Causes and effects of the Lake Victoria ecological revolution

Goudswaard, Pleun Cornelis

CHAPTER 9

What happened and who did what

Kees (P.C.) Goudswaard

Institute of Biology, University of Leiden, P.O. Box 9516,

2300 RA Leiden, The Netherlands

Introduction

In the chapters of this thesis the effects of fisheries, species introductions and eutrophication on the fish stocks of Lake Victoria have been discussed. It is obvious that human induced effects are the main causes of the changes in Lake Victoria. In this last chapter an attempt will be made to combine the information from the previous chapters and from the literature to acces the events. Ogutu-Ohwayo (1990a) and Witte et al. (1992b) have described the decline of the haplochromines. Wanink (1989) discussed the increase of dagaa (*Rastrineobola argentea* Pellegrin). The temporary massive increase of water hyacinth (*Eichhornia crassipes* von Martius) has been described by Njuguna (1991) and Williams & Hecky (2005). Several other aspects of the changes in the Lake Victoria ecosystem are poorly documented. It is for instance obvious that snails and lake flies have increased in numbers, but quantitative data on their changes in abundance are lacking, or incomplete (Kaufman, 1992; Mbahinzireki, 1992; Witte et al., 1992a).

In the previous chapters mainly attention was paid to interrelationships between one of the indigenous species (or a species group) and human induced changes. However, these effects are interrelated and feedback mechanisms will exist. To clarify this, a simplified semi-quantitative picture of human induced effects in the Lake Victoria ecosystem and their interrelationships is given in Fig. 9.1. Depicted are positive and negative correlations between the increased human population and the stock sizes of different organisms. Based on the shifts in

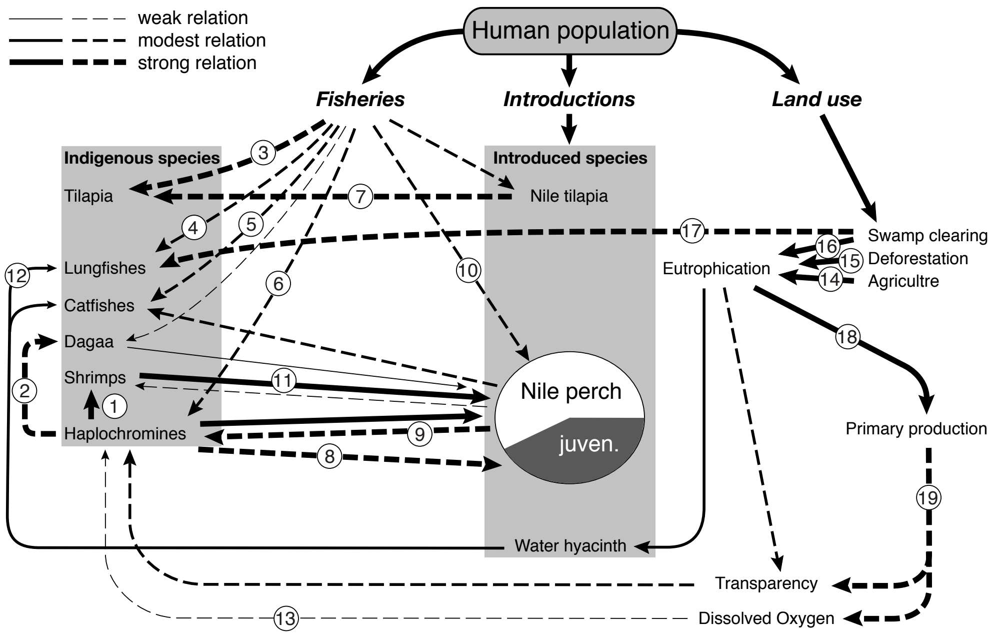

Fig. 9.1 *Diagram of positive and negative relations in the Lake Victoria ecosystem*

abundance of populations of fishes and other organisms in the lake between the early 1970s and the end of the 1990s, three levels of effect are distinguished: weak, moderate and strong.

