inequity

To ensure constant supply to the factories after the trawling ban became effective in the 1990s (Mbuga et al. 1998), a new social-economical interaction emerged: processors invested in building infrastructure to better store Nile perch at landing sites and sponsored fishermen with nets and gear via agents, who would then ensure fixed prices and supply of fish (Mbuga et al. 1998, Geheb et al. 2008, Johnson 2010). Lakeshore societies thus developed a stronger economic hierarchy from processor through agent to fisher, with many fishers then entering a situation of credit towards agents or processors (Geheb et al. 2008). Fishing effort continues to increase and fisher communities to restructure. In the Nile perch fishery in some areas, many agents (middlemen) have become boat owners and landing site or camp managers who employ camp supervisors and laborers to operate full fleets and with whom they arrange credits and loans to ensure a constant fish supply. The structure is likely quite diverse, however, and there are reports of wealthy boat owners striking deals with factories and thus taking a trader's role.

Economic input to society is nonlinear, with larger swaths of income distributed to big owners, and much less reaching fishers and laborers. Besides stocks and the international economy and regulations, local social-economic settings and interactions can have complex effects on both social stability and benefits reapable by owners through fishing. Individual cost-to-benefit ratio of fishing and risk-taking behavior is variable. Competition for landing sites among owners, for example, can influence costs and prices by leading to a local monopoly of the fisheries by few owners. Competition among owners can lead to conflict and violence: there are reports of piracy in the southern part of the lake, which leads to increased costs in security and uneven distribution of fish resources. Also, there are chronic territorial conflicts over fish camp islands between Kenya and Uganda (Otieno 2013). Knowledge of the distribution of power, opportunities, and value of risk in society is key to the selection and implementation of appropriate policy measures. Here, we lack representation of the potential response diversity of society, which is a great impediment to measuring and predicting society's reactions and adaptations to ongoing changes in the system.

Changes to the relative weight of interactions

Management policies can profoundly influence the connectedness of a system, for example, by creating tighter networks of communication. Increased economic disparity caused an increase in illegal fishing practices in the 1990s. In an effort to improve compliance and better implement fishing regulations, Tanzania established a comanagement approach to the fisheries in 1997, in the form of Beach Management Units (BMUs) (Kateka 2010). These local groups were established to increase stakeholder participation in surveillance and management of the fisheries, and similar structures were later implemented in Uganda and Kenya (Mkumbo 2002, Kateka 2010). Their success has been mixed, however: BMUs have effectively suppressed poisoning and dynamiting as fishing techniques, but they lack an adequate legal status, and by establishing their own bylaws, BMUs can sometimes abuse their position and authority (Geheb et al. 2007, Njiru et al. 2007). Importantly, they have also increased fishing efficiency through improving communication networks (Eggert and Lokina 2009) (Fig. 3: strengthening of interactions Nile perch and dagaa fishing effort has a negative effect on Nile perch, dagaa, and haplochromines), helping fishers get to good fishing sites faster and reducing the negative feedback of declining stocks on fishers.

Changes in the sign of interactions or feedbacks

Fertilizer subsidies, which might promote agriculture and alternative sources of income, would nonetheless reinforce positive feedback loops through nutrient enrichment, and thus be overall destabilizing. A fishing limiting policy, such as a licencing fee, could add a minus to fishing effort and change the signs of the loops in that way, though if it is not applied to all fisheries, such a policy could have a backlash effect and lead to higher exploitation of alternative fisheries or to increased land use for agriculture. In short, the effect of any single policy or change depends on its ripple effects through the broader system.

Changing the number of pathways in the system

In a bid to prevent and eliminate illegal, unregulated, and unreported fishing, the Lake Victoria Fisheries Organisation has pushed to promote eco-labeling of Nile perch. For this, they established codes of practice with help from the Marine Stewardship Council (Kolding et al. 2014). In 2009, the German cooperative Naturland launched its eco-label for the small capture Nile perch fishery, certifying the sustainability of Nile perch products exported to Germany. The label is based on ecosystem, fishery, social, and hygiene criteria, and covers eight landing sites and 1000 fishermen in Tanzania (Bukoba), though there is currently no known study that evaluates the effects of eco-labeling on the stocks, society, or economy. However, seen through our diagram, Naturland's policy—i.e., supporting a small-scale

