Seeing the water for the fish: building on perspectives of Lake Victoria

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To my parents

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Chapter 1

Seeing the water for the fish: building on perspectives of Lake Victoria, general introduction

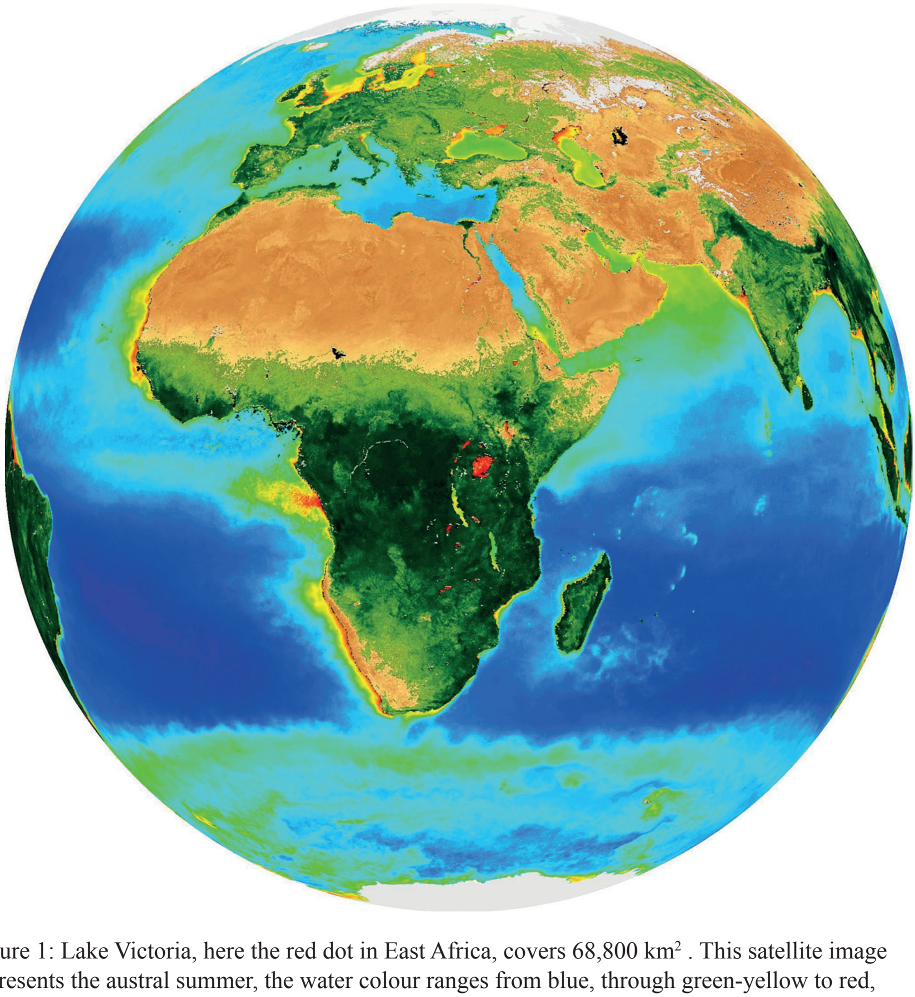

Figure 1: Lake Victoria, here the red dot in East Africa, covers 68,800 km^2 . This satellite image represents the austral summer, the water colour ranges from blue, through green-yellow to red, depending on chlorophyll concentration: red indicates high chlorophyll – i.e. high phytoplankton biomass. Image retrieved from seawifs.gsfc.nasa.gov/SEAWIFS.html/

Seeing the water for the fish

The water and fish of Lake Victoria attracted and enabled human settlement on its shores. To use these resources, the environment of and around Lake Victoria was controlled: swamps and bush were cleared to make the water accessible and the environment liveable. The more accessible its resources became, the more people came to use them, and the more its environment was adapted for use and adapted itself to change. This gradual human and nature co-evolution hit a tipping-point thirty years ago when Nile perch (*Lates niloticus*), a species that had been introduced thirty years previously, suddenly invaded and fully changed the services that the lake could provide. Indeed, the few Nile perch that had been introduced to Lake Victoria in 1954 turned into an international export product that now yields approximately 250 million US dollars yearly (Ogutu-Ohwayo and Balirwa 2006, Kayanda *et al.* 2009, van der Knaap and Ligtvoet 2010).

Concomitant to the Nile perch establishment and boom, many native species disappeared, including the majority of a 500-species strong diversity of haplochromine cichlids (Seehausen 2000). Following the haplochromine collapse, two native species – the shrimp *Caridina nilotica* and the cyprinid *Rastrineobola argentea* (dagaa) – started thriving, the latter inviting a fishery onto itself (Wanink 1999). Rapidly growing human populations on the lakeshores adapted to these changes in resources: exploitation of both Nile perch and dagaa increased, as well as the further transformation and use of the lake's surroundings – agriculture, cattle herding and poultry farming now complete the fishing industry (van der Knaap and Ligtvoet 2010). Already in the 1960s, increased land-use was causing the eutrophication of Lake Victoria (Hecky *et al.* 2010). Data have suggested increasingly fluctuating stocks since the 1990s, as well as altered Nile perch population size-structure (Mkumbo and Mlaponi 2007, Kolding *et al.* 2008), prompting the fear that Nile perch are being overfished. However, the changes are not consistent with those expected from fishing alone, and thus eutrophication has been hypothesized to play an important role on the dynamics of the Lake's system (Kolding *et al.* 2008).

Lake Victoria is the world's second largest lake. It covers a surface area of approximately 68,800 km^2 over three countries (fig. 1): Uganda, Kenya and Tanzania, and its drainage basin extends further west to Rwanda, Burundi and the Democratic Republic of Congo. Its size, rapidly changing ecosystem and complex socio-economic surroundings make it a difficult system to measure and understand. However, it is increasingly clear that to understand the changes in Nile perch stocks, the system needs to be put in its broader system context. The project entitled SEDEC – Disentangling the Social and Ecological Drivers of Change in Lake Victoria – is a collaborative endeavour to understand the lake's fisheries through an ecosystem perspective. This project brings together four PhD researchers from three departments to study socio-economic, environment and fishery effects on Lake Victoria's system and the Nile perch fishery. This particular study is the fourth element of the collaborative project, and combines knowledge from the different fields to understand how eutrophication and fishing are driving changes in the system, using a modelling approach.

In this thesis: a matter of perspectives

While defining this thesis' project, I reviewed literature and reports on Lake Victoria: at first all appeared to be scattered with contradicting and conflicting information and no straightforward means to align opposing views. I started assembling a database, to sort where, when and by whom different results had been obtained.

However, it soon became clear that studies do not overlap, data that appeared contradictory or different have a different origin in space, time and methodology. The apparent conflict in observations and understanding stems from the sheer size, complexity and rate of change of Lake Victoria's ecosystem: each observation and derived understanding is true, in its context. Each context reflects one in an infinite number of possible sampling points – represented by each Lake Victoria user observation or scientist's study. With this in mind, instead of trying to identify whether fishing or eutrophication is the root cause of changes in Lake Victoria's system, I aimed to understand how these two drivers influence the system.

The second chapter in this thesis represents an attempt to combine data from the database: find out how different elements of Lake Victoria that had been studied independently fit together, in their context. For this, we grouped data collected in a narrowed-down area outside the Mwanza Gulf (in Tanzania) covering three distinct years and described the food web there before, during and after the Nile perch boom. We used a mass-balance approach, i.e. we described the food web in units of biomass, and assumed that the food web was closed and that thus all flows of biomass in and out of every food web group would sum to zero. With this assumption, we could find which data could actually be combined, as well as obtain – by difference – data values that were missing.

In the third and fourth chapter of this thesis, we combine perceptions of the radical changes that took place thirty years ago. The Nile perch boom was a surprise: it happened rapidly and had dramatic consequences, but took place a long time after the introduction of Nile perch. In chapter three we study how this perceived delay inspired contradicting hypotheses concerning what might have prevented or triggered the Nile perch boom, we then provide a baseline against which to compare expected and observed Nile perch appearances. In chapter four, we investigate whether one of these hypotheses – that Nile perch recruitment was initially slow because native haplochromines predated on Nile perch eggs – would produce a delayed but sudden invasion. For lack of data against which to calibrate this model, we put it in the broader context of the role of diversity in the invasion success of an introduced predator, and investigated the effects of diversity loss on the resilience of an ecosystem.

In the fifth chapter we build a physiologically structured population model calibrated to Nile perch to investigate mechanisms behind the growth of Nile perch individuals and populations. We here go to the core of the SEDEC's main question, looking at how resource abundance and availability – our proxies for enrichment consequences at the level of Nile perch – influence the growth of Nile perch and viability of fishing mortality rates.

Chapter six represents a true compilation of perspectives; it is a synthesis of the knowledge of Lake Victoria scientists from around the world, representing all levels of expertise on Lake Victoria's fish, history, limnology, societies and functioning. This synthesis yields a social-ecological description of Lake Victoria, from which we can unravel the resilience of this system to changes, and see the water for the fish. In my concluding remarks I reflect on the results of chapters 2 to 6 in the context of the system as a whole.

Chapter 2

Collapse and reorganization of a food web of Mwanza Gulf, Lake Victoria*

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Summary

Lake Victoria in East Africa is the world's second largest freshwater system. Over the past century the ecosystem has undergone drastic changes. Some 30 years after the introduction of Nile perch (*Lates niloticus*) and Nile tilapia (*Oreochromis niloticus*) in the 1950s, the highly diverse community of native haplochromines collapsed, leaving a system dominated by only four species: the native cyprinid dagaa (*Rastrineobola argentea*) and shrimp (*Caridina nilotica*), as well as the introduced Nile perch and Nile tilapia. More recently, an unexpected resurgence of haplochromines has been reported. To understand these changes in terms of ecosystem functioning and of changes in growth of trophic groups, we created mass balances of the food web near Mwanza, Tanzania, before, during, and after the Nile perch boom (1977, 1987, and 2005), using the application ECOPATH. We connected these mass balances with a dynamic model assuming linear trends in net growth rates of the trophic groups. Our analysis suggests that the Nile perch boom initially altered the biomass distribution over trophic levels. Also, results indicate that not only fishing but also changes at the detritivores' trophic level might have played an important role in driving changes in the system. Both the mass balances and the dynamic model connecting them reveal that, after a major distortion during the Nile perch boom, the biomass distribution over the main trophic levels had largely recovered its original (1977) state by 2005. However, no such return appeared in terms of community structure. Biodiversity in the new state is dramatically lower, consisting of introduced species and a few native surviving species. We conclude that at an aggregate level Lake Victoria's ecosystem has proved to be resilient in the sense that its overall trophic structure has apparently recovered after a major perturbation. By contrast, its intricate functional structure and associated biodiversity have proved to be fragile and seem unlikely to recover.

Introduction

Lake Victoria in East Africa is a unique freshwater system as it is the world's largest tropical lake and is geologically and hydrologically different from its neighboring African great lakes (Bootsma and Hecky 2003). The high haplochromine diversity that characterized Lake Victoria until the 1980s became an iconic example of speciation (Kaufman 1992). Then, following the well- documented introduction of Nile perch, the lake's system has become a textbook study of the effects of species introductions and invasions on ecosystems (Witte *et al.* 2007a).

Nile perch (*Lates niloticus*) and Nile tilapia (*Oreochromis niloticus*) were introduced in the 1950s, but the first major ecosystem shift only became noticeable 30 years later (Reynolds and Greboval 1988), when the very diverse and complex haplochromine-based ecosystem was replaced by a system dominated by only four species: the native dagaa (*Rastrineobola argentea*) and lake atyid shrimp (*Caridina nilotica*) and the exotic Nile perch and Nile tilapia (Reynolds and Greboval 1988, Goudswaard *et al.* 2008). Since the Nile perch boom in the 1980s, its fishery has been the main source of income for ever-growing lakeside populations (Balirwa 2007).

New transformations in Lake Victoria's ecosystem have been occurring since the 1990s: stocks of haplochromines have increased after their collapse in the 1980s and the Nile perch population is dominated by smaller individuals than previously (Katunzi *et al.* 2003, Mkumbo *et al.* 2007). The system is now being exploited at an industrial scale and its resources, mostly Nile perch and dagaa, are exported internationally (Balirwa 2007). The lake's fisheries are said to support 30 million lakeshore inhabitants (Awange and Ong'ang'a 2006). Because of ongoing and unpredictable changes to fish stocks, fishing communities and economies built on the fishing industry now fear for the sustainability of the stocks (Balirwa 2007).

Many different processes affect Lake Victoria's ecosystem, such as species introductions and invasions, fishing, eutrophication, damming, and pollution (Ogutu-Ohwayo *et al.* 1997). However, most research on Lake Victoria has focused on studying the direct effects of species introduction and removal on a select group or food chain and has been mainly centred on fish. An understanding of the role and function of each group or species and their interrelations in the wider ecosystem perspective is still lacking (Goudswaard *et al.* 2006). In this study we compile and structure available data on pieces of the system to better understand the food web. Our aims are to uncover processes underlying changes in the system and to provide a better basis for unravelling the functioning of this dynamic food web.

We limit our study to the northern part of the Mwanza Gulf in Tanzania. This is an area of the lake in which the most extensive and comprehensive research has been undertaken, first sporadically by the East African Freshwater Fisheries Organization (EAFFRO) several decades ago, then from 1977 for 15 years by the Haplochromis Ecology Survey Team (HEST). Starting in 1980, the Tanzania Fisheries Research Institute (TAFIRI) collaborated with HEST and then continued carrying out research and surveys in the Tanzanian part of Lake Victoria. Surveys are increasingly standardized and executed in parallel with those carried out by the fisheries research institutes of Uganda and Kenya, under the guidance of Lake Victoria's Fisheries Organization (LVFO).

Using published studies and unpublished survey data, we first create three mass balances of the food web, describing its trophic groups, their functions and their interactions before, during, and after the Nile perch boom. To understand how trophic groups might have changed between 1977 and 2005, we then connect these mass balances with a parsimonious dynamic model that assumes linear trends in net growth rates of the different trophic groups.

Methods

Mass balances and data

We use mass balances to describe the food webs: each trophic group is represented as a biomass, all of which are balanced by mass flows between groups. In these balances, all that is consumed and produced is accounted for. The area we modelled represents a habitat with a depth ranging from 6 to 25 m with a mud bottom and no specific refugium structure.

Our analysis was done with the ecosystem model ECOPATH (Christensen *et al.* 2005), in which, for each trophic group, production is a sum of growth, migration, and all mortalities (eq. 1) and consumption is divided into production and waste (eq. 2):

1) Production = catches + predation mortality + other mortality + biomass accumulation + net migration
2) Consumption = production + respiration + unassimilated food

Productivity, consumption, catches, diets, and either biomass or ecotrophic efficiency (the part of the production that is further used in the system [or 1-waste fraction]) are the key input values needed for an ECOPATH mass balance. We used life-history parameters and empirical relations to calculate the productivity and consumption of each group (see Appendix A for details) (Christensen *et al.* 2005). We assumed the system was closed and did not include import or export of matter to the system. We assume masses are balanced at least over the period of time modelled, and biomass accumulation is set to zero.

We first compiled a database in which we entered, for all studied groups and species of Lake Victoria, their life-history parameters as we found them in the literature. For each of the three periods, we chose a representative year with most data (1977, 1987, and 2005). Data used for our 1977 and 1987 food web depictions came from published literature, whereas for our 2005 mass balance we also used unpublished survey data obtained from TAFIRI and the LVFO (see Appendix B: table B1 for details). Then, through a literature search, we selected groups that were dominant in the type of habitat we modelled during the different years. The parameter values collected at our chosen site and years formed our *a priori* set of values. When necessary data were not found we used values collected as close as possible in time and space to that of our models. The opportunistic character of most fish makes their diets location- and time-specific, so while the existence of a feeding interaction is usually known, the exact diet is often unknown. We initially entered plausible best-guess diet values that represented an existing interaction for which the relative role of each prey to its predator reflected diet reports and prey availability. As first input to our mass balances we entered values for production and consumption from our *a priori* set, as well as catches and best-guess diets. We then entered either ecotrophic efficiency or biomass, depending on data availability, and let the application ECOPATH estimate the remaining parameter, based on the two master equations (Eqs. 1 and 2). All groups and species are represented in units of fresh mass. Our first calibration step consisted of changing production and consumption values within our *a priori* chosen ranges to obtain a mass-balanced model. In our second calibration step we tested and modified diets and obtained ranges of feeding values for which (1) feeding interactions described in literature were best represented, (2) models were mass-balanced, and (3) the produced food web resembled that reported for the Mwanza Gulf at each modelled time. This second calibration step produced the final sets of *a posteriori* estimates of production, consumption, and biomass values and diet ranges that made the models mass-balanced and created an output that best represented literature descriptions of the system (see Appendix B).

Food web processes

To further investigate changes in the position and trophic role of different groups in the food web, we first categorized them as a function of their main diet. This allowed us to compare groups with similar functions over the three different years, despite the big decline in species numbers after 1977. In each model, we then followed how the different trophic groups used biomass, relative to that produced through primary production. We distinguished, for each group, their relative biomass in the food web, consumption, and production. We then dissected consumption (relative to primary production) into predation mortality, catches, natural mortality, and waste, through respiration and unassimilated consumption.

Ecosystem indices

We compared the following system indices produced from the ECOPATH mass balances to study relative impacts of different drivers of change on system maturity, productivity, efficiency, and stability (Odum 1969, Christensen and Pauly 1992, Ulanowicz 2004, Christensen *et al.* 2005). (1) Primary production : respiration ratio is a measure of the system's maturity. A mature system is expected to have a production : respiration ratio close to 1. When this ratio is >1 it reflects an immature system whereas when it is <1 it reflects eutrophication. (2) The primary production : biomass ratio is also a measure of maturity and is expected to decrease as a system matures. (3) The quantity of biomass supported by the system's energy flow, here reflected in the system biomass : throughput ratio, is expected to increase with system maturity. (4) We compared mean trophic levels of catch, to identify the focus of fisheries. (5) Gross fishing efficiency measures fishery catches as a function of primary production and is expected to be <<1. A low gross efficiency indicates low exploitation or exploitation of the top predator. A higher gross fishing efficiency signals more efficient use of the system's production and exploitation of lower trophic levels. We did not compare the connectance index of our food webs, a ratio of realized to possible interactions in the system because we lack resolution within the trophic groups we modelled. (6) The system omnivory index is a more weighted measure of how connected the food web is than the connectance index; the higher the omnivory index, the more connected the food web (Christensen *et al.* 2005).

Dynamics

ECOPATH has a dynamic subroutine, ECOSIM, that is commonly used to distinguish the effects of bottom-up pressures (eutrophication) from those of top-down pressures (fishing) on systems. ECOSIM is based on ECOPATH mass balances and can be a good tool when it can be adapted and re-run to fit time series, and where one gains knowledge from changing assumptions regarding top-down and bottom-up pressures. However, the consistent data set we have gathered on Lake Victoria is limited to three snapshots and these could be linked by a multitude of different dynamics. Therefore, in absence of consistent time series to falsify hypotheses generated by ECOSIM, we conducted a simpler, parsimonious dynamic analysis by calculating the linear changes in net growth rates of the different trophic groups that link our three mass balances. For each trophic group, using the application MAPLE, we derived and solved the straight-line equation that went through each of the three states (see Appendix C for an analytical solution to estimate intercept and slope of net growth rates for each trophic group). These linear trends provide a baseline for the dynamics in the period between 1977 and 2005 and yield a first approximation to the nonlinear development of relative biomasses of the major trophic groups during the whole period of observation. It is important to note that the fact that we work with relative biomasses does not hamper our analysis of linear patterns in net growth rates. Translating these relative biomasses into absolute values would affect the estimated net growth rate of each group equally and therefore not affect the differences in net growth rates.

Results

Mass balances

We distinguished 15 trophic groups in the 1977 mass balance, seven of which are monospecific (fig. 1, table 1). Nile perch was present but rare; only adult and subadult individuals were caught, in low numbers and mostly as by-catch (Goudswaard *et al.* 2008). Three species and one trophic group fill the piscivore function: Nile perch, two catfish species (*Bagrus docmak* and *Clarias gariepinus*), and piscivorous haplochromines. In our model, two haplochromine groups, zooplanktivores and prawn-eaters, as well as dagaa (*Rastrineobola argentea*), process benthic macroinvertebrates and zooplankton. Two tilapiine species (*Oreochromis esculentus*, *Oreochromis niloticus*), two haplochromine groups, the shrimp *Caridina nilotica*, and a zooplankton group occupy the detritivore/phytoplanktivore niche. All piscivores feed on zooplankton and shrimp in their juvenile stages (table 1). Detritivorous and zooplanktivorous haplochromines as well as native tilapia (*O. esculentus*) are the dominant fish groups.

Our 1987 model represents the peak of the Nile perch boom in the Mwanza part of the lake (fig. 1, table 2). In this model we only have nine trophic groups, with

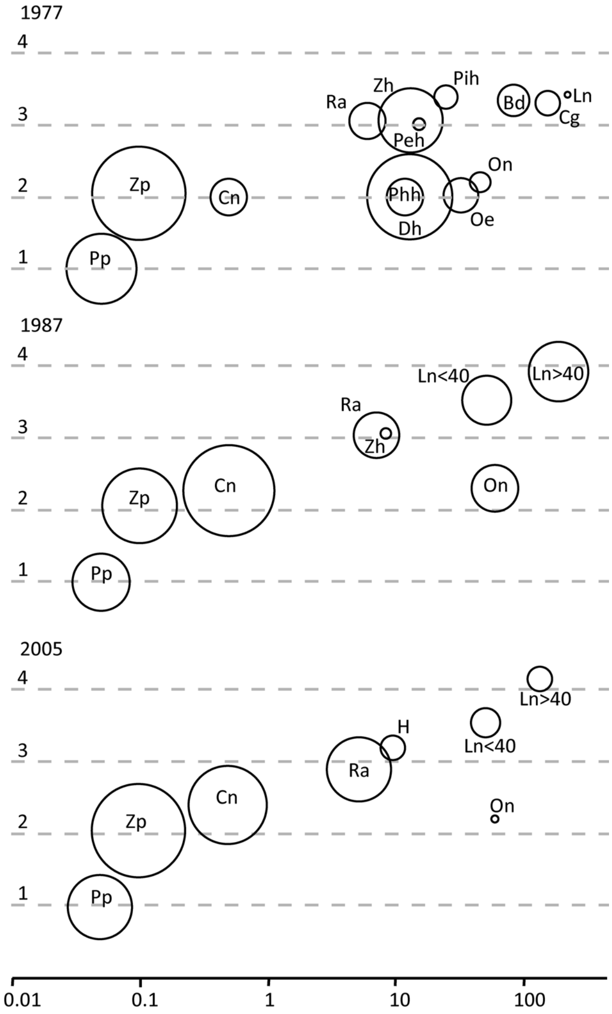

Figure 1: Relative biomasses of 1977, 1987 and 2005 food web groups. On the x-axis is the log of the maximum hypothetical length of the groups (logL_∞), on the y-axis are trophic levels (horizontal dotted lines). The area of each group's circle represents the percent biomass it represents relative to total: the sum of all pictured groups is 100%. Bd: *Bagrus docmak*; Cg: *Clarias gariepinus*; Cn: *Caridina nilotica*; Dh: detritivorous haplochromines; H: Haplochromines; Ln: *Lates niloticus* (Nile perch); Ln>40cm: Large Nile perch; Ln<40cm: small Nile perch; Oe: *Oreochromis esculentus*; On: *Oreochromis niloticus* (Nile tilapia); Peh: prawn-eating haplochromine; Phh: phytoplanktivorous haplochromine; Pih: piscivorous haplochromine; Pp: phytoplankton; Ra: *Rastrineobola argentea* (dagaa); Zh: zooplanktivorous haplochromines; Zp: zooplankton. While the detritus group is included in all mass-balances, for clarity we have removed it from this figure.

the number of multispecies groups reduced to three. Here Nile perch is divided into two different trophic groups, smaller or larger than 40 cm, to capture the ontogenetic shift in diet: large Nile perch is the only piscivore and consumes more dagaa (*R. argentea*) than previously, while smaller Nile perch here feeds mostly on the shrimp *C. nilotica*. Small Nile perch, dagaa, and zooplanktivorous haplochromines carry out the task of eating benthic macroinvertebrates and zooplankton, broadening their diets slightly (tables 1–3). Nile tilapia, *C. nilotica* shrimp, and zooplankton are the three remaining groups that feed on phytoplankton and detritus (table 2). Dominant species are the introduced Nile perch and Nile tilapia (native tilapia is no longer a representative component of the food web) as well as the native dagaa and shrimps. Planktivorous species ate bigger prey than they did in our 1977 food web (Wanink and Witte 2000a, Katunzi *et al.* 2003).

We have the same number of groups in our 2005 model as in the 1987 one (fig. 1, table 3). Nile perch is still the only piscivore, but its diet has reverted to include mostly haplochromines. There has been a shift in size structure of the Nile perch population as here smaller individuals are more abundant than large ones. Haplochromines are again an important component of the food web and most of them feed primarily on benthic macroinvertebrates, *C. nilotica* and zooplankton, thus moving up the food web and reaching a higher trophic level than before (tables 1–3, fig. 1), (Katunzi *et al.* 2003, Kishe-Machumu *et al.* 2008). Dagaa has slightly shifted down in trophic level as well as increased in relative biomass. The biomass of Nile tilapia is low in our model, despite reports that their stocks have increased. This is related to the fact that it does not contribute much to energy transfers at the scale of the Mwanza Gulf food web: it is the top predator of a much smaller trophic web than the one we describe, in a more sheltered and structured habitat.

Food web processes

To study the functioning of the food webs in the different periods, we sum different trophic groups into larger functional groups (table 4). Comparing these functional groups between the 1977 system and the less diverse but more productive

Table 1: Diet ranges for which the 1977 mass balance model output most resembles the literature description of the food web.

Predator	Prey	Diet contribution
L. niloticus	Piscivorous haplochromines	[0.05-0.1]
	B. docmak	[0-0.5]
	Prawn-eating haplochromines	[0-0.5]
	R. argentea	[0.05-0.1]
	Zooplanktivorous haplochromines	[0.1-0.15]
	Phytoplanktivorous haplochromines	[0.05-0.1]
	Detritivorous haplochromines	[0.2-0.35]
	C. nilotica	[0.2-0.25]
	Zooplankton	[0-0.1]
Piscivorous haplochromines	Piscivorous haplochromines	[0-0.03]
	Prawn-eating haplochromines	[0-0.02]
	O. esculentus	[0.02-0.1]
	R. argentea	[0.1-0.2]
	Zooplanktivorous haplochromines	[0.1-0.2]
	Phytoplanktivorous haplochromines	[0.02-0.04]
	Detritivorous haplochromines	[0.2-0.25]
	C. nilotica	[0.1-0.2]
	Zooplankton	[0.1-0.2]
C. gariepinus	*R. argentea*	[0.1-0.2]
	Zooplanktivorous haplochromines	[0.1-0.2]
	Phytoplanktivorous haplochromines	[0-0.02]
	Detritivorous haplochromines	[0.2-0.3]
	C. nilotica	[0.2-0.3]
	Zooplankton	[0.2-0.3]

B. docmak	*R. argentea*	[0.1-0.2]
	Zooplanktivorous haplochromines	[0.1-0.2]
	Phytoplanktivorous haplochromines	[0-0.02]
	Detritivorous haplochromines	[0.2-0.3]
	C. nilotica	[0.2-0.3]
	Zooplankton	[0.2-0.3]
Prawn-eating haplochromines	*C. nilotica*	1
O. esculentus	Phytoplankton	1
O. niloticus	Zooplankton	0.2
	Phytoplankton	0.8
R. argentea	Zooplankton	1
Zooplanktivorous haplochromines	Zooplankton	1
Phytoplanktivorous haplochromines	Phytoplankton	1
Detritivorous haplochromines	Detritus	1
C. nilotica	Detritus	1
Zooplankton	Zooplankton	0.5
	Phytoplankton	0.95

(in terms of fishery landings) 1987 system, we observe that the biomass distribution went from pyramid-shaped to top-heavy, through a big increase in the relative biomass of the piscivorous (Pisc) and a decrease of the zooplanktivores and benthic macroinvertebrate eaters (Zoobenth) (fig. 2, centre value of each box; fig. 3). This structural change was supported by increased productivity of the phytoplanktivore and detritivore (Phytdet) trophic group: Phytdet more than doubled in productivity (from ~12% in 1977 to 26% in 1987; fig. 2) without changing much in relative biomass and detritus consumption (21.2% of primary production in 1977, 23.4% of primary production in 1987; fig. 2). In this way, as much primary production was being processed by the Phytdet group, but more energy made its way up the food web to the Pisc group. This can be explained by the fact that with the diversity collapse in the Phytdet group, haplochromines were replaced by the small, fast-growing shrimp *Caridina nilotica* (fig. 1).

Table 2: Diet ranges for which the 1987 mass balance model output most resembles the literature description of the food web.

Predator	Prey	Diet contribution
L. niloticus > 40cm	*L. niloticus > 40cm*	[0-0.1]
	L. niloticus < 40cm	[0.2-0.28]
	R. argentea	[0.3-0.5]
	O. niloticus	[0-0.01]
	Zooplanktivorous haplochromines	[0-0.01]
	C. nilotica	[0.25-0.3]
	Zooplankton	[0.01-0.05]
L. niloticus < 40cm	*L. niloticus* < 40cm	[0.07-0.09]
	R. argentea	[0.2-0.3]
	C. nilotica	[0-1]
	Zooplankton	[0-1]
R. argentea	*C. nilotica*	[0.15-0.25]
	Zooplankton	[0.8-0.85]
	Phytoplankton	[0-1]
O. niloticus	*C. nilotica*	0.2
	Zooplankton	0.05
	Phytoplankton	0.7
	Detritus	0.05
Zooplanktivorous haplochromines	*C. nilotica*	[0.1-0.4]
	Zooplankton	[0.6-0.9]
C. nilotica	Zooplankton	[0.2-0.3]
	Phytoplankton	[0.2-0.3]
	Detritus	[0.4-0.6]
Zooplankton	Zooplankton	[0-0.008]
	Phytoplankton	[0.92-1]

Between 1987 and 2005, biomass distributions over the food web regained a pyramid structure, with the Pisc group again smaller than the Zoobenth group (fig. 3). This was mainly caused by an increase in Zoobenth's relative biomass through the return of haplochromines and a boom in dagaa biomass (fig. 1). However, this structural recovery did not translate into a return to previous energy transfer pathways: in 2005, the Zoobenth group was intercepting a larger part of energy flowing from the Phytdet group to the Pisc group than previously. Reasons behind this are that returning haplochromines consumed larger prey than previously and that the dagaa boom resulted in higher predation on zooplankton (fig. 2, tables 1 and 3). These functional switches in the Zoobenth group reflect strongly in its increased predation on Phytdet (from 4.7% in 1987 to 9.7% in 2005; fig. 2), as well as in increased detritus burial values (18% in 1977, 22% in 1987, and 27.7% in 2005; fig. 2).

While the increase in fast-growing shrimp facilitated the Nile perch boom in 1987, the ensuing increase in haplochromines and dagaa and in their predation on lower trophic groups reduced again the fraction of primary production that made it up the food web. The models also reveal the increase in efficiency with which the system is being exploited, through the steady increase in the ecotrophic efficiency of the piscivore group (fig. 2), illustrating how a large part of Pisc production makes it to the next trophic level, here fisheries.

Ecosystem indices

A comparison of system indices yielded by the application ECOPATH shows that different stresses, namely introduction, extinctions, fishing, and eutrophication, have had an enormous effect on food web structure and functioning (table 5).

The primary production to respiration ratio shows a large increase between 1977 and 1987 and slighter decrease between 1987 and 2005. The values are hundreds of folds larger than the 1 value expected for mature systems. The primary production : biomass ratio also has an overall upward trend, but first decreases, and then increases. A third maturity index, the total biomass-to-system throughput,

Table 3: Diet ranges for which the 2005 mass balance model output most resembles the literature description of the food web.