The following paragraphs are focussing on the strong and moderate interactions in the diagram (Fig. 9.1). The interrelationships between indigenous species, the impacts of fisheries on these species, and the impacts of introduced species, and the effects of land use on the ecosystem successively are discussed.

Interactions among indigenous species

It has been suggested that there is a strong negative correlation between the abundance of haplochromines and shrimps (Chapter 5), and between haplochromines and dagaa (Wanink, 1991) This is concluded from the fact that, both, dagaa and shrimps increased strongly after the disappearance of the haplochromines. Thus, the high abundance of haplochromines before the 1980s seems to have controlled the abundance of dagaa and shrimp populations. Competitive release due to the decline of haplochromines in the 1980s may have caused the increase of dagaa (Wanink, 1998). The increase of the shrimps may have been caused by the decreased predation on their juveniles by haplochromines (Chapter 5).

Fisheries on indigenous species

Originally the indigenous tilapiine species were the main target of the local fishermen. They had a heavy impact on these species, and catches declined strongly between the 1930s and the 1940s (Fryer, 1973). In the past, fisheries also had a strong impact on several other fish species that are not included in the diagram. For instance, the cyprinid *Labeo victorianus* Boulenger once supported a small seasonal fishery that had a dramatic impact on their stock (Cadwallader, 1965). Moderate negative impacts of fisheries have been described for lungfish, *Protopterus aethiopicus* Heckel (Chapter 7 – Goudswaard et al., 2002b). Locally, there was a moderate impact on the catfishes *Clarias gariepinus* (Burchell) and *Bagrus docmak* Forskåll (Martens, 1979; Chapter 6 – Goudswaard & Witte, 1997). The effects of fisheries on haplochromines were locally strong. Initially this was especially the case in the Nyanza Gulf by an artisanal fishery (Marten, 1979), and later in the Mwanza Gulf as a result of bottom trawling (Witte & Goudswaard, 1985; Chapter 2). Lake-wide, however, the fishery pressure on haplochromines can be considered as moderate.

Introduced species

Three alien organisms that were thriving in Lake Victoria in the 1990s were: Nile tilapia (*Oreochromis niloticus* L.), Nile perch (*Lates niloticus* L.) and water hyacinth. Due to its opportunistic feeding behaviour, its higher reproductive success, and its assumed aggressiveness to other species, Nile tilapia successfully out-competed the indigenous tilapiines (Lowe-McConnell, 2000; Chapter 8 – Goudswaard et al., 2002a).

The effect of the introduced Nile perch has been strong and is complex. As has been suggested in Chapter 2, Nile perch had a chance for successful recruitment in the Nyanza Gulf, after a local reduction of haplochromines by fishery. After the decline of the haplochromines in the area, juvenile Nile perch were not prone anymore to high predation pressure. The disappearance of the haplochromines also eliminated competition for food with juvenile Nile perch. As a consequence of decreased predation pressure the Nile perch stock boomed in the Nyanza Gulf (Chapter 2). From this nucleus, other parts of the lake were colonised by waves of migrating, sub-adult, Nile perch (Chapter 2). These waves of Nile perch, invading new areas, had a strong negative effect on local haplochromine stocks (Chapter 2, Witte et al., 1992b). The strong impact of Nile perch on the haplochromine cichlids is supported by the observations that some haplochromine species did increase in number again, when the stocks of Nile perch declined due to heavy fishing (Witte et al., 2000).

It has been noted that Nile perch seem to prefer and grow fastest on haplochromine prey (Ligtvoet & Mkumbo, 1990; Kaufman & Schwartz, 2002). However, when the haplochromines had vanished, they gave way to shrimps, dagaa and juvenile Nile perch (see above). These, then, became the dominant prey of Nile perch (Hughes, 1986; Ogari & Dadzie 1989; Ogutu-Ohwayo, 1990b; Mkumbo & Ligtvoet, 1992; Katunzi et al., in press). The observation that the catch rate of Nile perch in the Mwanza Gulf declined after the haplochromines had vanished from their diet in 1987 (Ligtvoet & Mkumbo, 1990; Mkumbo & Ligtvoet, 1992; Chapter 2), may corroborate the importance of haplochromines as food for this predator. It should be noted, however, that the impact of the increased Nile perch fishery over time is a confounding factor.

