



The shift to smaller zooplankton in Lake Victoria cannot be attributed to the ‘sardine’ *Rastrineobola argentea* (Cyprinidae)

Jan H. Wanink ^{a,b,*}, Egid F.B. Katunzi ^c, Kees P.C. Goudswaard ^a, Frans Witte ^a,
Wim L.T. van Densen ^d

^aInstitute of Evolutionary and Ecological Sciences, Section Integrative Zoology, University of Leiden, P.O. Box 9516, 2300 RA Leiden, The Netherlands

^bHaplochromis Ecology Survey Team (HEST), P.O. Box 1866, Mwanza, Tanzania

^cTanzania Fisheries Research Institute (TAFIRI), P.O. Box 475, Mwanza, Tanzania

^dFish Culture and Fisheries Group, Wageningen Institute of Animal Sciences, Wageningen Agricultural University, P.O. Box 338, 6700 AH Wageningen, The Netherlands

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Abstract

After the population increase of introduced Nile perch (*Lates niloticus*) in Lake Victoria, a decrease in the relative abundance of herbivorous cladocerans and calanoids was reported for the pelagic zone. The shift from large herbivores to small-bodied predatory cyclopoids has been attributed to the increase of the zooplanktivorous cyprinid dagaa (*Rastrineobola argentea*), which rose concomitantly with the Nile perch. However, we observed that in the Mwanza Gulf of the lake cyclopoids dominated the zooplankton community already before the rise of dagaa. Furthermore, there are indications that dagaa takes fewer calanoids than expected from their representation in the environment, although a slight preference for cladocerans may exist. Calanoids dominated the diet of small Nile perch of about 4 cm length, but juvenile Nile perch did not occur in the study area until after the size shift in zooplankton. The lumped biomass of dagaa and small Nile perch is lower than the biomass of the original haplochromine-dominated community of zooplanktivorous fish. Thus, the decline of large zooplankters in the lake cannot be explained by intensified predation after the replacement of zooplanktivorous haplochromines by dagaa and Nile perch. Increased eutrophication, resulting in a shift in predominance from diatoms to cyanophytes, is suggested as an alternative explanation for the shift in zooplankton composition. © 2002 Ifremer/CNRS/Inra/Cemagref/Éditions scientifiques et médicales Elsevier SAS. All rights reserved.

Résumé

Le changement vers un plus petit zooplancton dans le lac Victoria ne peut être attribué à *Rastreobola argentea* (Cyprinidés). Suite à l'accroissement de la population de la perche du Nil (*Lates niloticus*) introduite dans le lac Victoria, une diminution de l'abondance relative des cladocères et des copépodes calanoïdes phytoplanctoniques a été reportée pour la zone pélagique. Le changement de grands herbivores, en petits prédateurs, de cyclopoïdes, a été attribué au grand nombre de cyprinidés zooplanctonivores « dagaas » (*Rastrineobola argentea*), qui a augmenté de façon concomitante avec la perche du Nil. Cependant, nous observons que dans le golfe de Mwanza, les cyclopoïdes dominaient la communauté de zooplancton avant l'accroissement du nombre de dagaa. De plus, il y a des indications que les dagaas prennent moins de calanoïdes que l'on aurait pu s'attendre d'après leur représentation dans ce milieu, bien qu'une légère préférence pour les cladocères semble exister. Les calanoïdes sont prépondérants dans l'alimentation des petites perches du Nil de 4 cm de longueur environ, mais les perches juvéniles n'ont pas été recensées dans la zone d'étude avant le changement de taille du zooplancton. La biomasse globale de dagaa et de petite perche du Nil est inférieure à celle des poissons zooplanctonivores d'origine, de la communauté dominante des haplochromines. Aussi, le déclin des grands zooplanctonophages dans le lac ne peut pas être expliqué par une augmentation de la prédation après le remplacement des haplochromines zooplanctivores par le dagaa et la perche du Nil. L'augmentation de l'eutrophisation, résultant d'un changement de la prédominance des diatomés vers celle des cyanophytes, est suggérée comme une explication alternative au

* Corresponding author: EEW, University of Leiden, P.O. Box 9516, 2300 RA Leiden, The Netherlands.

E-mail address: wanink@rulsfb.leidenuniv.nl (J.H. Wanink).

changement dans la composition du zooplancton. © 2002 Ifremer/CNRS/Inra/Cemagref/Éditions scientifiques et médicales Elsevier SAS. Tous droits réservés.

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1. Introduction

Although zooplankton in Lake Victoria has not been studied intensively (Mavuti and Litterick, 1991), a remarkable change in the relative abundance of cladocerans, calanoid and cyclopoid copepods has been reported in recent years (Mwebaza-Ndawula, 1994; Gophen et al., 1995). During the 1930s and 1950s, large-bodied calanoids and cladocerans dominated the zooplankton community (Worthington, 1931; Rzóska, 1957). After the increase of the introduced Nile perch (*Lates niloticus*) in the 1980s, which caused many changes in the ecosystem (Ogutu-Ohwayo, 1990; Barel et al., 1991; Witte et al., 1992a), small-bodied cyclopoids contributed more than 95% of the zooplankton species (Mavuti and Litterick, 1991; Mwebaza-Ndawula, 1994). This shift has been attributed to intensified predation pressure on the large herbivores by the sardine-like cyprinid dagaa (*Rastrineobola argentea*), of which the abundance increased during the 1980s (Gophen et al., 1995).