Predator	Prey	Diet contribution
L. niloticus > 40cm	*L. niloticus < 40cm*	[0.1-0.2]
	R. argentea	[0.25-0.35]
	O. niloticus	[0-0.005]
	Haplochromines	[0.4-0.55]
	C. nilotica	[0.01-0.1]
L. niloticus < 40cm	*L. niloticus* < 40cm	[0.05-0.1]
	R. argentea	[0.25-0.3]
	Haplochromines	[0.05-0.1]
	C. nilotica	[0.15-0.2]
	Zooplankton	[0.35-0.45]
R. argentea	*C. nilotica*	[0.15-0.2]
	Zooplankton	[0.55-0.65]
	Phytoplankton	[0.15-0.25]
O. niloticus	*C. nilotica*	0.05
	Zooplankton	0.15
	Phytoplankton	0.7
	Detritus	0.1
Haplochromines	*C. nilotica*	[0.2-0.4]
	Zooplankton	[0.6-0.8]
C. nilotica	Zooplankton	[0.35-0.45]
	Phytoplankton	0.1
	Detritus	[0.45-0.55]
Zooplankton	Zooplankton	0.05
	Phytoplankton	0.95

changes very little overall. Mean trophic level of the catch has an upward trend over the three years modelled, despite a slight decrease between 1987 and 2005. The initial increase reflects the fact that the fishery target is an introduced top predator, whereas the decrease is a consequence of increased catches of smaller Nile perch and dagaa. Gross efficiency overall trebles: showing a slight increase between 1977 and 1987, but then doubling between 1987 and 2005. This indicates an increase in fishing efficiency as well as an increase in catches of fish lower in the food web. The omnivory index increases between 1977 and 1987 and then remains stable.

Dynamics

We linked our three mass balances with linear changes in net growth rates of the different trophic groups (fig. 4; for details, see Appendix C). The Pisc group follows opposite trends in change of growth over time to that of the lower trophic groups: Zoobenth and Prim. Given the similar biomass of the Phytdet group in our three mass balances, the linear rate of change in that group remains zero. Linear changes in dynamics yield the nonlinear changes in biomass observed in the system (fig. 4). In fact, our analysis shows that the most simple explanation for the boom in the Pisc group in the late 1980s is a strong positive growth rate in the late 1970s followed by a continuous linear decrease in growth rate in the following decades, either through a reduced reproductive rate, an increased mortality, or a combination of both.

Table 4: Species and group aggregation as a function of their main role in the food web, *: only present in the 1977 models, **: only present in the 2005 model.

Trophic group and diet	Composition	Equivalent 1977 trophic level
PISC: piscivores	Nile perch; piscivorous haplochromines*; *Bagrus docmak**; (catfish) *Clarias gariepinus**(catfish)	3
ZOOBENTH: benthic macroinvertebrate and zooplankton feeders	Prawn-eating haplochromines* Zooplanktivorous haplochromines;* Haplochromines**; *Rastrineobola argentea* (dagaa)	3
PHYTDET: phytoplanktivores and detritivores	Phytoplanktivorous haplochromines*; Detritivorous haplochromines*; *Caridina nilotica* (atyid shrimp); *Oreochromis esculentus** (native tilapia); *Oreochromis niloticus* (introduced tilapia); Zooplankton	2
PRIM: primary producers and detritus	Phytoplankton Detritus	1

Table 5: Dimensionless system indices as produced by the three ECOPATH mass-balances (Odum 1969, Pauly *et al.* 1993, Ulanowicz 2004, Christensen *et al.* 2005).

Index	1977	1987	2005
Total primary production/ total respiration	369	789	763
Total primary production/total biomass	46	40	57
Total biomass/total throughput	0.009	0.009	0.007
Mean trophic level of the catch	2.8	3.5	3.1
Gross efficiency (catch/net p.p)	0.002	0.003	0.006
System omnivory index	0.05	0.15	0.15

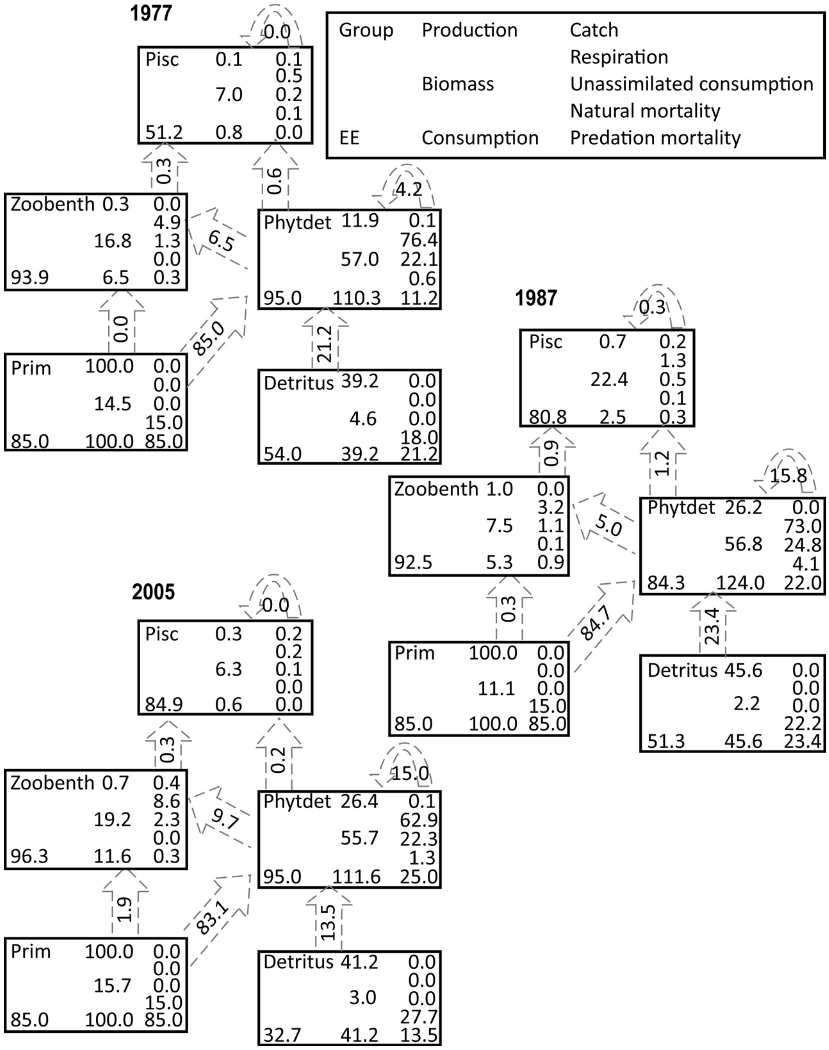

Figure 2: Biomass flows relative to total primary production through the food web in 1977, 1987, and 2005. Names in the upper left-hand box are laid out to match values in each box. All values are percentages and relative to primary production, except ecotrophic efficiency, which represents the part of the production further used in the system. Values in arrows represent biomass flows between connected trophic groups relative to total primary production. Abbreviations are: Pisc, piscivores; Zoobenth, benthic macroinvertebrate and zooplankton feeders; Phytdet, phytoplanktivores and detritivores; Prim, primary producers.

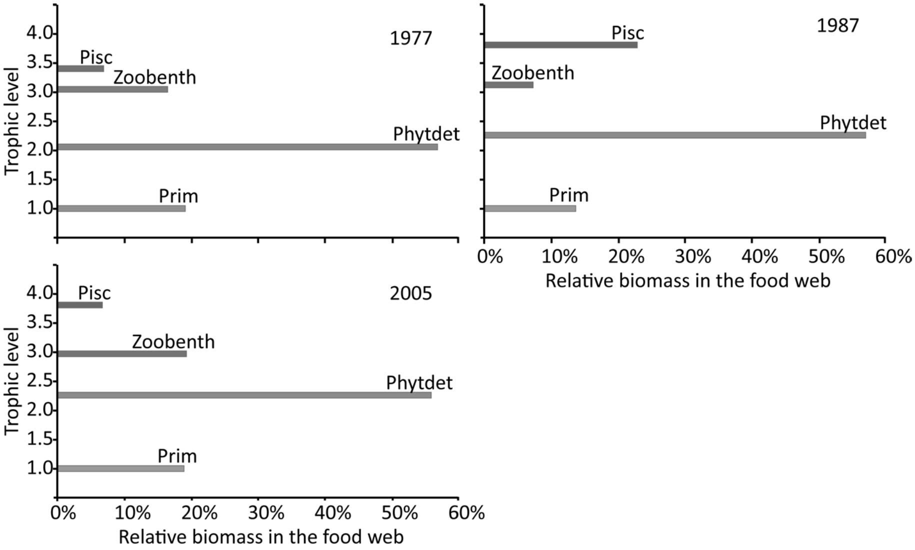

Figure 3: Relative biomass distribution over trophic groups in the food web in 1977, 1987, and 2005. The groups are placed along the y-axis following their trophic level, weighted to the relative abundance of component species and groups. See fig. 2 for an explanation of group abbreviations.

Discussion

Despite the uncertainty of our parameters and gross simplification of our food webs, our method of narrowing the *a priori* chosen ranges of parameter values allowed us to reveal how Lake Victoria's ecosystem moved through a sequence of strongly contrasting states over the past decades. Our analysis with the dynamic model shows that these contrasting states are paralleled in the changes in net growth rate of different functional groups, in particular Pisc and Zoobenth. While the food web seems to have regained the 1970s structure, no such recovery appears at a functional level because energy pathways are now fundamentally different and trophic groups have different members.

We suggest that the loss of key haplochromine trophic groups probably released smaller, more productive organisms from competition, allowed them to proliferate and to support the highly productive system that exists since the late

1980s. Detritivorous haplochromines dominated before the Nile perch boom. Their collapse could be the reason behind the abrupt increase of their direct competitors: the native detritivorous shrimp *C. nilotica*. Similarly, the collapse of phytoplanktivorous haplochromines might have released zooplankton from competition. These species shifts had several consequences: first, faster growing, more productive species replaced the haplochromines, perhaps explaining how the system could support the highly productive Nile perch fishery. Secondly, a release from competition and/or an increase in prey availability allowed for dagaa to flourish and for the more adaptable, returning haplochromines to find a new niche, feeding on macroinvertebrates.

The apparent recovery of zooplanktivores and benthic macroinvertebrate eaters, however, does not imply a restoration of the system to its 1977 organization on the haplochromine side; groups that disappeared were replaced by species that

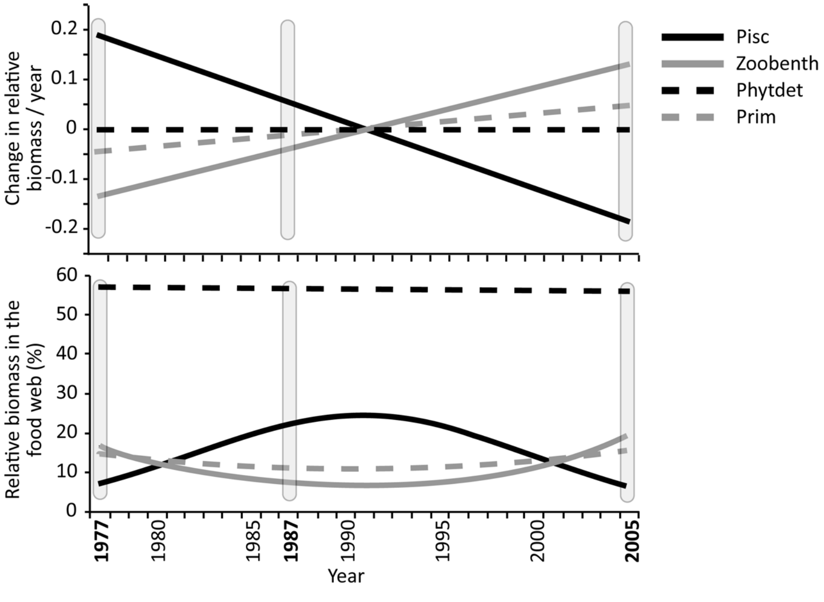

Figure 4: Dynamic model. Top panel: linear rates of change in relative biomass of each trophic group that link the observed relative biomasses in 1977, 1987, and 2005. Bottom panel: changes in relative biomass as inferred from linear dynamics; values obtained fit 1977, 1987, and 2005 observed relative biomasses (shaded years). See fig. 2 for an explanation of group abbreviations.

apparently evolved swiftly to change functions (Witte *et al.* 2007b, 2008). Also, after the Nile perch boom era, other zooplanktivores such as dagaa widened their diets to include more benthic invertebrates (Wanink and Witte 2000b, Katunzi *et al.* 2003). The return of haplochromines and the dagaa upsurge play an important role in the transfer of energy between detritivores/phytoplanktivores and piscivores and is a possible cause of the decrease in detritus processing and in piscivore production. Further insight to these and other processes at lower trophic levels is essential to construct an overall view of what drives the dynamics in the system. We suggest the fish-oriented perspective currently taken to study the lake needs to be broadened to a more general ecosystem approach.

Species' aggregation into groups and choice of species excluded from the models were based on data availability and on their reported importance in the food web. However, because studies on the lake have mostly focused on fish, existing data poorly account for limnological and environmental aspects of the ecosystem. As a result, the role of different phytoplankton and zooplankton groups as well as of macroinvertebrates and detritus could not be examined well in this study. There is also a lack of resolution when it comes to studying the diversity of different species-rich groups, especially in our 1977 mass balance. Despite this, since species and groups with low biomasses have little effect in model calibration, it seems reasonable to assume that the main interactions and patterns we describe are a good illustration of the trends of change in our food webs. While very difficult and complex, a more dynamic approach would probably allow a better grasp of the system's response to ongoing change (Mooij *et al.* 2010).

Whether it is fishing or eutrophication that predominantly drives change in Lake Victoria's ecosystem is an ongoing debate, the conclusion of which might have a great impact on how the lake's resources are managed (Kolding *et al.* 2008). Landings of Nile perch have increased and the dagaa fishery has properly taken off in the past decade (Balirwa 2007): this we see in the increased gross fishing efficiency index and in the decrease in mean trophic level of the catch between 1987 and 2005. An increased anoxic layer and the 1990s water hyacinth invasion are clear symptoms of increased nutrient loading (Hecky *et al.* 1994). However, through studying this particular food web in the system, we demonstrate how neither of the two chosen drivers has a distinct direct causal effect on observed changes in the food web. From the maturity indices we can conclude that overall the food web we model shows no sign of maturation, perhaps an unsurprising observation considering the disturbances to which the food web has been subjected. Between 1977 and 1987, the strong increase in production to respiration is paralleled in a decrease in primary production : biomass ratio, reflecting that excess production converted to some degree in accumulated biomass. The opposing trends of those two indices after the Nile perch boom might also reflect the opposite trend of the same process: less production leads to less biomass accumulation. However, the asymmetry in the changes in these two ratios can also indicate that top-down and bottom-up processes have had non-complementary effects on the food web. While the effects of both processes are indistinguishable from these ratios, they seem to emphasize the fact that no single driver is behind changes in the Mwanza food web, as it appears that the system changed differently before and after the Nile perch boom and that different stressors have sometimes synergistic and at other times conflicting effects on these indices.

The system's reaction to external pressures, including not only fishing and eutrophication but also species introductions, depends very strongly on interactions within the food web. In turn, these interactions in large part are directed by processes maintaining the food web's functional and structural integrity.

In light of our observations we need to reformulate our questions about Lake Victoria's ecosystem: we should not ask whether fishing or eutrophication cause changes, but rather how fishing and eutrophication influence the dynamics of the system, bearing in mind the functional and response diversity that characterizes it and having first a good grasp of how species interact and of population dynamics. However, it is important to realize that the ability of trophic groups to respond to ongoing pressures is likely to become more unpredictable and less flexible as pressures increase and diversity declines (Loreau *et al.* 2001).

Moreau *et al.*'s (1993) models of the Kenyan side of the lake in 1971 and 1985 showed comparable changes in biomass distributions to those we described: the Nile perch boom made the food web top-heavy. Underlying processes however appear to be slightly different: in Kenya, following the decline in haplochromines, diets of Nile perch shifted from fish to macrozoobenthos, whereas in our models larger Nile perch remain primarily piscivorous (Mkumbo and Ligtvoet 1992) and it is mainly detritivores and planktivores that take over the task of processing macro-benthic invertebrates and zooplankton. This illustrates the importance of local conditions in determining food web interactions and points out the functional heterogeneity of Lake Victoria's ecosystem. Our depictions of the system and its changes are likely to be site specific, other patterns and changes may well be observed in neighbouring regions, driven by other habitat and environmental conditions.

Currently, the Nile perch fishery is regulated by a minimum allowable catch size limit (Kolding *et al.* 2008). This supposes that the sustainability of the fishery only depends on how many fish of a certain size class allow for the whole population to survive, and that this rule is generalizable over the whole lake at all times of year. However, our study shows that sustaining the top predator has so far relied on massive changes to the structure of the food web around it, and this dependence on processes internal to the food web might very strongly affect population dynamics, e.g., efficiency, growth rates, and size structure, and thus influence the reaction of the system to any management policy (Pine *et al.* 2009). Comparing our work with that of Moreau *et al.* (1993), we conclude it is likely that these food web rearrangements are site-specific. To manage the Nile perch fishery it is necessary to understand resource-dependent dynamics of Nile perch populations. Such knowledge would allow the adaptation of management plans to both local resource availability situations of Nile perch populations and to local fishing needs or practices.

We are clearly far from comprehending the mechanisms of change in this fascinating system. Much attention has been focused on top-down drivers of change, such as the introduction and exploitation of species, but it is likely that ongoing eutrophication of the lake is also a major player in the apparent restructuring of its system. To understand and manage such a changing system we need to take a step beyond arguing what the causes of the changes are to identifying how structures and functions of the food web influence and define responses of its components to ongoing pressures (Eero *et al.* 2011). Only by gaining and integrating knowledge of different drivers of change to the ecological and evolutionary mechanisms of adaptation and transformation will we be able to suggest potential responses of the system to different pressures on the lake.

Chapter 3

Was *Lates* late? A null model for the Nile perch boom in Lake Victoria

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"The real purpose of scientific method is to make sure Nature hasn't misled you into thinking you know something you don't actually know" Robert M. Pirsig in Zen and the Art of Motorcycle Maintenance

Summary

Nile perch suddenly invaded Lake Victoria between 1979 and 1987, 25 years after its introduction in the Ugandan side of the lake. Perch then replaced the native fish diversity and irreversibly altered the ecosystem and its role to lakeshore societies. The delay in the Nile perch boom generated several hypotheses regarding its growth at low abundances and a hunt for triggers of the sudden boom – all hypotheses having important implications for the management of perch stocks. We use a parsimonious growth model to predict when the Nile perch invasion should have been expected, given its growth rate, initial stock size and introduction year. We find exponential growth explains the timing of the perch boom at the scale of Lake Victoria, suggesting that complex mechanisms are not necessary to explain its invasion. However, the boom started in Kenya before Uganda, indicating perhaps that Allee effects act at smaller scales than that of the whole Lake. The Nile perch invasion of other lakes suggests that habitat differences may also have an effect on invasion success. Our results suggest there is probably no single management strategy applicable to the whole lake that would lead to both efficient and sustainable exploitation of its resources.

"The trigger for the Nile perch irruptions is not known; it is interesting and mysterious that the fish should have persisted for so long and at such low densities before the explosion." (Kaufman 1992)

Introduction

Nile perch were first introduced surreptitiously to the Ugandan side of Lake Victoria in 1954 after a decline in native tilapia and other major food fishes (Pringle 2005a, Goudswaard *et al.* 2008). While a few Nile perch individuals were sighted over the years, this introduction did not initially cause any apparent changes to the system. Nine years after the unofficial introductions, authorities in Uganda and Kenya carried out proper introductions of both adult and fingerling Nile perch. Twenty years after this, the first major catches of Nile perch were reported in Uganda, and over the course of four years, between 1982 and 1985, Nile perch had replaced most indigenous species in catches. The same occurred a few years later in Tanzania, at the opposite end of the lake, between 1983 and 1987 (table 1) (Pringle 2005a, Goudswaard *et al.* 2008).

The sudden Nile perch invasion and haplochromine collapse caused major social and economic changes in lakeside populations (Pringle 2005b, Balirwa 2007, Chapman *et al.* 2008). The fisheries of native species used to provide only for a local and regional market and were managed on small scale- and value-investments. Nile perch, however, are exported internationally and processed at a larger scale (in filleting factories) (Balirwa 2007). To allow factories and export businesses to operate at capacity requires maintaining constant high catches of Nile perch. Since the mid-1990s however, Nile perch catches have been fluctuating, and some haplochromine species have increased in abundance (Witte *et al.* 2000, 2007a). Uncertainty in catches and the resurgence of haplochromine species have been interpreted – though not unanimously – as indicative that Nile perch stocks are being overfished (Njiru *et al.* 2006, Mkumbo *et al.* 2007, Kayanda *et al.* 2009). A key consideration when determining maximum sustainable yields of a stock lies in understanding the behaviour of the fished population at low densities.

A common question among lake Victoria scientists is why did it wait 25 years after its introduction to do so (Kaufman 1992, Verschuren *et al.* 2002)? Also, while Nile perch successfully invaded and became dominant in lakes Victoria, Kyoga and Nabugabo – where they were introduced – they are only found in low densities in lakes Chad, Turkana, Albert and the man-made Lake Volta (Ogutu-Ohwayo 1988, 1990, Achieng 1990, van Zwieten *et al.* 2011) – where they are native. Therefore, the Nile perch 25-year invasion delay, compounded with its cannibalistic tendencies and the fact that it has not colonised all environments with equal success, have led to several hypotheses regarding the viability of the stock below a certain density.

Kitchell *et al.* (1997) performed a modelling study aimed at understanding the balance between fishing pressure on Nile perch and predation pressure of Nile perch on haplochromines. While identifying the caveats of their modelling approach, the authors stated that increased fishing pressure might reduce cannibalism and have a compensatory, i.e. beneficial, effect on recruitment, implying that growth rates of the population would be higher at low population densities.

Table 1: How the Nile perch was introduced and invaded, from Goudswaard *et al.* (2008)

Year	Event	Location
1954	Illegal introduction of unknown number (& size) of Nile perch	Jinja, Uganda
1960	Catch of 8 Nile perch between 28-43 cm long	Jinja, Uganda
May 1962 - September 1963	Official introduction of 35 subadults (16-43 cm) and 339 fingerling Nile perch	Entebbe, Uganda
1963	Official introduction of 8 individuals (size unknown)	Nyanza Gulf, Kenya
1979-1982-1983	Onset of Nile perch boom	Kenya- Uganda-Tanzania
Until 1985	Catches of adult and subadult Nile perch	Mwanza, Tanzania
1986 - 1985 - 1987	Peak of Nile perch boom	Kenya- Uganda-Tanzania
1981-1985	First wave of Nile perch boom	Kenya-Uganda
1983-1987	Final wave of Nile perch boom	Tanzania

A later ecosystem study (Walters *et al.* 1997) came to the opposite conclusion: assuming haplochromines are competitors or predators of juvenile Nile perch, increased fishing pressure on Nile perch would release predation pressure on haplochromines and lead to an increase in their abundance, which in turn would lead to a decrease in Nile perch recruitment. This scenario would imply that growth rates of the population would decrease below a certain Nile perch population density: the depensatory effect of haplochromines on recruitment would create an Allee effect. The strength of this hypothesis was later reinforced by the observation that the depensation effect might even have slowed down the invasion of Nile perch, and that the Nile perch boom was only made possible by the prior decline in haplochromine abundance (Walters and Kitchell 2001).

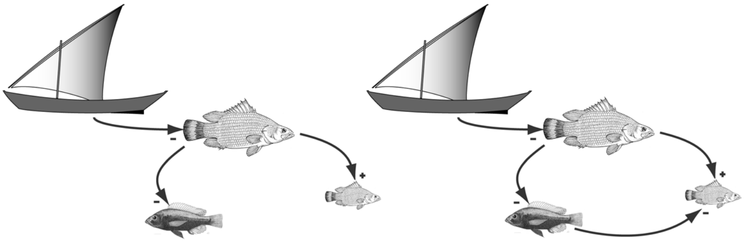
Goudswaard *et al.* (2008), from their own most complete description of the Nile perch invasion wave, state that the 25 year time-span between the introduction and invasion is remarkable, as is the fact that the Nile perch invasion appears to have started in Kenya rather than in Uganda, where they were first introduced. They hypothesize that depensation by haplochromines might be behind this pattern: indeed haplochromine stocks collapsed first in Kenya, and might thus have allowed for Nile perch to boom (Goudswaard *et al.* 2008).

A recent comparative study of Nile perch diets in the Mwanza Gulf before and after the resurgence of haplochromines (Kishe-Machumu *et al.* 2012) indicates that haplochromines are the preferred prey of Nile perch and that cannibalism mostly occurs when they are absent. The authors hypothesise that the return of haplochromines will therefore either compensate for the negative effects of cannibalism or – if they have no depensation effect – allow for an increase in Nile perch stocks.

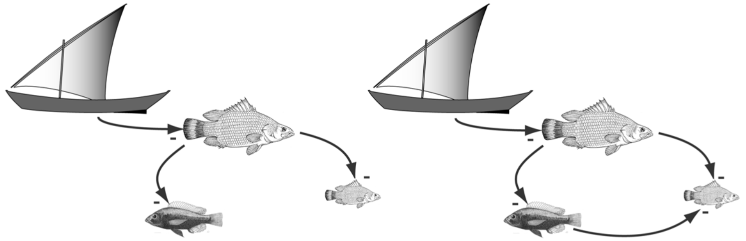
Based on these hypotheses, we can draw four alternative stock-recruitment relationships for Nile perch in Lake Victoria: a) Recruitment is a function of stock-size, there is no cannibalism or depensatory effect b) Haplochromines have a depensatory effect on Nile perch recruitment; c) In the absence of haplochromines, Nile perch have a negative effect on their own recruitment through cannibalism;

d) There is an alternation of depensation by haplochromines and cannibalism on recruitment (fig. 1).

Each of these descriptions implies a different possible prediction about the future of Nile perch stocks, and can lead to very contrasting optimal actions for the management of Nile perch (table 2). For example, if haplochromines have a strong depensatory effect, the system could have alternative stable states, where either Nile perch or haplochromines are dominant but do not co-exist in high abundances (this thesis, chapter 4). In such a case, the return of haplochromines indicates that fishing pressure on Nile perch should be reduced, or else stocks might collapse. If on the


a) Trophic cascade

b) Depensation


c) Cannibalism

d) Depensation and cannibalism

Figure 1: Different stock-recruitment relationships hypothesised for Nile perch. The top and right-hand fish of each panel represent Nile perch adult and young, respectively, the left hand fish represents haplochromines. a) There is no negative effect on recruitment; b) haplochromines have a negative effect; c) Nile perch have a negative effect; d) both haplochromines and Nile perch have a negative effect. To read the effect of any single component of each diagram on another it is connected to, follow arrows and multiply the signs: e.g. in d) the effect of fishing, via haplochromines on juvenile Nile perch is overall negative (-*-*-), whereas the effects of fishing, via large Nile perch, on juveniles is positive (-*-): they here cancel each-other out. In b) however, fishing has a negative effect following both pathways (-*-*- vs. -*+)

other hand Nile perch exerts a negative effect on its recruits, fishing pressure on Nile perch should probably be managed so as to best maintain an abundant enough stock of haplochromines in the system – as hypothesized by Kitchell *et al.* (1997), or Nile perch might undergo strong population cycles (Claessen *et al.* 2000).

Recruitment interferences can produce Allee effects and are most apparent at low population densities (Taylor and Hastings 2005): their presence is therefore difficult to identify while the Nile perch population is well established. We use the limited information there is on the Nile perch introduction to estimate when its upsurge should have been expected, and compare this with available data, to identify and discuss the importance of various stock-recruitment interferences.

Then, for lack of better knowledge on Nile perch migration, we assume Nile perch dispersed through the lake, and investigate what minimum requirements would have been for Nile perch to disperse across the lake in the time observed. We use these results for a broader discussion on Nile perch migration and as a theoretical baseline against which to compare further research on Nile migration.

Methods

Data

Goudswaard *et al.* (2008) published the most consistent compilation of data on the Nile perch introduction and invasion, gathering and standardising data from trawl surveys that had been carried out with different vessels, engines, and net sizes. Even though these data are not necessarily representative of the actual total biomass present in the lake – because different mesh-sizes are differently selective of fish-sizes – the standardisation by Goudswaard *et al.* (2008) makes them comparable, at least in terms of the timing of the observed changes. For each country or area surveyed, the authors arbitrarily define the onset of the boom as the moment when the density first reached 45 kg per hour of trawl (table 1).

The number and size of fish illegally introduced in 1954 is unknown, but was probably sufficient to produce a viable population, since eight sub-adult Nile

Table 2: The effects of different types of stock recruitment relationships (c.f. fig.1) on the introduction, settlement and removal of Nile perch, with theoretical management possibilities for the maintenance of sustainable Nile perch stocks. Np=Nile perch, H=haplochromines.

Stock-recruitment relation	Description	Introduction of Nile perch	Established Nile perch	Fishing Nile perch	Theoretical management options
a) Trophic cascade	Np have a negative effect on H and a positive effect on their own recruitment	Np eats its way into the top position of the food web.	High abundance of Np maintains low abundances of H.	Lower abundance of Np lead to increase in H. Np recruitment declines with adult stock.	Fish less
b) Depensation	Np have a negative effect on H and a positive effect on own recruitment. H have a negative effect on Np recruitment.	Too high an abundance of H might prevent or slow the establishment of Np.	High abundance of Np maintains low abundances of H.	Lower abundance of Np lead to their sudden collapse and the dominance of H.	Cull H. Introduce more Np.

c) Cannibalism	Np have a negative effect on H and on own recruitment.	Np establishment proceeds as normal in the presence of H, may be slowed by cannibalism in the absence of H.	High abundance of Np maintains low abundances of H. Np dominated by large individuals and recruitment is low.	Lower abundance of Np lead to more recruitment and increase in H abundance. Np population is stunted	Fish less. Shift fishing effort from large to smaller Np.
d) Depensation & cannibalism	Np have a negative effect on H and on own recruitment. H have a negative effect on Np recruitment.	Too high an abundance of H might prevent or slow the establishment of Np. Too low an abundance of H might slow the establishment of Np.	High abundance of Np maintains low abundances of H. Np dominated by large individuals and recruitment is low.	Lower abundance of Np leads to less cannibalism but more depensation. Np recruitment declines with adult stock.	Fish less.

perch were caught in 1960. These were too small to be the introduced individuals themselves and were assumed to be their progeny (Goudswaard *et al.* 2008).

Timing of the boom

Data on the introduction and invasion of Nile perch in Lake Victoria are quite few and scattered and produce no insight into the mechanisms or biology behind the invasion process. For this reason, we use a model of precision equal to those data, i.e. the logistic growth model, and with independent estimates of growth and carrying capacity, measure how many years after its introduction to Lake Victoria Nile perch growth would have reached its upsurge phase, and how soon thereafter it would slow down and reach carrying capacity. We compare these two metrics – the time of onset of the boom and time to carrying capacity – with the observed time of the Nile perch boom and the year of the highest catch as compiled by Goudswaard *et al.* (2008).