The Nile perch had a strong positive effect on the production level of Lake Victoria (not indicated in Fig. 9.1). Annual landings increased from approximately 100.000 tons in the 1960s to over 500.000 tons at the end of the 1980s (Reynolds et al., 1995). However, the Nile perch stock apparently could not cope with this level of exploitation and showed signs of over-fishing (Pitcher & Bundy, 1995; Balirwa et al., 2003).

Between 1989 and 1997 the water hyacinth increased strongly in the lake. This alien species apparently provided a suitable habitat for lungfish and the catfish *C. gariepinus*. Bugenyi & Van der Knaap (1997) attributed the modest recovery of both species to the spread of the water hyacinth. On the other hand it has been suggested that the low oxygen levels below the water hyacinth were not favourable to haplochromines and juveniles of other fish species (Williams & Heckey, 2005; Balirwa, 1998). However, after 1998 the water hyacinth declined and a restoration of the pre water hyacinth situation may be expected.

Land use and eutrophication

Three major factors are distinguished concerning land use in the Lake Victoria Basin: agriculture, deforestation and swamp clearing. Together they increased the eutrophication of the lake (Balirwa, 1998; Scheren et al., 2000; Ntiba, 2001; Verschuren et al., 2002).

A direct effect of swamp clearing was the destruction of the lungfish habitat, which was supposed to be one of the main causes of the lungfish decline (Chapter 7 – Goudswaard et al., 2002b). As mentioned above, this may have been partly diminished by the increase of water hyacinth. Eutrophication also caused phytoplankton blooms. The daily integral phytoplankton productivity per unit area was two times higher both inshore and offshore in the 1990s than in the 1960s (Mugidde, 1993).

Eutrophication and the related phytoplankton blooms had two major effects on the water quality, viz. a decrease of water transparency and a decrease of dissolved oxygen levels (Ochumba & Kibaraa, 1989; Hecky et al., 1994; Seehausen, 1997; Wanink et al., 2001; Witte et al., 1999, 2005). Long term hypoxia in large parts of the lake makes the environment less suitable for fish. The occasional sudden up-welling of anoxic water of Lake Victoria, has resulted in massive fish kills (Fish, 1957; Ochumba, 1990; Wanink et al., 2001). Nevertheless, the populations of Nile perch and dagaa, which are supposed to be sensitive to hypoxia, increased strongly, whereas, most of the haplochromine cichlids, that are relatively hypoxia tolerant (Verheyen et al., 1986; Chapman et al., 1996; Witte et al., 2005), declined. Consequently, hypoxia does not seem to have played a major role in the decline of the haplochromine stocks (Witte et al., 2005). In contrast, a decrease of water transparency may have had a negative impact on haplochromines. Species diversity in haplochromine cichlids is lower in turbid than in clear water. This holds both within Lake Victoria as well as among different East African lakes (Seehausen et al., 1997; Witte et al., 2005) and could be explained by the findings that visual information is important in haplochromines for social interactions and foraging (Seehausen, 1997; Seehausen et al., 2003; Witte et al., 2005).