Before the upsurge of the piscivorous Nile perch, haplochromine cichlids dominated the zooplanktivorous fish community (Goldschmidt et al., 1990). After the decline of the haplochromines, the original zooplanktivores were replaced by dagaa and juvenile (< 5 cm) Nile perch (Ogari and Dadzie, 1988; Ligtvoet and Witte, 1991; Wanink, 1991; Goldschmidt et al., 1993, Katunzi et al., in prep.). It has been assumed that dagaa exerts a higher predation pressure on the large zooplankters than the haplochromines (Gophen et al., 1995). Mwebaza-Ndawula (1994) suggested that the combined predation pressure by dagaa and small Nile perch might have caused the decline of large zooplankton. This author also mentioned the increased eutrophication in the lake as a possible cause, by inducing competition between the herbivorous zooplankters, which may lead to the disappearance of some species.

In this paper we reevaluate the data from the northern part of the lake, which led to the hypothesis that the size shift was caused by the increase in dagaa (Gophen et al., 1995), and add comparable data from the southern waters. In addition to the landing statistics previously used, we provide direct estimates of dagaa abundance in the Mwanza Gulf, from where our zooplankton data also originate. Besides comparing the timing of the observed changes in the fish and the zooplankton communities, we investigate the food preferences of haplochromine zooplanktivores, dagaa and juvenile Nile perch, and compare their biomass densities. This should improve our assessment of the impact

of the changes in Lake Victoria's zooplanktivorous fish on the structure of the zooplankton community.

2. Material and methods

2.1. Zooplankton

Changes in the relative abundance of cladocerans, calanoids and cyclopoids (excluding nauplii) in the northern part of Lake Victoria were estimated from the original papers quoted in Gophen et al. (1995). Additional data from the southern waters (Mwanza Gulf) were based on published papers and our own work (Table 1). All samples were taken during daytime, mostly by hauling a net through the whole water column, although in some studies only the surface or the bottom layer was sampled.

The values for relative abundance given in this paper are averages per year. However, there was a large variation in the coverage of individual months (Table 1). In 1927, samples were taken on a 3-h base during a period of 36 hours. The data for 1950 and 1956 represent single sampling days. A monthly sampling program was used in the other studies, except in 1983, when samples were taken every fortnight.

2.2. Fish

Trends in the abundance of dagaa were estimated in two ways. First, we used published data on the annual yield of the fisheries in the three riparian countries (Kenya, Tanzania and Uganda) based on the annual statistics reports (Wanink, 1999). Secondly, we used a small research vessel for a series of surface trawls at night, when most adult dagaa dwell close to the surface (Wanink, 1992; Wanink et al., 1999). Boat and gear have been described elsewhere (Goudswaard et al., 1995). At the 14-m deep sampling station G in the Mwanza Gulf (details in Witte, 1981) the following number of standard trawls (10 or 15 min) were done in nine successive years, from 1981 to 1989: 1, 4, 16, 9, 5, 14, 4, 22, 4. The number of dagaa in each haul was counted and the standard length (SL) of the fish was measured to the nearest mm.

In order to compare zooplanktivore biomass (haplochromines, dagaa and small Nile perch) in the Mwanza Gulf before and after the population changes following the Nile perch boom, we used data from monthly bottom trawling programs (in daylight) by the research vessels Mdiria and

Table 1
 Details of zooplankton sampling programmes used in this paper. Note that the programmes from 1983 and 1990 extended two months into the next year. In addition to station depth we have indicated from which part of the water column (if not the whole column) the samples originate (0 m = surface). Mesh sizes refer either to the used plankton net or to the sieve after sampling by a water sampler.

Location	Year	Sampling months	Depth (m)	Sample (m)	Mesh (μm)	Source
<i>Northern waters</i>						
Offshore (North-East)	1927	Nov	67	whole	140	Worthington (1931)
Offshore (North-West)	1956	Apr	?	whole	140	Lind (1968); Rzóška (1957)
Offshore (Bugala)	1990	Mar–Feb	65	whole	300	Mwebaza-Ndawula (1994)
Pilkington Bay	1956	Apr	8	whole	140	Lind (1968); Rzóška (1957)
Pilkington Bay	1990	Mar–Feb	8	whole	300	Mwebaza-Ndawula (1994)
<i>Mwanza Gulf</i>						
Mwanza	1950	Aug	?	surface	140	Lind (1968); Rzóška (1957)
Nyamatala Island	1973	Apr–Dec	8	whole	90	Akiyama et al. (1977)
Nyamatala Island	1974	Jan–Dec	8	whole	90	Akiyama et al. (1977)
Station G	1983	Mar–Feb	14	0–3	150	Hoogenboezem (1985)
Station G	1988	Oct–Dec	14	11–14	150	Katunzi et al. (in prep.); this study
Station G	1989	Jan–Sep	14	11–14	150	Katunzi et al. (in prep.); this study
Luanso Bay	1988	Oct–Dec	5	2–5	150	Katunzi et al. (in prep.); this study
Luanso Bay	1989	Jan–Sep	5	2–5	150	Katunzi et al. (in prep.); this study

