Invertebrates of East African Soda Lakes 8

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Abstract

Soda lakes are among the world's most productive natural ecosystems, but the fauna consists of only a few specialized groups which can attain high biomass, seasonally or throughout the year. The invertebrate fauna is generally poor in species diversity. Protozoa are restricted to a few ciliates dominated by *Condylostoma* and *Frontonia* spp. The zooplankton biomass is dominated by a calanoid, *Paradiaptomus africanus*, with a maximum value of 1.17 g m^{-3} reported in Lake Nakuru, Kenya. Rotifers dominate in terms of species diversity, with six species/lake being the highest recorded number at six. Cladocerans are rare and include some euryhaline forms also common in other Rift Valley lakes, such as *Alona* sp., *Macrothrix triseralis*, *Moina* and *Ceriodaphnia* spp. Rotifera are represented by a few euryhaline and halobiontic species such as *Brachionus dimidiatus*, *B. plicatilis* and *Hexarthra jenkinae*. At times, *B. dimidiatus* can attain extremely high abundances (800 million m^{-3}). The major food sources for zooplankton grazers are the large cyanoprokaryote *Arthrospira fusiformis*, Bacteria and detritus. Larger rotifers such as *B. plicatilis* obtain 48 % of their diet from fragments of *A. fusiformis*, whereas the smaller *B. dimidiatus* remove particles < 2 µm. Assimilation of this cyanoprokaryote was low. Despite this food constraint, secondary production of rotifers can exceed that of calanoids by a factor of 100x in soda lakes and over 600x in freshwater lakes. The macroinvertebrate community of soda lakes is dominated by insects of the order Heteroptera, Family Corixidae (water boatmen), genera *Micronecta* and *Sigara* and Family Notonectidae (backswimmers), genus *Anisops*. Other taxa include nematodes, oligochaetes, chironomids (non-biting

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midges), culicine mosquitoes, an anostracan (*Branchinella spinosa*) and ostracods (mussel shrimp). The chironomid community consists of halobiontic forms such as *Microchironomus deribae*, *Kiefferulus disparilis* and *Tanytarsus minutipalpis*. *M. deribae* can increase to enormous numbers seasonally and become a nuisance for lakeshore residents around soda lakes. In Lake Nakuru, Kenya, a high secondary production of 120 mg dry mass m^{-2} day^{-1} was recorded for *M. deribae*, but this is lower than the highest secondary production value of 182 mg dry mass m^{-2} day^{-1} for chironomids reported from the saline Australian Lake Werowrap. Secondary production can be high seasonally in soda lakes, but the biomass turnover rate (*P*/*B* ratio) of zooplankton and macroinvertebrates is low, probably because of the seasonal food limitations (e.g. *Anisops* is predatory on calanoids and fish) or the poor food quality of detritus and decomposing cyanoprokaryotes in the system. Soda lakes have simple food chains and are ideal as natural experimental models to study food web dynamics and energy flow in lakes.

8.1 Soda Lakes in East Africa

Saline lakes are restricted in their global distribution compared with the more common freshwater lakes (Hammer 1986). Soda lakes represent another set of saline lakes. They have a worldwide distribution but are mainly confined to (sub)tropical latitudes in continental interiors. Due to their hostile nature, they are often remote from the main centres of human activity. This is perhaps one reason why few studies have been conducted on these soda lakes.

Saline and soda lakes are more abundant in the Eastern Rift than in any other African ecoregion. Streams that feed the lakes flow over highly alkaline volcanic rocks, bringing Natron (a naturally occurring salt consisting of sodium carbonate and sodium bicarbonate) into the lakes' waters. Many of these lakes are endorheic, and high ambient temperature in the Rift Valley increases the evaporation rate, thereby enhancing the water's alkalinity by raising the concentrations of Na^{+}, HCO_3^{-} and CO_3^{2-}. Whereas the pH of natural freshwater lakes often ranges between 6 and 8, that of the soda lakes ranges from 9 to 12. Many of the soda lakes fluctuate in size and change in water salinity with dry and wet periods (Fig. 8.1). Soda lakes vary in shape from broad, shallow pans to narrow, deep depressions.

