

RESEARCH ARTICLE

Available Online at <http://www.aer-journal.info>

Zooplankton Communities of Lake Victoria and its Effects on the Fishery

K. Nyakeya^{1*}, J. E. Chemoiwo², J. M. Nyamora³, E. Kerich⁴ and Z. Gichana⁵

^{1*}*Kenya Marine and Fisheries Research Institute, Baringo Station, P.O. Box 31 Kampi ya Samaki; kobinginyakeya@gmail.com*

²*School of Science, Department of Biological Sciences, University of Eldoret, P.O. Box 1125, Eldoret.*

³*Kenya Marine and Fisheries Research Institute, Mombasa Station, P.O. Box 81651, Mombasa*

⁴*Directorate of Research and Innovation, University of Eldoret, P.O. Box 1125, Eldoret.*

⁵*Kisii University, P.O. Box 408, Kisii.*

Abstract

*This study is a review on the zooplankton of Lake Victoria and its effects on the fishery. A general introduction on zooplankton is given followed by an overview of Lake Victoria, and change in zooplankton ecology and their effects on the fishery. Three main groups of zooplankton communities do occur in the lake: cyclopoids, cladocerans and rotifers. There has been a shift with cyclopoids dominating from cladocerans. Although the Nile perch has been blamed for the decline of the cladocerans due to upsurge of dagaa that saw predation of the cladocerans, this may not be substantiated because such changes were witnessed as earlier as 1950s when *L. niloticus* had not been introduced. Therefore, other reasons such as eutrophication, predation and/or cannibalism, poor/variability in sampling protocols and pollution may have been responsible. However, other water bodies within the basin also support the same zooplankton community structure as that of the lake, which may confirm that there have been shifts ecologically. From the review, it is also evident that zooplankton supports the fish composition and distribution in L. Victoria. The paper recommends for harmonized and standardized study methods for zooplankton in the lake.*

Keywords: Lake Victoria, Zooplankton, Ecological Shift, Invasive Species

Introduction

Zooplankton, also called micro-plankton, is small secondary producing aquatic organisms ranging between 0 and 1500 μm total body length. They live in the water column and usually their vertical and/or diel distribution is governed both by abiotic and biotic factors (Mwebaza-Ndawula, 2004). Zooplankton can be found in both marine and fresh water systems. They play an intermediate role between organisms in the lower and upper trophic levels (Kelly *et al.*, 2013). They are therefore the main players when it comes to the functioning and productivity of these ecosystems because

they are important in energy transfer. They also regulate the population of phytoplankton by grazing on them and thus have cascading effects on zooplankton prey assemblages. Of significance, they act as source of protein for fish and some of them are good bioindicators of water quality (Hoxmeier & Wahl, 2004).

The occurrence of zooplankton may not necessarily be uniform in an aquatic system (Castro *et al.*, 2007; Mulimbwa *et al.*, 2014) and under several instances they display both longitudinal and latitudinal patterns (Yurista and Kelly, 2009). Dietzel *et al.* (2013) pointed out that such a behavior by

zooplankton are important ecologically as they shape the fish composition, distribution and abundance, general invertebrates and phytoplankton (Casper & Thorp, 2007).

The zooplankton structure differ from one habitat to another (Lévesque *et al.*, 2010) and this may be as a result of climatic changes, physico-chemical parameters variations, biological interactions (Semyalo *et al.*, 2009; Oyoo-Okoth *et al.*, 2011; Omondi *et al.*, 2011), depth, transparency (Semyalo *et al.*, 2009), conductivity, anthropogenic activities that result into fresh water degradation and organic pollution via discharging rivers (Dietzel *et al.*, 2013). Feeding by fishes and other invertebrates, and algal blooms may also affect their distribution (Semyalo *et al.*, 2009).

In Lake Victoria, zooplankton communities have been studied, but there exists conflicting information about their distribution and abundance. This is because some scientists have argued that there have been some changes in their abundance whereas others say this has not happened. There is need also to try to understand their relationship with the fishery of L. Victoria. This paper, therefore, try to unearth the above arguments by reviewing the available literature through an overview of the Lake Victoria basin to understand dynamisms that may have contributed or influenced the state of environmental ecology of the lake. Zooplankton occurrence and distribution is then accounted for as ecological shift is highlighted. The probable causes of zooplankton changes are then articulated in detail. To discern this, the zooplankton structure in the adjacent water bodies of Lake Victoria is also given. Lastly, the effect of zooplankton distribution on Lake Victory fishery is explored before the concluding remarks and recommendations.

Lake Victoria Basin

Lake Victoria is the second largest freshwater body globally with a total area of 68,800 km². It is regarded as a shallow lake whose depth is 84 m in deep areas and 40 m in shallow ends (Hutchinson, 1957; Beadle, 1972; Hecky & Bugenyi, 1992). Apart from the three East African states sharing the lake (Kenya, Uganda and Tanzania), its catchment covers part of Rwanda and Burundi. Most of the surface water ending up in Lake Victoria come from the Kenyan rivers followed by rivers from Tanzania. Of great importance, however, is River Kagera, traversing through Rwanda and Burundi thus it is the largest and longest basin in the region. In spite of all these rivers, the main contributor to Lake Victoria waters is precipitation (COWI, 2002).

The L. Victoria basin (Figure 1) has over 50 million people with an annual growth of over 3% per annum. The lake plays a vital role in terms of the economics, politics and the social welfare of the riparian communities and even beyond through the Nile which is the mainstay of the Egyptian agricultural production. It is the leading freshwater body in terms of fisheries production globally with annual yield of more than 500,000 tonnes per year. However, of late there have been concerns over the dwindling fish stocks. Some of the reasons that have been cited to be responsible for fish declines include: pollution as a result of intensive agricultural activities in the catchments, mining, eutrophication, overfishing, climate change, hydropower generation and transport. In addition to the above, the most notorious challenge is to sustain the lucrative fishery that emerged out of the Nile perch introductions, and at the same time restore and conserve the lost fish diversity. It is against the aforementioned backdrop that Lake Victoria is designated a biodiversity hot spot (Okeyo-Owuor, 1999) having lost over 300 species in the last eight decades.