Kiboko between 1977 and 1990. Details of the vessels and their gear are described elsewhere (Goudswaard and Ligtoet, 1988; Goudswaard et al., 1995). Data from before 1984 (R.V. Mdiria) originate from various locations in the Mwanza Gulf. Nile perch < 5 cm total length (TL) did not occur in these samples. Average catch rates ($\text{kg}\cdot\text{h}^{-1}$) per year of all haplochromines were taken from Witte et al. (1995). We assumed that 27% (in weight) of the total haplochromine catch consisted of zooplanktivores (Goldschmidt et al., 1993). Fresh weight (FW) was converted into dry weight (DW) using the relationship $\text{DW} = 0.246 \text{ FW}$ (Douthwaite, 1976), in order to achieve an estimate of biomass comparable to the dry biomass estimated for haplochromines and Nile perch in later years.

From 1984 onwards, the data (R.V. Kiboko) refer only to station G. The numerical abundance ($\text{n}\cdot\text{h}^{-1}$) of haplochromine zooplanktivores was estimated from subsamples of the catch. Standard length of every fish from the subsamples was measured to the nearest mm, and biomass was estimated using the formula $\ln \text{DW (mg)} = 2.747 \ln \text{SL (mm)} - 4.456$ (Wanink and Goudswaard, 1994). The same procedure was followed for Nile perch < 5 cm TL found in the subsamples, using the formulas $\text{TL (mm)} = 1.22 \text{ SL (mm)} + 0.17$ and $\ln \text{DW (mg)} = 3.349 \ln \text{SL (mm)} - 6.777$ (Wanink and Goudswaard, 1994). We selected Nile perch < 5 cm TL, because only this size class is zooplanktivorous (Ogari and Dadzie, 1988; Katunzi et al., in prep.).

Since dagaa was sampled by another technique, its biomass was not directly comparable to that of the haplochromine zooplanktivores and small Nile perch. However, in 1982 the abundance of dagaa, in terms of fresh weight, has been estimated to be one-third of that of the haplochromine zooplanktivores (Goldschmidt et al., 1993). After converting the fresh weight of dagaa to dry weight with the relationship $\text{DW} = 0.224 \text{ FW}$ (Douthwaite, 1976), we have used this as a basis. From here, we have estimated the biomass of dagaa for the period 1981–1989 using the trend from the nightly surface trawls. For the years before 1981,

we have set dagaa biomass to the mean value calculated over 1981–1984, before the changes in the Mwanza Gulf.

3. Results

3.1. General trends

Relative abundance of cyclopoids, calanoids and cladocerans in Lake Victoria, from all available studies which allowed for their calculation, have been plotted as a function of time (Fig. 1a-c). Cyclopoids, which comprised only about 10% of the three types of zooplankton in 1927, showed a continuous increase until the last sampling date in 1990, when their fraction amounted to 70–90%. A less steep but consistent decrease was found in calanoids and cladocerans, which respectively formed about 50 and 40% of the zooplankton in 1927 and only 10–20 and about 2% in 1990. Except for the low value for cladocerans near Mwanza in 1950, the patterns for the northern and the southern waters were fairly similar.

Like Gophen et al. (1995), we compared the trends in the zooplankton in the northern waters with the trends in the annual landings of dagaa in the Kenyan part of the lake (Fig. 1d). We support their conclusion that the catch data indicate an increase in dagaa after 1980. However, we do not believe that an increase in the dagaa population has caused the changes in the zooplankton community, because the graphs show that these changes had started already between 1927 and 1956, far before the population increase of dagaa. The pattern does not change when the combined zooplankton data for the northern and the southern waters are compared with the landing statistics for the whole lake.

3.2. Trends in the Mwanza Gulf

Between 1950 and 1989 the relative abundance of cyclopoids in the Mwanza Gulf increased from about 60 to