In our model equation (eq. 1), N represents Nile perch abundance (t/km^2), r the annual growth rate (yr^{-1}) and K the population carrying capacity (t/km^2).

$$\frac{dN}{dt} = r\,N\,(1 - \frac{N}{K}) \tag{1}$$

We used a growth rate of 0.73(yr^{-1}) derived by Downing *et al.* (this thesis, chapter 5). In their study, the authors use a physiologically structured population model fitted to Nile perch to find how resource abundances and the length at which they shift diets influence the growth rate. 0.73(yr^{-1}) represents the maximum growth rate under an unlimited mixed resource and a wide range of lengths at diet shift. We use a carrying capacity of 963200 tonnes for the whole lake, from a density of 14 (t/km^2) derived from Pitcher and Bundy (Pitcher and Bundy 1995) multiplied over the surface area of the lake (68,800 km^2) and set the initial "inoculum" (N_0) to four 20 cm-long Nile perch. Using equation 1 we calculate biomass growth over 35 years and identify the year where biomass first exceeds 5% of carrying capacity (approximately same density threshold as defined by Goudswaard *et al.* (2008)) as the year of the onset of the boom, and the year where biomass first exceeds 95% of carrying capacity as the peak of the boom.

We then evaluate how mild depensation would affect the timing of the Nile perch invasion. We do so by setting a lower growth rate (90%, 80%, 70% and 50 % of 0.73) until Nile perch reaches the 50%, 100% or 200% of the biomass used as our indicator of the onset of the boom. Furthermore we performed a semi-analytical sensitivity analysis to find which parameters determine the onset of the boom (appendix D).

Dispersal

Because the Nile perch boom did not take place over the whole lake simultaneously, we assume that Lake Victoria is larger than the homogeneous-distribution area of Nile perch, i.e. the area Nile perch would cover without dispersing, over which its density would increase homogeneously. Therefore, to describe the migration or dispersal of Nile perch across Lake Victoria, we need two parameters: firstly, one that reflects density-dependence – or the homogeneous-distribution area of Nile perch – that influences the threshold at which a population growth solely serves to increase population density to serving both as an increase in density and to expand over space; and secondly, a migration or dispersal rate, that sets a balance between energy allocation to growth and migration.

There is, to our best knowledge, no information on either the density-dependence of migration or on dispersal rates of Nile perch. A preliminary migration study carried out in the late 1980s found that Nile perch can swim 50 km in a single week, and up to 150 km in 6 months: an individual can thus cross the lake within a year (Ligtvoet and Mkumbo 1990). We therefore assume that there are no physiological boundaries to Nile perch dispersal, and instead focus our attention to effects of basic triggers of dispersal and use a parsimonious model.

We first investigate the effects of density-dependence by testing different territoriality scenarios and assume that Nile perch disperse according to their density: a highly territorial Nile perch would have a small free-distribution range and start moving at low population densities and a less-territorial Nile perch would have a large free-distribution range and start dispersing later. We divide the lake into different numbers of cells *n* of equal area to test the effects of territoriality: many small cells to fit a high-territoriality scenario and fewer large cells to represent a low-territoriality scenario. We create a one-dimensional model, where we assume the cells are distributed linearly, with the two extremities representing the most northern and southern parts of the lake and Nile perch diffuses in one dimension (*i*) (Eq 2). We also build a 2-dimensional lattice-model, where Nile perch can diffuse in two directions (*i* and *j*) (eq. 3). We fit a modified logistic growth model to each cell that includes migration to and from neighbouring cells (*i*-1 ; *j*-1 and *i*+1; *j*+1) at a migration rate *m* (yr^{1}). We include border conditions, so that biomass cannot leave the lattice.

2)
$$\frac{dN_i}{dt} = rN_i\left(1-\frac{N_i}{K_i}\right) + m\left(N_{(i-1)} + N_{(i+1)} - 2\,N_i\right)$$

3)
$$\frac{dN_{i,j}}{dt} = rN_{i,j}\left(1-\frac{N_{i,j}}{K_{i,j}}\right) + m(N_{(i-1,j)} + N_{(i+1,j)}+N_{(i,j-1)} + N_{(i,j+1)} - 4\,N_{i,j})$$

The dispersal rate *m* is a function of the number of areas the lake is subdivided into (*n*). For every value of *n* tested (n_i=2; 3; 4; 5; 10; 20 and $n_{i,j}$=5,5; 10,10; 20,20), we calibrate *m* so that the onset of the boom in the first and last cells fit observations for Kenya and Tanzania respectively.

Results

Timing of the Nile perch boom

Our logistic growth model yields an onset of the boom in 1979, with carrying capacity reached in 1987 (fig. 2). This result fits the data following which the initial illegal stocking of Nile perch carried out in 1954, actually took seed and produced a viable population. This finding is robust to whether the later official introduction was successful or not: indeed, by 1963, the population introduced in 1954 would already have grown to produce a biomass twentyfold larger than that of the 35 adults and 339 fingerlings introduced in 1963. The later official introductions therefore represent a “drop in the Nile perch sea” and have no effect on the timing of the Nile perch boom.

Even though there is a lot of uncertainty in the initial stocking size (N_0), we find the assumption that a few sub-adults constituted the initial introduction realistic, considering that it is probably not larger than the official introduction that occurred later in Uganda for example. The timing of the boom is mostly dependent on the growth rate (appendix D), and a change in the initial stocking size has an effect 20 times smaller than that of the growth rate. Indeed, we find that doubling the initial population size to 10 individuals only leads to the onset of the boom occurring one year earlier than expected, but also yields a stronger mismatch with the observations of 1960. A smaller initial population-size leads to the peak of the Nile perch-boom taking place one year later. An initial stock-size of 4 * 20 cm individuals produce a population larger than the catches of 1960, as well as a timing for the onset and peak of the boom that matches observations. The growth rate we use, derived from Downing *et al.* (this thesis, chapter 5) is realistic and close to the average over all age-classes derived by Kitchell *et al.* (1997) (between 0.6 yr^1 for adults and 0.8 yr^1 for the youngest cohort) (Kitchell *et al.* 1997). Though the elasticity analysis illustrates how sensitive the results are to *r*, a growth rate of 0.8 yr^1 — which is a high estimate of growth rates for large fish such as Nile perch — would only yield a difference of two years on the onset of the boom, probably not enough to change the perception of a delayed invasion.

Depensation, whereby growth of Nile perch would have been lower than maximum at low population densities would delay the Nile perch boom, even if the depensatory effect has a very low biomass threshold (table 3). Indeed, the result is much more sensitive to the strength of the depensation than to the duration of the depensatory effect, indicating that any strong effect on growth early on in the invasion process would probably have delayed the Nile perch invasion.

Nile perch migration wave

We adjusted the dispersal parameter *m* so that is was sufficiently large to bring enough individuals across the lake, and for the boom to occur there in 1985, and small enough not to dilute the first cell too much and delay the first boom (fig. 3). The value of *m* is dependent on the size of each cell: the more cells we divide the lake into, the larger *m* needs to be for the migration wave to reach the last cell, and that this should occur within the time limit. Therefore, our one-dimensional model can only reproduce the migration wave for a number of cells smaller than 4. In a two dimensional model, where biomass can diffuse in four directions, the migration only takes place as a wave at lower values of *m*, and thus for a low resolution in term of number of cells. At higher dispersal values, the migration occurs homogeneously over the lake (fig. 4). Comparing observations of a migration wave going through the lake with our lattice model, we might suggest the Nile perch has quite a large territory. Should Nile perch be found to be a very territorial fish, we could only reproduce the observed migration wave without altering results for the timing of the boom by increasing the carrying capacity of the system.

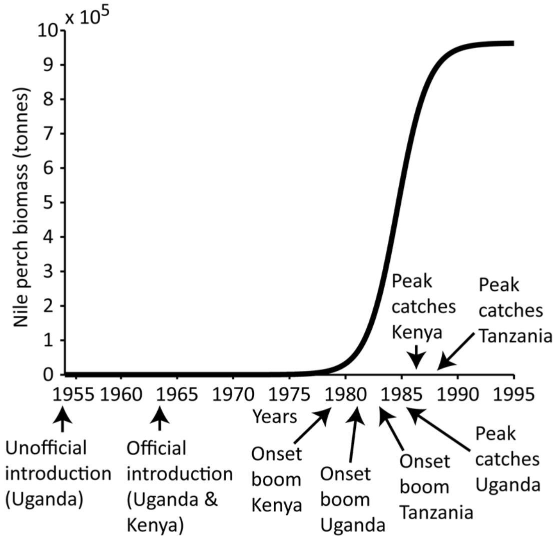


Figure 2: The logistic curve, with N_0=0.00039 tonnes, r=0.73 yr^{-1}; K=963,200 tonnes. The onset of the boom phase matches observations of the timing of the Nile perch boom.

Table 3: Effects of depensation on the year of onset and peak of the Nile perch boom. We illustrate depensation as a lower population growth rate when the Nile perch population is at low densities. The upper value in each cell represents the calculated onset of boom under each depensation scenario, and the lower value represents the peak of the boom. Depensation tests are read as follows: in columns – reduced growth rate as a percentage of 0.73. In rows: Nile perch biomass until which depensation is effective (arbitrarily centred around the indicator of the onset of the boom B_{ini}) (rows) on the timing of the start and peak of the Nile perch boom (top and lower year in each cell, respectively), in bold, the standard, no-depensation situation.

		Depensation effect (% r)				
		100%	90%	80%	70%	50%
Depensation threshold (%B_{ini} t)	50%	1979	1982	1985	1989	2003
		1987	1990	1993	1998	2012
	100%	**1979**	1982	1985	1990	2004
		1987	1990	1994	1998	2013
	200%	1979	1982	1984	1990	2004
		1987	1990	1994	1999	2014

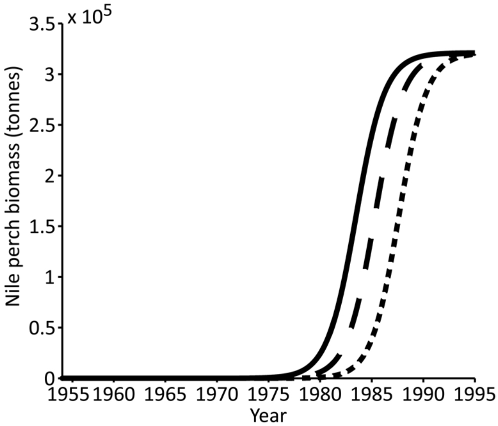


Figure 3: Nile perch dispersal wave with onset in the north in 1979 and in the south in 1984 (n=3 and m=0.11). The solid line represents the first wave in the north of the lake, the dashed one in the second segment of the lake, and the dotted line represents the final wave in the southernmost part of the lake. Adding resolution to the dispersal process (i.e. increasing n), would require an increase in m, which delays the dispersal wave in the north and speeds it up in the south.

Discussion

The timing of the Nile perch boom

With independently determined values for growth, carrying capacity and reasonable estimates for the biomass of Nile perch initially introduced, our logistic model yields an onset of the boom and time to carrying capacity that match the coarse observations of the Nile perch boom in Lake Victoria. Therefore, the timing and speed of the Nile perch invasion in Lake Victoria should not appear surprising or remarkable. Half a kilo of unhindered Nile perch takes 33 years to invade Lake Victoria (1954-1987), due to a constant exponential growth that becomes apparent only in its latest stages, with no external triggers for the boom necessary.

Furthermore, Kudhongania and Cordone (1974) Nile perch stock measures broadly fit within the predictions of the model. They estimated that the standing stock of Nile perch in 1969-1970 was 402 tonnes, through conversion of trawl data by the swept area method (Witte and van Densen 1995): our logistic growth model indicates the population would have crossed the 400 tonnes threshold in 1972. Given the level of approximation in the data conversion method and the uncertainty as to the number of individuals initially introduced, we find this is a reasonably nice fit to our model.

A population growth model with three key parameters fits the data, simple logistic growth is therefore the most parsimonious explanation behind the Nile perch invasion. These results rely on uncertain data – we do not know how many or what age Nile perch were initially introduced in 1954 nor if individuals have a significantly different growth rate at introduction. However, the findings are robust to the uncertainty in both stocking-size and growth rate, as variations within the uncertainty range would only change results by a couple of years – which fits the uncertainty in the observations and would probably not have affected the common perception of the delay in the Nile perch boom. To summarise: the parameter settings are realistic, the results are reasonably robust and leave us no reason to conclude differently than that the Nile perch invasion occurred as should have been expected as it entered its new resource-rich environment.

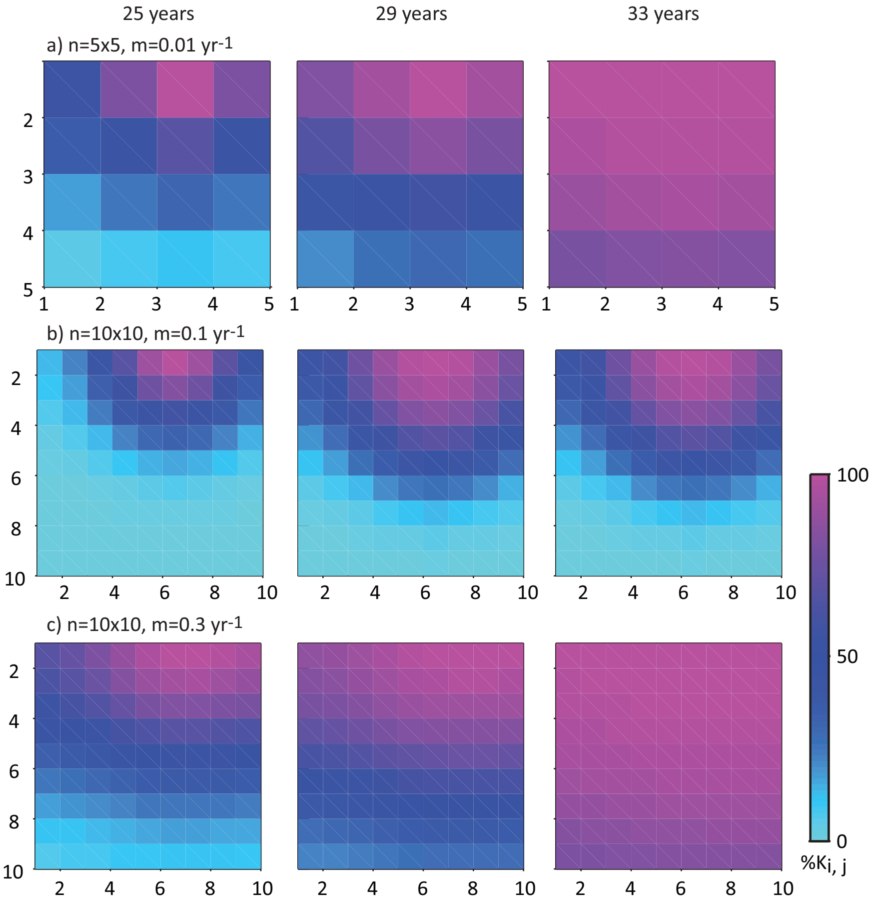


Figure 4: Nile perch dispersal in two dimensions. If the number of cells is small (e.g. panels a) a small dispersal rate *m* can produce a colonisation wave, where the expansion starts after 25 years, and the lake fills in 33 years. As the number of cells increase (b and c), representing a more territorial behaviour of Nile perch, a high dispersal rate is necessary for a colonisation of the lake in 33 years, However, then the dispersal is also more homogeneous (c versus b).

The migration process

The Nile perch boom took place first in the north of the lake – though interestingly in Kenya before Uganda – where it was introduced and then crossed the lake as a wave or front, reaching the southernmost part three years later (Goudswaard *et al.* 2008). This indicates that Nile perch did not disperse completely freely and therewith increase in abundance homogeneously over the whole lake, but migrated from one end to the next. To reproduce this migration with a simple linear dispersal model, we must assume that Nile perch are not very territorial and have a broad dispersal range. Should further research on Nile perch migration and spatial behaviour find that Nile perch has a low dispersal range, that there are effective barriers to its distribution or that Nile perch has territorial behaviour, the model would need to be adapted: either an increase in the carrying capacity of the lake or a more complex expression of its migration would be necessary to illustrate the migration process without affecting the timing of the Nile perch boom at the scale of the whole lake.

Further considerations

Our results indicate that a prior decline in haplochromine abundance was not a prerequisite for the Nile perch invasion. Nonetheless, they do not exclude the possibility that negative interactions – such as depensation or cannibalism – influence Nile perch growth. Our results here suggest that such processes did not have any significant effect on the timing of the Nile perch invasion on the large temporal and spatial scales that reflect the resolution of the observations on the Nile perch invasion in Lake Victoria. However, Goudswaard *et al.* (2008) point out that the Nile perch boom started in Kenya before Uganda, and match this observation with the decline of haplochromines that appears to have taken place in Kenya first (Goudswaard *et al.* 2008). While we find that the timing for the upsurge in Kenya could have been expected, perhaps some mechanism did delay the invasion from happening first in Uganda. Our findings provide us with a new perspective from which to look at the mystery of the Nile perch invasion: indeed, instead of asking what triggered the onset of the boom in Kenya, we might now ask what delayed the boom in Uganda.

Lake Victoria is the world's second largest lake, and it constitutes a very heterogeneous assemblage of habitats that contain different combinations of species (i.e. foodwebs). Therefore, processes such as depensation and cannibalism as well as fishing-pressure and the compensatory effects of eutrophication are probably not homogeneously distributed over the lake: each of these processes might very well influence Nile perch growth and dynamics at a smaller foodweb or habitat scale. Growth-influencing processes might be seasonal and cancel each other out over the year: Nile perch distributions vary seasonally and geographically (Mkumbo *et al.* 2007) and therefore, a strong depensation-season might be followed by a high productivity and growth season. Also at larger time scales, one could hypothesize that eutrophication in the lake might have produced more resources for juvenile Nile perch and compensated for the depensatory effects of haplochromines. We here find that there was no prevalent effect of any such process on the Lake Victoria-scale, but do not dismiss the fact that these processes occur at smaller scales, or in different areas. In fact, Nile perch are not dominant in all the lakes in which they are found: in lakes Albert, Chad, Turkana and the man-made lake Volta for example, they co-exists at low abundances with tilapia, haplochromines or other species (Ogutu-Ohwayo 1988, Achieng 1990, van Zwieten *et al.* 2011). Nile perch is therefore not immune to environmental factors or interspecific interactions that can limit its growth. It should also be noted that Nile perch are natives of lakes Albert, Chad and Turkana, as well as of the River Volta and it is likely Nile perch and other species in these water bodies have a long history of co-evolution, a history that probably should not be forgotten when considering the future of Nile perch stocks in Lake Victoria.

In similar ways to Lake Victoria, Nile perch were introduced to lakes Nabugabo (in 1960) (Gee 1964) and Kyoga (in 1955) (Gee 1969, Pringle 2005a), where they successfully invaded the system and depleted native haplochromine stocks (Ogutu-Ohwayo 1988, 1990). In the case of Lake Nabugabo, there are no data illustrating how and when the invasion took place, all that is known is that by 1991 Nile perch was already dominant in the lake's open waters and most native species had either disappeared or greatly declined in abundance (Chapman *et al.* 1996, 2003). The case of Lake Nabugabo gives a nice illustration of the role of different habitats on the success of Nile perch invasions. Indeed, Nile perch invaded open waters of Lake Nabugabo successfully, but not so much wetland and swamp habitats that thus provided a refugium for some native cichlids and lungfish (Chapman *et al.* 1996).

In Lake Kyoga however, the Nile perch invasion occurred much sooner than could have been expected. Nile perch were caught lake-wide already in 1962 (Gee 1964), and catch reports indicate the boom occurred between 1963 and 1968 (Ogutu-Ohwayo 1995). Using our model (K=24,080, N_0=147 individuals (Pringle 2005a) of unknown length – we assume 20-30 cm) we expect a Nile perch boom to occur between 1969-1975 or 1971-1977 – probably much later than observed. The speediness of the Nile perch invasion in Lake Kyoga might be related to the maturity of the individuals introduced, or to higher productivity of this environment. Lake Kyoga is a lot shallower than Lake Victoria, as it has an average depth of six meters, whereas Lake Victoria has an average depth of 40 meters. This might have played a role, perhaps allowing for more efficient predation, reproduction and establishment. In an interesting parallel, Kudhongania and Cordone's 1969-1970 survey of Lake Victoria found no Nile perch beyond 29 meters of depth (Kudhongania and Cordone 1974): the Nile perch shifted to deeper waters in the 1980s (Witte *et al.* 1995).

Conclusions

Simple logistic growth suffices to explain the timing of the Nile perch boom and fits the principle of parsimony (Ockham's razor). Testing the null hypothesis as we do here does not prove that Nile perch do not suffer depensatory or cannibalistic effects. Instead our analysis sets a new baseline from which to compare deviations in the invasion or establishment process of Nile perch and from which to better identify the mechanisms that might cause such deviations.

Furthermore, the fact that no single process dominates or influences Nile perch growth at the scale of the whole lake should be taken as an indicator that important population-dynamic driving processes probably occur at smaller time- and space- scales, e.g. seasonally or within different habitats. Therefore, further research should not operate from the *a priori* assumption that a consistent depensatory process influences Nile perch growth, and instead needs to identify the scales at which these processes have effect as well as how these scales compare to and are influenced by exploitation patterns. Importantly, any single management strategy aimed at maintaining sustainable stocks of Nile perch is probably not applicable to the lake as a whole, and would be most effective if based on dynamics observed at the scale of exploitation.

Chapter 4

The resilience and resistance of an ecosystem to a collapse of diversity[*]

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"Magic's easy, you just find the place where everything is balanced and push". Terry Pratchett in Equal Rites.

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Summary

Diversity is expected to increase the resilience of ecosystems. Nevertheless, highly diverse ecosystems have collapsed, as did Lake Victoria's ecosystem of cichlids or Caribbean coral reefs. We try to gain insight to this paradox, by analysing a simple model of a diverse community where each competing species inflicts a small mortality pressure on an introduced predator. High diversity strengthens this feedback and prevents invasion of the introduced predator. After a gradual loss of native species, the introduced predator can escape control and the system collapses into a contrasting, invaded, low-diversity state. Importantly, we find that a diverse system that has high complementarity gains in resilience, whereas a diverse system with high functional redundancy gains in resistance. Loss of resilience can display early-warning signals of a collapse, but loss of resistance not. Our results emphasize the need for multiple approaches to studying the functioning of ecosystems, as managing an ecosystem requires understanding not only the threats it is vulnerable to but also pressures it appears resistant to.

Introduction

Diverse systems are generally considered more constant (Tilman *et al.* 2006), reliable (Naeem and Li 1997), predictable (Berlow 1999), and less prone to change (Dovčiak and Halpern 2010) or invasion (Elton 1958) than simple systems. In spite of this, diverse systems have been known to suddenly collapse: from the global scale prehistoric mass extinctions (Whiteside and Ward 2011) to the smaller scale recent cases of Caribbean coral reefs (Bellwood *et al.* 2004), and of Lake Victoria's cichlid diversity (Witte *et al.* 1992).

Biodiversity is known to benefit systems through several mechanisms. Ecosystem experiments reveal that species-rich systems can exploit resources more efficiently than species-poor systems (Naeem *et al.* 1996, Cardinale 2011). This mechanism is known as complementarity and illustrates how systems that contain a high diversity of species can reach a higher biomass. Also, a large number of species can imply some level of functional redundancy: the loss of one species has a smaller effect in a diverse system than in a species-poor one. This is the insurance effect (Yachi and Loreau 1999, Tilman *et al.* 2006). High species diversity also implies higher chances of having beneficial species – which is known as the sampling (or selection) effect. Furthermore, it is often argued that for co-existence to be possible, even functionally redundant species need to differ in some aspects, including in their susceptibility to threats or to changes to their system (response diversity) (Loreau *et al.* 2001, Elmqvist *et al.* 2003). Response diversity, sampling and insurance effects are said to increase the resilience of an ecosystem.

Though it seems clear from experiments that diversity has effects on the stability of an ecosystem in the broad sense, diversity has seldom been explicitly connected to ecosystem resilience. We here describe the resilience of a system by the size of its basin of attraction in the stability landscape (Holling 1973), which can also be though of as the maximum perturbation a system can withstand and remain in the same state (Scheffer *et al.* 2001). While it has been suggested that diversity loss can cause loss of system resilience by reducing the size of the basin of attraction of an ecosystem state (Folke *et al.* 2004), mechanisms associating diversity to critical transitions have not yet been identified.

Critical transitions – such as those that shape the dynamics of a shallow lake shifting between its clear and turbid states (Scheffer *et al.* 1993) – occur when environmental conditions change and reshape a basin of attraction. This can reduce a system's resilience until it easily and rapidly slips into an alternative state – or basin of attraction. A sudden system collapse can also happen when a perturbation knocks a system out of its basin of attraction into an alternative one (Scheffer *et al.* 2001, Beisner *et al.* 2003). Critical transitions and alternative attractors require the presence of positive feedbacks: a weak feedback makes a system react smoothly to environmental changes (Scheffer *et al.* 2001). However, a strong enough positive feedback can yield alternative stable states, in which case a system can exist in different states for the same range of environmental conditions. The presence of alternative attractors in systems has important management consequences because they imply hysteresis, whereby the shift from one state (basin of attraction) to the next does not occur under the same conditions as the reverse shift back to the initial state (Scheffer *et al.* 2001).

Diverse ecosystems have been associated with critical transitions, yet the feedbacks behind these transitions have not yet been linked to diversity, but rather to keystone species (Barkai and McQuaid 1988, Stromayer and Warren 1997, Scheffer *et al.* 2001). The idea that diverse communities as a whole exert a feedback on their environment or on new-coming species is however not new (Drake 1990). Such a diversity-emergent feedback might also be associated to the story of Lake Victoria's diversity collapse. In this case, more than 500 species of haplochromine cichlids that used to occupy every trophic level of Lake Victoria's system suddenly disappeared and were replaced by the introduced Nile perch (Witte *et al.* 1992, Seehausen *et al.* 1997a) – though only 30 years after the introduction of Nile perch. One hypothesis for this delayed and sudden shift is that native cichlids might have initially controlled their introduced predator through predating on Nile perch eggs, but that increased eutrophication and fishing caused a slow decline in cichlid diversity. This gradual diversity loss eroded the resilience of the system until the egg-predation control mechanism failed, allowing Nile perch to suddenly boom (Goudswaard *et al.* 2008). Inspired by this hypothesis, we investigate – using a simple multi-species model –

how a strong positive feedback can emerge from a diverse system and how it affects the mechanisms that confer resilience to diverse systems, looking for insight into the paradox of diversity collapses. We here primarily aim to investigate the role of diversity itself in shaping the resilience of systems when an inconspicuous diversity-emergent feedback is at play and to understand some of the implications of diversity loss for a system in the presence of such a feedback.

Methods

Model

To describe the native diverse community, we used a Lotka-Volterra competition model (eq. 1), in which native species (N_i) differ from each other in their competition coefficient ($\alpha_{i,j}$), chosen randomly from a uniform distribution. We assumed interspecific competition to be lower than intraspecific competition ($0< \alpha <1$), allowing a diverse community to emerge. The diagonal elements of the competition matrix ($\alpha_{i,i}$) – that reflect intraspecific competition – are by definition equal to one. As an option, we inflict an extra species-specific and biomass-dependent mortality rate ($m_{F,i}$) on native species (by default, $m_{F,i}=0$). This extra mortality might for example represent a fishing pressure to which different species are unequally vulnerable.

In this model, the introduced predator (I) (eq. 2) grows from feeding on all species of the native community with an attack rate g, following a sigmoidal (or Holling type III) functional response (eq. 1) with a half saturation value H and assimilation efficiency e. The sigmoidal functional response is commonly used for fish populations and assumes reduced predation at low prey densities. We tested the effects of this assumption by trying our model using a type II functional response (see appendix E for results).

We assume that the predator has no food preference and feeds on each species proportionally to its biomass. The introduced predator has a loss rate (i.e. mortality and respiration) of m. In addition, each species of the native community causes additional mortality to the introduced predator that is proportional to its biomass ($p_i N_i$) and has no cost or benefit to the native species. By default we assumed the feedback rate p_i to be the same for all native species. Parameters are chosen so as to produce viable diverse communities; we test the effects of different parameter values in the model analysis (parameter descriptions given in table 1).

1) $$\frac{dN_i}{dt} = r N_i \left(1 - \frac{\sum \alpha_{i,j} N_j}{K_i}\right) - g I \frac{N_i}{N_{tot}} \frac{N_{tot}^2}{N_{tot}^2 + H^2} - m_{F,i} N_i$$

2) $$\frac{dI}{dt} = e g I \frac{N_{tot}^2}{N_{tot}^2 + H^2} - m I - I \sum p_i N_i$$

Where $N_{tot} = \Sigma N_i$ and $\alpha_{i,i}$=1

Analysis

We explored the effects of different levels of diversity as well as of diversity loss through simulations of different scenarios. To test the effects of diversity on the outcome of the introduction of an invader, we first simply ran simulations with different numbers of native species (respectively 30, 20 or 10 species), and no extra mortality on the native species ($m_{F,i}$=0).

To analyse the effects of diversity loss we applied two methods. In the one method, we tested the effects of sudden extinctions of individual species. For this we ran the simulations – again with different initial numbers of species – and set the biomass of a random native species to zero at chosen time steps. Our other method consisted in testing the effects of species-specific mortality rates within the native community. For this we ran the simulations, also starting with different initial numbers of species, but this time with the extra mortality ($m_{F,i}$).

To gain further insight into the effects of diversity on the feedback mechanism, we carried out numerical bifurcation analyses to identify system states for different parameter values, changing a control parameter incrementally and finding the equilibrium biomasses. We then tested the effects of diversity in two-dimensional bifurcation analyses by repeating the parameter analyses but with different numbers of species.

Simplifying the model to include only one strong keystone species, we conducted a more thorough model analysis (appendix F). We carried out phase plane analyses, identifying conditions under which populations do not change over time; we found system equilibria and analysed their stability. Through our phase plane analyses we exposed the different possible system dynamics that our model yields. Then, in bifurcation analyses, we modified parameters two-by-two and delimited parameter spaces over which the different dynamics occur and determined how the system might change from one type of dynamic to the next (results of this analysis are in appendix F). All simulations were carried out with GRIND for MATLAB (http://www.aew.wur.nl/UK/GRIND) that solves differential equations with a Runga-Kutta method.

Table 1: Model parameters

Parameter	Name	Dimensions
g	Predator foraging rate	Time^{-1}
H	Feeding half saturation	Biomass
r	Native per capita growth rate	Time^{-1}
$\alpha_{i,j}$	Competition coefficient	
K_i	Prey carrying capacity	Biomass
e	Conversion efficiency	
m	Predator background mortality rate	Time^{-1}
p_i	Predator mortality caused by prey *i*	Time^{-1} Biomass^{-1}
$m_{F,\,i}$	Extra mortality rate on native species *i*	Time^{-1}

Results

In our model, a high number of native species can effectively suppress the introduced predator (fig. 1). However, following species extinctions or an increase in species-specific mortality, a less diverse system can undergo a catastrophic collapse and shift to a state where the introduced predator has invaded and dominates (fig. 1c1 and 1c2, see appendix E for results obtained using functional response type II). When running the model with consecutive native species' extinctions, we see that at high diversity, each extinction usually only leads to a slight decrease in the total biomass of the native community (fig. 1a1, 1b1), but when starting from a lower initial diversity a few consecutive species' extinctions causes a relatively large biomass loss that ultimately leads to collapse (fig. 1c1).