fishery on the Nile perch—might be translated by adding a role to some owners, whereby their connection between the regional market and the Nile perch fishery is subject to regulations (Fig. 3: LocMar --> owners --> Nile perch fishing effort) and where owners connect the regional and international market (Fig. 3, IntMar --> owners --> LocMar). One of the loops that would then emerge is a negative feedback loop connecting the regional market to fisheries, Nile perch stocks, the international market, local societies, and the regional market (Fig. 3: LocMar --> owners --> Nile perch fishing effort --o Nile perch --> IntMar --> Soc&econ (or owners) --> LocMar). This constraint on the middleman (owner) would differ from the loops we have so far accounted for in that the owner's role merges with that of the local and regional economy and society (Fig. 3, Soc&econ). Such a loop might have beneficial social-economic repercussions since it could reduce economic disparity (note that we separated owners from society to be able to reflect differences in economic benefits and incentives). However, in itself, this policy still only adds a pathway to harvesting Nile perch: a small-scale fishery might be sustainable if taken on its own, but as long as it operates in parallel with other harvesting policies, the stocks might yet be vulnerable to unsustainable harvesting. Therefore, for a policy like that of Naturland to actually ensure sustainable Nile perch harvesting, it needs to outcompete existing harvesting strategies (effectively connecting itself to other fisheries with a minus sign in our diagram). While not all owners are party to the policy, sustainable harvesting might happen if the label succeeds in influencing consumption patterns in the international market (and) or if different incentives to harvest sustainably are presented directly to fishermen and fishing site owners.

Quantitative versus structural changes to the system

Overall, we find that policies and changes that alter the connectedness of the system influence the self-regulatory capacity of the system. Connection strength changes are probably the most common and insidious changes in the system, as they can be an uncalculated side effect of various other policies (as for example, the case of BMUs). Also, given the heterogeneity in conditions and processes over the whole lake, differences in connectedness across the system influence the generalizability of policy interventions: interaction strengths are not the same across the whole lake or even permanent in time (Boxes 2 and 3). Changes in the sign and number of interactions, however, as for example the Naturland eco-labeling policy, can alter system dynamics without necessarily altering the integrity of regulating feedback mechanisms, though the effects of such structural changes are dependent on the configuration and dynamics of the system as a whole.

DISCUSSION

Here, we put together pieces of Lake Victoria's social-ecological system in a qualitative, conceptual model and achieve greater understanding of the system's functioning from a good prior knowledge of the processes behind dynamics, as well as from the key elements and interactions that are specific to Lake Victoria.

The interconnection diagram highlights the multiple pathways to any single phenomenon in the system. As an example, the threat to fisheries stems not only from fishing effort but also from other environmental factors: eutrophication, hypoxia, and anoxia reduce fish growth and survival rates, thereby increasing the stocks' vulnerability to fishing pressure. Complete overharvesting of Lake Victoria's fishes, be it Nile perch, dagaa, or tilapia, would not necessarily be an easy task: the number of fishers and crafts on the lake has increased dramatically since the early 1990s, but technologies have not followed suit everywhere. Paddling is still the dominant method of propulsion in a large part of the lake, and where engines are available, fuel costs, and in the case of the Nile perch fishery, costs related to the hygienic storage of fish during longer periods, as well as dangerous boating conditions, all impose limits on the distance from shore that is exploited. Dagaa is also difficult to harvest efficiently, despite being a productive species: fishing of dagaa occurs mostly on moonless, windless nights, using lamps that attract insects and zooplankton and then the zooplanktivores, including dagaa. However, even if all stocks are not currently overfished, the threat to Lake Victoria's fisheries is real. Indeed, native tilapia (ngege [*Oreochromis esculentus*]) was successfully reduced to low numbers using quite simple methods before the introduction of Nile perch and Nile tilapia. Even though the dagaa fishery might not be the most important direct threat to dagaa stocks, it could be an important influence on haplochromines since the two fisheries are connected through fishing methods and markets. The adaptability of fishers and markets to changes in stocks might reduce the self-regulating character of exploitation (i.e., dampen the negative feedback of exploitation loops) and make a stock collapse even less predictable or even avoidable. In this way, while overfishing is not necessarily currently the biggest threat to fisheries on Lake Victoria *per se*, it becomes an important threat in the presence of environmental change and eutrophication, and in the context of the full, interconnected system.