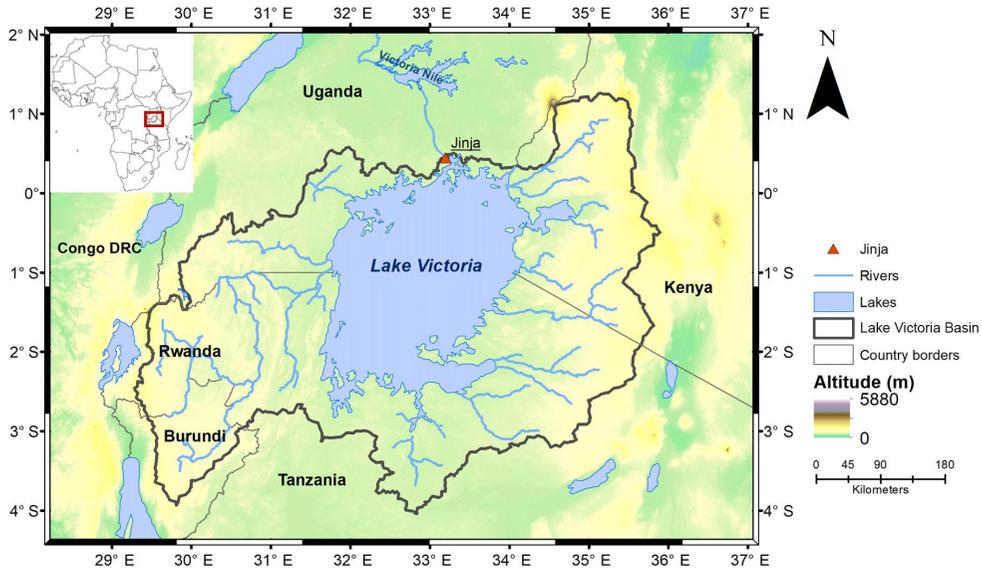


Figure 1: Major Lake Victoria catchment area (Source: Vanderkelen *et al.*, 2018).

Zooplankton Occurrence and Distribution

There is not much data on the zooplankton in Lake Victoria (Mavuti & Litterick, 1991) although it is agreed among scientists from the region that the system is made up of three major zooplankton communities namely: Copepoda, Cladocera, and Rotifera although others such as *Chaoborus* larvae exist in small numbers (Plate 1). The Zooplankton species composition is almost uniform over the lake and among the cyclopoid copepods, 6 of the 8 species are common. The *Thermocyclops oblongatus* Sars, are not found in Tanzania waters whereas *Thermocyclops decipiens* Kiefer is

found in the Kenyan waters only (Mwebaza-Ndawula, 2004).

The calanoid species, *T. galeoides* Sars and *T. stuhlmanni* Mrazek have a global distribution in the lake. Seven out of 10 Cladocera spp. are found in the entire lake. Whereas *Daphnia barbata* is only found in the Kenya waters, *Chydorus sphaericus* O.F.M. and *Alona* spp. are hardly found in the Tanzania waters (Mwebaza-Ndawula, 1994). A total of 16 rotiferan spp. out of 24 are distributed lake wide. The remaining 8 spp. are missing in Tanzania portion of the lake except *Platyias patulus*, which is also not encountered in the Ugandan records.

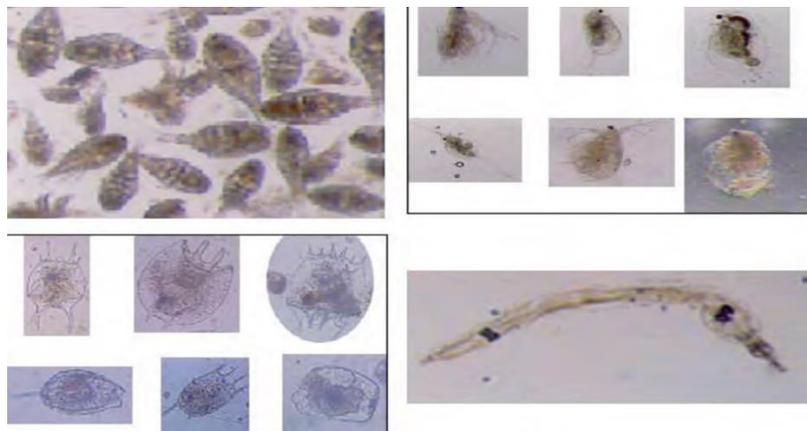


Plate 1: The three groups of zooplankton of Lake Victoria: Copepoda and Cladocera top left and right respectively; Rotifera on bottom left; and *Chaoborus* larva displayed on the bottom right (Source: Mwebaza-Ndawula *et al.*, 2004).

Changes in Zooplankton Abundance in L. Victoria

There has been a pronounced zooplankton structure in L. Victoria in the recent years (Ogello *et al.*, 2013; Mwambungu 2004; Mwebaza-Ndawula, 1994) as illustrated in Figure 2 below. Although there have been refuting claims recently that there has not

been any change in the abundance of zooplankton with a major dominance by the small-sized copepods, studies conducted by such authors as Worthington (1931), Rzóska (1957) documented the dominance of large-bodied calanoids and cladocerans in the 1930s and 1950s, which started to decline in the 1950s.