We use two-dimensional bifurcation analyses to systematically check the effect of species diversity on the position of the critical transitions for different parameter settings (fig. 2). As diversity increases, the range of conditions over which

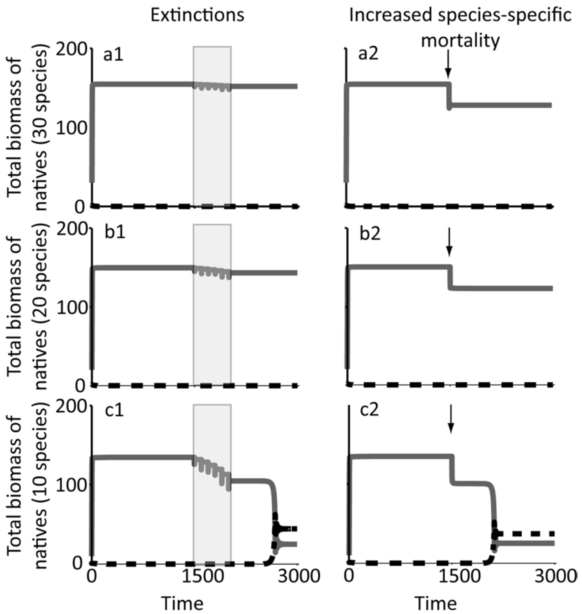

Figure 1: The effects of diversity and diversity loss on the outcome of the introduction of a predator into a diverse native community. Initially, native species prevent the introduced predator from invading. After species' extinctions (shaded areas) or an increase in species-specific mortality $m_{F,I}$ (arrow), at low diversity, the feedback mechanism fails and the introduced predator invades very suddenly. Low diversity communities have a lower initial biomass and the effect of diversity loss has a larger effect on the total biomass of less diverse systems. (p=0.0015; e=0.6; r=1; g=0.7; H=20; m=0.22; $\alpha_{i,j}$=0.3; K_i=50, $m_{F,i}$=[0,0.5]).

the system has alternative attractors also increases. Increased diversity thus makes the system more resilient to invasion by pushing the threshold to collapse away, but once a diverse system has collapsed, it is also further away from the conditions necessary for recovery. This effect is limited when competition coefficients ($\alpha_{i,j}$) are higher (fig. 2b and 2d), but it is exacerbated by both low competition and high

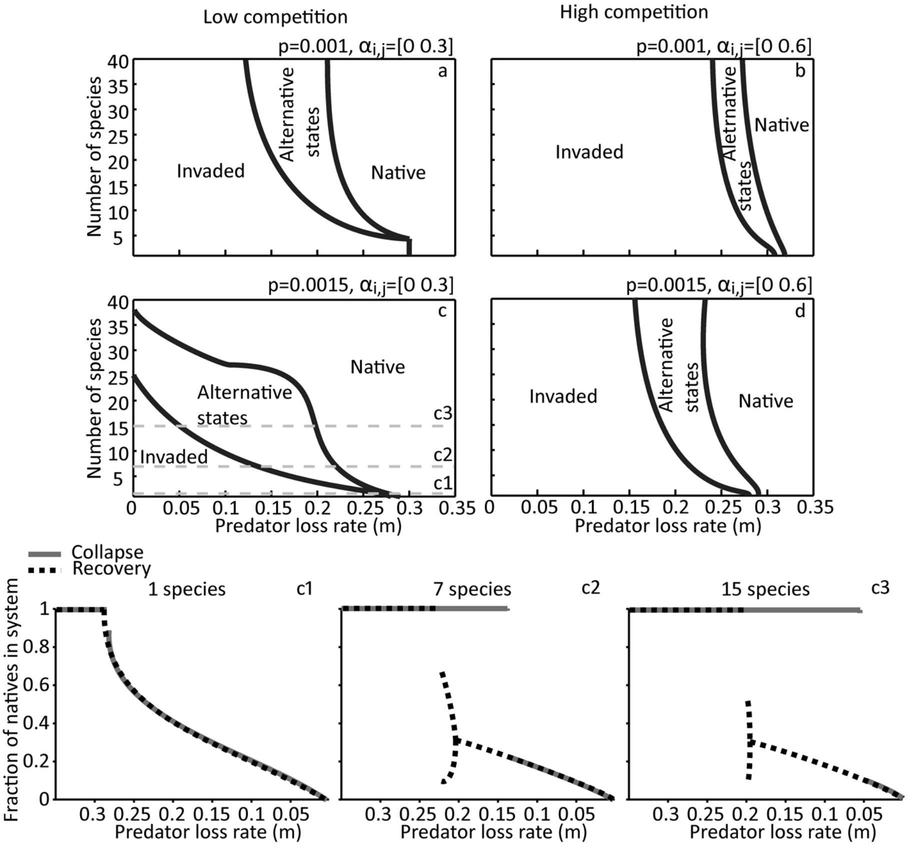

Figure 2: Effect of diversity and predator loss rates on dynamics. Stronger competition decreases the range of predator loss rates for which there are alternative stable states (b and d, versus a and c). In (c) with 25-38 native species, the predator only dominates if it is already dominant. At higher diversity, it cannot invade. To make a), b), c) and d), we ran the model in two sets of 20 runs for each number of species, starting in a native state and decreasing the predator loss rate (*m*); then starting from the invaded state and increasing *m*. Lines are averages of 20 runs. c1), c2) and c3) represent cross sections of c) at 1, 7 or 15 species: following equilibria as the system shifts from native to invaded and back. (e=0.6; r=1; g=0.7; H=20; m=0.2; K_i=50).

feedback rate (p_i) (fig. 2c). The predator is more easily suppressed when competition between native species is lower, i.e. there is a larger range of parameter conditions under which the system is in a native-only state for low competition values (fig. 2a and 2c).

In our simplified keystone-species model, one productive species can resist invasion by the introduced predator (appendix F), but in a diverse community each species needs a lower carrying capacity and the feedback rate can be weaker.

The way we model our diverse native community – where interspecific competition is lower than intraspecific competition – implies a certain level of complementarity between species. Weak competition reflects high niche complementarity, and translates into more efficient use of resources and thus higher productivity (fig. 3a). Therefore, our diverse communities make up a higher biomass than species-poor communities (c.f. fig. 1). When competition is strong ($\alpha_{i,j}$ closer to 1), fewer species bring the total biomass of the community to its maximum, which also implies that a diversity decline in a highly competing community leads to a more abrupt loss of biomass than in a more complementary community (fig. 3b, dashed lines).

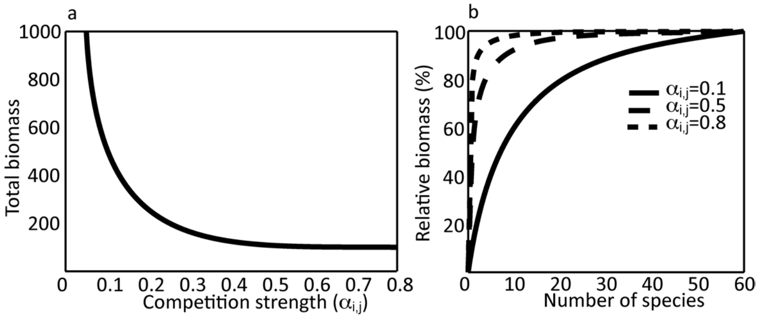

Figure 3: Biomass-diversity relationship. When interspecific competition is lower than intraspecific competition several species can make up more biomass than a single species on a given amount of resource. When competition is stronger (high $\alpha_{i,j}$), a few species quickly make up the total biomass (right hand panel). This also illustrates how when competition is high, the decrease in biomass with diversity loss happens more suddenly and at a lower diversity (dashed lines). The total biomass made up by 100 species decreases with increasing interspecific competition strength (left hand panel). Here it is complementarity that increases the productivity in the system.

Discussion

We here show with a very simple model how a community-wide feedback can make a diverse community more resilient to invasion than a species-poor system and how this feedback might imply that the loss of a few species could lead to a critical transition. The mechanism through which a diverse community acquires this resilience – here through increased productivity – is relevant for many other ecosystems that have alternative states, for instance systems that can switch to an overgrazed state (van de Koppel *et al.* 1997).

The small feedback mechanism we model could indeed stand as a possible explanation to Lake Victoria's mystery: the collapse of most cichlid species happened within a few years, but only thirty years after the introduction of Nile perch. The diversity collapse and Nile perch boom followed long-term increases in fishing pressure and eutrophication, two processes that had negative impacts on native species (Verschuren *et al.* 2002). Interestingly, the collapse of haplochromine cichlids in Lake Victoria was accompanied by an increase in the abundance of the shrimp *Caridina nilotica*, a competitor of the largest cichlid trophic groups (this thesis, chapter 2). This shrimp became an important food source for Nile perch, but is an unlikely threat to juvenile Nile perch: it could thus represent a case where the insurance effect – seen in shrimp replacing vanishing haplochromines – decreased the resilience of the community to invasion by providing more food for Nile perch but without negatively affecting Nile perch recruitment.

Caribbean coral reefs show similar albeit more complex diversity collapses that can also be compared to the mechanism we model. The native diverse state comprised high coral cover and grazing fish. With fishing and eutrophication, fish stocks and coral cover declined, and a single species of urchins took over the task of grazing on macro-algae. This simplified system rapidly collapsed leaving a fully barren state (Bellwood *et al.* 2004). One of the main feedbacks maintaining the coral state is grazing pressure by a diverse assemblage of grazing herbivorous fish that use corals as a habitat (Hoey and Bellwood 2011). Additionally, a recent study by Price *et al.* (2011) demonstrates how coral diversity promotes functional diversity in fish: this could represent another important feedback mechanism that might greatly increase a reef's resilience but that might also set it up for a catastrophic shift should a minimum diversity threshold be crossed.

An essential ingredient of our model is the productivity-diversity relationship. This relationship has been observed in many experiments and systems (Loreau *et al.* 2001, Tilman *et al.* 2006, Carvalheiro *et al.* 2011). In our model this relationship emerges from complementarity, as we assume lower inter- than intraspecific competition values. In real systems, however, this relationship can also be driven by other mechanisms: through resilience to microbes (Schnitzer *et al.* 2011), functional diversity (Yachi and Loreau 1999, Paquette and Messier 2011) or through niche partitioning (Cardinale 2011).

Despite its simplicity, our model allows us to differentiate resilience obtained from the diversity-productivity relationship to resistance acquired from the insurance effect. Because the collapse threshold is here a biomass-limit, productivity makes the system more resilient to an invasion by increasing its distance from the point of collapse (fig. 3). In contrast, the insurance effect reduces the effect of each species' extinction on the total biomass of the native community (fig. 3b) and thus increases the system's inertia – or resistance. Resilience and resistance each seem to have their own trade-off: the ability to ward-off invasion that comes with increased productivity – resilience – also comes at the cost of increasing the range of conditions for which there are alternative attractors. The insurance that comes with functional redundancy – resistance, even though it does not lead to hysteresis on its own, does not in itself give the ability to withstand invasion. In this perspective, Caribbean reefs seem to display more of a resistance effect: low diversity stands of grazing urchin initially succeeded in preventing algal growth – the loss of species did not initially reduce the critical biomass necessary to control the invading algae. The resilience of this urchin-dominated community was however already compromised, as pathogens wiped out this low-diversity system and critically reduced its productivity. Perhaps this illustrates a mechanism similar to that seen by Schnitzer *et al.* (2011), whereby diversity in grasslands increased the resilience of plants to disease and lead to a strong diversity-productivity relationship.

This distinction between resistance acquired through the insurance mechanism and resilience obtained through the diversity-productivity relationship is relevant when identifying the causes of diversity decline. Habitat destruction, such as forest clearing, might for example kill different species indiscriminately across system functions, whereas eutrophication or climate change might primarily affect species carrying out a single function – possibly species that compete quite strongly. Our study suggests that these different threats, though they might have the same impact on the number of species present, might have very different effects on ecosystem resilience and on the reversibility of a collapse.

The difference in how a system becomes more vulnerable – be it through a decrease in the system's inertia (resistance) or through changing the size of the system's basin of attraction (resilience) – will probably also affect the foreseeability of a critical transition. When loss of diversity implies a change in the basin of attraction, the system can present early warning symptoms of resilience loss: the rate at which it recovers from minor disturbances is lower, this is known as critical slowing down. A system that looses in resistance, however, is not expected to show any such symptoms (Scheffer *et al.* 2009).

The mechanism we model is very simple and general: all species are prey to the invader, and all contribute to prevent invasion. In reality, it is more likely species all have different effects – the shrimp in the Lake Victoria hypothesis we present could be a good example of this. Our results here show a clear-cut biomass threshold above which the system is resistant to invasion and above which both the insurance effect and increased productivity can further increase resilience of the system. However, this threshold becomes blurred in situations where species are not equally efficient at controlling the invader or equally susceptible to predation and where some species are competitively superior to others. The overall effects of species' extinctions are then even less predictable.

Our model illustrates how a small, no-cost feedback inconspicuously applied by individual species can be amplified in a diverse community to have a huge impact: consequences of diversity loss are not necessarily linear and not only a function of the number of species that are lost, a fact that is of high relevance to ecosystem monitoring and management. In effect, we show that both the level of functional redundancy that characterizes a community and the way in which the community is disassembled – across or within functional groups – might play a role on the resilience of a system and on the reversibility of a collapse. It is also important to remember that a small feedback mechanism is invisible until it fails, and consequences of diversity loss will tend to be very unpredictable. These findings reinforce the view that the key to preventing unexpected ecosystem changes lies in managing the resilience of ecosystems, and that resilience management should focus on maintaining biodiversity (Steneck *et al.* 2011).

Our results therefore emphasize the necessity to have a broad view on system processes and functioning, taking into account not only the pressures it is vulnerable to, but also the ones it appears resilient to. Such insight can be gathered not only from past collapses in other systems but also from understanding the mechanisms that structure communities and confer resilience to a system.

Chapter 5

Effects of resources and mortality on the growth and reproduction of Nile perch in Lake Victoria

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Third fisherman: "[...] Master, I marvel how the fishes live in the sea.
First fisherman: "Why, as men do a-land; the great ones eat up the little ones [...]" William Shakespeare in Pericles

Summary

A collapse of Nile perch stocks of Lake Victoria could affect up to 30 million people. Furthermore, changes in Nile perch population size structure and stocks make the threat of collapse imminent. However, whether eutrophication or fishing will be the bane of Nile perch is still debated. We here unravel how fish population growth and size-structures respond to changes in resources and fishing mortality. We parameterise a physiologically structured model to Nile perch and analyse the influence of ontogenetic diet shifts and relative resource abundances on existence boundaries of Nile perch and describe the populations on either side of these boundaries. Our results show that ignoring ontogenetic diet shifts can lead to over-estimating the maximum sustainable mortality of a fish population. Size-distributions can be indicators of processes driving population dynamics. However, the vulnerability of stocks to fishing mortality is dependent on its environment and is not always reflected in size distributions. We suggest that the ecosystem — instead of populations — should be the indicator of the state of its components.

Introduction

Lake Victoria, in East Africa, is a complex ecosystem that has undergone many unexpected changes in response to external pressures. In the 1950s, Nile perch, tilapia and other species were introduced to boost the lake's productivity and to compensate for the decline of native species (Pringle 2005a). The rapid invasion of Nile perch took place in the 1980s and coincided with the collapse of their dominant prey: the 300-500 species-strong native haplochromines nearly vanished from the lake (Witte *et al.* 1992, Goudswaard *et al.* 2008).

Nile perch is a highly prized commercial fish, and its success in Lake Victoria prompted a rapid increase in fishing effort and the development of an international Nile perch export industry (Pringle 2005a, Balirwa 2007). An estimated 30 million people now depend on the lake's fisheries (Awange and Ong'ang'a 2006). Since its invasion of Lake Victoria, Nile perch has therefore been both beneficial to lakeshore societies and economies and detrimental to the diversity of native fish.

Even though Nile perch are widely blamed for the collapse of their main prey, it is generally acknowledged that haplochromine populations were previously already declining, likely in response to fishing and perhaps also increased eutrophication and the subsequent deterioration of the lake's water quality (Witte *et al.* 1992, 2008). Indeed, in the 1960s Lake Victoria already showed signs of eutrophication: the phytoplankton community had shifted from a dominance of algae to that of cyanobacteria, and zooplankton communities shifted to a dominance of smaller species. Eutrophication increased over the decades, and manifested itself in the presence of more widespread and longer lasting anoxia, fish-kills from the sudden mixing of anoxic water, as well as in the invasion of the introduced water hyacinth in the 1990s (Hecky *et al.* 2010). The Nile perch invasion and haplochromine collapse was also followed by other changes in the food web: the boom of the native cyprinid *Rastrineobola argentea* (dagaa) and of the shrimp *Caridina nilotica* might be a result of the decline of their haplochromine competitors, though their success might also be a consequence of differential sensitivity to eutrophication (this thesis, chapter 2).

Surprisingly perhaps, Nile perch continued thriving after the disappearance of haplochromines. Nile perch are life-history omnivores, as they switch from a diet consisting of invertebrates when they are small to piscivory at larger sizes. In the absence of haplochromines as a resource to support them, Nile perch were found to feed longer on the native shrimp *Caridina nilotica* and only shifted to a predominantly cannibalistic life-stage when too large to consume shrimp efficiently (Hughes 1986, Ogari and Dadzie 1988, Mkumbo and Ligtvoet 1992).

Over the past twenty years, Nile perch catches have been fluctuating and populations seem to have undergone changes in size-structure. Also, haplochromines are recovering in some areas and appear frequently in Nile perch stomach contents (Kishe-Machumu *et al.* 2012), raising concerns that Nile perch are being overfished.

However, Kolding *et al.* (2008), found that changes seen in the size-structure of Nile perch populations in Uganda and Tanzania between the 1990s and 2005 are not explained by fishing pressure alone: where overfishing was expected to cause a decline in both mean and maximum length of Nile perch, they often found a decline in mean length, but never in maximum length. This has led to the hypothesis that eutrophication – through changes in the diet and resource availability – might be driving changes in Nile perch stocks and population dynamics.

Indeed, much research has confirmed that species that undergo ontogenetic diet shifts, such as Nile perch, on the one hand play an important role in shaping the structure and composition of their foodwebs through selective predation (Werner and Gilliam 1984), and on the other hand respond to the productivity and abundance of their different prey in changes of their own growth rates and population size-structure (Osenberg *et al.* 1992, Persson *et al.* 1998, de Roos *et al.* 2003a). The productivity of different resources, combined with the size- or stage-specific ability to consume one or other resource can lead to complex population cycles (Persson *et al.* 1998, de Roos and Persson 2003). These processes can both be the product and the cause of behavioural changes – such as increased cannibalism (DeAngelis *et al.* 1979) and/or habitat shifts (Persson and Greenberg 1990). Behavioural changes in turn influence population size-structure and dynamics by playing on the amount of resource available to any size-class and in this way affecting intra- and inter-cohort competition (Claessen *et al.* 2000, 2004, van de Wolfshaar *et al.* 2011), as well as community composition (Werner and Gilliam 1984, de Roos *et al.* 2003a).

Furthermore, changes in the size-structure and condition of Nile perch have been linked to the availability of suitable prey (Ogutu-Ohwayo 1999). There are therefore solid reasons to hypothesize that the large changes in the foodwebs of lake Victoria are linked to the fluctuations in Nile perch stocks and population size-structure.

Considering its high societal and economic importance, it is important to manage the Nile perch fishery effectively and prevent its collapse. To manage Nile perch, we need to look beyond the effects of fisheries alone and understand how eutrophication and fisheries drive changes in the populations. Such understanding can only be established on sound knowledge of Nile perch individual growth and population dynamics accounting both for energy intake and mortality.

We here present and parameterise a model for Nile perch growth that allows us to test the effects of differences in length at ontogenetic diet shift, prey abundance and type on Nile perch growth and size-structure. We aim to provide a basic diagnostic tool to assess the viability of Nile perch stocks under different resource and harvesting pressures.

With this model, we first estimate existence boundaries for Nile perch in the resource-mortality space: we determine the maximum mortality a population can withstand given the abundance of resources in the system. We then analyse the influence of length at ontogenetic diet shifts and relative resource abundances on the maximum sustainable mortality rate. Finally, we describe growth of individuals in- and outside these boundaries. These population- and individual-level descriptions of Nile perch allow us to map population size-structure indicators as a function of mortality as well as of resource-driven growth.

Methods

We develop a physiologically structured model for Nile perch to study its individual-growth and lifetime reproductive output under different feeding strategies and maximum sustainable mortality scenarios. We use the Escalator Boxcar Train approach to implement the model in continuous time (de Roos *et al.* 1992). This is a useful and tractable method to analyse the effects of individual-level life-history characteristics – such as length, weight or age – on population dynamics and gives us a grasp of mechanisms driving observed dynamics. We analyse two versions of the model: a single-resource model, mostly used to calibrate Nile perch life-history parameters, and a more realistic model where Nile perch feeds on two resources and that allows us to study the effects of differential resource availability and of different ontogeny scenarios.

Single resource model

The basic growth function for Nile perch is comparable to the specialized von Bertalanffy growth function (VBGF), where rates of resource assimilation and of metabolic loss scale to body size (table 1, eq. 1, model parameters are in table 2). The consumption rate follows a Holling type II (saturating) functional response (eq. 2). Growth in length scales to weight following an allometric scaling (eq. 3). After maturity length, a fraction of weight is allocated to gonad tissue, and the remainder goes into somatic tissue. Growth in length is related to the somatic fraction of body weight, for all individuals. To avoid a decrease in length in cases where body weight is lost (e.g. when resources are scarce and the fish starves), we set a theoretical-length auxiliary variable that directly relates to weight (eq. 3), and a realised-length state variable that either does not change or increases (eq. 4). We use the possible discrepancy between realized and theoretical lengths to determine the condition or fitness of the fish: following weight loss, realised-length is larger than theoretical-length and the fish are lean and in a reduced condition (eq. 5). When their condition falls below a certain fitness ratio, starvation adds to the Nile perch's mortality rate (eq. 6). The cohort we follow decreases in density as a function of background mortality, starvation mortality and fishing mortality (eq. 7).

Reproductive events happen yearly (Ogutu-Ohwayo 1988, Mkumbo 2002), when individuals in the cohort spawn (eq. 8). Individuals do not shed as much gonad tissue as is available if this brings it below the fitness ratio (eq. 8), and therefore do not starve because of reproduction nor reproduce if starving. The number of offspring resulting from a reproductive event is the product of the gonad tissue weight, the number of eggs per gram of gonad tissue, the density of the reproducing cohort and an egg-survival ratio (eq. 9). The full reproductive output is a sum over all reproductive events of the number of new offspring.

Two-resource model

We use this more complex model to study the effects of the ontogenetic diet shift of Nile perch: juvenile perch eat mostly macro-invertebrates (such as the shrimp *Caridina nilotica*, or insects) and adult Nile perch are predominantly piscivorous (eating haplochromine cichlids or feeding on their own young).

The two-resource model can differ from the single-resource model in the following aspects: each resource has a distinct abundance; encounter rate and efficiency with which they are assimilated. For most analyses we assume equal encounter rates and assimilation efficiencies, though we investigate the effects of differences in prey assimilation and encounter in our sensitivity analyses. Nile perch individuals cannot feed on both resources simultaneously, and shift from one prey-type to the next at a certain length. We describe the ontogenetic resource shift with two hill functions reflecting a length-determined preference for either resource (eq. 10a, 10b). In this model, the consumption rate on each resource thus depends not only on the resource density, but also on Nile perch preference, as reflected in the two functional responses (eq. 11a, 11b). Thus the assimilation part of the growth equation becomes a sum of the assimilation rate of each resource (eq. 12).

Parameterisation

Most parameter values were found in literature, parameters that were not found were varied to fit length-at-age data best (detailed parameterisation in appendix G).

Analyses

We follow the approach of de Roos *et al.* (1990) to determine existence boundaries for the Nile perch population. The existence boundary is the combination of parameters for which the lifetime reproductive output of one cohort is equal to 1. It gives the minimum parameter values above which a population can be sustained, but it does not inform on the equilibrium biomass of Nile perch. Indeed, since we do not model resource growth, there is no feedback of foraging by Nile perch on food availability. We determine these existence boundaries by simulation of a single cohort at different food availabilities (kept constant) by summing the yearly reproductive output of Nile perch until the end of their life. The resource concentration at which the average per capita reproductive output N_{new} equals one, is found numerically. This resource concentration can be regarded as the minimum resource carrying capacity necessary for Nile perch population to remain constant at a given mortality rate, and can be paralleled to the R^* in Tilman's resource competition model (Tilman 1981).

When depicting existence boundaries as a function of resource concentration and mortality, the minimum R^* (R^* at μ_f=0) represents the minimum resource necessary for the population to grow and produce an equivalent population under only background (natural) mortality. This value of minimum resource concentration increases with increasing fishing mortality until it reaches the maximum added mortality the population can sustainably withstand under infinite resources. Within the existence boundaries (i.e. $R>R^*$), the Nile perch population grows; beyond the boundaries ($R<R^*$), the population declines and the level of added mortality is considered unsustainable. We describe the viability of the population as the potential to withstand additional mortality pressure: i.e. as the distance to the existence boundary.

To unravel the effects of a changing environment – described in resource abundance, relative resource composition and fishing mortality – on Nile perch growth, viability and length frequency distribution, we proceed in a stepwise manner.

First we analyse the effects of ontogeny alone: assuming the two resources are identical in encounter rate and conversion efficiency, we map the resource-mortality space of Nile perch undergoing no ontogenetic diet shift; an early ontogenetic diet shift (shift from shrimp to fish diet between 10 and 20 cm, also referred to as low Lshift); and a late ontogenetic diet shift (shift from shrimp to fish diet between 50 and 60 cm, also referred to as high Lshift). In all three ontogenetic scenarios, we find the existence boundaries as a function of resources and mortality (R^*) and describe Nile perch physiological traits, such as length, body-mass and growth rate.

In a second step we carry out Monte-Carlo sensitivity analyses on the two Lshift models. To help interpret the results of the sensitivity analyses, we do hierarchical cluster analyses of the sensitivity matrices following the method of Klepper (1989). This yields clusters of parameters that have the same or opposite effects on model results (the full sensitivity and cluster analysis is described in appendix H).

Results

Existence boundaries of Nile perch

In our model, Nile perch can reach a maximum sustainable mortality rate of 0.00231 day^{-1} (0.84 yr^{1}) under unlimited resources. The critical resource concentration (R^*) is sensitive to feeding behaviour: it is lowest when there is only one resource and increases when two resources and an ontogenetic diet shift are taken into account. Ignoring diet ontogeny can therefore lead to overestimating the maximum growth rate of a Nile perch population at any resource abundance in the system. If we take into account changes in length at ontogenetic diet shift and consider the resource to be mixed, we find a good estimate for the maximum sustainable mortality of Nile perch is closer to 0.002 day^{-1} (0.73 yr^{1}). In the two-resource model R^* increases with length at ontogenetic diet shift (Lshift) (fig. 1). Further, in the two-resource models we see that for any given mortality rate, there is a range of possible critical resource abundances, depending on the relative resource composition. Thus, Lshift and resource composition are essential determinants of the existence boundaries of Nile perch. This implies that a change in composition of the resource is enough to shift the cohort from positive to negative growth, even at a fixed mortality rate.

Effects of relative resource composition and feeding behaviour on viability

To see how resource composition and Lshift influence the viability of Nile perch we calculated the critical mortality rate for a fixed total resource abundance but under varying resource composition (fig. 2). When the shift to the second resource happens early (low Lshift), Nile perch growth is highest under high abundances of the second resource: fish are here the limiting resource. At high Lshift, Nile perch populations can withstand the highest mortality rate when there are similar amounts of both resources: shrimp are a more limiting resource. Therefore, with a length at ontogenetic diet shift that matches the relative resource abundance (i.e. high Lshift when shrimp are most abundant, low Lshift when fish are most abundant), the critical mortality rate can be maintained (fig. 2). There is nonetheless a physiological limit to how far Nile perch can adapt length at ontogenetic diet shift to relative resource abundance, since Nile perch smaller than 5 cm are inefficient piscivores, and Nile perch larger than 60 cm are inefficient shrimp-eaters. Though size-selective predation rates might refine these results, we here identify the environment of lowest vulnerability – or where the highest mortality rate can be sustained – as one in which fish are an abundant prey and Nile perch have a low Lshift.

Mapping population growth as a function of resources and mortality

Equilibrium biomass, length-at-age and length-frequency distributions at different Lshift and relative resource compositions indicate that Nile perch grow faster and to larger sizes when the resource is mostly composed of fish (fig. 2 panels b and d). The highest peak in biomass, however, is reached when shrimp are the dominant resource (fig. 2, panels a1 and c1). Interestingly, at high Lshift and high

Table 1: Model equations

	Subject	Equation
1)	Growth	$\frac{dW}{dt} = A\ H\ W^{d} - k\,W^{n}$
2)	Functional response	$H = \frac{\eta\, R}{1 + (h\, \eta\, R)}$
3)	Theoretical length	If $L < l_m$, $L_h = \frac{W^{1/b}}{a}$, else $L_h = \frac{W^{1/b}}{a\, A_f}$
4)	Realised length	$L = \max(L, L_h)$
5)	Condition	$c = \frac{W}{a\, L^{b}}$
6)	Starvation mortality	If $c < \sigma$, $\mu_s = s\, \frac{L}{L_h}$ else $\mu_s = 0$
7)	Population density	$\frac{dN}{dt} = -(\mu_0 + \mu_s + \mu_f)\, N$
8)	Gonad mass	When $L > l_m$, if $c\, A_f > \sigma$, $\frac{dWe}{dt} = \frac{1}{365}\, W\, (1 - A_f)$ Else $\frac{dWe}{dt} = \frac{1}{365}\, W - a\, L^{b}\, \sigma$
9)	Reproductive output	$N_{new} = W_e\, E_{no}\, N\, J$
10a)	Preference resource 1	$p_{r1} = \frac{r_{L1}^{\xi}}{L^{\xi} + r_{L1}^{\xi}}$
10b)	Preference resource 2	$p_{r2} = 1 - \frac{r_{L2}^{\xi}}{L^{\xi} + r_{L2}^{\xi}}$
11a)	Functional response resource 1	$H_1 = \frac{\eta_1\, R_1\, p_{r1}}{1 + (h\, \eta_1\, R_1\, p_{r1}) + (h\, \eta_2\, R_2\, p_{r2})}$
11b)	Functional response resource 2	$H_2 = \frac{\eta_2\, R_2\, p_{r2}}{1 + (h\, \eta_1\, R_1\, p_{r1}) + (h\, \eta_2\, R_2\, p_{r2})}$
12)	Growth on 2 resources	$\frac{dW}{dt} = (A_1\, H_1 + A_2\, H_2)\, W^{d} - k\, W^{n}$

Table 2: Model parameters and variables

Parameter	Description	Units	Values
R, R_1, R_2	Resource density	$g\ m^{-2}$	[1-40]
η, η_1, η_2	Encounter rates	$m^2\ g^{-1}\ d^{-1}$	0.06
h	Handling time	d	9
A, A_1, A_2	Conversion efficiency		0.65
d	Consumption exponent		2/3
k	Metabolic loss rate	d^{-1}	0.0012
n	Respiration exponent		1
a	Length-weight allometric scalar		0.0089
b	Length-weight allometric exponent		3.106
l_m	Length at maturity	cm	77
A_f	Adult somatic growth ratio		0.975
J	Egg-juvenile conversion ratio		$1.575e^{-5}$
σ	Starvation ratio		0.74
μ_o	Background mortality rate	d^{-1}	$7.9e^{-4}$
μ_f	Fishing mortality	d^{-1}	
E_{no}	Number of eggs per g of gonad tissue	$\#\ g^{-1}$	7480
l_0	Initial length	cm	0.083
s	Starvation mortality rate	d^{-1}	0.1
r_{L1}, r_{L2}	Upper and lower bounds of Lshift	cm	10-20; 50-60
x	Slope of the diet shift hill-function		8
Auxiliary variables			
w_{egg}	Initial weight	g	
L_h	Theoretical length	cm	
c	Condition		
μ_s	Starvation mortality	d^{-1}	
E_{no}	Number of eggs per fish	#	
H	Functional response	d^{-1}	

State variables		
W	Weight	g m^{-2}
L	Length	cm
N	Cohort size	#
W_e	Gonad weight	g m^{-2}
N_{new}	New individuals	#

fish-prey abundance (fig. 2 panels d), Nile perch grow to very large sizes but produce a relatively low biomass and the maximum sustainable harvest rate is half that of when Nile perch shift diets earlier (fig. 2, panels d versus b). Length is here not indicative of fishing mortality, as both high and low maximum and mean length can be reached for similar mortality rates (fig. 2 panels b and c), and both high and low mortality rates can lead to similar maximum and mean length values, depending on Lshift and relative resource composition (fig. 2 panels a versus c and b versus d). We see clear stage-specific growth rates at high Lshift: when shrimp are abundant, Nile perch grow fast until they reach shift length (fig. 2, panel c1). When fish are an abundant resource however, Nile perch grow fastest after the shift (fig. 2, panel d1).