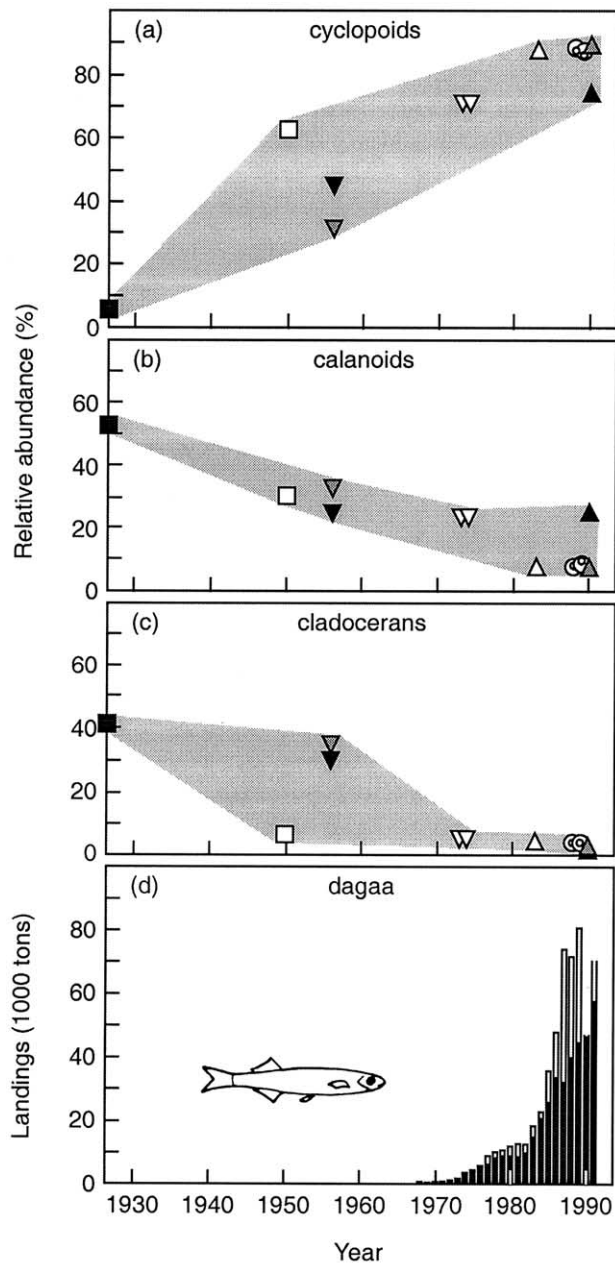


Fig. 1. Changes in zooplankton and *Rastrineobola argentea* (dagaa) in Lake Victoria between 1927 and 1991. (a–c) The relative abundances of cycloids, calanoids and cladocerans were calculated from the following sources (sampling and station details in Table 1): filled squares (Worthington, 1931), unfilled squares and filled downward triangles (Rzóska, 1957), unfilled downward triangles (Akiyama et al., 1977), unfilled upward triangles (Hoogenboezem, 1985), unfilled small and large circles (Katunzi et al., in prep.; this study), filled upward triangles (Mwebaza-Ndawula, 1994). The filled symbols (black = offshore station; grey = Pilkington Bay) represent the data from the northern waters used by Gophen et al. (1995). Unfilled symbols represent the stations in the Mwanza Gulf (small circles = shallow station Luanso Bay). (d) Annual landing data for dagaa are given for the Kenyan waters (black bars) and the whole lake (black plus stacked open bars). No data for the Tanzanian waters were available for 1990 and 1991.

about 90%. In the same period the calanoids decreased from about 30 to about 10%, while the cladocerans as well, which

comprised only 7% in 1950, decreased to about 4% in 1989 (Fig. 2a). The strong increase in the annual landings of dagaa in the Tanzanian waters started in 1985 (Fig. 2b), a few years after the start in the mid-1970s in the northerly Kenyan waters (Fig. 1d). This reflects the time delay between the northern and the southern parts of the lake in the upsurge of the voracious Nile perch (Witte et al., 1995), which was a major cause of the disappearance of the haplochromines (Witte et al., 1992b). Our direct estimate of dagaa abundance in the Mwanza Gulf (Fig. 2c) agrees with the landing statistics and shows that from 1985 onwards much higher densities occurred than before. Since the fractions of cycloids, calanoids and cladocerans did not change between 1983 and 1989, we conclude that the increase in dagaa in the Mwanza Gulf has not caused the changes in the zooplankton community.

Although the dagaa population increased dramatically during the 1980s, this does not necessarily imply an increase in the predation pressure on the zooplankton. As expected, the zooplanktivores were relatively good survivors amongst the haplochromines, but eventually most of them disappeared from the Mwanza Gulf (Wanink, 1991; Witte et al., 1992b). To estimate the possible changes in predation pressure, regardless of species composition and food preferences, we have plotted the biomass density of zooplanktivorous haplochromines, dagaa and small Nile perch as a function of time (Fig. 2d). Nile perch appears to be an insignificant zooplanktivore in terms of biomass. Since the decrease in biomass of the haplochromines was much larger than the increase in biomass of dagaa, the overall biomass density of zooplanktivores in the 1980s appeared to be smaller instead of larger than in previous years.