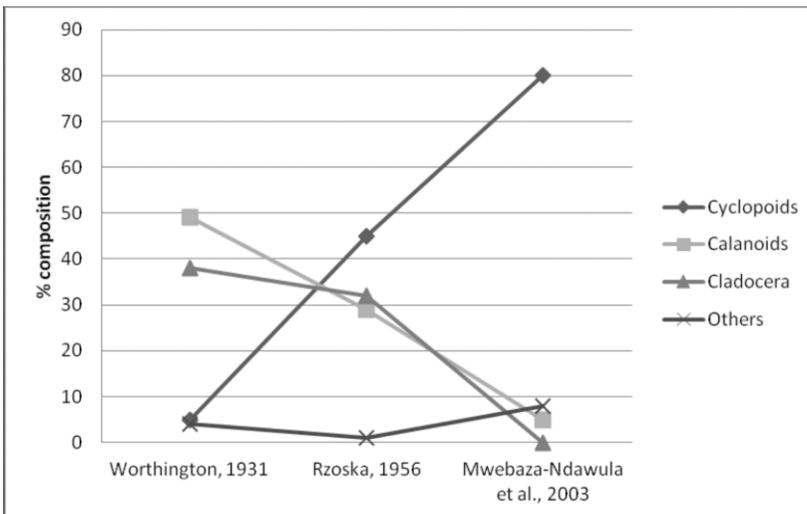


Figure 2: Shift in percentage composition of zooplankton in Lake Victoria between the 1930s and 1990s (Source: Ogello *et al.*, 2013).

What Caused the Changes?

Introduction of Exotic Invasive Species

Invasive aquatic species are nonnative (from another geographic region, usually another continent) species that cause ecological and/or economic harm to a natural or managed ecosystem (Dukes and Mooney 2004). They are organisms entered and

continent) species that cause ecological and/or economic harm to a natural or managed ecosystem (Dukes and Mooney 2004). They are organisms entered and

manifested in the aquatic environment from outside of their natural habitat and their introductions can be either intentional or unintentional. Invasive aquatic species often cause both economic and ecological harm. Their impacts are devastating on native biota and can cause extinctions thus impacting negatively on the local ecosystems (Ehrenfeld, 2003). They reproduce rapidly, out-compete native species for food, water and space, and are one of the main causes of global biodiversity loss.

One of the reasons cited for the ecological change in zooplankton diversity of L. Victoria is the introduction of the Nile perch (*Lates niloticus*) in the 1980s, which is cited to have caused many changes in the ecosystem (Ogutu-Ohwayo, 1990). It is argued that the *L. niloticus* preyed on the haplochromines, which led to their decline and thus the upsurge of the *R. argentea* that put much pressure on cladocerans (Mavuti and Litterick, 1991; Mwebaza-Ndawula, 1994). According to Gophen *et al.* (1995), this shift intensified predation pressure on the large herbivores by the sardinelike cyprinid dagaa, *R. argentea*, of which the abundance increased during the 1980s (Figure 3). However, this may not be true

because changes in the distribution and abundance of zooplankton communities were reported as early as 1950s (Worthington, 1931; Rzóska, 1957) and as such the Nile perch had not blossomed because it was also introduced into the lake in those years. This therefore means that other factors may have had the changes.

As much as there may be conflicting claims on as a factor that may have contributed to zooplankton shift in Lake Victoria, scientific evidence has proved that bigger bodied zooplankton are preferred by predators in the ecosystem hence there is more exerted pressure on them. This affects the general structure of zooplankton such that smaller bodied ones blossom. According to Brooks and Dodson (1965), predation plays a key role in shaping zooplankton community. This is because larger zooplankton can easily be seen or located by their predators hence are most affected by predation that may result into their eventual extinction (Hrbacek *et al.*, 1961; Lazzaro, 1987). It is possible then that with the upsurge of *R. argentea* courtesy of *L. niloticus* introduction, predation on bigger bodied cladocerans may have been intensified resulting into their decline.