To follow how population size-structure changes with total resource abundance, relative resource composition, length at ontogenetic shift and mortality, we measure the mean and maximum average length of a cohort under low and high total resource abundance, low and high mortality rate and over the whole range of relative resource compositions, at low and high Lshift (fig. 3).

As indicated in our previous results, Nile perch reach higher maximum lengths at high fish abundance in the resource. Mean length follows the same pattern at low Lshift, but not at high Lshift, where highest mean length occurs under a mixed resource composition. The average mean and maximum lengths are higher when there is more total resource (fig. 3, panels b) and lower when mortality increases (fig. 3, panels c). However, mean length is more sensitive to mortality than is maximum length.

Shaded areas in the graphs of figure 3 represent areas of negative population growth. We find no consistent trend in changes of mean and maximum length as a population becomes overfished. At low Lshift, lower mean and maximum lengths accompany a shift to negative growth when it stems from a decrease in fish abundance or an increase in mortality rate (fig. 3, →A, →B). At high Lshift an increase in shrimp abundance can cause a shift to negative growth rate accompanied by an increase in maximum length and decrease in mean length (fig. 3, →C). A decrease in Lshift at high shrimp abundance can cause negative growth, with a decrease in both length indicators, though much more marked decrease in mean length than maximum length (fig. 3, →D). An increase in Lshift however can lead to a decreased mean length but stagnant maximum length (fig. 3, →E). A decrease in total resource abundance can lead to a slight decrease in both indicators (fig. 3, →F).

Sensitivity analyses

Both models have approximately the same sensitivity to parameter changes (see appendix H for details). Fishing mortality is the parameter with the strongest sensitivity coefficient. In the low Lshift model, the model variables are more or less

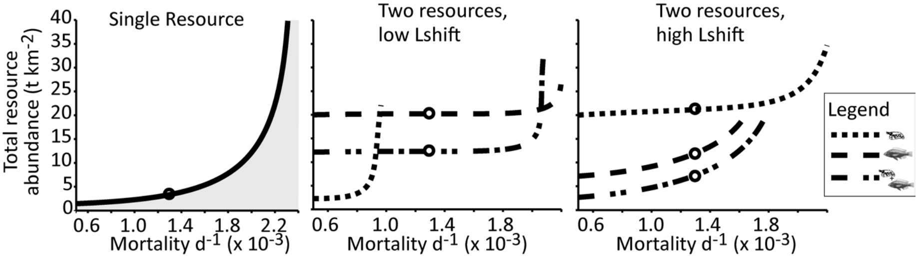

Figure 1: Critical resource concentrations (R^*) with no, low and high length at ontogenetic diet shift (Lshift). The curved lines were obtained by finding, for each combination of R_1 and R_2, the value of μ_f at which the lifetime reproductive output is 1. The shaded area represents areas of negative growth ($R<R^*$), we have not added it to the two-resource graphs out of clarity. The circles represent the minimum resource necessary to support the average fishing mortality calculated by Kolding *et al.* (2008). In the right hand panels: the dotted line represents R^* when shrimp is the dominant resource; the dashed line when fish is the dominant resource and the dashed-dotted line that of a mixed resource composition.

equally sensitive to parameters relating to either resource, in the high Lshift model, variables are more sensitive to the parameters relating to the consumption of the first resource than to their second resource counterparts (e.g. η_1 has a stronger effect than η_2). This is a consequence of Nile perch feeding longer on R_1 and less time on R_2 in the high Lshift model.

Discussion

In this study, we determine how total resource abundance, relative resource composition, and length at ontogenetic diet shift influence the vulnerability of Nile perch populations to fishing mortality. Also, we describe how resources and mortality shape Nile perch populations, and we link common indicators of sustainable fishing to actual population viability. We find that fishing is not the sole driver of changes in population size-structure, and that fish-length metrics are therefore poor indicators of the sustainability of fishing. We suggest that the state of an ecosystem can be a good indicator of how much its fish stocks can be sustainably harvested, and therewith reinforce the validity of the "ecosystem approach to fisheries" paradigm.

Taking into account relative resource abundance and an ontogenetic diet shift can show considerably reduced population growth rates. Broader ecosystem views are therefore necessary to understand and manage fish stocks, as resource composition and use determine the rate at which the population can be harvested. This also implies that negative population growth rates are not necessarily only a consequence of increased fishing or of decreased total resource abundance. Negative growth rate ($R<R^*$) can also stem from a decrease in fish as a resource or from an increase in length at diet shift.

The growth rates we obtain fall within range of values calculated by Pitcher and Bundy (Pitcher and Hart 1995). Our existence boundary curves indicate that at average fishing mortality (calculated for Tanzania between 1985 and 2002 as 0.48 yr^1 (Kolding *et al.* 2008)), Nile perch is most efficient (i.e. requires the lowest amount of resource) on a mixed diet and with a high length at ontogenetic diet shift. Overall, Nile perch can sustain the highest fishing mortality rate either when on a fish-dominated diet, at low Lshift or when on a shrimp dominated diet, at high Lshift (fig. 1). However, at high Lshift, the amount of resources necessary to sustain that mortality are much higher, and any increase in fishing mortality has a much stronger effect on the minimum resource necessary to maintain the population.

We find that Nile perch grow fastest on a diet dominated by fish and largest on a fish-dominated diet and a high Lshift (fig. 2, 3). The latter might appear to be an unlikely situation, since Nile perch are thought to shift to piscivory early in life when fish are an abundant prey (Kishe-Machumu *et al.* 2012). However, a high Lshift combined with high fish resource abundance could represent a situation where haplochromines are scarce, leading to a lack of suitably sized fish-prey for smaller Nile perch, and larger Nile perch have a cannibal piscivorous phase – as was seen in the late 1980s (Mkumbo 2002). To test to what extent ontogeny and prey availability drives the observed length frequency distributions, we would need to know the influence of inter-cohort dynamics and of feedbacks from the environment. Modelled Nile perch length-age distributions at equilibrium are only a good approximation for length-frequency distributions in the absence of inter-cohort dynamics (e.g. competition), and environmental feedbacks, such as growth rates of the different prey consumed by Nile perch.

The fact that the different prey that the Nile perch consumes cannot perfectly substitute each other is relevant in the context of the effects of past and possible changes in the food webs of Lake Victoria. In the 1980s, for example, the increase in shrimp abundance is thought to have effectively compensated for the decline in haplochromines in an ecosystem-function perspective. Indeed, the compensatory growth of shrimp may have maintained detritus-processing rates (this thesis, chapter 2). However, we here show that the dominance of shrimp rather than fish in the system, as well as the observed higher length at ontogenetic diet shift probably increased the vulnerability of the Nile perch population to fishing mortality.

In this study, the ontogenetic niche shift and relative resource abundances can lead to differences between growth rates of specific life-stages, and therefore uncouple the responses of mean and maximum length to changes in mortality or resources. Differences in size- and stage-specific growth rates are common in

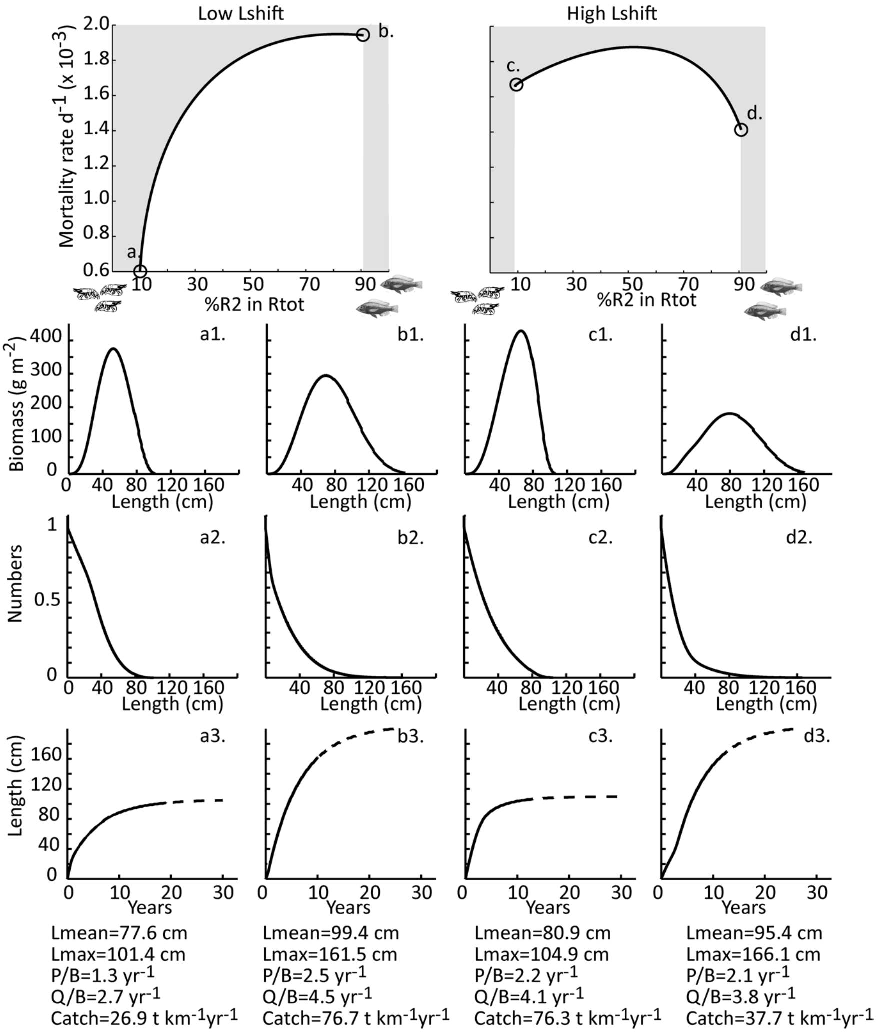

Figure 2: Equilibrium resource composition for Nile perch at low and high lengths at ontogenetic diet shift (Lshift) (10-20 cm and 50-60 cm respectively) over different relative resource abundances. The two curved lines in top panels represent equilibrium resource concentrations (*R**) of Nile perch under a fixed total resource abundance of 16 t/km^2; shaded areas represent areas of negative growth ($R<R^*$). Panels a1-d1 represent biomass/length in the areas circled in panels above. Panels a2-d2 represent length frequency distributions. Panels a3-d3 illustrate growth of a cohort, the solid lines end at the maximum realised length at critical mortality, the dotted lines represent the length that would be reached with no mortality. Values for mean length, max length, productivity (*P/B*), consumption (*Q/B*) and total harvest biomass at equilibrium figure under the four scenarios.

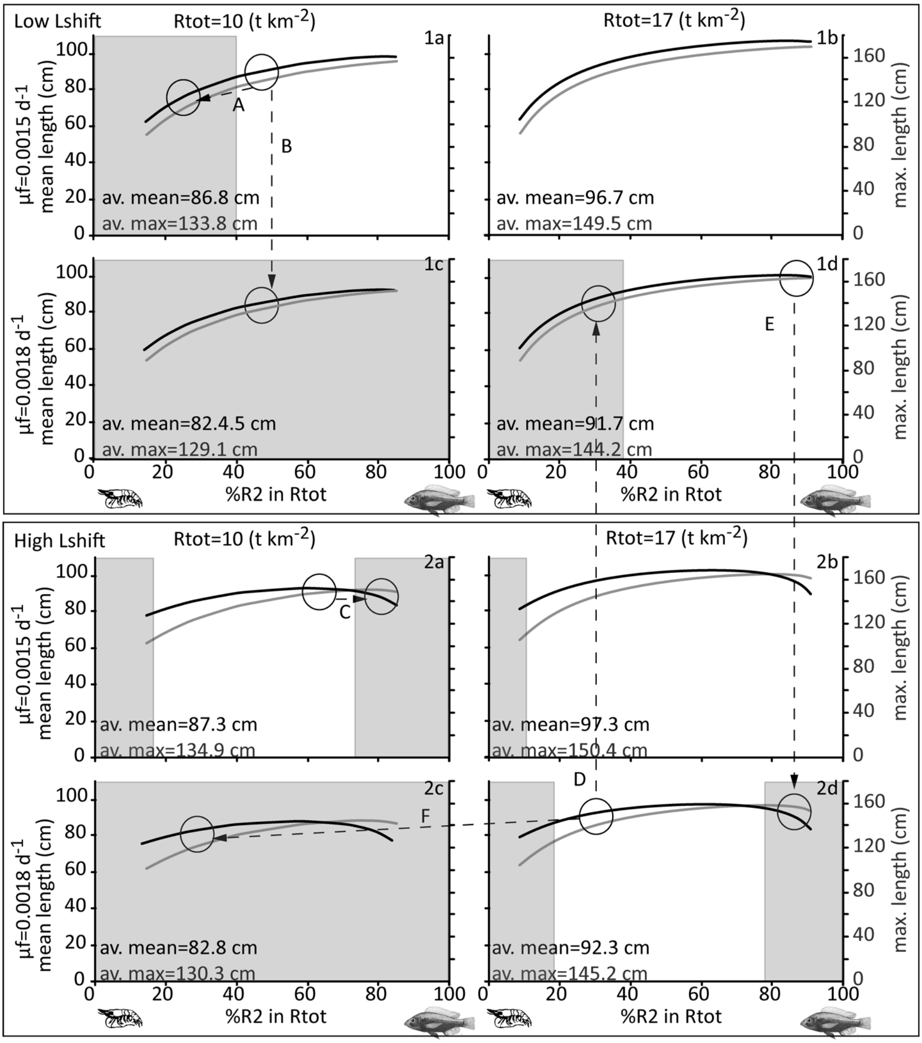

Figure 3: Comparing the effects of total resource abundance, relative resource abundance, length at ontogenetic diet shift and fishing pressure on mean and maximum length of Nile perch. Black lines represent mean lengths, values on left-hand y-axes; grey lines represent maximum lengths, with values on right-hand y-axes. Shaded areas are areas of resource-mortality space where the Nile perch population declines ($R_{tot}<R^*$). A-E represent scenarios where population switches from positive to negative growth through: A) an increase in relative shrimp abundance; B) an increase in mortality; C) an increase in relative fish abundance; D) a decrease in Lshift; E) after an increase in Lshift and F) following a decrease in R_{tot}.

populations undergoing ontogenetic niche shifts, and can drive complex population dynamics by influencing interactions between cohorts or with the different resources exploited, and ultimately lead to feedbacks and alternative stable states (de Roos and Persson 2002, Claessen *et al.* 2004, van Kooten *et al.* 2005, de Roos *et al.* 2007).

We illustrate the effects of such processes in a diagram (fig. 4). Limited growth of the juvenile stages can for example stem from high competition within this life stage (fig. 4, loop A). This can lead to a stunted juvenile population and to low recruitment to the adult stage (e.g. de Roos *et al.* 2003a, van Leeuwen *et al.* 2008). In turn, lower densities in adult stages might release adults from competition and allow them to grow fast, attain large sizes and reproduce abundantly, re-creating a competition strain on the first resource (Osenberg *et al.* 1992): such a loop produces a low mean length of fish and a high maximum length. When competition is strongest on the second resource (fig. 4, loop B), adults find themselves in a growth bottleneck; they are stunted and produce few offspring. This reduces competition on the first resource, and allows an abundance of fast growing juveniles to mature and again strongly compete for the second resource. This feedback loop can produce a high mean length and lower maximum length.

Changes in the productivity of either resource, or in the behaviour of fish (e.g. change in length at ontogenetic shift or increased cannibalism) (e.g. Claessen *et al.* 2000, 2002, Claessen 2003) or of fishers (through increased fishing pressure on a size group) (e.g. Persson *et al.* 2007, van Kooten *et al.* 2007, van de Wolfshaar *et al.* 2011) represent negative feedbacks and can affect the size class that suffers the growth bottleneck and can thus weaken the positive feedback loops. Breaking positive feedback loops can lead to critical transitions, and systems characterised by strong positive feedback loops and critical transitions may have alternative stable states (Scheffer *et al.* 2001, Scheffer and Carpenter 2003).

The ubiquity of processes driving stage-specific growth rate in populations that undergo ontogenetic niche shifts is of particular importance to the assessment and management of Nile perch stocks in Lake Victoria. Indeed, it opposes current interpretation of a decrease in mean and maximum lengths as indicators of overfishing: a decline in mean or maximum length can stem from an increase in mortality, but also from a decrease in resource availability, or simply a change in which resources are most available to any given life stage. Importantly, a stagnation or increase in mean and maximum length is not a sign that the population is being fished sustainably and overfishing can occur even without an increase in the fishing mortality incurred by a population.

We must stress, however, that while our model and the values we use reflect realistic growth for Nile perch, our assumption that fishing mortality is a constant and equal rate for the whole population is very simplistic. This implies that it is not the trends or the values for mean and maximum length that are the important result, but the process that they here uncover, i.e. stage-specific growth rates.

In its current form, our model is an appropriate tool to infer consequences of different eutrophication scenarios. For example, it allows us to test the effects of relative resource abundance and availability that might stem from changes in the oxygen and/or visibility of the environment that influence the distributions and interactions of Nile perch, fish and invertebrate prey differently (Witte *et al.* 2000, Wanink *et al.* 2001, Ngupula and Mlaponi 2010, Goudswaard *et al.* 2011). However, given the model's sensitivity to the functional response parameters, before increasing its complexity to include feedbacks of resource depletion and re-growth on Nile perch dynamics, we need to understand better the foraging behaviour of Nile perch. Until such knowledge becomes available, we suggest this model could be combined to the approach of Kitchell *et al.* (1997), to uncover the indirect effects of harvesting and growth of Nile perch –including the effects of resource availability and ontogeny – on predation rates by Nile perch on its resources. This can be done by refining size-specific predation and harvest rates and might lead to finding the balance between a healthy, diverse ecosystem and that of a productive and sustainable fishery.

While here we fit our model to Nile perch, the ontogenetic diet shift is the mechanism behind the differences in vulnerability and growth rates. The opportunistic character of Nile perch – or its adaptability with regards to diet and length at ontogenetic shift – sets the amplitude of these differences. In their general form, our findings probably apply to other fish than Nile perch.

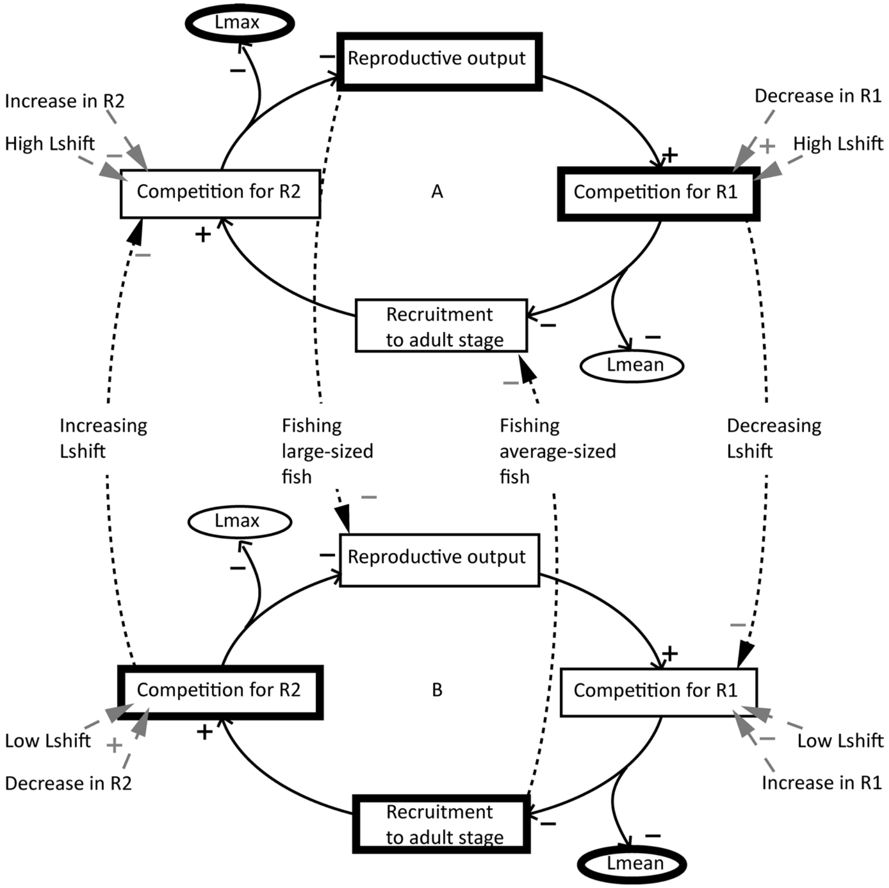

Figure 4: Growth cycles: Feedback loop A represents the juvenile-bottleneck or adult-release loop, whereby strong competition on the first resource (R_1) limits the number of individuals that make it to adulthood and the exploitation of the second resource (R_2), thus releasing adults from competition and allowing them to grow large and reproduce abundantly, re-creating a competition strain on the first resource: this loop produces a low mean length of fish and a high maximum length. Feedback loop B represents the adult-bottleneck or juvenile release loop, where adults are limited, produce few offspring, thus reducing competition on the first resource, and allowing an abundance of juveniles to mature and strongly compete for the second resource. Loop B can produce a high mean length, and lower maximum length. Reinforcing effects of additional drivers on each loop are illustrated with dashed arrows. Dotted arrows represent behaviours that might cause a shift from one loop to the other. The delay in behaviour change, after which loop-switches occur, and the rate at which the switches happen would determine whether these two loops occur under the same conditions (alternative stable states). Lshift=length at ontogenetic diet shift; Lmax=maximum length; Lmean=mean length.

Conclusion

Our results support the idea that fishing probably does not act alone in driving changes in Nile perch population dynamics. However, our results do not support the view that current trends in size distributions exclude the possibility that the stocks are being over-fished.

We suggest that a Nile perch population can be identified as having a higher vulnerability to fishing pressure when Nile perch stomach contents do not match the abundance of prey in the system, or when Nile perch delay their ontogenetic diet shift to piscivory. Such situations can occur both seasonally and site-specifically, and therefore management strategies should be adaptive. Such a management approach requires involving fishing communities in the current understanding of the system and in the monitoring of the stock and system as a whole. It would allow great steps to be made in both making the exploitation of Nile perch safer and in increasing our understanding of the system's dynamics.

We here show that population indicators are not only useful to show what processes are driving population dynamics, but can also point to appropriate management strategies: e.g. help guide which size-class should or should not be harvested or to understand the effects of a given management strategy. However, the viability of the population – indicating how much it can be harvested – is best determined by looking at the overall state of the system. We therefore conclude that the ecosystem – not population traits – should be used as an indicator of the health of its components.

Chapter 6

Synthesis Part One:

Chain reactions in the social-ecological system of Lake Victoria

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"Man wants to see nature and evolution as separate from human activities. There is the natural world, and there is man. But man also belongs to the natural world. If he is a ferocious predator, that too is part of evolution. If cod and haddock and other species cannot survive because man kills them, something more adaptable will take their place. Nature, the ultimate pragmatist, doggedly searches for something that works. But as the cockroach demonstrates, what works best in nature does not always appeal to us." Mark Kurlansky, in Cod: a biography of a fish that changed the world.

Summary

Lake Victoria, in East Africa, provides resources and services to millions of lakeshore inhabitants. The dynamics of these resources and services are variable, complex and poorly understood. Additionally, some of the perspectives of different lake scientists, users and stakeholders appear to be in disagreement as to the state of Lake Victoria's ecosystem and fisheries, thus creating a barrier to constructive discussion regarding this system's future. We here provide a social-ecological description of Lake Victoria's system using three different approaches: in a first step, we describe past and present trends in elements of the socio-economic and ecological subsystems. We then derive interactions between these elements, combine all subsystems into an interaction diagram and carry out a loop analysis on it to get a better grasp of the cascading chain of effects throughout the system as a whole and of how – conceptually at least – certain feedbacks in the system can be disrupted. In a final step, we bring together experts in all fields of study of Lake Victoria and ask them 10 critical questions regarding the state of the system, the answers of which we use to understand trends and drivers of resilience of Lake Victoria. We find that the social-economic subsystem is increasingly resilient to the collapse of contributing markets, but that it still is vulnerable to fishery collapses. The spatial heterogeneity and variability of Lake Victoria, as well as the biological diversity in central areas of the lake could increase the resilience of fisheries to harvesting. However, this resilience is reduced by eutrophication that causes irreversible loss of biodiversity to the system.

Introduction

The state of Lake Victoria's Nile perch fishery is the subject of strong debates between stakeholders and scientists. Owners of filleting factories argue that they are operating their factories at decreasing capacity; some scientists read decreasing trends in stocks from survey data (Mkumbo and Mlaponi 2007, Kayanda *et al.* 2009) while others see a total stock that fluctuates around a stable average despite increased fishing effort – an effect attributed to increased productivity (Kolding *et al.* 2008).

Nile perch was introduced to Lake Victoria in the 1950s and became dominant in the system by the end of the 1980s (Goudswaard *et al.* 2008), it has since become the product of an export industry (Pringle 2005a). An estimated 30 million people live in the lake's basin and both depend on (directly or indirectly) and have an influence on its resources (Awange and Ong'ang'a 2006), the management of these resources is therefore crucial.

So far, Nile perch management measures have included banning trawling and destructive methods such as poisoning, and increasing the minimum mesh-size of gillnets (van der Knaap *et al.* 2002). This latter measure is difficult to implement and monitor, given that Lake Victoria is the world's second largest freshwater lake by area (68,800 km^2), that its fisheries are open access and that it is shared by three countries (Tanzania, Uganda and Kenya). Furthermore such policies are immediately detrimental to the filleting factories that need to process the fish for export markets (Johnson 2010).

Therefore, whether Nile perch stocks are currently overexploited or not, the risk of their overexploitation is real. However, the sustainable management of fish resources is a skill not yet mastered: not only in Lake Victoria, but worldwide, an increasing proportion of fisheries is becoming fully- and over-exploited (FAO 2011). The collapse of fisheries and this apparent failure to sustainably exploit or manage fish stocks first led, in the 1990s, to the establishment of a set of fishing guidelines that exist under the framework of the Ecosystem Approach to Fisheries (EAF) (Garcia *et al.* 2003, Garcia and Cochrane 2005).

The EAF framework takes into account the feedbacks between exploited fish stocks and their environment, and aims at understanding how factors such as pollution, climate change, diversity and more influence fish stocks and, in this way, influence the sustainability of their exploitation. However, despite these considerations, management of fisheries based on an ecosystem approach has had little success (Garcia *et al.* 2003).

The ineffectiveness of management based on the EAF is largely associated to the poor accounting of socio-economical effects and responses to management policies and to ecosystem changes (De Young *et al.* 2008). The human component of ecosystems – i.e. the users of ecosystem services – makes these systems adaptive, in that actors can influence their resilience (Folke *et al.* 2010), and therefore invites adaptive management strategies.

The social-ecological systems (SES) perspective fully integrates the human component and takes into account interactions and complexities within and between social, ecological and economic systems and subsystems (Ostrom 2009). However, linking the social and ecological perspectives leads to a paradigm shift with regards to the use and management of ecosystem services: in this broader perspective, aiming for a maximized production of a single service is incompatible with the maintenance of economic and ecological resilience for example (Walker *et al.* 2004).

The SES approach appears particularly fitting to Lake Victoria, for ecological, social and economic reasons. Indeed, whether Nile perch stocks are currently overexploited or not, the whole ecosystem is influenced by eutrophication, which impoverishes the system by driving an irreversible decline in biodiversity, and beyond a certain threshold, threatens to cause a collapse of stocks (Kolding *et al.* 2008). Also, Nile perch is not the only exploited fish – the native pelagic cyprinid *Rastrineobola argentea* (known as dagaa in Tanzania, omena in Kenya and mukene in Uganda, from hereon referred to as dagaa) also boomed after the Nile perch invasion (Wanink 1999), and since the 1990s there has been a resurgence of endemic pelagic haplochromine cichlids: these two groups now constitute a fishery that is double that of Nile perch in terms of catches (Kayanda *et al.* 2009). Furthermore, since the explosion of Nile perch in the lake, the social and economic drivers of effort have changed: the risks and opportunities that face fisher-communities have changed with increasing human population sizes (Medard, in preparation). The European market to which Nile perch is predominantly destined imposes hygiene standards and sets prices for the fish, influencing their exploitation (van der Knaap and Ligtvoet 2010).

We here try to analyse the social-ecological system of Lake Victoria using three distinct approaches. In one approach, we scour the literature and data to describe past and present trends of change in the different subsystems (i.e. socio-economic and ecological) and their components.

In a second approach, we identify the interactions that connect the components of each subsystem, we then integrate these subsystems into a simplified feedback diagram. We carry out a qualitative loop analysis on this diagram, isolating positive and negative feedbacks through the system, reading chain reaction effects of external changes through the system and their influences on the feedbacks.

In a third approach, we invited experts in different fields of study of Lake Victoria to answer and discuss ten critical points of contention relating to trends and interactions in lake Victoria's system. These questions are critical in that they constitute a barrier to further constructive discussion that would lead to an effective approach to managing Lake Victoria's resources.

Trends

Eutrophication

From the 1960s already, well before the Nile perch boom, effects of eutrophication – driven by human population growth around the lake and subsequent changes in land-use and -exploitation (Verschuren *et al.* 2002, Hecky *et al.* 2010) – started becoming apparent. The phytoplankton community underwent a transition from a diatom-dominated community to one increasingly dominated by N-fixing cyanobacteria, and primary production increased. In turn, the zooplankton community shifted to be dominated by small-sized species (Hecky *et al.* 2010). The lake is not nutrient limited (Silsbe *et al.* 2006), indicating that increases in nutrients will not lead to increased primary production.

Since the 1990s, effects of eutrophication and fishing have become more apparent and Lake Victoria's system is still undergoing many changes. The water hyacinth (*Eichhornia crassipes*) – that first appeared in the lake in 1989 (Chapman *et al.* 2008) – had by 1995 produced large mats that severely disturbed fishing operations and altered the physico-chemical environment of the water under them, until they were managed with the introduction of a weevil (*Neochetina eichhorniae*) (Njiru *et al.* 2002, Wilson *et al.* 2007). Eutrophication and increased productivity have lead to increased hypoxic and anoxic conditions, effects that are amplified by climate warming (Sitoki *et al.* 2010), and that have negative effects on the diversity of the haplochromine cichlids, a globally unique species flock of some 500 ecologically varied endemic species (Seehausen *et al.* 1997a, Witte *et al.* 2007a) which in turn influences food web interactions (Hecky *et al.* 1994, 2010, Verschuren *et al.* 2002) as well as system functioning (Cardinale *et al.* 2012).

In inshore areas, terrestrial runoff is behind light-limitation from high levels of chromophoric dissolved organic matter (CDOM) 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, though there is a lot of spatial heterogeneity in the effects of eutrophication (Silsbe *et al.* 2006, Loiselle *et al.* 2008). Spatial and temporal variations in primary productivity are now primarily driven by climate (Cózar *et al.* 2012).

Food web and fishing

Before the introduction of Nile perch, the main fishing targets in Lake Victoria were the native tilapia *Oreochromis esculentus* and *Oreochromis variabilis*. The introduction of gillnets in the 1920s as a new fishing tool led to the quadrupling of catches per unit effort. Fish were initially sold by number rather than weight, thus inviting catches of small fish (Balirwa 1998). As native stocks were declining from overexploitation, eutrophication and habitat destruction, Nile tilapia (*Oreochromis* *niloticus*) and other tilapiine species were introduced, at the same time as Nile perch (between 1954 and 1964) – 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 2005b). From 1965, Nile tilapia replaced native tilapia, became the main commercial catch (Balirwa 1998), and is currently an important product for local and regional markets (Njiru *et al.* 2008).