Interestingly, here we find that even though high connectivity of fisheries at the level of owners and markets may be detrimental to stocks (Box 2), it can also make the social-economic system more robust to the loss of the international market. A loss of the international market would cause a dramatic loss of revenue, but there is no shortage of demand for fish products, in general, and fishing markets have diversified. Dagaa, haplochromines, and small Nile perch are sold locally and regionally for human consumption and as animal feed. Tilapia and Nile perch fetch higher prices on the same markets. Furthermore, a shutdown of all international trade is considered highly unlikely. In the same way as when the European market closed in 1997, Israel and Asia and other African countries could perhaps serve as alternative markets (van der Knaap et al. 2002). Nonetheless, it is important to remember that lakeshore societies have grown and developed fast, and a lack of long-term investments or permanent structures contributes to the high and increasing income disparity in lakeshore populations, which in turn can influence societies and contribute to their increased volatility (Wilkinson and Pickett 2009).

The rapid Nile perch invasion created a strong dependence on fisheries (as exemplified during the water hyacinth blooms), which probably makes societies quite vulnerable to a loss of stocks, especially since there are few other sources of steady income. Indeed, as the Nile perch fishery grew, migrant settlements that started off as temporary became villages—with bars, makeshift cinema halls, and brothels—though they often lack essential

permanent structures such as medical units or schools (Geheb et al. 2008). Investment opportunities lie mostly in high profit margin activities rather than in durable or saving schemes, the economic life is deeply monetized since there is little self-sustenance, and most goods must be bought (Beuving 2010). People in these boom villages easily fall into a poverty trap. General health status is low, and there is a high HIV-AIDS infection and prevalence rate (van der Knaap and Ligtvoet 2010). Therefore, alternative sources of income are undoubtedly highly dependent on the fisheries—the services sold in villages and camps are targeted at fishers. These will not provide a safety net should fisheries collapse. Agriculture, chicken farming, and livestock herding are among the few sources of income that are independent of fisheries. Following this analysis, we suggest new metrics with which to bridge social and ecological changes in future studies: investments in infrastructure and the sources of these investments might provide a usable proxy for the dependence of societies on their resources. Such data might also inform the sustainability or durability of development around Lake Victoria. While investment in urban and transport infrastructure in the early 20th century and in fish processing infrastructures in the 1980s heralded priority areas of future development around the lake, there was no comparable spending on agricultural infrastructure.

This model does not yet encompass the full complexity of Lake Victoria's societal components (e.g., Box 4). We lacked the references and detail needed to generalize the different processes that drive societal dynamics, and how these induce individuals to take risks, drive investment, and frame decision-making processes. In short, our model strongly underrepresents the response diversity of society (all those processes hidden in the feedback between society and the local market). In the same way, our model lacks resolution in terms of biodiversity (Box 5). We can represent functional diversity to a small degree—which underlies in part the haplochromine-dagaa interrelation—but the full biodiversity and richness of the ecosystem, which sets the stage for the adaptability of the system to changes and disturbances, is not represented. These two elements—biodiversity and social structure—are directly relevant to any medium-term predictions on system dynamics, to policy-making, and to the assessment of the social-ecological system's current state. Also, it is important to remind the reader that the ecosystem we describe has a strong aquatic bias. In truth, any visitor to the lake will first encounter a large diversity of birds, insects, and vegetation, all of which influence and are influenced by changes in the aquatic, terrestrial, climatic, and human systems. This, however, is at least a first step in bridging the social-economic-(aquatic)-ecosystem, in hopes that encouraging further work on bridges to avian and terrestrial ecology might be possible in the future.

Box 5: Diversity changes

Even though the resurging offshore haplochromine community has largely recovered in biomass and retained a 40-strong species diversity (Seehausen et al. 1997*b*), of which 15–20 species are pelagic, this is only a small fraction of the 1970s haplochromine diversity. Indeed, 65–70% of both benthic and pelagic species dwelling over soft bottoms in the sublittoral waters (6–14 m deep) of the Mwanza Gulf seem to have been irreversibly lost (Kishe-Machumu 2012, Witte et al. 2013) (Fig. 4). In the pre-Nile perch system, an estimated minimum of 500 different species of haplochromines occupied almost every function in the food web, from detritivorous species through to piscivores. Fishing pressure on Nile perch (Fig. 3: Nile perch fishing effort --o Nile perch --o haplochromines), as well as morphological adaptations to changed environmental conditions and major habitat shifts are possibly associated with the reappearance of haplochromines (Kitchell et al. 1997, Seehausen et al. 1997*b*, Schindler et al. 1998, Witte et al. 2000, 2008, Balirwa et al. 2003, Mkumbo and Mlaponi 2007, van Rijssel and Witte 2013). Dominant haplochromines of the Mwanza Gulf in 2006–2008 and 2010–2011 were found to be predominantly the former zooplanktivores and detritivores/phytoplanktivores (Kishe-Machumu 2012). However, diets of haplochromine species recovering since the 1990s changed: they contained more macro-invertebrates than in the 1970s and early 1980s (Kishe-Machumu et al. 2008). Although in recent years haplochromines seem to have reverted to zooplanktivory, they are less specialized than they were in the 1970s and 1980s (Kishe-Machumu 2012, van Rijssel and Witte 2013).