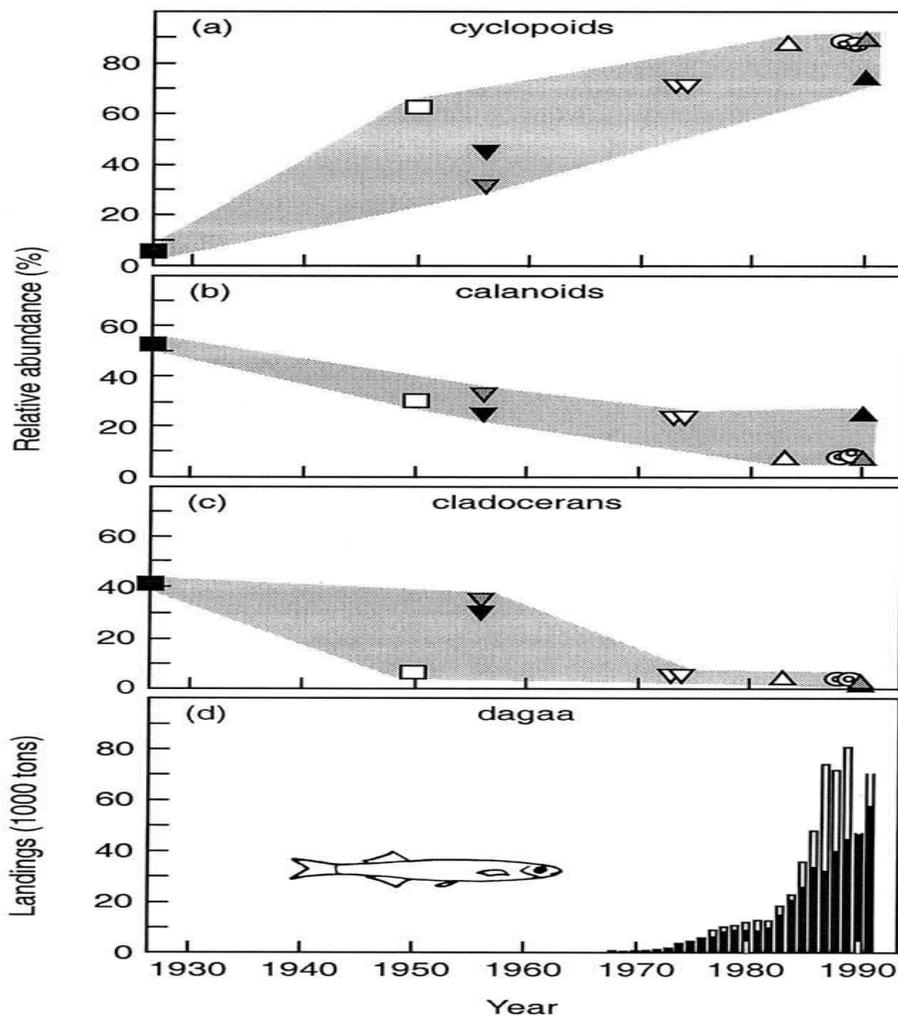


Figure 3: Changes in zooplankton and *R. argentea* (dagaa) in Lake Victoria between 1927 and 1991. (a-c) The relative abundances of the three groups (d) Annual landing data for dagaa in Kenyan waters (black bars) and the whole lake (black plus stacked open bars) (Source: Wanink *et al.*, 2002).

Eutrophication

Eutrophication is another possible reason for the witnessed changes in zooplankton community. Mwebaza-Ndawula (1994) cited eutrophication as the factor responsible for the changes witnessed in zooplankton composition which insinuated unnecessary competition between the herbivorous zooplankters, leading to the disappearance of some species. *Thermocyclops* are cyclopoids that are nutrient loving and therefore thrives in

nutrient-rich environments as compared to bigger bodied cladocerans. This has been confirmed in other studies observed at semi-arid water systems of Morocco (e.g. Leitão *et al.*, 2006). Cyclopoids feed mainly on rotifers (Rao & Kumar, 2002) whose composition, distribution and abundance is highly favoured by eutrophic and hypereutrophic conditions.

Thermocyclops have been documented to be more abundant in the waters of Lake

Victoria, which is experiencing eutrophication (Sitoki *et al.*, 2014). The density of nauplii, also a cyclopoid increases tremendously with the increase in nutrients at the expense of diatoms. According to Silva *et al.* (2009), increased nutrient concentration favours the growth of cyclopoids.

Pollution

Zooplankton community structure can be affected by pollution. In a study conducted by Uriarte and Villate (2004) in two estuaries of the Basque coast, Spain reported that pollution affects zooplankton abundance and distribution. According to them, pollution enhances the growth of cyanobacteria, which acts as food base for the zooplankton. Such a scenario is evident in Lake Victoria where rotifers are known to thrive in poor water quality conditions such as the Winum Gulf of Lake Victoria (Sitoki *et al.*, 2012). The nearshore areas of Lake Victoria are more prone to pollution emanating from non-point and point sources of pollution that could account for the higher turbidity and conductivity, and the lower pH values and Dissolved oxygen levels. Similar trends have been documented by Badsı *et al.* (2010) in a polluted lagoon in Southern Morocco. Calanoids and cladocerans feed on plants and consequently may be affected by phytoplankton diversity and abundance due to eutrophication and sedimentation from anthropogenic activities around Lake Victoria (Sitoki *et al.*, 2014). The phytoplankton structure in Lake Victoria has changed due to pollution such that the once diatom dominated lake is currently dominated by blue green algae which cannot be consumed by the calanoids and cladocerans explaining the reason as to why cyclopoids are on the increase.

Variability in Sampling Strategies

Zooplankton structure can change in both season and in terms of the habitat and such variation is difficult to verify statistically (Evans & Sell, 1983; Livings *et al.*, 2010). In such a situation the accuracy and

precision of the estimation and the establishment of community shifts in response to local gradients and temporal environmental changes. Sampling approaches that ignore time and space result to poorly designed surveys that may significantly underestimate diversity (Vieira *et al.*, 2017). Zooplankton sampling can be undertaken using different methods namely collecting a known volume of sub-surface water by bucket or by bottle-sampler and filtration through a plankton net (Peixoto *et al.*, 2008), collecting with a suction pump (Santos-Wisniewski & Rocha, 2007), sampling at several depths using a Van Dorn bottle followed by filtration (Keppeler, 2003), collection by vertical hauls with a plankton net at specific layers of the water column (Simões & Sonoda, 2009), horizontal hauls at surface (Waichman *et al.*, 2002) or sampling using a Schindler-Patalas trap (Bezerra-Neto *et al.*, 2009).

The foregoing protocols may be associated to personal preferences, system constraints and the objectives of different zooplankton community studies (Mack *et al.*, 2012). A best sampling technique can work for each group of zooplankton investigated (for example: macrozooplankton - large mesh net, microzooplankton - small mesh nets (Vannucci, 1968), and protozoasurface collections (Lahr & Lopes, 2006). While species richness and evenness are usually dependent on mesh size, diversity indexes are typically less influenced by mesh selection (Riccardi, 2010). So, the challenge is to provide a good sampling method for all groups at once. However, in most studies conducted in Lake Victoria have either knowingly or unknowingly been carried out using just one method at a given time and space. Such results may not be accurate. Kozłowsky-Suzuki and Bozelli (1998) compared the efficiency of three different samplers (vertical haul, Schindler-Patalas trap and suction pump) in a Brazilian coastal lagoon. The performance of the vertical haul with plankton net was found to be the most inefficient, except for the

copepods, and the sampling with suction pump was considered the most efficient for all the taxa analyzed. Therefore, similar studies conducted in Lake Victoria using vertical hauls may have reported the presence of copepods at the expense of cladocerans hence reporting a misrepresentation of zooplankton communities.