While the Nile perch introductions had little immediate effect, in the 1980s many changes took place quite rapidly. Nile perch suddenly became dominant in the whole lake, and contributed to driving haplochromine stocks to collapse (Witte *et al.* 1992). Ecological niches left vacant by vanishing haplochromines were filled in short succession by two native species, first the detritivorous shrimp *Caridina nilotica* (Goudswaard, Witte, & Wanink, 2006) and then the zooplanktivorous cyprinid dagaa (*Rastrineobola argentea*) (Wanink *et al.* 2002).

Nile perch became the product of a large fishery and export industry of higher investment. This new source of income attracted migrants to the lake shores (Kolding *et al.* 2008) and led to increased fishing effort as well as catches on Nile perch throughout the 1980s (Muhoozi 2002). The population size-structure of Nile perch has changed since its first introduction, probably both as a response to the environment – through diet changes – and through size-selective fishing (this thesis, chapter 5).

Although dagaa is native to Lake Victoria, a fishery for it only first developed in the 1960s, at first of small scale. The stocks of dagaa however rapidly increased after the Nile perch boom and haplochromine collapse, and became the lake's second most important fishery by the 1990s (Wanink 1999), and it is currently a dominant commercial fishery of the lake in terms of biomass (Tumwebaze *et al.* 2007). Neither predation by Nile perch nor increased fishing pressure have caused a decrease in the stocks of dagaa: together with resurging pelagic haplochromines, they now constitute about 50% of the lake's fish biomass (Wanink 1999, Kayanda *et al.* 2009). Dagaa have however undergone adaptive behavioural and morphological changes (Wanink and Witte 2000a) and their maximum size and size at maturity have decreased (Wanink 1999, Manyala and Ojuok 2007) – primarily as a response to increased fishing (Sharpe *et al.* 2012). Fishing effort has been on a steady increase (Mkumbo *et al.* 2007), though 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).

Haplochromine populations in the offshore and pelagic waters were on a steep decline from the late 1970s and collapsed to near-zero in the wake of the Nile perch boom (Kolding *et al.* 2008). Haplochromine biomass however started recovering in the early 1990s (Seehausen *et al.* 1997b) and quickly achieved pre-collapse pelagic stock biomass (Witte *et al.* 2007b). Even though the resurging offshore haplochromine community has retained a 40-strong species diversity (Seehausen *et al.* 1997b), at least 15 to 20 pelagic species have been irreversibly lost (Witte *et al.* 2000, 2012). In the pre-Nile perch system, an estimated 500 different species of haplochromines occupied almost every function in the food web, from detritivorous species through to piscivores. Fishing pressure on Nile perch, as well as morphological adaptation to changed environmental conditions and major habitat shifts are possibly associated with the reappearance of haplochromines (Kitchell *et al.* 1997, Seehausen *et al.* 1997b, Witte *et al.* 2000, 2008, Balirwa *et al.* 2003, Mkumbo and Mlaponi 2007). In the current system however, the diets of recovering species have changed, they are now predominantly zooplanktivores and benthivores (Witte *et al.* 2000, Kishe-Machumu *et al.* 2012). Haplochromines – that now represent up to 80% of the pelagic fish biomass (Tumwebaze 1997) – have shifted from being an important by-catch of the dagaa fishery (50% of the catch) to becoming a target that is sold to regional markets (Ngupula and Mlaponi 2010).

The shrimp *C. nilotica* increased in abundance after the Nile perch boom (Goudswaard *et al.*, 2006). It is thought their increase was due to a release from competition or predation by haplochromines (Goudswaard *et al.* 2006, Ngupula and Mlaponi 2010, this thesis, chapter 2). Local declines in shrimp have been reported, which have been attributed to the resurgence of haplochromines (Ngupula and Mlaponi 2010).

Socio-economics

Abundant stocks lead to increased exploitation when there are markets and organisational structures and institutions that allow fishers to build livelihoods on them. Before the introduction of Nile perch, fishing, along with agriculture and livestock herding constituted the economic foundations of lakeshore societies. Following the introduction of gillnets to help the tilapia fishery, it became commercial – a process further helped by urban infrastructure development (including road and rail) around the Lake (Balirwa 1998).

The advent of the Nile perch boom in the 1980s changed societies dramatically. Filleting factories were constructed around the lake and the fish exported to Europe (Pringle 2005a, 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% (Johnson 2010). People migrated to the lake to enter the fisheries, accelerating human population growth and altering the kinship relations that had existed previously (Medard, in preparation). Nile perch catches reached a peak in 1990, and effort has increased since. 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). European regulations led to import bans several times in the late 1990s because of poor hygiene, during these periods, Nile perch exported to alternative markets, such as Japan — though at lower prices — and fishing effort was temporarily reduced (van der Knaap *et al.* 2002). The European market can influence the production costs through adding regulations and quality requirements on the products they buy, but can also modify the value of Nile perch, as a function of its competition with other products on the European market (Johnson 2010).

Trawling was effectively banned in the 1990s. To ensure constant supply to the factories, a new socio-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 (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 debt towards agents or processors (Geheb *et al.* 2008).

The dagaa fishery properly developed in the early 1990s, when landing camps started organising themselves, also presenting a strong social structure, from trader, to owner, through manager and labourers, with women drying the fish. This small fish is destined to domestic and regional markets (Gibbon 1997). Catch that is successfully dried and cleaned of sand is destined for human consumption – it serves as a cheap source of protein for the poor and middle-class, and the rest sells as animal fodder. Traders play an important role checking the quality of the product as well as establishing its price (Gibbon 1997).

Human population growth around the lake is increasing at a higher rate than the African average (Odada *et al.* 2009). Fishing effort continues to increase, and fisher communities to restructure: in the Nile perch fishery, many agents have become boat owners and landing site managers, operating full fleets. Entry to fisheries used to be done through the dagaa fishery (Geheb *et al.* 2008), but as the relations within the fishery network are increasingly contractual, and fisheries have become more specialised, entry to either fishery can mostly only be done at the labourer level. Employment is based on good reputation rather than family ties – and it is difficult to increase in rank: the social and economic disparities are higher (Medard, in preparation).

Interactions

We create a diagram integrating the ecological food web and socio-economic components of Lake Victoria’s system and base ourselves on past trends to draw the interactions between the different components. We proceed in three steps, first illustrating the ecological subsystem, then the socio-economical and fisheries subsystems, and finally group these two perspectives, with fish and fisheries as the bridge between socio-economical and ecological perspectives.

From expert opinions in each field, we selected the significant elements, then connected the interdependent elements and added signs to these connections: if an increase in the value (biomass, concentration or economic value) of an element causes an increase in a dependent element, we added a plus (+) sign, if on the other hand an increase in one causes a decrease in the other, we added a negative (-) sign. Note that we cannot account for strongly non-linear interactions, when signs of the interactions may even be dependent on the system's state. In such cases we base the sign of the interactions on current state of the system.

We analysed the diagram through qualitative modelling (Levins 1974), using an algorithm to find all possible feedback loops in the diagram. Such feedback loop is negative ('self-regulating') when each element has a negative effect on itself, through the loop. This is the case if the product of the signs of the interactions in the loop is negative, as for example a predator-prey loop where an increase in prey abundance has a positive effect on the predator, but an increase in the predator has a negative effect on the prey. A positive feedback loop ('reinforcing ') emerges when the product of the signs in the loop is positive, such as that of a rush to resources: more fish-catches attracts more fishermen which in turn leads back to higher catches. Each element can be part of many different loops, but appear only once in a single loop. Reading interactions in this qualitative loop context provides insight to the controlling or reinforcing factors behind dynamics of different elements.

To make our diagram more parsimonious, we eliminate the elements that are only flanked by unidirectional positive interactions, as they add nothing to dynamics.

Ecological subsystem

The basic resource of the system is represented in nitrogen and phosphorus (N and P) that contribute to an increase in phytoplankton biomass which in turn is consumed by zooplankton and fish (fig. 1). The major source of nutrient input to the lake is lakeshore societies, through agriculture, sewage, industrial waste, land clearing and coastline degradation (Silsbe 2004). An increase in nutrients has a non-linear effect on the system: indeed, while there is an initial phase of increase in biomass, as nutrient input continues increasing, biomass reaches a ceiling and then declines. We try to account for this strong non-linearity by adding phytoplankton's self-shading property and contribution to detritus. Detritus in turn also increases shading and consumes oxygen (fig. 1).

The shrimp *C. nilotica* is an important detritivore and prey for juvenile Nile perch as well as haplochromines in the current system (this thesis, chapter 2). Light is of primary importance for haplochromines, because they rely on colour vision for successful breeding and efficient feeding (Seehausen *et al.* 1997a). Poor light conditions cause the demise of haplochromine species diversity through hybridisation (Seehausen *et al.* 1997a, Seehausen 2009).

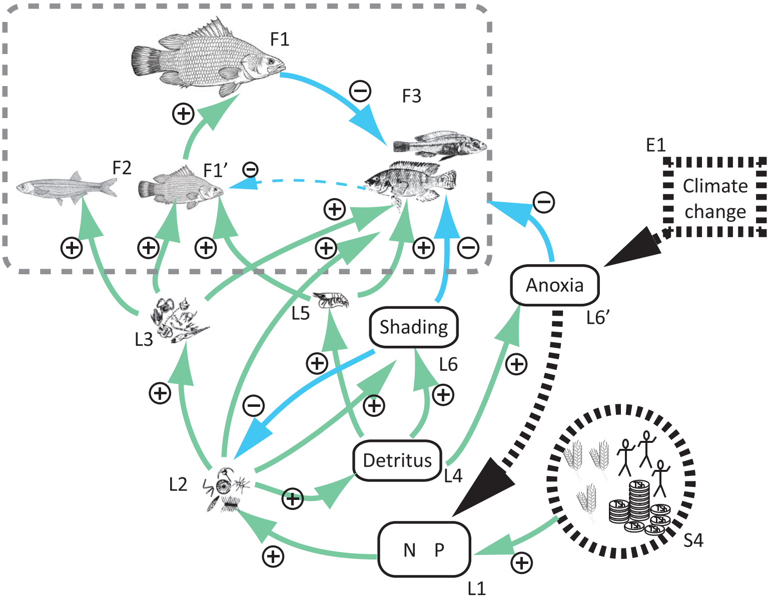


Figure 1: Ecological interactions. Green arrows represent growth processes (also identified by + sign); blue arrows represent mortality processes (associated to - signs); Thick dotted lines and arrows represent complex systems/interactions not further developed; E1=climate change; F1=large Nile perch; F1'=small Nile perch; F2=*R. argentea*; F3=haplochromines; L1=Nitrogen and Phosphorus; L2=phytoplankton; L3=zooplankton; L4=detritus; L5=*C. nilotica*; L6=shading; L6'=anoxia; S4=local and regional economy and society.

We connect anoxia negatively to fish, as they have lower tolerances to reduced oxygen levels, and that oxygen promotes growth at the level of individual fish (van Dam and Pauly 1995). It is a complex non-linear process, but ultimately however, reduced oxygen is detrimental to all species. 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, thus potentially increasing predation rates of Nile perch by haplochromines as well as hybridisation rates between haplochromine species (Vonlanthen *et al.* 2012). In a later step, the seasonal upwelling of deep anoxic waters can lead to large fish-kills (Ochumba 1990, Gophen *et al.* 1995).

Additionally, oxygen plays a complex role in biogeochemical cycles: denitrification – a process that releases nitrogen – takes place primarily in anoxic conditions, which in turn also promote phosphorus release. 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). The effects of climate change on Lake Victoria's food web and dynamics are thus likely to hinge on the oxygen-related biological and chemical processes.

The interaction between small Nile perch and haplochromines is here in a dashed line: it has long been speculated that through either competition or predation, haplochromines play a negative role on the growth of small Nile perch (Walters *et al.* 1997, Walters and Kitchell 2001, Goudswaard *et al.* 2008). However, a recent study suggests that such an interaction did not play a significant role at the scale of the whole lake (this thesis – chapter 3). Such a process should only be included in cases and areas where there is a demonstrated negative stock-recruitment relationship.

Society and fisheries

We here illustrate how catches of small Nile perch, dagaa and haplochromines feed a regional market whereas large Nile perch catches go to a European export market (fig. 2). The markets convert these catches into investment power: on the one hand, the economy grows, there is further investment in alternative sources of income (e.g. agriculture and farming, but could also include support businesses such as transport or entertainment), and human populations grow. This growth feeds back into the regional market. The local and regional markets invest in boat-owners to ensure their supply of fish. Owners in turn capitalise their investment into effort, thus further increasing catch.

By separating landing-site and boat owners from the rest of society, we get the means to reflect social, political and economical disparity: Industries invest in owners, and they can themselves invest in further effort and gain. Labour is cheap, always abundant enough and plays a role in every industry, we therefore neglect their impact on owners. As the economy grows, fishers and labourers gain

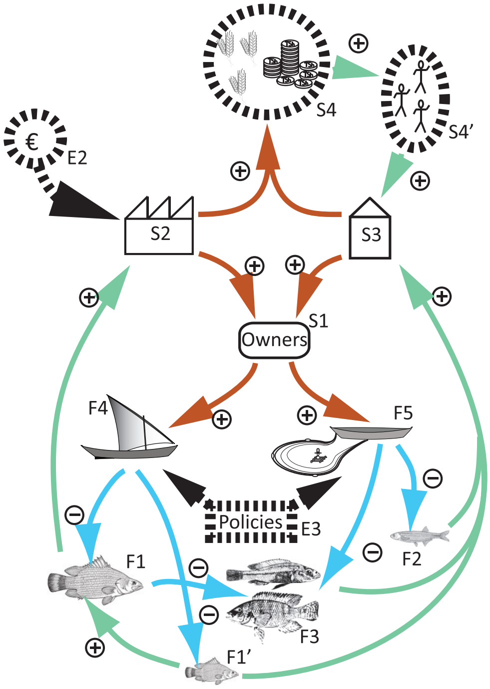


Figure 2: Social-economic interactions. Green arrows represent growth processes (also identified by + sign); blue arrows represent mortality processes (associated to - signs); rust arrows represent investment; Thick dotted lines and arrows represent complex systems/interactions not further developed; E2=international economy; E3=policies; F1=large Nile perch; F1'=small Nile perch; F2=*R. argentea*; F3=haplochromines; F4=Nile perch fishing effort; F5=*R. argentea* fishing effort; S1=boat and landing-site owners.

in alternative means of earning an income, they thus become less dependent on the fishing industry.

We have added two external drivers to this diagram: the international economy and policies. The international economy, driven by many more products, trends and fashions than the resources of Lake Victoria, can establish the price Nile perch fetches, as well as quality requirements of the Nile perch they import (Johnson 2010). This international influence determines many of the costs in the Nile perch industry (e.g. installing and maintaining storage and hygiene facilities) and therefore sets the catch level necessary to offset costs and reap a benefit (van der Knaap *et al.* 2002, van der Knaap and Ligtvoet 2010).

The social-ecological system

We combine both diagrams and simplify the model to make it manageable. We summarise the positive interactions that dominate the ecological perspective into two main processes: the positive effects of nutrient input that promote growth in fish species, and the negative effects that come from enrichment, but are represented by anoxia and shading (fig. 3).

We remove small Nile perch from the fish groups. Instead, Nile perch as a whole contribute to both the regional and international markets. We merge society and the economy into one, since they are connected with positive interactions, they here directly contribute to nutrient enrichment.

Analysis

Our socio-ecological system diagram has 25 loops. We exclude one from our analysis – the direct feedback between local market and society, since it holds no emergent information. Among the remaining 24 loops, we separate nutrient-driven processes, including nine ‘enrichment’ loops (table 1), in which nutrients lead to stock growth; nine ‘eutrophication’ loops (table 2), where stronger nutrient input

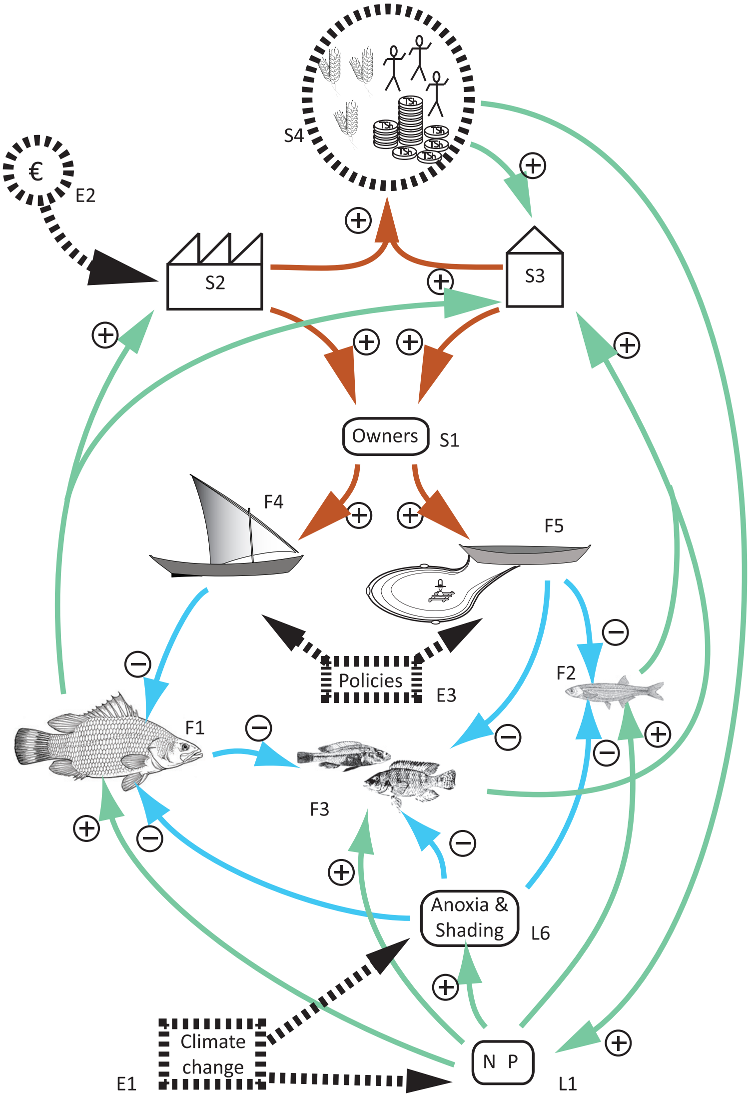


Figure 3: Social-ecological system interactions. Green arrows represent growth processes (also identified by + sign); blue arrows represent mortality processes (associated to - signs); rust arrows represent investment; Thick dotted lines and arrows represent complex systems/interactions not further developed;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

leads to anoxia and shading. Additionally, we have six exploitation loops (table 3) that describe dynamics from the different stocks through to the markets and back.

Positive enrichment loops go from nutrient promoting the growth of the stocks, through the positive effect on markets, then society and back to nutrient input (table 1). Negative eutrophication feedback-loops link nutrients to anoxia and shading; their negative effect on stocks that cascades to markets; 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 obtain inverse loops, where enrichment is self-regulating and eutrophication and exploitation are self-reinforcing (tables 1, 2 and 3, shaded rows). These inverted-sign loops describe longer chain reactions stemming from the presence of alternative sources of income for society: for example, if nutrient enrichment leads to higher Nile perch stocks, 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, thus negatively influencing the local and regional market and lead to a decrease in human population growth, which would lead to a decrease in nutrient input (table 1, row 6). Taken in isolation, such a scenario assumes that nutrient enrichment only has a positive effect on Nile perch, not on dagaa. Also, it assumes a single fishery target with no alternative stimuli for the regional market. 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.

It is important to note that a certain level of nutrient input can amount to enrichment for one species, but represent eutrophication for another: haplochromine species for example are particularly sensitive to low light (Seehausen *et al.* 1997a), dagaa is perhaps more sensitive to de-oxygenation than Nile perch (Wanink *et al.* 2001), though because it is a faster growing species, it appears to respond more to increased productivity. At all stages of enrichment and eutrophication however, the relative strength of fishing induced mortality of a stock versus its response in growth and fluctuations therein to nutrient input plays a very important role: it determines the sustainability of the stocks. Without external management, enrichment would most likely always lead to further nutrient enrichment, but this would only translate to increased stock growth until the negative consequences of eutrophication start kicking-in and if fishing effort does not cause mortality rates that exceed growth rates (i.e. stock collapse).

This diagram allows us to see the effects of change in a broader context, but it has limited predictive value: indeed, it cannot account for non-linearity and for adaptation in either human or fish populations to changes in stock or in environmental conditions. However, with a short time frame in mind, it can give an idea of the far reaching effects of any single action on the whole system. We indicated three external forces: climate change, the international economy and policies. These could trigger a cascading collapse along a positive feedback loop.

Table 1: Enrichment loops and their signs. Shaded rows represent loops with inverted sign. N;P=Nitrogen and Phosphorus, Np=Nile perch; IntMar=international market; Soc&Econ=society and economy; LocMar=local and regional market; Haplo=haplochromines; Dagaa=*R. argentea*; →=positive interaction; −○=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−○Haplo→LocMar→Soc&Econ →N;P	-
7.	N;P→Np→IntMar→Owners→Dagaa effort−○Dagaa→LocMar→Soc&Econ →N;P	-
8.	N;P→Haplo→LocMar→Owners→Np effort−○Np→IntMar→Soc&Econ→N;P	-
9.	N;P→Dagaa→LocMar→Owners→Np effort−○Np→IntMar→Soc&Econ →N;P	-

Table 2: Eutrophication loops and their signs. Shaded rows represent loops with inverted sign. 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=*R. argentea*; →=positive interaction; −○=negative interaction

	Loop	Sign
1.	N;P→Anox&Shade−○Np→IntMar→Soc&Econ→N;P	-
2.	N;P→Anox&Shade−○Np→LocMar→Soc&Econ→N;P	-
3.	N;P→Anox&Shade−○Haplo→LocMar→Soc&Econ→N;P	-
4.	N;P→Anox&Shade−○Dagaa→LocMar→Soc&Econ→N;P	-
5.	N;P→Anox&Shade−○Np−○Haplo→LocMar→Soc&Econ→N;P	+
6.	N;P→Anox&Shade−○Np→IntMar→Owners→Dagaa effort−○Haplo →LocMar→Soc&Econ→N;P	+
7.	N;P→Anox&Shade−○Np→IntMar→Owners→Dagaa effort−○Dagaa →LocMar→Soc&Econ→N;P	+
8.	N;P→Anox&Shade−○Haplo→LocMar→Owners→Np effort−○Np→IntMar →Soc&Econ→N;P	+
9.	N;P→Anox&Shade−○Dagaa→LocMar→Owners→Np effort−○Np→IntMar →Soc&Econ→N;P	+

Table 3: Exploitation loops and their signs. Shaded rows represent loops with inverted sign. Np=Nile perch; IntMar=international market; Soc&Econ=society and economy; LocMar=local and regional market; Haplo=haplochromines; Dagaa=*R. argentea*; →=positive interaction; --o=negative interaction

	Loop	Sign
1.	Np→IntMar→Owners→Np effort−○Np	-
2.	Np→LocMar→Owners→Np effort−○Np	-
3.	Haplo→LocMar→Owners→Dagaa effort−○Haplo	-
4.	Dagaa→LocMar→Owners→Dagaa effort−○Dagaa	-
5.	Np−○Haplo→LocMar→Owners→Np effort−○Np	+
6.	Np→IntMar→Soc&Econ→LocMar→Owners→Np effort−○Np	-

At this stage, we can draw three main messages. A first is that fishing –by taking out nutrients – cannot compensate for the system-wide effects of nutrient enrichment: enrichment must be tackled separately. A second message is that a sustainable fishing effort must take into account the growth rate of the targeted stocks but that growth rates are not linearly increasing functions of nutrient enrichment. Finally, economic input does not distribute itself evenly through society, it is a function of the opportunities available to the different members of society.

Synthesis of expert opinions

We asked experts to answer 10 questions judged critical (table 4) and to qualify their answers. These questions emerged from scientific meetings and discussions held in Dar Es Salaam and Amsterdam in May 2012.

Only one question – the aspect of whether or not Nile perch are being overfished – yielded a clear lack of consensus: as many replied yes as no, and a majority expressed a clear opinion on the matter. Two questions produced full consensus: all agreed that the dagaa fishery has both an ecological and an economic limit. The seven remaining questions yielded ambivalent responses but the discussions around

Table 4: Critical questions regarding the state of Lake Victoria

1. Are Nile perch stocks declining?
2. Are Nile perch stocks over-exploited?
3. Is eutrophication influencing Nile perch stocks positively or negatively?
4. Is there an ecological limit to the dagaa fishery?
5. Is there an economic limit to the dagaa fishery?
6. Are the different fisheries connected positively or negatively?
7. Would the fisheries benefit or loose-out if the international market were to vanish?
8. Can the system recover to its previous state?
9. Is the Nile perch in Lake Victoria an economic success <u>or</u> an ecological failure?
10. Is self-regulation by over-fishing or eutrophication inevitable?

these questions had some very interesting overlaps, and the perspectives of scientists in different fields complemented each other nicely, producing excellent material for a social-ecological perspective of the system: that is, material to assess requirements for a resilient Lake Victoria. We here draw from the answers given by experts to discuss the resilience of the social-economical subsystem, of the fisheries, and of the ecological subsystem and food web.

Socio-economical resilience

One of the interesting new insights drawn is that the system's economical resilience to the disappearance of markets appears to have increased: most respondents agreed that a loss of the international market would cause a dramatic loss of revenue, but that there is no shortage of demand for fish products in general, and that fishing markets have diversified. Dagaa and haplochromines are sold locally and regionally for human consumption and as fodder. Tilapia and Nile perch fetch higher prices on the same markets. Furthermore, a shutdown of all international trade is highly unlikely. In the same way as when the European market closed in 1997, Israel and Asia and other African countries could serve as alternative markets.

Even though the economy might be resilient to a shutdown of important markets, the economy would probably not be very resilient to a loss of fisheries. Indeed, the Nile perch fishery has attracted migrants seeking work, opportunity and a high-life to the lakeshore (Beuving 2010). As the Nile perch fishery grew, migrant settlements that started off as temporary became villages, that have bars, make-shift cinemas and brothels, though they do not necessarily have essential permanent structures such as medical units or schools (Geheb *et al.* 2008). Investment opportunities mostly lie in high profit-margin activities rather than in durable or saving schemes, people in these boom villages do not easily escape the poverty trap, the general health status is low and there is a high HIV-AIDS infection rate (Beuving 2010, van der Knaap and Ligtvoet 2010). Also, alternative sources of income are very highly dependent on the fisheries – the services sold in villages and landing sites are targeted at fishers – they would not provide a safety net, should fisheries collapse. Agriculture and livestock herding are among the few sources of income that are not fishery dependent, they currently complement the fishing industry well, but are probably not able to replace it.

Resilience of fisheries

The number of fishers and crafts targeting Nile perch on the lake has been on a steady increase since the early 1990s. The spatial distribution of this effort is heterogeneous: the centre of the lake is largely unexploited, harvesting is restricted to a short distance from the shore (Peter, in preparation). Heterogeneity in spatial allocation of fishing effort could act as a source of resilience of Nile perch stocks to increased fishing pressure, as the unharvested part may act as a buffer against over-harvesting. With increased eutrophication however, these unharvested populations might have reduced growth or survival rates.

No system is unlimited, however, spatial heterogeneity might make it more difficult to reach the limits of exploitation of Nile perch stocks. For dagaa, exploitation limits are also difficult to reach: it is a very productive species that is difficult to harvest efficiently. Nonetheless, fishing does have an influence on individual and population growth rates (Sharpe *et al.* 2012), and continued eutrophication could reduce their resilience to fishing by further reducing growth rates.

In the harvested part of the lake, Nile perch stocks are showing contrasting trends. In some areas – for example the Nyanza Gulf in Kenya and the Speke Gulf in Tanzania – stocks are declining, in others not (Taabu, in preparation). Increased effort and no decrease in stocks is probably a sign of increased productivity that compensates for harvest mortality. Increased effort combined with decreased stock and no relent in catches is either indicative that harvest rates do not reflect stock size and are primarily market driven, or that fishers' per capita catch is declining, and is probably illustrative of the fact that economic benefits derived from the Nile perch fishery are not percolating evenly through society. Increased economic disparity, stemming from strong top-down market drive could reduce social resilience.

While it is highly unlikely that Lake Victoria will become fully hypertrophied and that the system will die from a catastrophic anoxic event, eutrophication will probably impact the fisheries negatively: Nile perch populations are already not benefiting uniformly from a compensation of fishing through productivity. Furthermore, anoxia might be decreasing Nile perch recruitment success. The dagaa stocks still appear to be increasing, though they have adapted to changing environmental conditions, perhaps already as far as they could (Wanink and Witte 2000a).

Resilience of the ecosystem

Eutrophication has had dramatic, though not altogether negative consequences on Lake Victoria's system. The collapse of haplochromines was in part caused by eutrophication, in part by Nile perch predation, in part by a combination of the two: nutrient enrichment helped support the highly productive Nile perch stocks that fed on haplochromines (Witte *et al.* 1992, 2012). Added to the fact that ever-increasing human populations are continuously contributing to nutrient enrichment of the system, the loss of diversity might well be helping maintain Lake Victoria in a state of eutrophication and preventing its remediation to a state of higher water quality (Chapman *et al.* 2008). Lake Victoria appears resistant to eutrophication remediation.

Decreased eutrophication will therefore probably not be spontaneous but require management. Management policies could include improving agricultural practices as well as rebuilding coastal wetland areas, in turn this would benefit the re-emergence of now rare species (Goudswaard and Witte 1997, Njiru *et al.* 2002, Chapman *et al.* 2008).

In the case of Lake Victoria, a less eutrophied state that harbours a high abundance of haplochromines could produce larger and faster growing Nile perch, if these are harvested properly, they could co-exist with the haplochromines (Kitchell *et al.* 1997, this thesis, chapter 5). Haplochromines are recovering in terms of total abundance, but it is only a few species that are making up this abundance (Witte *et al.* 2012) and they are much more limited functionally than previously (Kishe-Machumu *et al.* 2008). Much haplochromine diversity is thus probably irreversibly lost and a diverse system would only re-emerge in an evolutionary time-span. This reduced diversity implies that the system is less resilient: system functioning would be reduced by further diversity loss (Cardinale *et al.* 2012).

Conclusions

Past trends are a good reminder of the complex and unexpected ways in which a system can respond to change. Even when we do understand how certain processes – such as species introductions or extensive harvesting – operate, predicting their full chain of consequences is impossible. The diagrams we draw to describe Lake Victoria's social-ecological system serve as a tool to keep in mind leading processes taking place in the system. However non-linearity in these processes and more importantly – the adaptive capacity of the system – make it impossible to use such diagrams as predictors. Instead, the system needs to be understood in the context of whether or not it is, and will continue, providing needed services. With this in mind, we have used the social-ecological system's perspective to qualify the resilience, i.e. the system's ability to maintain a functional integrity in the face of on-going changes and pressures.

Trends in the system illustrate the strong coupling of ecological and socio-economic subsystems: increased stocks and changes in species abundances brought in migrant fishers and offered alternative fisheries to exploit. As a consequence, social and economic systems are becoming more structured, and the driver of fishing effort is probably shifting from the ecosystem to the economy: it is not only stocks but also market pressures that act as incentives to fish (Johnson 2010).

At a social level, the structuring of fisheries from labourer through landing-site owner, traders and factories, and competition within the labourer network are making it increasingly difficult for an individual to switch from the dagaa to the Nile perch fishery (Medard, in preparation). However, the dagaa and Nile perch stocks are still strongly connected ecologically and economically: there is a large niche overlap between dagaa and haplochromines: either as competitors for resources, as prey for Nile perch, or as alternative fisheries to Nile perch. Our loop analysis illustrates how such system-connectedness implies that individual stocks cannot effectively be managed in isolation, as this would probably have cascading effects onto other stocks, and create a feedback on the management target.