4. Discussion

4.1. More dagaa, thus smaller zooplankton?

For their suggestion that the increase in dagaa during the 1980s has caused the shift from large-bodied calanoids and cladocerans to small-bodied cycloids, Gophen et al. (1995) compared lumped zooplankton data from 1927 and 1956 with data from 1990. That seemed to be a valid approach, according to their remark that in the former two years calanoids and cladocerans were the dominating zooplankton types (90–55% by numbers) in the offshore waters, whereas their proportions were less than 5% in 1990. However, plotting the data per year showed that a large increase in the relative abundance of cycloids (from 6 to 45%) occurred already between 1927 and 1956 (Fig. 1a). This cannot have been caused by the increase of dagaa during the 1980s.

In the Mwanza Gulf, the only location in the lake for which a direct estimate of the population change in dagaa is available, cycloids had reached a relative abundance of almost 90% at least two years before the rise in dagaa

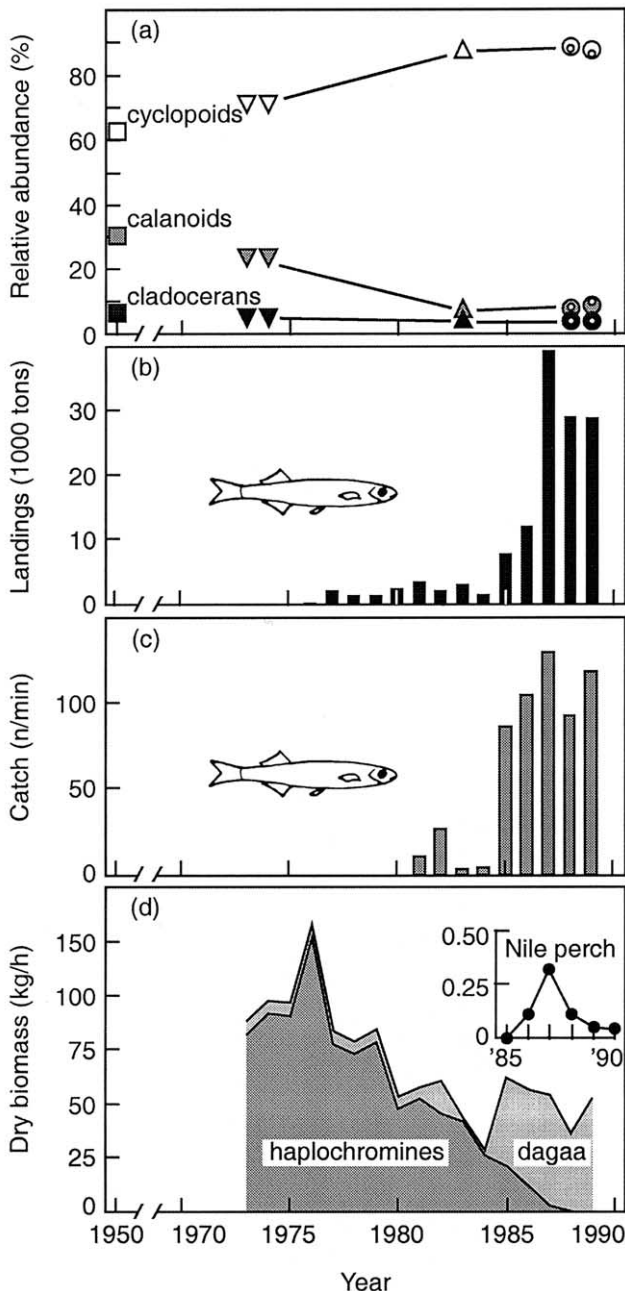


Fig. 2. Changes in zooplankton and zooplanktivores in the Mwanza Gulf between 1950 and 1990. (a) Relative abundances of cyclopoids, calanoids and cladocerans (sources in Fig. 1). The small circles (shallow station Luanso Bay) are unfilled for clarity but should be identical to the surrounding larger circles. (b) Annual landings of *Rastrineobola argentea* (dagaa) for the Tanzanian waters. (c) Dagaa catch rate by the small research vessel at station G. (d) Biomass density of zooplanktivores. Values for zooplanktivorous haplochromines and dagaa are stacked. Data for small Nile perch are given separately, because densities were too low to visualize them in the area graph.

(Fig. 2). Six years later, at the end of the study period, the proportion was still the same. The decrease in biomass density of the zooplanktivores in spite of the rise in dagaa (Fig. 2d) provides additional support for the idea that the predation pressure on the zooplankton has not increased during the 1980s. It is not possible, however, to predict the

effect of this biomass reduction on the individual zooplankton types, without knowledge of the food preferences of the different zooplanktivorous species.

4.2. Food selection by the zooplanktivores

Not much is known about the food preferences of the haplochromine zooplanktivores. The daytime diet of six species regularly caught at station G has been described as “cyclopoid and calanoid copepods and to a lesser extent cladocerans” (Goldschmidt, 1989). Since most of the investigated stomachs were from fish caught during 1983 and 1984 (Goldschmidt et al., 1990), when the relative abundances of calanoids and cladocerans at station G amounted to only 4.5 and 7.7% respectively (Fig. 2a; Hoogenboezem, 1985), the aforementioned description of the diet might indicate a preference for calanoids, although this is rather speculative. One of these six species, *Haplochromis piceatus*, has its peak distribution at a water depth of around 8 m over mud bottoms (Goldschmidt et al., 1990). In this shallower area, cladocerans comprised a considerable amount of the diet of *H. piceatus* (Galís, 1990). The diet of *H. tanaos*, a species with a high abundance between 2 and 6 m over sandy substrates, was dominated (67%) by cladocerans (van Oijen and Witte, 1996).