Cannibalism

Another reason for the dynamic changes in zooplankton abundance in L. Victoria could be attributed to feeding mechanisms employed by different groups. Whereas the feeding of a majority of cladocerans, has been classified as herbivorous, the nutrition of copepods is regarded as predaceous. Consequently, it has been documented elsewhere that copepods predate on the cladocerans (Gliwicz, 1994; Gliwicz & Umana, 1994) a situation that could be happening in the L. Victoria waters where the number of copepods is on the rise while that of cladocerans is on the decline. However, according to Santer and van den Bosch (1994), some of the copepod species and stages feed on protists and algae but they are very selective when compared with cladocerans (Jurgens *et al.*, 1996). Copepods actively select their food, while most cladocerans are filter feeders. This also may be the reason as to why copepods are

on the rise in L. Victoria compared to cladocerans. The copepods will therefore go for bigger bodied cladocerans thus depleting their populations.

How does Zooplankton of L. Victoria Relate to other Adjacent Water Bodies?

Now that there are reported changes in zooplankton abundance in L. Victoria, are there such changes in other lakes within the same geographical region? Looking at data from the adjacent L. Kivu, similar trends as those observed in L. Victoria are evident. Low proportion of cladocerans, has been reported (Amarasinghe *et al.*, 2008). Copepods on the other hand has been said to constitute over 90% of the existing zooplankton in the waters of L. Kivu and this is so during the rainy seasons. Rotifers were also numerically low in numbers (Fig. 4). During the dry seasons, cladocerans increase in numbers to about 20% of the zooplankton population but they do not supersede the copepods which although decrease somehow, still remain dominant.

While reviewing data from the Small Water Bodies (SWBs) within the L. Victoria catchments, a similar trend is depicted as that one of L. Victoria as far as the zooplankton composition, distribution and abundance is concerned. Copepods are represented by over 95% dominance as compared to cladocerans and the rotifers.

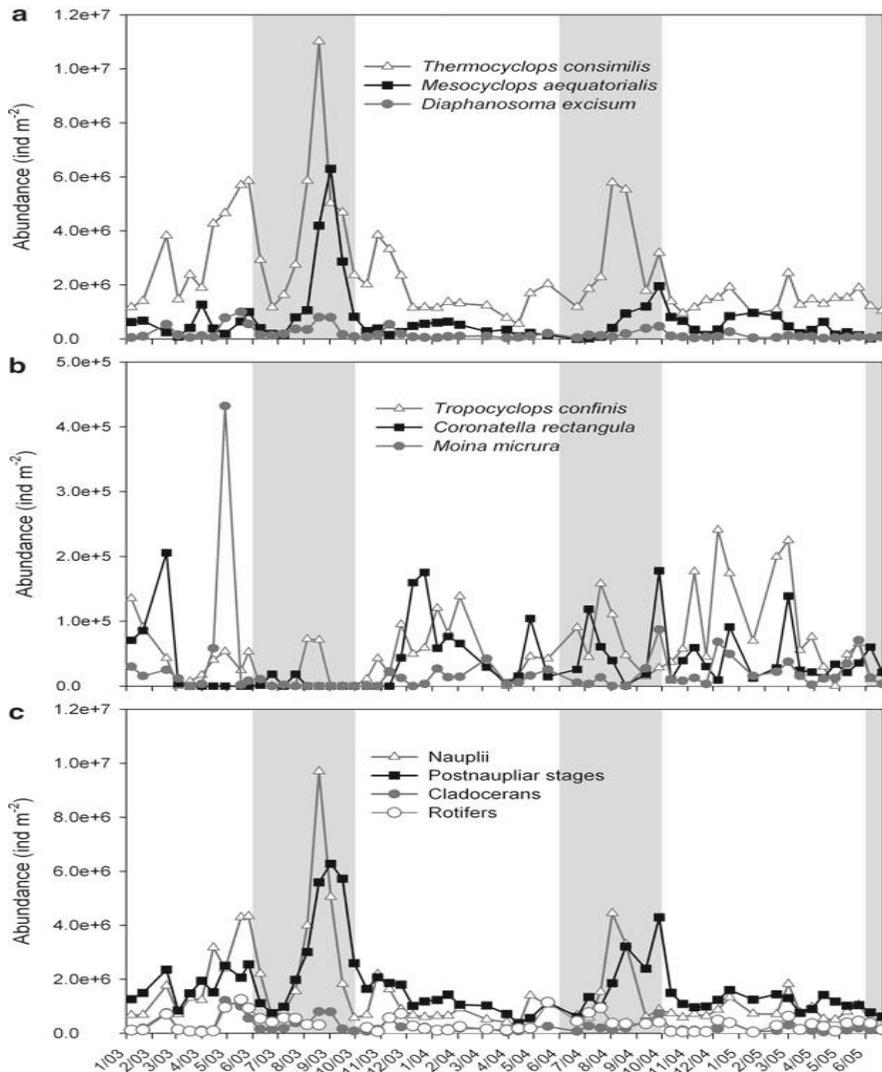


Figure 4: Variation of metazooplankton abundance in the 0–60 m water column of Lake Kivu (Ishungu basin) from January 2003 to June 2005. Note the different scales on the Y-axis for a, b and c. The light grey boxes indicate the dry season periods (Adapted from Descy *et al.*, 2012).

Effects of Zooplankton Distribution on Fish in L. Victoria

Zooplankton feed on phytoplankton thereby regulating their population. Phytoplankton form the main source of energy for the zooplankton which converts algal food into quick source of protein for fish. All fish larvae depend on the distribution and abundance of zooplankton a source of food for their survival. This, therefore, means

that the abundance of fish in L. Victoria is dependent on the abundance of zooplankton because it is through fish larvae recruitment that the fishery of the lake is dependent on.