In our feedback diagrams, we linked all fields of research at their boundaries, thus shifting the focus from each field's central themes to the interconnections between fields. The diagrams show how a change in any part of Lake Victoria's system can trigger chain reactions across the system. Many of these chain reactions contain or are part of feedback loops, indicating that changes in the system can initiate and drive new dynamic regimes. By analyzing this interconnected system, we find multiple pathways to what may at first appear to be singular, linear phenomena. The presence of multiple pathways can be dangerous since it can lead to a misinterpretation of mechanisms driving change, but it can also be advantageous: by understanding different pathways that regulate a single process, we obtain multiple tools with which to manage change.

We investigate the mechanisms of change through the social-ecological model. Changes to the structure of the system, which can be brought about through evolution and adaptation in the social-ecological system (for example, a broadening of a species' diet creating a new interaction, a species extinction leading to a loss of an interaction, or technical or cultural changes in the social system) or through the implementation of policies, can dramatically alter systems dynamics and responses to change. Though our analysis is not quantitative, we can nonetheless see that differences in relative strengths of interactions, which can be understood as a change in the system state, can greatly influence the vulnerability of system elements to further change. Such quantitative changes and differences can be quite pervasive in both time and space. The dominant processes shaping the Lake Victoria's dynamics have changed over time and are heterogeneous in space. This heterogeneity implies that multiple system states exist, which means on the one hand that studies on any part of the system must be understood in their specific space–time context, and on the other hand that the scope of management actions must be scale adapted.

The system's heterogeneity can also explain some of the scientific disagreement that prevails regarding the state of the fisheries.

Efforts ought to be made to determine the spatio-temporal scales at which different processes dominate. Lake Victoria's complex, changing, and interconnected system calls for an adaptive management approach capable of embracing this heterogeneity. Adaptive management requires in large part that stakeholders have a common understanding and knowledge of their system (Ostrom 2009). By combining knowledge from different fields and perspectives, we tried to develop such common knowledge. This knowledge should not be interpreted as absolute. Rather, it will wax and develop as users and scientists learn from further changes in Lake Victoria's system and from the system's responses to management. Choices of management policies need not and will not wait for more or better knowledge of the system's dynamics: they are part of the learning processes.

This little history of Lake Victoria highlights how nearly all regulations or policies that have been put in place in Lake Victoria have only ever targeted fishing. Almost nothing has been done to halt or reverse eutrophication. In part, this is because the main sources of eutrophication—i.e., land burning—have only recently been defined. Though eutrophication already displayed effects in the 1960s, it has only recently been acknowledged as a potential and in fact important driver of change in Lake Victoria's system. Indeed, this is to our knowledge the first interdisciplinary study to put eutrophication and fisheries in Lake Victoria on an equal footing, and perhaps in this way signals a turning point in the understanding of drivers of change in Lake Victoria. Eutrophication is ongoing, has damaging consequences for Lake Victoria's system, cannot compensate for or be remediated by fishery policies, and must be addressed for the general health of the system, its users, and fisheries. Additionally, any fishery-oriented policy is likely to be ineffective in the absence of a parallel eutrophication and broader lake basin management policy. Associated policy options must be processed and understood by societies to be made operational, yet we still lack a lot of knowledge about social dynamics and interactions. Furthermore, biodiversity is likely to be key in helping to process excess nutrients, restore better water quality, and value and enjoy the host of nonfishery-related ecosystem services that the lake also provides. The full role of biological diversity and its potential to recover in Lake Victoria are largely unknown. Our study points to society and diversity as two key subjects Lake Victoria scientists need to unravel.

Responses to this article can be read online at:
http://www.ecologyandsociety.org/issues/responses.php/6965

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