The first study on the diet composition of dagaa reported a dominance of cladocerans (65%) over copepods (Corbet, 1961). Although the fish were collected in the northern waters of the lake during the 1950s, when the relative abundance of cladocerans in these waters still amounted to 30–35% (Fig. 1c), the data suggest a positive selection for cladocerans. It must be noted, however, that most of the investigated fish were collected on a single day, from an inshore area over a sandy bottom. Dagaa caught at station G in the Mwanza Gulf during 1983 and 1984 possibly showed a slight preference for cladocerans, whereas calanoids, which were as scarce as the cladocerans (Fig. 2a), seemed to be avoided (Hoogenboezem, 1985).

In 1988 the diet of small Nile perch in the Mwanza Gulf was studied in relation to food availability at the 5-m deep station Luanso Bay (Table 1) and the 14-m deep station G (Katunzi et al., in prep.). Few cladocerans were taken and a shift from cyclopoids to calanoids as the main prey was observed in perch sizes increasing from 1 to 4 cm total length. The sizes of cyclopoids and calanoids found in the stomachs were both larger than the mean values sampled in the water column.

4.3. What caused the shift in the zooplankton?

The data presented in this paper do not support the idea that the population increase of dagaa has caused the observed shift in the zooplankton from large-bodied calanoids and cladocerans to small-bodied cyclopoids. Even the combined predation of dagaa and Nile perch after their upsurge is unlikely to be the causative factor. The overall

predation pressure on zooplankton is more likely to have decreased rather than increased after the changes in the fish community.

If the haplochromine zooplanktivores, like dagaa, took a high proportion of cyclopoids, the reduction in zooplanktivore biomass may have initiated a shift towards a higher relative abundance of cyclopoids, which could have been enhanced by the fact that cyclopoids are predators of calanoids and cladocerans. Experiments with cyclopoids from the Mwanza Gulf showed that they mainly fed on cladocerans and possibly on copepod nauplii (Akiyama et al., 1977). In Lake Malawi, *Mesocyclops aequatorialis*, also a common species in Lake Victoria (Mavuti and Litterick, 1991), causes significant mortality in calanoids and cladocerans (Irvine and Waya, 1993). This cyclopoid species makes an incision through the carapace of its prey and ingests the inner contents. Because of this feeding technique, *M. aequatorialis* can take cladocerans and calanoids (which are preferred over cyclopoids and nauplii) with sizes up to, or even exceeding the predator's body length (Irvine and Waya, 1993).

In addition to the changes in the fish community after the Nile perch boom, a strong increase in lakeflies (chaoborid and chironomid midges) has been reported (Kaufman, 1992; Mbahinzireki, 1992; Witte et al., 1992a). Since *Chaoborus* larvae feed on zooplankton, population changes may affect the structure of the zooplankton community. It has been shown that *Chaoborus edulis*, a common species in Lake Victoria (Goldschmidt et al., 1990), selects strongly for cladocerans in Lake Malawi (Irvine, 1995). However, the lakefly increase in Lake Victoria was apparently restricted to chironomids, while chaoborids may even have decreased (Okedi, 1990; Wanink and Goudswaard, 2000).

All published explanations for the size shift in Lake Victoria's zooplankton refer to the changes in the fish fauna after the upsurge of Nile perch. We have shown, however, that the relative abundance of cyclopoids, calanoids and cladocerans had changed already before the introduction of the perch in the mid-1950s (Fig. 1). Although our data on decreasing biomass density of zooplanktivores (Fig. 2d) do not exclude the possibility that biomass decreased already before the start of the monitoring program, the results of a trawl survey during 1969 do not point into this direction (Kudhongania and Cordone, 1974).

More likely, a general trend towards eutrophication may explain the shift in zooplankton composition. Although an increase in primary productivity was noticed between 1960–1961 and 1989–1991, at the same time a shift in predominance from diatoms to nutritionally less valued cyanophytes took place (Gophen et al., 1993, 1995; Hecky, 1993; Mugidde, 1993). Analysis of a sediment core showed that changes in the phytoplankton composition followed increased deposition rates of nitrogen (starting in the 1920s) and phosphorus (starting in the 1950s), and were clearly underway before the introduction of Nile perch in the mid-1950s (Hecky, 1993).

5. Conclusion

Between the late 1920s and the late 1980s, a gradual shift from large-bodied calanoids and cladocerans to small-bodied cyclopoids occurred in the zooplankton community of Lake Victoria. The decrease in herbivorous calanoids and cladocerans may have been caused by concurrent changes in the phytoplankton, initiated by an increase in the load of nitrogen and phosphorus. Although large time lapses exist between successive zooplankton samples, it is clear that the changes were well underway before the introduction of Nile perch in the mid-1950s. Therefore, we reject the suggestion that the population increase of the zooplanktivorous cypriid *Rastrineobola argentea* during the 1980s has caused the observed shift in the zooplankton.