Taking the food web characteristics that exist between zooplankton and fishes of L. Victoria, it is evident that such fish species as *Rastrineobola argentea*, *Oreochromis niloticus* and the larvae of *Lates niloticus*. Ingest its food from zooplankton. It is

reported that the aforementioned fish species feed mainly on cyclopoid copepods and these are the major constituent of zooplankton communities of L. Victoria (Oyoo-Okoth *et al.*, 2011). On the other hand, fish larvae eat small-bodied rotifers, mainly distributed along the shallow inshore areas of the lake. In addition, the young *L. niloticus* feed solely on *Caridina nilotica* (Semyalo *et al.* 2009). In the absence of zooplankton in L. Victoria, it therefore, means that *L. niloticus*, which is of commercial importance will collapse.

Mature *L. niloticus* is a predator that feed majorly on *R. argentea* and other pelagic haplochromines which derive their food from the zooplankton. Some copepod species such as *Mesocyclops* spp. and *Chaoborus* spp. predate on cladocerans. These species are in turn eaten by fish thus affecting their distribution and abundance (Irvine and Waya, 1995). In a nutshell, zooplankton distribution, composition and abundance in L. Victoria is, therefore, a key connection in terms of energy flow integrating carnivorous invertebrates and pelagic fishes for production of major commercial fishes such as *O. niloticus* and *L. niloticus*.

Conclusion

Going by the reported studies, L. Victoria is dominated by three main groups namely Cyclopoids, Cladocerans, and Rotifers. There have been changes in relative abundance from large bodied calonoids and Cladocerans to the smaller bodied Cyclopoids. This is supported by the same occurrence in other adjacent SWBs within the basin. The changes in zooplankton community has been attributed to the introduction of the Nile perch, eutrophication, pollution, poor or variability in sampling methods and cannibalism.

Although it is argued that so much research in zooplankton community of Lake Victoria has been undertaken especially since the 1990s (Mbahinzireki, 1994; Okedi, 1990; Mavuti & Litterick, 1991; Mwebaza-Ndawula, 1994; Mwebaza-Ndawula *et al.*,

2003a), in our opinion, the studies conducted lack consistence. There are no regular or periodic studies that have been conducted to provide reliable data that could give predictable trends in zooplankton structure. The same scenario is depicted in earlier studies as well where very little inconsistent research was carried out (Worthington, 1931; Rzoska, 1957; Akiyama *et al.*, 1977; Hoogenboezem, 1985; Macdonald, 1956). This then means that the lake has been covered sparingly in both littoral and inshore. To some extent the picture reflected in the studies so far carried out may not be true: no wonder the refuting claims on the reasons of the current zooplankton structure in the lake. Consequently, we are also persuaded to conclude that lack of capacity may be another contributor to unclear reporting of the zooplankton of Lack Victoria. Not all the limnologists who have studied zooplankton of Lake Victoria are specialists in zooplankton ecology. Further to this, Lake Victoria is a transboundary resource shared by the three East African countries: Kenya, Uganda and Tanzania. Research by scientists from each country is not conducted uniformly. There is therefore, a difference in terms of standards and protocols employed that may lead into several biasness in terms of equipment use (i.e. different sampling net sizes), identification keys and to some extent professional judgement during identification. It is also, concluded that the abundance of zooplankton influences the distribution of fishes in the lake although there is scanty data to support this.

Recommendations

There is need for more studies on the zooplankton of L. Victoria and its impacts on the fishery. It is also, recommended that capacity building in zooplankton ecology be enhanced in the region. There is need for harmonized sampling protocol in the three East African countries to enhance collection of reliable data that could be able to depict the real picture in the lake ecosystem.

References

- Abila, R. (1995). *Biomass and spatial distribution of benthic macroinvertebrates in Lake Kanyaboli, Kenya*. MSc Thesis. Moi University, Eldoret. 151 p.
- Akiyama, T., Kajumulo, A. A. & Olsen, S. (1977). Seasonal variation of plankton and physical chemical condition in Mwanza Gulf, Lake Victoria. *Bull. Freshwat. Fish. Res. Lab*, 27, 49-61.
- Amarasinghe, P. B., Ariyaratne, M. G., Chitapalpong, T. & Vijverberg, J. (2008). Production, biomass and productivity of copepods and cladocerans in south-east Asian water bodies and the carrying capacity for zooplanktivorous fish. In Schiemer, F., Simon, D., Amarasinghe, U. S., & Moreau, J. (Eds). *Aquatic ecosystems and development: Comparative Asian perspectives*. Germany, The Netherlands: Margraf and Backhuys Publishers.
- Badsì, H., Ali, H. O., Loudiki, M., Hafa, M. E. & Aamiri, R. A. (2010). Ecological factors affecting the distribution of zooplankton community in the Massa Lagoon (Southern Morocco). *Afric. J. Env. Sci. Tech.*, 4, 751-762.
- Bezerra-Neto, J. F. & Pinto-Coelho, R. M. (2002). A influência da larva de *Chaoborus brasiliensis* (Theobald, 1901) (Diptera, Chaoboridae) na distribuição vertical da comunidade zooplancônica da lagoa do Nado, Belo Horizonte, estado de Minas gerais. *Acta Sci Biol Sci*, 24, 337-344.
- Brooks, J. L. & Dodson, S. I. (1965). Predation and composition of plankton. *Science*, 150, 26-35.
- Casper, A. F. & Thorp, J. H. (2007). Diel and lateral patterns of zooplankton distribution in the St. Lawrence River. *River Res. Appl.*, 23, 73-85.
- Castro, B. B., Marques, S. M. & Gonçalves, F. (2007). Habitat selection and diel distribution of the crustacean zooplankton from a shallow Mediterranean lake during the turbid and clear water phases. *Freshwat. Biol.*, 52, 421-433.
- Descy, J. P., F. Darchambeau, F. & Isumbisho, M. (2012). Lake Kivu: Limnology and biogeochemistry of a tropical great lake. *Aquatic Ecology Series* 5, DOI 10.1007/978-94-007-4243-7_7, © Springer Science+Business Media B.V. 2012.
- Dietzel, A., Mieleitner, J., Kardaetz, S. & Reichert, P. (2013). Effects of changes in the driving forces on water quality and plankton dynamics in three Swiss lakes – long-term simulations with BELAMO. *Freshwat. Biol.*, 58, 10-35.
- Dukes, J. S. & Mooney, H. A. (2004). Disruption of ecosystem processes in western North America by invasive species, *Rev Chil Hist Nat*, 77, 411–437.
- Ehrenfeld, J. G. (2003). Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems*, 6, 503–523.
- Evans, M. S. & Sell, D. W. (1983). Zooplankton sampling strategies for environmental studies. *Hydrobiologia*, 99, 215-223.
- Gliwicz, Z. M. (1994). Retarded growth of cladoceran zooplankton in the presence of a copepod predator. *Oecologia*, 97, 458–461.
- Gliwicz, Z. M., & Umana, G. (1994). Cladoceran body size and vulnerability to copepod predation. *Limnology and Oceanography*, 39, 419–424.
- 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.
- Jürgens, K., Wickham, S. A., Rothhaupt, K. O. & Santer, B. (1996). Feeding rates of macro- and microzooplankton on heterotrophic nanoflagellates. *Limnology and Oceanography*, 41, 1833–1839.
- Hoxmeier, R. J. H. & Wahl, D. H. (2004). Growth and survival of larval Walleyes in response to prey availability. *Transactions of the American Fisheries Society*, 133, 45–54.
- Hoogenboezem, W. (1985). The zooplankton in the Mwanza Gulf (Lake Victoria) and the food of a zooplanktivorous cyprinid (*Rastrineobola argentea*) Hest Report, Rjksuniversiteit Leiden, The Netherlands.
- Hrbacek, J. (1962). Species composition and amount of the zooplankton in relation to fish stock. *Rozpr CSA V rada matem prir ved* 72, 1-116.
- Irvine, K. & Waya, R. (1995). The zooplankton: general sampling methods and estimation of biomass and development rates. In Menz, A. (Ed.), *The Fishery Potential and Productivity of the pelagic zone of Lake*