The main cause of the decline of haplochromines

During the past decades, there has been a dispute about the causes of the decline of the haplochromine stock in Lake Victoria. Over-fishing (Acere, 1988; Bundy and Pitcher, 1995; Kudhongania & Chitamwebwa, 1995), eutrophication (Hecky et al., 1994; Bundy and Pitcher, 1995; Seehausen et al., 1997, Verschuren et al., 2002) and predation by Nile perch (Barel et al., 1985, 1991; Ogutu-Ohwayo, 1990a, Witte et al., 1992b; Goldschmidt, 1996) have been mentioned as the causes for this decline. In a recent paper (Witte et al., in press) it has been argued that predation by Nile perch and eutrophication were the main factors determining the fate of haplochromines, and that it was impossible to distinguish between these two factors. However, the data in this thesis suggest that, although massive extinction of haplochromines might be the result of a combination of factors, it seems that Nile perch played a key role in the process. This is supported by the increased decline of the haplochromines in different areas, each time after a local increase of Nile perch (Chapter 2), and by the recovery of some haplochromine species after the decline of the Nile perch in the 1990s (Witte et al., 2000). One of the arguments for the contribution of eutrophication to the loss of haplochromine diversity in the 1980s, was the observation of intermediate phenotypes in murky waters along the rocky shores (Seehausen et al., 1997a). These “hybrids” were noticed for the first time several years after the Nile perch boom (Seehausen, 1997). Nile perch is not common in the structural complex rocky habitat. In the open waters of the Mwanza Gulf, where Nile perch boomed in the 1980s, amalgamation of species has not been observed and, consequently, cannot explain the dramatic decline of the number of haplochromine species. It is necessary to make a distinction between the decline in abundance of individuals and the decline in species diversity of haplochromines. Nile perch predation is likely to have an impact on both abundance and diversity (Witte et al., 1992b), whereas eutrophication may mainly have an impact on diversity (Seehausen et al., 1997). This is supported by the following observation. After the decline of the Nile perch in the 1990s, the abundance of zooplanktivores in the Mwanza Gulf increased to a level similar to that in the 1970s. In spite of this recovery in biomass, the number of species had declined from 12 in the 1970s to only three in the 1990s (Witte et al., in press). Thus, low species diversity does not need to indicate a low abundance of haplochromines.

Did the Nile perch act alone?

During the past decades many fish species have declined or even vanished from Lake Victoria. The Nile perch has often been blamed to be the culprit. However, the diagram (Fig. 9.1) shows that several changes in the ecosystem of Lake Victoria were not, or only partly, related to the Nile perch boom. (1) The indigenous tilapias were strongly affected by the fishery and by the introduced Nile tilapia. (2) Fishery had a moderate negative impact on lungfish, catfishes and haplochromines. (3) There was a strong effect of swamp clearing on lungfish. (4) There was a negative impact of eutrophication on the haplochromines. Moreover, man aided the introduced Nile perch, by locally reducing the haplochromines. As a consequence, juvenile Nile perch found an open niche resulting in a large recruitment. In conclusion, Nile perch had a strong effect on the Lake Victoria ecosystem, but did not act alone.

The future of the Lake Victoria ecosystem

As shown in Fig. 9.1 the relations between Nile perch, haplochromines and shrimps are complicated. The abundance of adult Nile perch has a negative impact on the abundance of haplochromines. Due to the negative correlation between haplochromines and the stocks of dagaa, juvenile shrimps and juvenile Nile perch, an increase in abundance of Nile perch indirectly has a positive effect on these three stocks. On their turn, haplochromines and adult shrimps have a positive impact on the abundance of adult Nile perch. Haplochromines seem to be the most preferred prey of Nile perch (Ligtvoet & Mkumbo, 1990; Kaufman & Schwartz, 2002). Based on a model of Kaufman & Schwartz (2002), Balirwa et al. (2003) suggested that biodiversity and fisheries in Lake Victoria could go hand in hand. They state that “according to the model, a key in sustainability in Nile perch fishery is to maintain sufficient fishing pressure to ensure an abundance of haplochromine prey but not so much pressure as to threaten the Nile perch stock itself”. It has also been noticed that the diversity of haplochromines may be improved by a reduction of eutrophication (Seehausen et al., 1997a; Balirwa et al., 2003; Witte et al., 2005). Though, in principle this seems correct, the foregoing studies did not consider the negative impact of a high abundance of haplochromines on juvenile Nile perch, juvenile shrimps and dagaa, as suggested in this thesis (Fig. 9.1). From a fisheries point of view, a decline of Nile perch production is not desirable. Therefore, it remains an important question at what density the negative impact of haplochromines on juvenile Nile perch will overrule their positive impact on adult Nile perch. This level not necessarily needs to be the same as that at which the shift from haplochromines to Nile perch took place. Responses of complex communities to environmental changes are often characterized by hysteresis and sudden shifts (Scheffer & Carpenter, 2003; Van Nes & Scheffer, 2004).