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References

- Akiyama, T., Kajumulo, A.A., Olsen, S., 1977. Seasonal variations of plankton and physicochemical condition in Mwanza Gulf, Lake Victoria. *Bull. Freshw. Fish. Res. Lab.* 27, 49–61.
- Barel, C.D.N., Ligtvoet, W., Goldschmidt, T., Witte, F., Goudswaard, P.C., 1991. The haplochromine cichlids of Lake Victoria: an assessment of biological and fisheries interest. In: Keenleyside, M.H.A. (Ed.), *Cichlid fishes: behaviour, ecology and evolution*. Chapman and Hall, London, pp. 258–279.
- Corbet, P.S., 1961. The food of non-cichlid fishes in the Lake Victoria basin, with remarks on their evolution and adaptation to lacustrine conditions. *Proc. Zool. Soc. Lond.* 136, 1–101.
- Douthwaite, R.J., 1976. Fishing techniques and foods of the pied kingfisher on Lake Victoria in Uganda. *Ostrich* 47, 153–160.
- Galis, F., 1990. Ecological and morphological aspects of changes in food uptake through the ontogeny of *Haplochromis piceatus*. In: Hughes, R.N. (Ed.), *Behavioural mechanisms of food selection*. Nato ASI series, vol. G20. Springer-Verlag, Berlin, pp. 281–302.
- Goldschmidt, T., 1989. Reproductive strategies, subtrophic niche differentiation and the role of competition for food in haplochromine cichlids