- Malawi/Niassa (69-83). Chatham, UK: Natural resource Institute.
- Keppeler, E. C. (2003). Abundance of zooplankton from different zones (pelagic and littoral) and time periods (morning and night) in two Amazonian meandering lakes. *Acta Sci Biol Sci*, 25, 287-297.
- Koziowsky-Suzuki, B. & Bozelli, R. (1998). Evaluation of the efficiency of three samplers on estimating the zooplankton abundance of Cabiúnas lagoon. In Esteves, F. A. (Ed.), *Ecologia das lagoas costeiras do parque nacional da restinga de Jurubatiba e do Município de Macaé (RJ)*, 442.
- Lahr, D. J. G. & Lopes, S. G. B. C. (2006). Morphology, Biometry, ecology and Biogeography of Five Species of *Diffugia leclerc*, 1815 (Arcellinida: Diffugiidae), from Tiete River, Brazil. *Acta Protozool*, 45, 77-90.
- Lazzaro, X. (1987). A review of planktivorous fishes, their evolution, feeding behaviours, selectivities and impacts. *Hydrobiologia*, 146, 97-167.
- Leitao, A. C., Freire, R. H. F., Rocha, O. & Santaella, S. T. (2006). Zooplankton community composition and abundance in two Brazilian semiarid reservoirs. *Acta Limnologia Brasiliensia*, 18(4), 451-468.
- Lévesque, S., Beisner, B. E. & Peres-Neto, P. R. (2010). Meso-scale distributions of Lake Zooplankton reveal spatially and temporally varying trophic cascades. *J. Plankton Res.*, 32, 1369-1384.
- Livings, M. E., Schoenebeck, C. W. & Brown, M. L. (2010). Comparison of Two Zooplankton Sampling gears in Shallow, Homogeneous lakes. *The Prairie Naturalist* 42(1/2).
- Macdonald, W. W. (1956). Observations on the biology of Chaoborids and Chironomids in Lake Victoria and on the feeding habits of the Elephant snout fish (*Mormyrus kanume* Forsk). *J. Anim. Ecol.* 25, 36-53.
- Mack, H. R., Conroy, J. D., Blocksom, K. A., Stein, R. A. & Ludsins, S. A. (2012). A comparative analysis of zooplankton field collection and sample enumeration methods. *Limnol Oceanogr Meth*, 10, 51-43.
- Mavuti, K. M. & Litterick, M. R. (1991). Composition, distribution and ecological role of zooplankton community in Lake Victoria, Kenya waters. *Verh. Internat. Verein. Limnol.*, 24, 1117-1122.
- Mbahinzireki, G. B. (1994). Initial results of benthic fauna studies in the northern Lake Victoria. In E. A. Okemwa, A. Getabu & E. Wakwabi (Eds.), *Proceedings of the 2nd EEC Regional Seminar on 'Recent Trends of research on Lake Victoria Fisheries'* September 1991, Kisumu, Kenya. Nairobi: ICIPE Science Press.
- Mulimbwa, N., Raeymaekers, J. A. M. & Sarvala, J. (2014). Seasonal changes in the pelagic catch of two clupeid zooplanktivores in relation to the abundance of copepod zooplankton in the northern end of Lake Tanganyika. *Aquat. Ecosyst. Health Manage.*, 17, 25-33.
- Mwambugu, J. A. (2004). The diversity of benthic mollusks of Lake Victoria and Lake Burigi. *Tanzania Journal of Science*, 30(1), 21-32.
- Mwebaza-Ndawula, L. V., Kiggundu, K. & Pabire, W. G. (2003). Diversity and abundance of invertebrate in Victoria basin lakes, Uganda. *Journal of Agricultural Science*, 8, 209-220.
- Mwebaza-Ndawula, L. (1994). Changes in relative abundance of zooplankton in northern Lake Victoria, East Africa. *Hydrobiologia*, 272, 259-264.
- Okeki, J. (1990). Observations on the benthos of Murchison Bay, Lake Victoria, East Africa. *Afr. J. Ecol.*, 28, 111-122.
- Okeyo-Owuor, J. B. (1999). Social Economics of Lake Victoria Fisheries: A Review of Biodiversity and Social Economic Research in Relation to Fisheries in Lake Victoria. LVEMP.
- Ogello, E. O., Obiero, K. & Munguti, J. M. (2013). Lake Victoria and the common property debate: Is the tragedy of the commons a threat to its future? *Lakes, Reservoirs and Ponds*, 7(2), 101-126.
- Oyoo-Okoth, E., Muchiri, M., Ngugi, C. C., Njenga, E. W., Ngure, V., Orina, P. S., Chemoiwa, E. C. & Wanjohi, B. K. (2011). Zooplankton partitioning in a tropical alkaline-saline endorheic Lake Nakuru, Kenya: Spatial and temporal trends in relation to the environment. *Lakes Reserv.: Res. Manage.*, 16, 35- 47.
- Peixoto, R. S., Cem, S. Á., Guimaraes, A. S. & Mala-Barbosa, P. M. (2008). Seasonal