A wide array of off-shoot businesses have flourished alongside the Nile perch and dagaa fisheries, including bars, hotels, shops and brothels (Beuving 2010). Because there is a diversity of markets for the lake's resources, these alternative sources of income could provide the social and economic system with quite a high resilience to the loss of economic input from Europe. However, because these sources of income are dependent on the fisheries, they are probably not resilient to a fishery collapse. The lake's fisheries appear to have a high intrinsic resilience to over-exploitation: the lake is too vast to be fully harvested in its entirety with the current fishing practices, and the stocks are quite productive and mobile. However, two processes reduce this resilience: on the one hand eutrophication, that can affect stocks lake-wide and decrease individual and population growth rates and survival, thus reducing the maximum amount stocks can be harvested. On the other hand diversity loss can imply a loss of response diversity, and lead to a higher vulnerability to environmental changes and diseases, which can cause population collapse. Reduced diversity can also lead to lower efficiency of the system (Schindler *et al.* 2010, Cardinale *et al.* 2012), and probably acts in maintaining the system in its eutrophied state.

Therefore, while it is essential to maintain the resilience of Lake Victoria's system for its sustainability, this is not sufficient, and active management to remediate eutrophication is also necessary. In the meantime, fishing management should take into account the system's reduced resilience through eutrophication.

Chapter 7

Synthesis Part Two:

Concluding remarks

What we learned

The resources of Lake Victoria lured human populations to its shores and drove human population growth. In turn, human population growth and activities triggered past and present trends of change in the lake's system: species introductions reduce native diversity; fishing alters the stocks; land-use and agriculture cause eutrophication and climate change influences biogeochemical processes. In this way, the main anthropogenic drivers of change in Lake Victoria have, to a large extent, been identified and accepted.

Our approaches to understanding the system's responses to different drivers fall in three broad categories. 1) Studies of drivers and their specific effects tell us about the *limits* imposed by each driver: as for example the maximum sustainable fishing mortality, minimum sustainable oxygen levels, or minimum necessary resource concentrations. 2) By superimposing these single perspectives we obtain a more complete description of the layers of limits that define the possible *states* of the system. 3) Integrating the different perspectives reveals how the drivers influence each other, defining new limits and determining *transitions* from a state to another.

In this thesis, we use different techniques and a combination of these three approaches to unravel how different drivers influence Lake Victoria's ecosystem states. In the first study (chapter 2), we compile data to build a description of three of the states Lake Victoria's system has existed in: diverse, invaded and re-settling (approach 2). We then study how Lake Victoria's system might have transited from a diverse to invaded state (chapters 3 and 4 – approach 3). In chapter 5, we look at mechanisms of growth that determine how much Nile perch can be harvested (approach 1) and finally, in the synthesis (chapter 6) we combine the different processes that drive change in Lake Victoria's socio-ecological system at an interdisciplinary level, to determine what factors might help maintain Lake Victoria in its current state, and what factors might push it to its next, unknown, destination (approach 3).

Chapters 2, 4 and 6 reveal the essential role of diversity in the adaptive capacity of Lake Victoria's ecosystem: functional and response diversity allowed the food web to recover structurally from the Nile perch invasion and haplochromine collapse: there were enough species for some to survive external pressures, and those that survived could pick up the roles of extinct species (chapter 2). We then illustrate how diverse systems that are characterised by efficiency (Naeem *et al.* 1996, Cardinale *et al.* 2011) can produce higher resilience than diverse systems characterised by higher functional redundancy (Yachi and Loreau 1999, Tilman *et al.* 2006) (chapter 4). In Lake Victoria, this not only has consequences in explaining whether the invasion of Nile perch was the cause or the consequence of diversity loss, but it also has implications for the future of the lake, in a situation where haplochromines are recovering in abundance, but not in species or functional diversity. We discuss, in chapter 6, how diversity in social as well as economic systems can increase resilience to an economic collapse, and find that the advice of Steneck *et al.* (2011) should be heeded: a resilient economy needs to be founded on a diversity of goods and services that have a degree of independence from each other.

In chapters 3 and 5 we understand growth of Nile perch at two very different resolutions: at the scale of the lake, no specific mechanism is necessary to explain the speed of invasion of Nile perch. However, at a food web level, resources available and Nile perch feeding behaviour can have a strong influence on how fast and how large Nile perch grow.

We draw two contrasting characteristics from these findings. On the one hand, while lake Victoria is a unique system in many ways – in its size, history and socio-economic impact – it is above all multiple: the heterogeneity that characterises this huge lake implies that drivers of change are having locally-specific consequences. No "one rule fits all" approach can guarantee the efficient and sustainable management of Lake Victoria's resources, a contextual and adaptive approach is needed.

On the other hand, our findings are generalizable to other populations, ecosystems and social-ecological systems. We here use Lake Victoria and Nile perch as case studies, but the processes described: growth, exploitation, eutrophication, diversity loss, invasion and resilience are ubiquitous. Our understanding of processes taking place in Lake Victoria can guide us in understanding other systems – for example, using the intricate relationship between Nile perch and haplochromines as inspiration, we highlight how a gradual loss of diversity can cause a critical transition to an alternative stable state.

Also, other systems can teach us about Lake Victoria: this is particularly important while the availability and resolution of data do not allow us to calibrate our models to trends in the system. In chapter 5, we find that the feedback of resources as well as fishing effort on stage-specific growth rates play an important role in the variability of the Nile perch population size structure. However, our understanding of predator-prey interactions of Nile perch is not refined enough to match the specificity of model needs: we cannot accurately quantify the effect of these feedbacks and use our model as a predictive tool. Thankfully, a large body of science exists on fish population dynamics (de Roos *et al.* 2003), and from it we can glean indicators of the state of the system – e.g. where growth bottlenecks are occurring.

We go beyond the biological approach and take both an ecosystem and social-ecological perspective to understand mechanisms that shape Lake Victoria's system. By breaking from the linear resource-management perspective and exploring the system in all its dimensions, the human component of the system – users and stakeholders – gains in adaptive capacity. The limits to the human component's capacity lie in how many dimensions of the system exist – i.e. in the system's diversity and complexity. Therefore, the human systems need to find a balance with its natural environment so as to co-evolve sustainably, this balance can only be found through multidisciplinary approaches.

> *"So long, and thanks for all the fish!"*
> Douglas Adams in The Hitchhiker's Guide to the Galaxy

Appendices

Appendix A: Chapter 2 – Creating ECOPATH mass-balances

The following tables summarize the ECOPATH parameters, empirical relations and constants used in our mass-balances, following the ECOPATH userguide (Christensen et al. 2005).

Table A1: Input parameters needed to create an ECOPATH mass-balance

Parameter	Description	Unit
Biomass (*B*)	Average biomass per unit area in the habitat area where the group occurs	t/km^2
Production to biomass ratio (*P/B*)	Equivalent to the instantaneous rate of total mortality (*Z*)	yr^{-1}
Consumption to biomass (*Q/B*)	Rate of intake of food by a group over time	yr^{-1}
Ecotrophic efficiency (*EE*)	Fraction of production that is further used in the system	
Production over consumption (*P/Q*)	Ratio between production and consumption, corresponds to gross food conversion efficiency	
Unassimilated consumption	Fecal fraction, part of consumption that returns to detritus	
Detritus import	Rate of entry of detritus into the system	t/km^2/yr
Fishing landings	Represent the non-discarded part of the catch, expressed as flows	t/km^2/yr
Diets	Expressed as the fraction each prey contributes to the overall diet of a group	

Table A2: Empirical equations used to calculate productivity and consumption (Christensen *et al.* 2005), as well as quantifying *Caridina nilotica** stocks (Goudswaard *et al.* 2006).

Productivity	$P/B = Z = M + F$ $P/B = K\,(L_\infty - \bar{L}) / (\bar{L} - L')$
Consumption	$Q/B = 10^{C_1} - W_\infty^{-C_2}\ 10^{-C_3}\ 10^{A\ C_4}$
Natural mortality	$M = K^{C_5}\ L_\infty^{-C_6}\ C_7$
Fishing mortality	$F = Y / B$
Length	$L_\infty = L_t / (1 - e^{(t - t0)})$
Weight-length	$W = a\ L^b$
Shrimp weight-length relationship*	$FW = L^{C_8}\ e^{-C_9}\ /\ C_{10}$

Table A3: Parameters needed for the empirical equations.

P	Production	t/km^2/yr
B	Biomass	t/km^2
Z	Total mortality rate	yr^{-1}
M	Natural mortality rate	yr^{-1}
F	Fishing mortality rate	yr^{-1}
K	von Bertalanffy growth function parameter expressing rate at which asymptotic length is approached	yr^{-1}
L_∞	Asymptotic length	cm
$\bar{L}$	Mean length	cm
L'	Length at entrance into fishery	cm
Y	Yield	t/km^2
Q	Consumption	t/km^2/yr
W_∞	Asymptotic weight	G
A	Tail aspect ratio parameter	

L_t	Length at age t	cm
t	Age	yr
t_0	von Bertalanffy growth function parameter expressing hypothetical age of a fish of length 0	yr
W	Weight	g
L	Length	cm
a	Scaling factor in W-L relationship	
b	Exponent in W-L relationship	
DW	Dry weight	G
FW	Fresh weight	g

Table A4: Constants used in empirical relations (Christensen *et al.* 2005)

C_1=7.964	C_6=0.279
C_2=0.204	C_7=4.439
C_3=6.583	C_8=2.7
C_4=0.083	C_9=4.876
C_5=0.65	C_{10}=0.2

Appendix B: Chapter 2 – Gathering data on Lake Victoria

For each of the three periods modelled, we chose a representative year with most data (1977, 1987 and 2005). Data used for our 1977 and 1987 food web depictions came from published literature whereas for our 2005 mass-balance we also used unpublished survey data obtained from the Tanzanian Fisheries Research Institute (TAFIRI) and the Lake Victoria Fisheries Organization (LVFO) (table B1). We entered five of the six necessary parameters (table B2) and let the application ECOPATH calculate the remaining one, based on the two master equations. After two calibration steps we obtained mass-balanced models depicting the food web in the three chosen years (tables B3, B4 and B5).

Table **B1:** Sources of parameters for the different groups in each model.

Trophic group	Model	Source
Adult/Sub-adult Nile perch	1977	(Witte and van Densen 1995, Palomares and Pauly 1998).
Adult Nile perch	1987	(Ligtvoet and Mkumbo 1991, Witte and van Densen 1995, Palomares and Pauly 1998, Goudswaard 2006),
Juvenile Nile perch	1987	(Ligtvoet and Mkumbo 1991, Witte and van Densen 1995, Palomares and Pauly 1998, Goudswaard 2006),
Adult Nile perch	2005	(Palomares and Pauly 1998, Mkumbo *et al.* 2007, Njiru *et al.* 2008, Kolding *et al.* 2008), Trawl survey data (TAFIRI, LVFO)
Juvenile Nile perch	2005	(Palomares and Pauly 1998, Mkumbo *et al.* 2007, Njiru *et al.* 2008, Kolding *et al.* 2008), Trawl survey data (TAFIRI, LVFO)
Piscivore haplochromines	1977	(Goldschmidt *et al.* 1993, Goudswaard 2006)
Zooplanktivore haplochromines	1977	(Goldschmidt *et al.* 1993, Goudswaard 2006)
Phytoplanktivore haplochromines	1977	(Goldschmidt *et al.* 1993, Goudswaard 2006)
Detritivore haplochromines	1977	(Goldschmidt *et al.* 1993, Goudswaard 2006)
Prawn-eating haplochromines	1977	(Goldschmidt *et al.* 1993, Goudswaard 2006)
Zooplanktivore haplochromines	1987	(Witte 1992, Witte and van Densen 1995, Froese and Pauly 2009)

Haplochromines	2005	(Moreau *et al.* 1993, Froese and Pauly 2009), Trawl survey data (TAFIRI, LVFO),
Rastrineobola argentea	1977	(Wanink and Witte 2000b)
Rastrineobola argentea	1987	(Witte and van Densen 1995, Wanink and Witte 2000b, Manyala and Ojuok 2007, Froese and Pauly 2009), HEST 1988-1990,
Rastrineobola argentea	2005	(Wanink and Witte 2000b, Manyala and Ojuok 2007, Froese and Pauly 2009), (HEST 1988-1990) Total catches survey data
Clarias gariepinus	1977	(Witte and van Densen 1995, Goudswaard and Witte 1997, Palomares and Pauly 1998, Froese and Pauly 2009),(HEST 1988-1990),
Bagrus docmak	1977	(Witte and van Densen 1995, Goudswaard and Witte 1997, Froese and Pauly 2009)
Oreochromis esculentus	1977	(Witte and van Densen 1995, Goudswaard *et al.* 2002, Froese and Pauly 2009), (EAFFRO 1974)
Oreochromis niloticus	1977	(Witte and van Densen 1995, Goudswaard *et al.* 2002, Froese and Pauly 2009), (EAFFRO 1973-1975)
Oreochromis niloticus	1987	(Witte and van Densen 1995, Goudswaard *et al.* 2002, Froese and Pauly 2009), (HEST 1988-1990)
Oreochromis niloticus	2005	(Witte and van Densen 1995, Njiru *et al.* 2008), Trawl survey data (TAFIRI, LVFO, HEST 1988-1990)

Table **B2:** Summary of all parameters used for fish groups in the three different models (*a posteriori*). *Values in Italics are calculated using the empirical relations advised by ECOPATH makers*. **Values in Bold are found either as is or are averages from literature values**. Values underlined are best guesses. *Values underlined and in italics are calculated, using a best-guess parameter*. **Values in bold underlined are found in literature but either refer to a similar species, or to a close-by lake.** *P/B*=Production over Biomass; *Q/B*=Consumption over Biomass; *K*=von Bertalanffy growth exponent; *M*=natural mortality rate; *F*=Fishing mortality rate; W_∞=asymptotic weight; L_∞=asymptotic length; *SL*=standard length; *TL*=total length; *a*=scaling factor in W-L relationship; *b*=exponent in W-L relationship; *A*=tail aspect ratio parameter (Christensen *et al.* 2005) (c.f. appendix A).

Trophic group	Model	Biomass (t km^{-2})	*P/B* (=*Z*) (yr^{-1})	*Q/B* (yr^{-1})	Catch (t km^{-2} yr^{-1})	*K* (yr^{-1})	*M* (yr^{-1})	*F* (yr^{-1})	W_∞ (g)	L_∞ (cm)	*SL* (cm)	*TL* (cm)	*a*	*b*	*A*
Adult/Sub-adult Nile perch	1977	0.05	*0.27*	*2.46*	0.00	**0.14**	*0.27*	0.00	*181479.84*	**228.00**			**0.01**	**3.16**	**1.09**
Adult Nile perch	1987	**6.00**	*0.68*	*2.81*	*2.10*	**0.17**	*0.33*	**0.35**	*93857.88*	**185.00**			**0.01**	**3.16**	**1.09**
Juvenile Nile perch	1987	**4.00**	*1.83*	*6.41*	*1.40*	**1.00**	*1.48*	**0.35**	*1659.57*	*51.49*		*40.00*	**0.01**	**3.16**	**1.09**
Adult Nile perch	2005	**0.85**	*0.66*	*3.54*	*0.17*	**0.25**			*33135.68*	**133.00**			**0.01**	**3.16**	**1.09**
Juvenile Nile perch	2005	**1.27**	*3.98*	*6.53*	*3.19*	**1.00**			*1659.57*	*51.49*		*40.00*	**0.01**	**3.16**	**1.09**
Piscivore haplochromines	1977	**0.42**	*2.73*	*10.56*		**0.90**			*191.09*	*25.16*	**19.00**	*21.00*	**0.01**	**3.00**	**1.30**
Zooplanktivore haplochromines	1977	**2.59**	*0.57*	*15.69*		**0.90**			*27.46*	*13.18*	**9.00**	*11.00*	**0.01**	**3.00**	**1.30**
Phytoplanktivore haplochromines	1977	**0.90**	*0.36*	*56.62*		**0.90**			*20.63*	*11.98*	**8.00**	*10.00*	**0.01**	**3.00**	**1.30**
Detritivore haplochromines	1977	**4.28**	*0.57*	*39.23*		**0.90**			*27.46*	*13.18*	**9.00**	*11.00*	**0.01**	**3.00**	**1.30**
Prawn-eating haplochromines	1977	**0.12**	*1.00*	*14.17*		**0.90**			*45.33*	*15.57*	**12.00**	*13.00*	**0.01**	**3.00**	**1.30**

Zooplanktivore haplochromines	1987	0.20	*2.66*	*20.60*	0.00	**1.12**	*6.61*	*8.20*	7.00	*7.70*	**0.01**	**3.00**	**1.30**
Haplochromines	2005	**0.82**	*5.06*	*47.08*	**1.65**	**1.50**	*11.23*	**9.78**		**9.29**	**0.01**	**3.00**	**1.30**
Rastrineobola argentea	1977		*1.51*	*20.14*		**1.42**	*1.69*	**6.10**			**0.01**	**3.14**	**1.90**
Rastrineobola argentea	1987		*5.24*	*27.66*		**3.00**	*2.74*	*7.12*	**6.40**	*7.04*	**0.01**	**3.14**	**1.90**
Rastrineobola argentea	2005		*1.60*	*31.30*	**5.21**	**3.00**	*1.09*	**5.30**			**0.01**	**3.14**	**1.90**
Clarias gariepinus	1977	**0.40**	*0.19*	*3.66*		**0.08**	*33274.80*	**157.00**			**0.01**	**3.09**	**1.26**
Bagrus docmak	1977	**0.65**	*0.20*	*2.80*		**0.08**	*8952.12*	**85.00**			**0.01**	**3.08**	**1.44**
Oreochromis esculentus	1977		*0.48*	*27.45*		**0.31**	*669.00*	**32.40**			**0.01**	**3.23**	**1.32**
Oreochromis niloticus	1977		*0.18*	*21.89*		**0.25**	*2029.76*	**46.00**			**0.04**	**2.86**	**1.32**
Oreochromis niloticus	1987		*0.18*	*5.38*		**0.25**	*4882.52*	*60.79*		**56.00**	**0.02**	**3.07**	**1.32**
Oreochromis niloticus	2005	0.09	*12.47*	*18.89*	**1.04**	**0.5**	*4570.00*	**59.5**		**54.00**	**0.02**	**3.07**	**1.32**

Table B3: Mwanza 1977 mass-balance. *TL*=Trophic Level,; *B*=Biomass; *P*=Production, *Q*=Consumption; *EE*=Ecotrophic Efficiency (Part of the production that is further used in the system).

Group name	*TL*	*B* (t km^{-2})	*P/B* (yr^{-1})	*Q/B* (yr^{-1})	*EE*	*P/Q*
L. niloticus	3.41	0.05	0.27	2.46	0	0.11
Piscivore haplochromine	3.38	0.42	2.73	10.56	0.44	0.26
C. gariepinus	3.31	0.40	0.18	3.66	0.99	0.05
B. docmak	3.33	0.65	0.20	2.80	0.93	0.07
Prawn-eating haplochromine	3.00	0.12	1.00	14.17	0.92	0.07
O. esculentus	2.00	0.54	0.48	27.45	0.95	0.02
O. niloticus	2.21	0.28	0.18	21.89	0.95	0.01
R. argentea	3.05	0.92	1.52	20.14	0.95	0.08
Zooplanktivore haplochromine	3.05	2.59	0.57	15.68	0.93	0.04
Phytoplanktivore haplochromine	2.00	0.90	0.36	56.62	0.98	0.01
Detritivore haplochromine	2.00	4.28	0.57	39.23	0.95	0.01
C. nilotica	2.00	0.86	4.00	36.36	0.95	0.11
Zooplankton	2.05	5.25	20.00	145.00	0.95	0.14
Phytoplankton	1.00	3.21	300.00	0.00	0.85	
Detritus	1.00	1.00			0.53	

Table B4: Mwanza 1987 mass-balance. *TL*=Trophic Level,; *B*=Biomass; *P*=Production, *Q*=Consumption; *EE*=Ecotrophic Efficiency (Part of the production that is further used in the system).

Group name	*TL*	*B* (t km^{-2})	*P/B* (yr^{-1})	*Q/B* (yr^{-1})	*EE*	*P/Q*
L. niloticus >40cm	3.92	6.00	0.68	2.81	0.52	0.24
L. niloticus <40cm	3.52	4.00	1.83	6.41	0.97	0.29
R. argentea	3.04	3.14	5.24	27.66	0.95	0.19
O. niloticus	2.31	3.57	0.16	5.63	0.95	0.03
Zooplanktivore haplochromines	3.05	0.20	2.66	20.60	0.16	0.13
C. nilotica	2.26	12.70	7.00	63.64	0.41	0.11
Zooplankton	2.05	9.07	40.00	145.00	0.95	0.28
Phytoplankton	1.00	4.94	350.00	0.00	0.85	
Detritus	1.00	1.00			0.51	

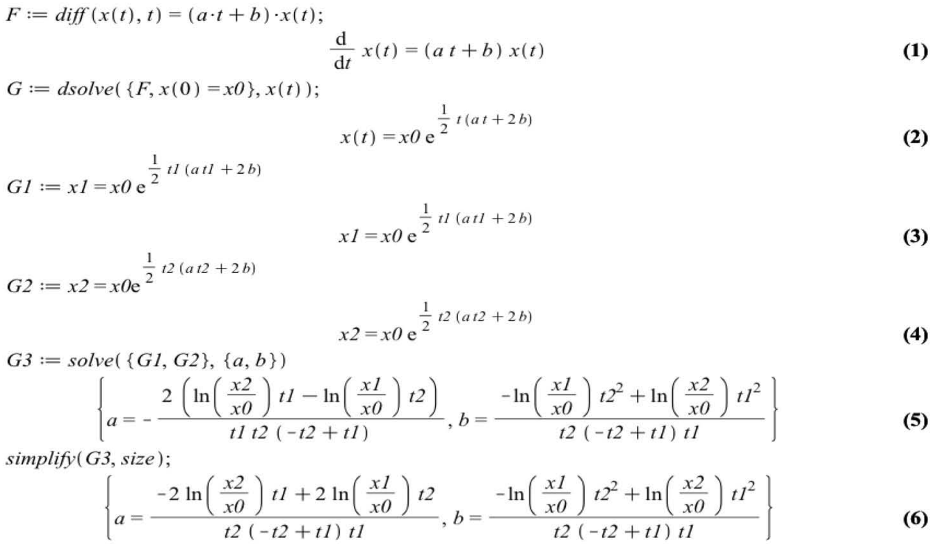
Table B5: Mwanza 2005 mass-balance. *TL*=Trophic Level,; *B*=Biomass; *P*=Production, *Q*=Consumption; *EE*=Ecotrophic Efficiency (Part of the production that is further used in the system).

Group name	*TL*	*B* (t km^{-2})	*P/B* (yr^{-1})	*Q/B* (yr^{-1})	*EE*	*P/Q*
L. niloticus >40cm	4.16	0.85	0.66	3.54	0.35	0.19
L. niloticus <40cm	3.56	1.27	3.98	6.53	0.90	0.61
R. argentea	2.92	5.64	1.60	31.30	0.95	0.05
O. niloticus	2.23	0.09	12.47	18.89	0.94	0.66
Haplochromines	3.20	0.82	5.06	47.08	0.99	0.11
C. nilotica	2.42	7.85	7.00	63.64	0.95	0.11
Zooplankton	2.05	10.81	40.00	145.00	0.95	0.28
Phytoplankton	1.00	5.30	350.00	0.00	0.85	
Detritus	1.00	1.00			0.00	

Appendix C: Chapter 2 – Linear dynamics

For each trophic group, we fitted a straight line between the relative biomasses of the three different years, representing a linear trend of changes in relative growth rate. We did this analytically, using MAPLE, first deriving (eq.1) then solving the straight-line equation (eq.2). We thus obtained changes in relative growth rate for each trophic group, from which we calculated relative biomasses of the different trophic groups in between the three modelled years.

Equations:



$F := diff(x(t), t) = (a \cdot t + b) \cdot x(t);$

$$\frac{d}{dt} x(t) = (a\,t + b)\, x(t) \tag{1}$$

$G := dsolve(\{F, x(0) = x0\}, x(t));$

$$x(t) = x0\, e^{\frac{1}{2} t (a t + 2 b)} \tag{2}$$

$G1 := x1 = x0\, e^{\frac{1}{2} t1\, (a t1 + 2 b)}$

$$x1 = x0\, e^{\frac{1}{2} t1\, (a t1 + 2 b)} \tag{3}$$

$G2 := x2 = x0 e^{\frac{1}{2} t2\, (a t2 + 2 b)}$

$$x2 = x0\, e^{\frac{1}{2} t2\, (a t2 + 2 b)} \tag{4}$$

$G3 := solve(\{G1, G2\}, \{a, b\})$

$$\left\{ a = -\frac{2 \left(\ln\left(\frac{x2}{x0}\right) t1 - \ln\left(\frac{x1}{x0}\right) t2 \right)}{t1\, t2\, (-t2 + t1)},\; b = \frac{-\ln\left(\frac{x1}{x0}\right) t2^2 + \ln\left(\frac{x2}{x0}\right) t1^2}{t2\, (-t2 + t1)\, t1} \right\} \tag{5}$$

$simplify(G3, size);$

$$\left\{ a = \frac{-2 \ln\left(\frac{x2}{x0}\right) t1 + 2 \ln\left(\frac{x1}{x0}\right) t2}{t2\, (-t2 + t1)\, t1},\; b = \frac{-\ln\left(\frac{x1}{x0}\right) t2^2 + \ln\left(\frac{x2}{x0}\right) t1^2}{t2\, (-t2 + t1)\, t1} \right\} \tag{6}$$

Parameters:

t=time (years)

a=intercept

b=slope

x0=relative biomass at time *t*=0

x1=relative biomass at time *t*=10

x2=relative biomass at time *t*=28

t1=10 years (1987)

t2=28years (2005)

Table C1: Linear dynamics obtained analytically, using eq. 6

Time	Pisc	ZooBenth	PhytDet	Prim	Detritus
0	7	16.8	57	14.5	4.6
10	22.4	7.5	56.8	11.1	2.2
28	6.3	19.2	55.7	15.7	3
slope	-0.013341995	0.009490729	-5.24972E-05	0.003284452	0.00649933
intercept	0.183025057	-0.128101234	-8.90084E-05	-0.043142616	-0.10625658

Table C2: Yearly change in growth rate of each trophic group to obtain changes in relative biomass in table 2.

Year	Time step	Pisc	Zoobenth	Phytdet	Prim	Detritus
1977	0	0.18303	-0.12810	-0.00009	-0.04314	-0.10626
1978	1	0.17635	-0.12336	-0.00012	-0.04150	-0.10301
1979	2	0.16301	-0.11387	-0.00017	-0.03822	-0.09651
1980	3	0.14967	-0.10437	-0.00022	-0.03493	-0.09001
1981	4	0.13633	-0.09488	-0.00027	-0.03165	-0.08351
1982	5	0.12299	-0.08539	-0.00033	-0.02836	-0.07701
1983	6	0.10964	-0.07590	-0.00038	-0.02508	-0.07051
1984	7	0.09630	-0.06641	-0.00043	-0.02179	-0.06401
1985	8	0.08296	-0.05692	-0.00048	-0.01851	-0.05751
1986	9	0.06962	-0.04743	-0.00054	-0.01522	-0.05101
1987	**10**	**0.05628**	**-0.03794**	**-0.00059**	**-0.01194**	**-0.04451**
1988	11	0.04293	-0.02845	-0.00064	-0.00866	-0.03801
1989	12	0.02959	-0.01896	-0.00069	-0.00537	-0.03151
1990	13	0.01625	-0.00947	-0.00075	-0.00209	-0.02501
1991	14	0.00291	0.00002	-0.00080	0.00120	-0.01852
1992	15	-0.01043	0.00951	-0.00085	0.00448	-0.01202
1993	16	-0.02378	0.01901	-0.00090	0.00777	-0.00552
1994	17	-0.03712	0.02850	-0.00096	0.01105	0.00098

1995	18	-0.05046	0.03799	-0.00101	0.01434	0.00748
1996	19	-0.06380	0.04748	-0.00106	0.01762	0.01398
1997	20	-0.07714	0.05697	-0.00111	0.02090	0.02048
1998	21	-0.09049	0.06646	-0.00117	0.02419	0.02698
1999	22	-0.10383	0.07595	-0.00122	0.02747	0.03348
2000	23	-0.11717	0.08544	-0.00127	0.03076	0.03998
2001	24	-0.13051	0.09493	-0.00132	0.03404	0.04648
2002	25	-0.14385	0.10442	-0.00138	0.03733	0.05298
2003	26	-0.15720	0.11391	-0.00143	0.04061	0.05948
2004	27	-0.17054	0.12340	-0.00148	0.04390	0.06598
2005	**28**	**-0.18388**	**0.13289**	**-0.00153**	**0.04718**	**0.07248**

Table C3: Relative biomass of each trophic group each year between those measured (bold)

Year	Time step	Pisc	Zoobenth	Phytdet	Prim	Detritus
1977	**0**	**7**	**16.8**	**57**	**14.5**	**4.6**
1978	1	8.35	14.85	56.99	13.91	4.15
1979	2	9.83	13.25	56.98	13.39	3.77
1980	3	11.42	11.94	56.97	12.93	3.44
1981	4	13.08	10.86	56.96	12.53	3.17
1982	5	14.79	9.97	56.94	12.18	2.93
1983	6	16.51	9.24	56.92	11.87	2.73
1984	7	18.18	8.65	56.89	11.62	2.56
1985	8	19.75	8.17	56.86	11.41	2.42
1986	9	21.17	7.79	56.83	11.23	2.30
1987	**10**	**22.40**	**7.50**	**56.80**	**11.10**	**2.20**
1988	11	23.38	7.29	56.76	11.00	2.12
1989	12	24.08	7.15	56.72	10.95	2.05
1990	13	24.48	7.09	56.68	10.92	2.00
1991	14	24.55	7.09	56.64	10.94	1.96

1992	15	24.30	7.15	56.59	10.98	1.94
1993	16	23.73	7.29	56.54	11.07	1.93
1994	17	22.86	7.50	56.48	11.19	1.93
1995	18	21.74	7.79	56.43	11.36	1.95
1996	19	20.39	8.17	56.37	11.56	1.97
1997	20	18.88	8.65	56.30	11.80	2.02
1998	21	17.25	9.24	56.24	12.09	2.07
1999	22	15.54	9.97	56.17	12.43	2.14
2000	23	13.83	10.86	56.10	12.81	2.23
2001	24	12.13	11.94	56.02	13.26	2.33
2002	25	10.51	13.26	55.95	13.76	2.46
2003	26	8.98	14.86	55.87	14.33	2.61
2004	27	7.57	16.81	55.79	14.98	2.79
2005	**28**	**6.30**	**19.20**	**55.70**	**15.70**	**3.00**

Appendix D: Chapter 3 – Sensitivity analysis

We performed an analytical sensitivity analysis by deriving the derivatives of the solution of the logistic growth model with respect to the growth rate (*r*), the carrying capacity (*K*) and the initial stock size (N_0). These derivatives can be interpreted as sensitivity coefficients.

The analytical solution of the logistic growth model is:

$$N(t) = \frac{e^{r\,t}\;K\;N_0}{(e^{r\,t} - 1)\;N_0 + K}$$

The derivatives of this solution to the initial stock size and parameters, reflecting the sensitivity of the change in population-size to changes in initial stocking and parameters are:

$$\frac{\delta N(t)}{\delta N_0} = \frac{e^{r\,t}\;K^2}{(e^{r\,t}\;N_0 - N_0 + K)^2}$$

$$\frac{\delta N(t)}{\delta K} = \frac{(e^{r\,t} - 1)\;e^{r\,t}\;N_0^2}{(e^{r\,t}\;N_0 - N_0 + K)^2}$$

$$\frac{\delta N(t)}{\delta r} = \frac{t\;e^{r\,t}\;K\;N_0(K - N_0)}{(e^{r\,t}\;N_0 - N_0 + K)^2}$$

We obtain the elasticity of the model to each parameter by scaling the sensitivity to population size:

$$E_{N_0}(t) = \frac{\delta N\;(t)}{\delta N_0}\,\frac{N_0}{N\;(t)};\; E_K(t) = \frac{\delta N\;(t)}{\delta K}\,\frac{N_0}{N\;(t)};\; E_r(t) = \frac{\delta N\;(t)}{\delta r}\,\frac{r}{N\;(t)}$$

Finally, we plot the elasticity of each parameter as a function of time so as to tell the effect of each parameter on population size as population grows (fig. D1).