- (Pisces) from Lake Victoria, Tanzania. Ann. Mus. Roy. Afr. Centr., Sc. Zool. 257, 119–132.
- Goldschmidt, T., Witte, F., de Visser, J., 1990. Ecological segregation in zooplanktivorous haplochromine species (Pisces: Cichlidae) from Lake Victoria. Oikos 58, 343–355.
- Goldschmidt, T., Witte, F., Wanink, J., 1993. Cascading effects of the introduced Nile perch on the detritivorous/phytoplanktivorous species in the sublittoral areas of Lake Victoria. Conserv. Biol. 7, 686–700.
- Gophen, M., Ochumba, P.B.O., Kaufman, L.S., 1995. Some aspects of perturbation in the structure and biodiversity of the ecosystem of Lake Victoria (East Africa). Aquat. Living Resour. 8, 27–41.
- Gophen, M., Ochumba, P.B.O., Pollinger, U., Kaufman, L.S., 1993. Nile perch (*Lates niloticus*) invasion in Lake Victoria (East Africa). Verh. Int. Ver. Limnol. 25, 856–859.
- Goudswaard, P.C., Ligtvoet, W., 1988. Recent developments in the fishery for *Haplochromis* sp (Pisces, Cichlidae) and Nile perch, *Lates niloticus* (Pisces, Centropomidae), in Lake Victoria. FAO Fish. Rep. 388, 101–112.
- Goudswaard, P.C., Mous, P.J., Ligtvoet, W., van Densen, W.L.T., 1995. Gears and boats. In: Witte, F., van Densen, W.L.T (Eds.), Research on Lake Victoria fish stocks and fisheries: a handbook for field observations. Samara Publishing Ltd., Cardigan, pp. 83–117.
- Hecky, R.E., 1993. The eutrophication of Lake Victoria. Verh. Int. Ver. Limnol. 25, 39–48.
- Hoogenboezem, W., 1985. The zooplankton in the Mwanza Gulf (Lake Victoria) and the food of a zooplanktivorous cyprinid (*Rastrineobola argentea*). HEST Report. University of Leiden, Leiden.
- Irvine, K., 1995. Ecology of the lakefly, *Chaoborus edulis*. In: Menz, A (Ed.), The fishery potential and productivity of the pelagic zone of Lake Malawi/Niassa. Natural Resources Institute, Chatham, pp. 109–140.
- Irvine, K., Waya, R., 1993. Predatory behaviour of the cyclopoid copepod *Mesocyclops aequatorialis aequatorialis* in Lake Malawi, a deep tropical lake. Verh. Int. Ver. Limnol. 25, 877–881.
- Kaufman, L., 1992. Catastrophic change in species-rich freshwater ecosystems: the lessons of Lake Victoria. BioScience 42, 846–858.
- Kudhongania, A.W., Cordone, A.J., 1974. Batho-spatial distribution patterns and biomass estimates of the major demersal fishes in Lake Victoria. Afr. J. Trop. Hydrobiol. Fish. 3, 15–31.
- Ligtvoet, W., Witte, F., 1991. Perturbation through predator introduction: effects on the food web and fish yields in Lake Victoria (East Africa). In: Ravera, O (Ed.), Terrestrial and aquatic ecosystems: Perturbation and recovery. Ellis Horwood, Chichester, pp. 263–268.
- Lind, E.M., 1968. Notes on the distribution of phytoplankton in some Kenyan waters. Br. Phycoll. Bull. 3, 481–493.
- Mavuti, K.M., Litterick, M.R., 1991. Composition, distribution and ecological role of zooplankton community in Lake Victoria, Kenya waters. Verh. Int. Ver. Limnol. 24, 1117–1122.
- Mbahinzireki, G.B., 1992. Distribution and abundance of two dipteran aquatic larvae in northern Lake Victoria. FAO Fish. Rep. 475, 39–39.
- Mugidde, R., 1993. The increase in phytoplankton primary productivity and biomass in Lake Victoria (Uganda). Ver. Int. Ver. Limnol. 25, 846–849.
- Mwebaza-Ndawula, L., 1994. Changes in relative abundance of zooplankton in northern Lake Victoria, East Africa. Hydrobiologia 272, 259–264.
- Ogari, J., Dadzie, S., 1988. The food of the Nile perch, *Lates niloticus* (L.) after the disappearance of the haplochromine cichlids in the Nyanza Gulf of Lake Victoria. J. Fish Biol. 32, 571–577.
- Ogutu-Ohwayo, R., 1990. The decline of the native fishes of Lakes Victoria and Kyoga (East Africa) and the impact of introduced species, especially the Nile perch, *Lates niloticus* and the Nile tilapia, *Oreochromis niloticus*. Environ. Biol. Fish. 27, 81–96.
- Okedi, J.Y., 1990. Observations on the benthos of Murchison Bay, Lake Victoria, East Africa. Afr. J. Ecol. 28, 111–122.
- Rzóska, J., 1957. Notes on the crustacean plankton of Lake Victoria. Proc. Linn. Soc. Lond. 168, 116–125.
- van Oijen, M.J.P., Witte, F., 1996. Taxonomical and ecological description of a species complex of zooplanktivorous and insectivorous cichlids from Lake Victoria. Zool. Verh. Leiden 302, 1–56.
- Wanink, J.H., 1991. Survival in a perturbed environment: the effects of Nile perch introduction on the zooplanktivorous fish community of Lake Victoria. In: Ravera, O (Ed.), Terrestrial and aquatic ecosystems: Perturbation and recovery. Ellis Horwood, Chichester, pp. 269–275.
- Wanink, J.H., 1992. The pied kingfisher *Ceryle rudis* and dagaa *Rastrineobola argentea*: estimating the food-intake of a prudent predator. In: Bennun, L (Ed.), Proc. VII Pan-Afr. Orn. Congr., PAOCC, Nairobi. pp. 403–411.
- Wanink, J.H., 1999. Prospects for the fishery on the small pelagic *Rastrineobola argentea* in Lake Victoria. Hydrobiologia 407, 183–189.
- Wanink, J.H., Goudswaard, P.C., 1994. Effects of Nile perch (*Lates niloticus*) introduction into Lake Victoria, East Africa, on the diet of pied kingfishers (*Ceryle rudis*). Hydrobiologia 279/280, 367–376.
- Wanink, J.H., Goudswaard, P.C., 2000. The impact of Lake Victoria's lakefly abundance on Palearctic passerines. Ostrich 71, 194–197.
- Wanink, J.H., Goudswaard, P.C., Berger, M.R., 1999. *Rastrineobola argentea*, a major resource in the ecosystem of Lake Victoria. In: van Densen, W.L.T., Morris, M.J. (Eds.), Fish and fisheries of lakes and reservoirs in Southeast Asia and Africa. Westbury Publishing, Otley, pp. 295–309.
- Witte, F., 1981. Initial results of the ecological survey of the haplochromine cichlid fishes from the Mwanza Gulf of Lake Victoria, Tanzania: breeding patterns, trophic and species distribution. Neth. J. Zool. 31, 175–202.
- Witte, F., Goldschmidt, T., Wanink, J.H., 1995. Dynamics of the haplochromine cichlid fauna and other ecological changes in the Mwanza Gulf of Lake Victoria. In: Pitcher, T.J., Hart, P.J.B (Eds.), The impact of species changes in African lakes. Chapman and Hall, London, pp. 83–110.
- Witte, F., Goldschmidt, T., Goudswaard, P.C., Ligtvoet, W., van Oijen, M.J.P., Wanink, J.H., 1992a. Species extinction and concomitant ecological changes in Lake Victoria. Neth. J. Zool. 42, 214–232.
- Witte, F., Goldschmidt, T., Wanink, J., van Oijen, M., Goudswaard, K., Witte-Maas, E., et al., 1992b. The destruction of an endemic species flock: quantitative data on the decline of the haplochromine cichlids of Lake Victoria. Environ. Biol. Fish. 34, 1–28.
- Worthington, E.B., 1931. Vertical movement of freshwater macroplankton. Int. Rev. Ges. Hydrobiol. Hydrogr. 25, 394–436.