- fluctuations of the microcrustacean assemblages in the littoral zone of lake Dom Helvécio (Parque estadual do Rio Doce, Mg). *Acta limnol Bras*, 20, 213-219.
- Riccardi, N. (2010). Selectivity of plankton nets over mesozooplankton taxa: implications for abundance, biomass and diversity estimation. *J limnol*, 69, 287-296.
- Rao, T. R. & Kumar, R. (2002). Patterns of prey selectivity in the cyclopoid copepod *Mesocyclops thermocyclopoides*. *Aquatic Ecology*, 36(3), 411-424.
- Rzóska, J. & Lewis, D. J. (1976). Insects as factor in general and human ecology in the Sudan. In J. Rzóska (Ed.), *The Nile, Biology of an Ancient River* (325-332). The Hague: Dr. W. Junk. B.V. Publishers.
- Santer, B. & van den Bosch, F. (1994). Herbivorous nutrition of *Cyclops vicinus* – The effect of a pure algal diet on feeding, development, reproduction and life-cycle. *Journal of Plankton Research*, 16, 171–195.
- Santos-Wisniewski, M. J. & Rocha, O. (2007). Spatial distribution and secondary production of Copepoda in a tropical reservoir: Barra Bonita, SP, Brazil. *Braz J Biol*, 67, 223-233.
- Semyalo, R., Nattabi, J. K. & Larsson, P. (2009). Diel vertical migration of zooplankton in a eutrophic bay of Lake Victoria. *Hydrobiologia*, 635, 383-394.
- Simoes, N. R. & Sonoda, S. (2009). estrutura da assembleia de microcrustáceos (Cladocera e Copepoda) em um reservatório do semi-árido Neotropical, Barragem de Pedra, estado da Bahia, Brasil. *Acta Scien Biol Sci*, 31, 89-95.
- Sitoki, L., Kurmayer, R. & Rott, E. (2012). Spatial variation of phytoplankton composition, biovolume, and resulting microcystin concentrations in the Nyanza Gulf (Lake Victoria, Kenya). *Hydrobiol.*, 691(1), 109-122.
- Silva, A. M. A., Barbosa, J. E. L., Medeiros, P. R., Rocha, R. M., Lucena-Filho, M. A. & Silva, D. F. (2009). Zooplankton (Cladocera and Rotifera) variations along a horizontal salinity gradient and during two seasons (dry and rainy) in a tropical inverse estuary (Northeast Brazil). *Pan-American Journal of Aquatic Sciences*, 4, 226-237.
- Uriarte, I. & Villate, F. (2004). Effect of pollution on zooplankton abundance and distribution in two estuaries of the Basque coast (Bay of Biscay). *Mer. Pl. Bul.*, 49(3), 220-228.
- Vanderkelen, I., Van Lipzig, N. P. & Thiery, W. (2018). Modelling the water balance of Lake Victoria (East Africa)-Part 1: Observational analysis. *Hydrology and Earth System Sciences*, 22(10), 5509-5525.
- Vannuccim, M. (1968). Loss of organisms through the meshes. *Monog Oceanog Meth* 2, 77-86.
- Vleira, L. C. G., Vital, M. C. V., Fernandes, A. P. C., Bonecker, C. C., Nabout, J. C., Kraus, C. N., Bernard, J. V. E., Velho, L. F. M. & Bini, L. M. (2017). Sampling sufficiency for estimating zooplankton diversity in neotropical floodplain lakes. *Lakes Reservoirs: Res Manag*, 22, 190-196.
- Waichman, A. V., Garcia-Davila, C. R., Hardy, E. R. & Robertson, B. A. (2002). Composição do zooplâncton em diferentes ambientes do lago Camaleão, na ilha da Marchantaria, Amazonas, Brasil. *Acta Amaz*, 32, 339-347.
- Worthington, E. B. (1931). Vertical movements of freshwater macroplankton. *Int. Rev. ges. Hydrobiol. Hydrogr.*, 25, 394-436.
- Yurista, P. M. & Kelly, J. R. (2009). Spatial patterns of water quality and plankton from high-resolution continuous in situ sensing along a 537-km nearshore transect of western Lake Superior, 2004. In M. Munawar & I. F. Munawar (Eds.), *State of Lake Superior. Ecovision World Monograph Series, Aquatic Ecosystem Health and Management Society* (439-471). Ont., Canada: Burlington.