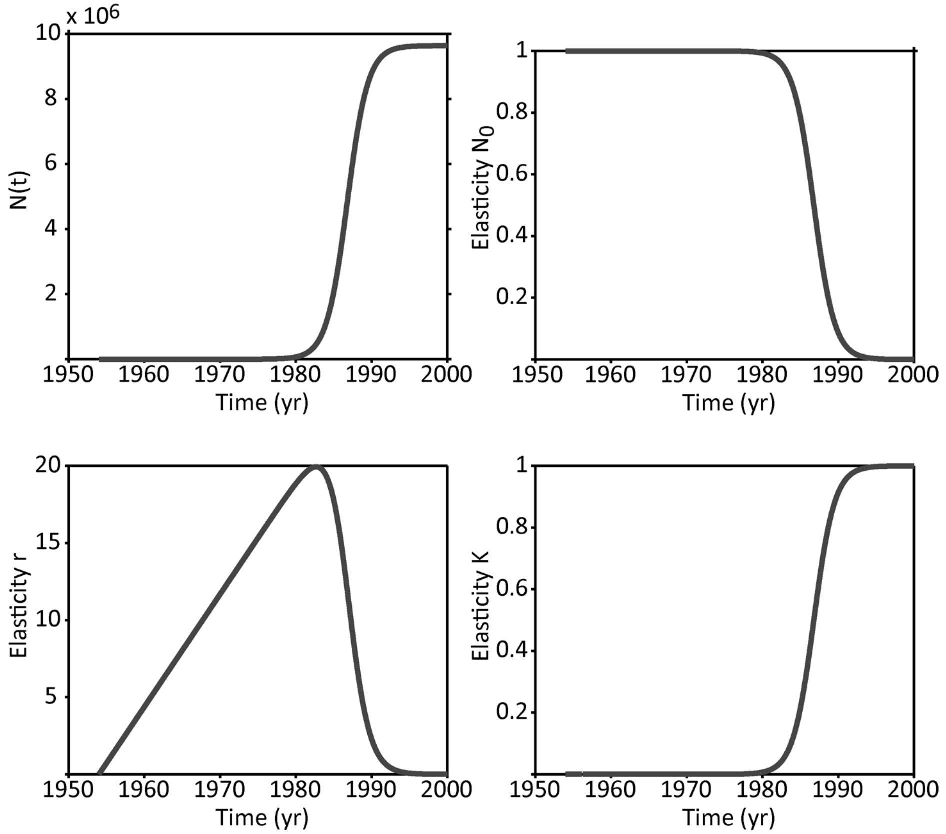


Figure D1: The sensitivity of the model to the parameters and initial conditions. (a) the original model with the default parameters (see figure 2), (b,c,d) the elasticity of resp. the initial conditions (N_0), the carrying capacity (K) and the growth rate (r).

Conclusion

The timing of the boom is almost entirely determined by the growth rate r. The initial stock size N_0 has also some impact but the exact value is relatively unimportant. The carrying capacity K has negligible effect on the timing of the boom, but it determines the equilibrium density.

Appendix E: Chapter 4 – Testing the functional response assumption

To test the extent to which these results are driven by our assumption of a sigmoidal functional response, we ran the model using a Holling type II –monod-saturating type – functional response. The only difference observed using a type II functional response is that after the sudden collapse of native diversity, the system does not systematically stabilise into a stable invader-dominated state, but goes into predator-prey cycles. The basic mechanism we describe, whereby a decrease in diversity leads to a collapse, and that the threshold to collapse is set by a biomass threshold is robust to the change in functional response. The cycles seen here typically arise from an oversimplification of the predator-prey interaction: the monod-relation assumes equal feeding rate at low prey densities, and these cycles tend to disappear when one assumes not all prey are simultaneously equally vulnerable to the predator (e.g. in presence of spatial refugia for the prey).

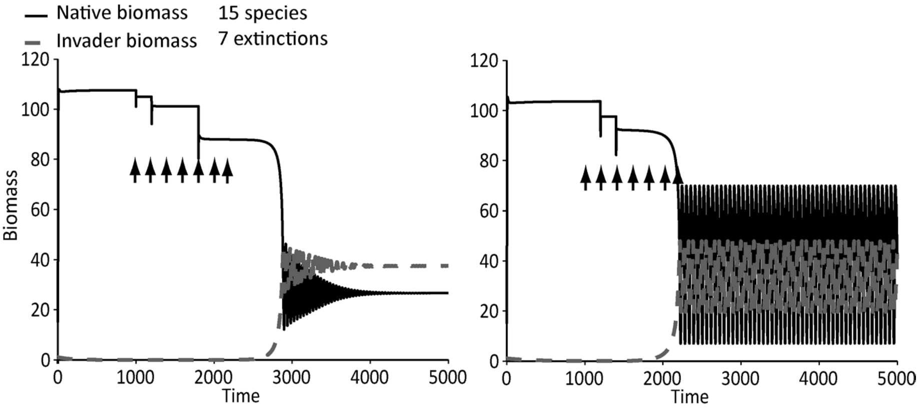


Figure E1: Invasion of the introduced predator when the predator-prey interaction is expressed with a Holling type II (monod) functional response. The mechanism we describe, following which the removal of native species eventually leads to a critical transition, is robust to the change in functional response. However, the monod functional response can lead to predator-prey cycles, thus making the results more complex to analyse, and overshadowing the basic mechanism we aim to describe. (p=0.0015; e=0.6; r=1; g=0.7; H=20; m=0.2; $\alpha_{i,j}$=[0 0,6]; K_i=50). The results appear different for a same set of parameter conditions because of the random choice of competition coefficient $\alpha_{i,j}$.

Appendix F: Chapter 4 – Single native species model analysis

For easier analysis of the effects of different parameters, we simplified the model to include only one native species and the introduced invader. We used increased productivity – obtained with higher values of carrying capacity – as a proxy for increased diversity. Analysis reveals that there are four possible system dynamics, seen in phase planes featuring different configurations of nullclines, or lines of zero growth (fig. F2a-F2d). The native species' nullcline is a curved line, where the native equilibrium is at highest biomass when invaders are absent, intersecting with the x-axis at carrying capacity, and at lowest biomass for high biomass of introduced predator. The introduced predator has two vertical nullclines representing native biomasses at which it can exist. The four configurations depicted in figure F2, with zero, one or two intersections between nullclines, are obtained by changing carrying capacity and predator loss parameters. We related each type of system dynamics to their area of the parameter space defined by control rate (*p*) and carrying capacity (*K*), illustrating how moving right along the x-axis (increasing *K*) causes the native isocline to stretch, and how moving up the y-axis (increasing *p*) causes the invader isoclines to merge. Intersections represent equilibria for both natives and the invader, the stability of these equilibria differs in the four configurations. At low carrying capacity there is not enough native-prey present to sustain an invader (fig. F2a), as carrying capacity increases, the native isocline intersects one invader isocline (fig. F2b): there is then enough native-prey for the predator, but the native species is not abundant enough to control the predator: the only system state is invaded. By increasing both *K* and *p*, the system enters alternative stable states parameter space (fig. F2c). Here initial conditions determine whether the predator or native species dominate. Increasing *K* or *p* further pushes the system through a Hopf bifurcation (fig. F2d), where the invaded state becomes unstable. Increasing control rate makes the two invader isoclines merge, predator losses are altogether too high and the only possible system state is the native one (fig. F2e).

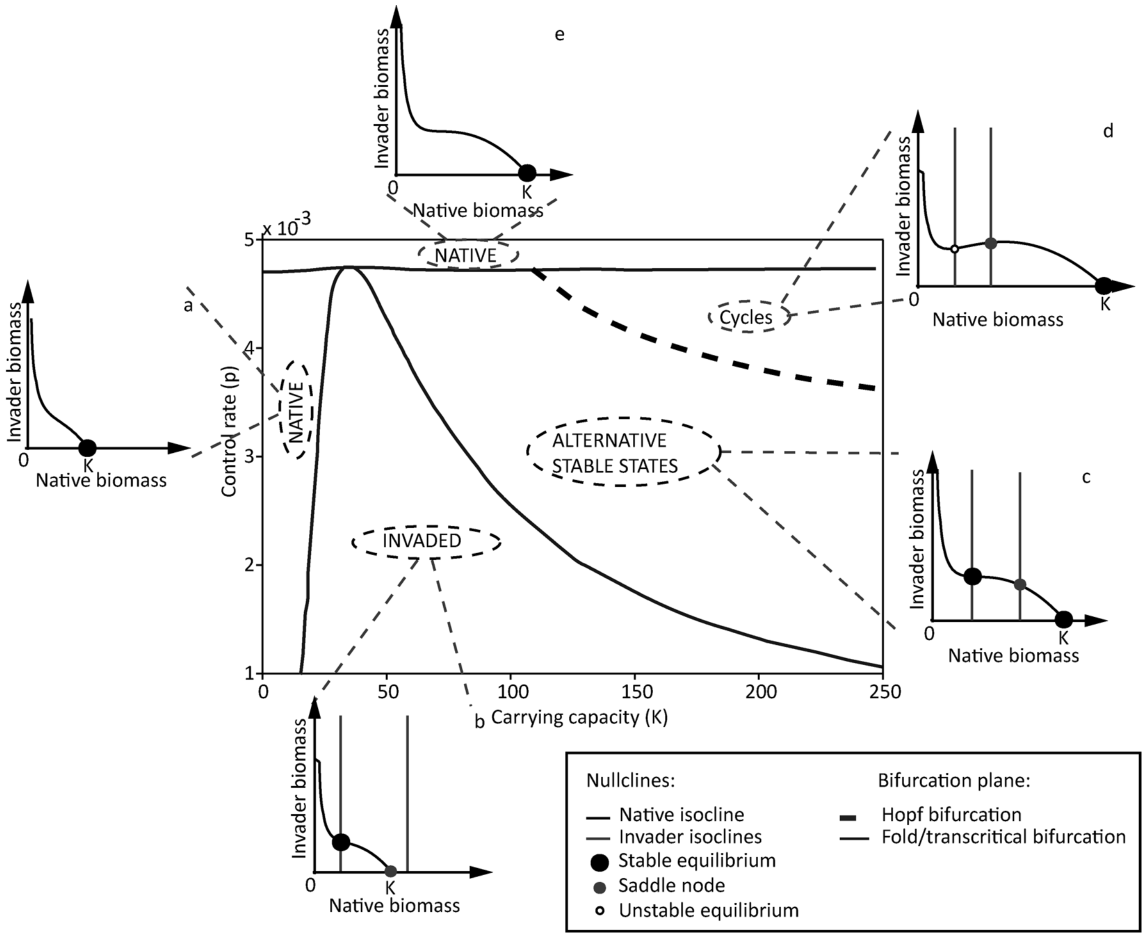


Figure F1: Parameter space illustrating how model dynamics occur under different parameter conditions. In a) there is one stable equilibrium, representing the native-only state; b) the only stable state is invaded, the native equilibrium is a saddle-node. c) With increasing *K* and *p* the native nullcline stretches to the right and the invader ones move left and closer to each other, here the system can exist in either the native-only or invader-dominated state; d) the invaded equilibrium is unstable. e) invader mortality is too high, the only possible equilibrium represents a native-only state.

Appendix G: Chapter 5 – Model parameterisation

The basic growth function for Nile perch is comparable to the specialized von Bertalanffy growth function (VBGF), assuming the respiration allometric exponent n=1 and the consumption exponent d=2/3 (eq. 1). Essington *et al.* (2001) find that these are realistic assumptions, as d does not differ significantly form the d=0.68 measured by Kitchell *et al.* (1997). With regards to the respiration allometric exponent, Essington *et al.* (2001) finds n=1 might underestimate consumption rates should the real value of n be smaller than 1, and over-estimate consumption should the real value of n be larger than 1. Although the model is sensitive to changes to the respiration exponent, Essington *et al.* (2001) find that the error in consumption rate estimated when assuming n=1 is smallest as long as the real value of n is smaller than but close to 1, as expected by fish activity and morphometrics (Jobling 1995). We therefore expect that the assumption of n=1 yields either reasonably accurate or at least consistently underestimated consumption rates. Natural mortality (0.29 yr^{-1}), was used by Kitchell *et al.* (1997) as well as calculated by Mkumbo (2002).

We set values for the metabolism loss rate (k), handling time (h) and encounter rate (η) by co-varying the three parameters within sensible ranges (k=[0.0008-0.002] (d^{-1}); h=[5-12] (d); η=[0.01-0.15] ($m^2\ g^{-1}\ d^{-1}$) and finding the combination of the three parameter values that yielded outputs of length-at-age, maximum length and asymptotic length matching literature values for Nile perch. More precisely, using Matlab, we ran the model for all combinations of those three parameters, assuming a conversion efficiency of A=65%, under a resource abundance R=10(g m^{-2}) to obtain outputs of length at year 1, year 11 (values in Kitchell *et al.* (1997)) as well as maximum length. We ran the model again for all combination of parameters but under R=1000 (g m^{-2}) (representing unlimited resources) to obtain the asymptotic length (L_∞). We then searched through those results and picked out the values and the parameters combination that produced them, that fit all our observational constraints (length year 1=[26.7-30.7] cm, length year 11=[155.2-159.2] cm, i.e. length at age ± 2cm from data in Hughes (1992), used by Kitchell *et al.* (1997). Lmax=[180-200] cm and L_∞=[200-220]). We refined the range of by calibrating the encounter rate (η) to produce individuals just mature at a minimum limiting resource 120% the density of Nile perch. Thus we obtained the following values: k=0.0012, h=9, η=0.06.

Unknown parameters involved in reproduction are A_f and J. The number of eggs per gram of gonad tissue (E_{no}) was measured by Ogutu-Ohwayo (1988). We adjusted A_f to match fecundity measured by Ogutu-Ohwayo (1988). Fecundity is defined as the number of ripe ova in the ovary prior to the next spawning season and was measured to be between 1 and 2 million for recently matured fish and reach about 16’000’000 in fish >150 cm. Gonad weight is expected to increase with fish length after maturity, therefore our fixed parameter A_f is a bit of a rough estimate of the gonadosomatic index (GSI: represents the fraction of total fish mass that is gonad tissue). We here used a value of A_f that overestimates the maximum GSI measured by Ogutu-Ohwayo (1988) but fits fecundity. Overestimating the overall mass of gonads relative to body-mass should here yield underestimates of body length. However, length is quite insensitive to gonad weight whereas fecundity is highly sensitive to gonad weight, which is why we calibrated A_f to best fit fecundity rather than GSI. This approach means that our model slightly underestimates asymptotic length.

The number of eggs spawned that in turn survives to become spawning individuals is set by the parameter J, representing a survival ratio. Stock-recruitment relationships are poorly understood in fish, but it was found that in most spawning fish populations out of 700 studied, individuals produced between 1 and 7 spawning recruits per year of maturity each (Myers *et al.* 1999). We therefore found the limits of the range of J values that correspond to the Nile perch cohort producing either 1 or 7 viable recruits at each spawning event over its mature life-time, we used the mean J for the study.

Appendix H: Chapter 5 – Sensitivity analyses

We carry out Monte-Carlo sensitivity analyses on the two Lshift models, in both cases at an equilibrium resource composition with a mortality rate of μ_f=0.0015 d^{-1} (low Lshift: R_1=5.8448 t km^{-2}, R_2=4.3966 t km^{-2}. High Lshift: R_1=5.8448 t km^{-2}, R_2=2.9483 t km^{-2}). To test the effects of changes in parameter values on the model output (abundance, weight, length, reproductive output) we first generated 10,000 sets of parameters by drawing their values independently from uniform distributions (±10%). We sampled the model outputs at a frequency of 3 times per year simulated, over 30 years. We include 1000 dummy variables – that have no effect on the model – in this sensitivity analysis (van Nes *et al.* 2003). After simulation, the sensitivity coefficients for each model output are calculated. These coefficients give the relative change in output as a result of changing the parameters over their distribution range and are scaled between 0 and 1 (Klepper 1989). This yields a matrix of sensitivity coefficients for each parameter-output combination at each sampled time-step. To qualify the sensitivity coefficients of the model parameters, we compare them to those of the dummy variables. We consider the parameters whose sensitivity coefficients are higher than 95% of the dummy variables' coefficients as having a significant effect on the model output.

To facilitate analysis of the sensitivity coefficients, we cluster the parameters that have a significant effect on the model into groups that have the same or opposite effects on the model behaviour (Klepper 1989). For this we use a hierarchical cluster analysis using group average clustering and the sine distance as a similarity measure.

Results

In both models, the sensitivity analyses revealed 19 out of the 29 parameters had an effect significantly different (to the 95 percentile) to that of 1000 dummy variables. Fishing mortality is the parameter with the strongest overall sensitivity coefficient, though it only has significant effect on density N. Initial values of weight (W_0) and density (N_0) as well as exponents (d, n, b) also have strong sensitivity coefficients. The strong sensitivity to the initial condition W_0 is caused by a high effect on the initial state of the cohort, even though it has no significant effect thereafter. N_0 affects N throughout the cohort life.

We separated the clusters at an arbitrary sine-distance level of 0.85. Overall and unsurprisingly, the cluster analysis reveals that parameters are clustered in similar ways in the two models. The state variables reproductive output (N_{new}) and length (L) are both sensitive to A_f, though the effect is strongest on N_{new}. Handling time and parameters that relate to the consumption of the first resource form one cluster (fig. H1 cluster I), to which predominantly both weight (W) and length (L), and to a lesser extent reproductive output are sensitive. The next parameter cluster (fig. H1 cluster II), comprises growth parameters and exponents as well as parameters relating to the consumption of the second resource and affects the same variables, albeit in the opposite way to cluster I. The last cluster (fig. H1, cluster III) includes parameters to which cohort density (N) is sensitive.

In the low Lshift model, the model variables are more or less equally sensitive to parameters relating to either of the two resources; in the high Lshift model, variables are more sensitive to the parameters relating to the consumption of the first resource than to their second resource counterparts (e.g. η_1 has a stronger effect than η_2). This is a consequence of Nile perch feeding longer on R_1 and less time on R_2 in the high Lshift model.

Discussion

We find a strong and differential sensitivity of model outputs to functional response parameters. This result indicates that the choice of functional response in more complex models that take feedbacks with the resource into account will have a significant impact on the results (Abrams 1987). Therefore, before adventuring further in dynamic models, it is worth exploring how Nile perch interacts with its different prey and try to quantify processes such as size-selection, behaviour at low or high prey density, and adaptive or prey-dependent functional responses.

Our analysis shows that with the model formulation we use, assimilation efficiency is the parameter from the numerical response that has the strongest overall effect. So far, we have simplifyingly assumed that the assimilation efficiency of both resources is equal (A_1=A_2). In reality however, shrimp is known to contain only approximately 70% of the calorific content of fish, implying that A_1<A_2 (Kitchell *et al.* 1997). Using a lower value of A_1 would lead to a higher R^*, by increasing the limiting effect of the first resource. We have so far also assumed that encounter rates for both resources are equal (η_1=η_2). In a more realistic approach these encounter rates would be a function of the size of both prey and predator and require a more complex formulation and are likely to have significant effect on population dynamics (Schindler *et al.* 1998, Claessen *et al.* 2002, van Kooten *et al.* 2005). Encounter rates are also influenced by the foraging method of the predator or the elusiveness of prey, of which we know little, if anything, for Nile perch and its prey.

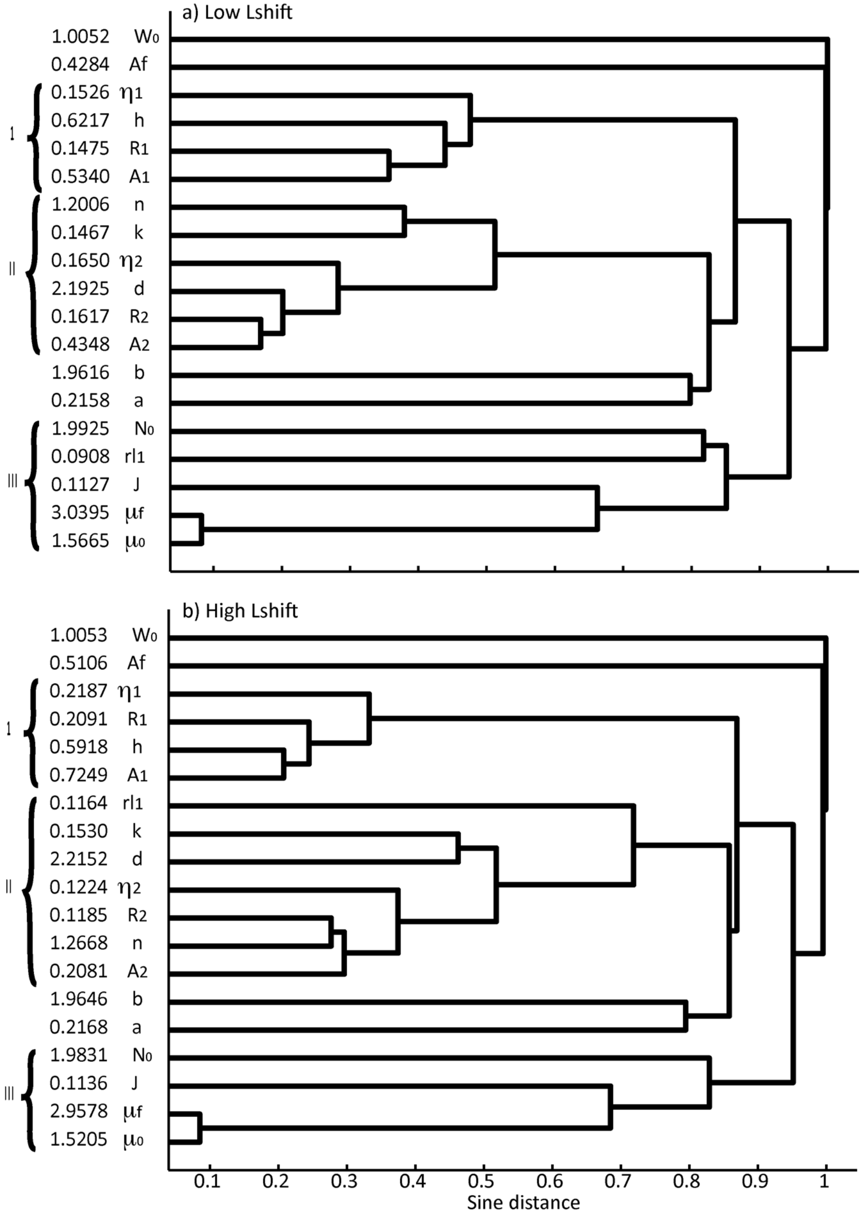


Figure H1: Cluster analysis of the parameters based on their sensitivity indices. Sensitivity analyses were carried out at equilibrium resource concentration. The value attributed to each parameter is its sensitivity coefficient: a high sensitivity coefficient reflects a strong effect on the model output. Clusters contain parameters that have similar or opposite effects on the model output.

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Summary

Lake Victoria, in East Africa, has undergone unpredictable changes since the early 1900s in response to multiple stressors, such as species introductions, eutrophication, exploitation and climate change. These changes culminated in the 1980s, when the introduced Nile perch invaded the system and the native diversity of haplochromines collapsed. Since then, some 30 million people who live in the lake's basin increasingly depend on the revenue and opportunities provided by the Nile perch fishery, as well as on the fishery of a small native cyprinid (dagaa) that flourished after the diversity collapse. With on-going anthropogenic disturbances and fluctuations in stocks, it is essential to understand how external drivers influence the system so as to manage it sustainably. This study aims at unravelling the effects of fishing and eutrophication on the food web, by taking a multidisciplinary and modelling approach.

We describe and compare pre-, per- and post-Nile perch boom food webs using a mass-balance approach and find that the system as a whole was structurally and functionally disturbed in the wake of the diversity collapse and Nile perch boom. The system recovered mostly at a structural level, but less so at a functional level and there are on-going adaptations in the different trophic groups of the food web (chapter 2).

Using two minimal models, we investigate the conditions and expectations for the Nile perch boom and compare with available data from that period. Our results indicate that basic exponential growth is sufficient to explain the Nile perch invasion at the scale of the whole lake, but that there are probably local food-web influences on Nile perch growth and establishment (chapter 3), such influences can affect the maximum rate at which Nile perch can be harvested, as well as the resilience and recovery of the system (chapter 4).

In chapter 5 we investigate population growth at a finer scale and find that different drivers can have the same effect: using a physiologically structured population model for Nile perch we find that a change in available resources – such

as the one that followed the Nile perch boom – can influence Nile perch population size-structure and thus confuse indicators of over-exploitation. Furthermore, these two processes can have synergistic effects, and an ecosystem perspective is therefore necessary to understand how changes are taking place.

Finally, we describe the social-ecological system of Lake Victoria by bringing together Lake Victoria experts of different disciplines. Our analysis illustrates how external influences can have cascading effects on the system. Also, we investigate the resilience of social, economical and ecological components of the system: it appears that social resilience needs a further build-up, and that mitigation of eutrophication is necessary to maintain ecological resilience. We conclude that even though diversity loss and anthropogenic influences have eroded the adaptive capacity of the ecosystem, the human component still has means to exploit its own adaptive capacity, and that it should be balanced with that of the ecosystem.

Samenvatting

Het Victoriameer, in Oost-Afrika, heeft sinds 1900 als gevolg van verschillende stressoren, zoals introductie van exotische soorten, eutrofiëring, overbevissing en klimaatverandering, grote veranderingen ondergaan. Deze veranderingen culmineerde in de jaren 1980, toen de geïntroduceerde nijlbaars het systeem binnendrong waarna de enorm diverse gemeenschap van inheemse cichilden (haplochromiden) instortte. Sindsdien zijn 30 miljoen mensen die rond het meer leven, voor hun inkomsten steeds afhankelijker geworden van de nijlbaarsvisserij, aangevuld door de visserij op een kleine inheemse karperachtige (dagaa) die sterk in aantal toenam. Met de huidige antropogene verstoringen en schommelingen in de visstanden, is het essentieel om te begrijpen hoe verschillende externe factoren het systeem beïnvloeden, en hoe het systeem duurzaam beheerd kan worden. Deze studie is gericht op het ontrafelen van de effecten van de visserij en eutrofiëring op het voedselweb, en heeft een modelmatige en multidisciplinaire benadering.

We beschrijven en vergelijken eerst de voedselketens in de periodes voor, tijdens en na de piek in de nijlbaarspopulatie door middel van het opstellen van massabalansen. Hieruit bleek dat het systeem structureel en functioneel verstoord was na de instorting van de diversiteit van cichilden en na de nijlbaarspiek. Het systeem herstelde vooral op een structureel niveau, maar in veel mindere mate op functioneel niveau, hoewel veel groepen in het voedselweb zich nog steeds aan het aanpassen zijn (hoofdstuk 2).

Met behulp van twee heel eenvoudige modellen, hebben we verder de oorzaak van de traagheid in de opkomst van de nijlbaarspopulatie nader onderzocht. Nijlbaars nam namelijk pas zo’n 20 jaar na introductie in enkele jaren zeer sterk in aantal toe. Onze resultaten geven aan dat exponentiële groei op de schaal van het grote meer alleen al voldoende is om dit patroon te verklaren, hoewel dat er lokaal waarschijnlijk ook andere factoren van invloed op de groei en vestiging van nijlbaars zijn geweest (hoofdstuk 3). Deze resultaten zijn ook van belang voor de maximale visserijdruk die nijlbaars kan ondergaan, evenals voor een schatting van de veerkracht en het herstel van het systeem (hoofdstuk 4).

In hoofdstuk 5 onderzoeken we de populatiegroei van nijlbaars op een fijnere schaal en zien we dat verschillende factoren hetzelfde effect op de populatiestructuur kunnen hebben. Met een fysiologisch gestructureerd populatiemodel van nijlbaars vinden we dat een verandering in de beschikbare voedselbronnen – bijvoorbeeld in de periode na de nijlbaars piek – de lengte-frequentie verdeling van de nijlbaarspopulatie kan beïnvloeden en daarmee een invloed kan hebben of indicatoren die aangeven of de populatie overbevist wordt. Bovendien kunnen visserij en eutrofiering synergetische effecten hebben, waardoor het om veranderingen te kunnen begrijpen noodzakelijk is het systeem van een ecosysteem perspectief te bezien.

Tot slot beschrijven we het sociaal-ecologische systeem van het Victoriameer waarbij we diverse deskundigen van verschillende disciplines bij elkaar hebben gebracht. Onze analyse laat zien hoe externe invloeden effecten kunnen hebben op het systeem en hoe die indirect in het systeem doorwerken. Ook hebben we de veerkracht van sociale, economische en ecologische componenten van het systeem onderzocht: het lijkt er op dat sociale veerkracht behoefte heeft aan een verdere opbouw, en dat de eutrofiëring een bedreiging is voor de ecologische veerkracht. We concluderen dat het verlies aan diversiteit en antropogene invloeden de adaptieve capaciteit van het ecosysteem hebben uitgehold, de menselijke component nog mogelijkheden heeft om de visexploitatie uit te breiden, maar dat dat wel een verkleining van de veerkracht van het ecosysteem tot gevolg kan hebben.

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Curriculum vitae

Andrea S. Downing was born in Geneva, Switzerland in 1982. She studied classical languages through secondary school and shifted focus to biological sciences at university. During her university studies, she spent a year at the Université de la Réunion, in the Indian Ocean, on an Erasmus program, and was awarded a graduate diploma of biology by the University of Geneva in 2004. She carried out her masters at James Cook University in Australia, studying coral bleaching and its monitoring. Throughout her studies, Andrea worked as a research assistant and teacher. In 2008, she started her PhD project at Wageningen University, studying the complex ecosystem of Lake Victoria with multiple modelling approaches.

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The Netherlands Research School for the
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- Uncertainty analysis
- Basic statistics
- Research Methodology 1: from topic to proposal
- Consumer-Resource interactions

Other PhD and Advanced MSc Courses

- Models of Biological Processes and Environmental Quality
- Techniques for Writing and Presenting Scientific Papers
- Scientific publishing workshop

Management and Didactic Skills Training

- Contributed as a scientific expert to two scientific and stakeholder workshops in Tanzania on Fishing pressure, eutrophication and their interactions on Lake Victoria’s ecosystem
- Organizer of the workshop on Seeing the water and the fish of Lake Victoria: combining perspectives
- Session Chair for the Netherlands Annual Ecology Meeting in 2010
- Practical supervisor for the MSc course Modelling Biological Systems and the MSc course Models of Biological Processes and Environmental Quality
- Guest lecturer for the course The Ecosystem Approach to Fisheries

Oral Presentations

- *Collapse and Reorganization of a Lake Victoria food web*. Netherlands Annual Ecology Meeting (NAEM), 9-10 February 2010, Lunteren
- *Unexpected effects of diversity loss.* NAEM, 8-9 February 2011, Lunteren
- *How does Nile perch respond to changes in its system, Lake Victoria?* NAEM, 8-9 February 2012, Lunteren
- *When diversity loss leads to a critical transition.* 96th ESA Annual Meeting, 7-12 August 2011, Austin, Texas
- *Unravelling the responses of Nile perch population dynamics to changes in Lake Victoria.* 97th ESA Annual Meeting, 5-10 August 2012, Portland, Oregon
- *Modelling food driven changes in Nile perch population dynamics.* 31st Congress of the International Limnological Society, 15-20 August 2010, Cape Town

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