Alkaline-saline lakes, or soda lakes, in tropical Africa are inhabited by specialized biota that can tolerate high water temperature (e.g. 40 °C in Lake Bogoria, Kenya, and even as high as 50 °C in Lake Natron, Tanzania; Hughes and Hughes 1992), high salinity and low oxygen solubility (Hecky and Kilham 1973; Talling 1992). Only a few specialized groups of zooplankton and macroinvertebrates are able to survive in soda lakes. Most of these organisms also possess highly developed strategies of diapause and dispersal that enable them to persist in arid landscapes where scarce aquatic habitats are hydrologically unstable and of marginal quality.

Due to the presence of high solar radiation, moderate temperature, unlimited carbon dioxide reserves in the form of carbonate-bicarbonate salts and other essential nutrients such as phosphate, the East African soda lakes (EASL) have high rates of photosynthesis (Grant 2006; Melack and Kilham 1974; Oduor and Schagerl 2007; Talling et al. 1973). Primary production rates of >10 g C $m^{-2}day^{-1}$ have been recorded, making these among the most productive aquatic

Fig. 8.1 Lake Eyasi (Tanzania) in 2010 almost completely dried up (photo: Michael Schagerl)

environments in terms of biomass anywhere in the world. Indeed, the highest primary productivity for a natural habitat was earlier recorded from some of these lakes in Ethiopia (Talling et al. 1973). This remarkable photoautotrophic primary production is presumably the driving force behind all biological processes in what is essentially a closed environment. Cyanobacteria (notably *Arthrospira*) species and heterotrophic Bacteria are the most abundant primary producers in these habitats (Grant 2006; Mwatha 1991).

Salinity is variable and high in the soda lakes. Total salts vary from about 50‰ in the northern lakes (Bogoria, Nakuru, Elmenteita, Sonachi) to saturation in parts of the Magadi-Natron basin in the south. The high alkaline and high salt concentrations of soda lakes seem to be too extreme for most forms of life to exist, but these lakes support a diverse group of microorganisms. These microorganisms, generally termed extremophiles, are adapted to the extremes of alkaline pH and high salt concentration (Grant 2006). In the highly productive soda lakes, abundant organic matter (Jirsa et al. 2013) supports a huge assemblage of heterotrophic Bacteria, probably involved in organic matter decomposition and nutrient recycling (Grant 2006; Mutanga et al. 2000). In the process of oxidizing organic matter, these heterotrophic microbes consume the available oxygen. As a result, in some of these lakes (e.g. Lake Chitu and Lake Arenguade, Ethiopia), no measureable dissolved oxygen is detected in areas deeper than 35 cm and no fish are present.

The dominant cyanoprokaryote *Arthrospira fusiformis* has evolutionarily developed a mechanism of adaptation to the hyperosmotic environment in soda lakes (see Schagerl and Burian, Chap. 12). How have the invertebrates coped with the same problem? Benthic invertebrates have several mechanisms to adapt to saline and alkaline lakes. Larvae have a lime gland to remove carbonate and bicarbonate ions from the blood and excrete them (see Schagerl and Burian, Chap. 12).

With an abundance of food and a paucity of competitors, soda lake invertebrate populations grow to astounding densities. It is estimated that 37 million brine flies can be found on one linear mile of shore at the Great Salt Lake (USA). It is not unusual to see soda lake shores covered with immense numbers of corixids on which huge flocks of birds converge and feast. The unconsumed invertebrate biomass decomposes on the lake shores, giving off an offensive and obnoxious smell to the surrounding area, which depreciates the aesthetic and recreational value of soda lakes.

The algal and invertebrate communities of soda lakes are highly sensitive to environmental change, and some taxa can become locally extirpated following salinity fluctuations well within known tolerance ranges. Several observations indicate that soda lake communities are regulated by a variety of environmental factors, among which salinity may be important but not necessarily decisive for survival. Other factors may include nutrient or food availability, temporal variation in dissolved oxygen, water-column transparency and the stability of various substrata available to benthic organisms (McClanahan et al. 1996; Melack 1976; Vareschi and Vareschi 1984).

The main saline or alkaline soda lakes are Bogoria (42 km^2), Nakuru (49 km^2), Elmenteita (19 km^2) and Magadi (105 km^2) in Kenya; Natron (900 km^2), Manyara (470 km^2) and Eyasi (1050 km^2) in Tanzania; and some lakes in the Ethiopian Rift Valley such as Lakes Arenguade, Abijata, Shala and Chitu. There are also other small lakes (<20 km^2) on the valley floor, including Lakes Solai, Sonachi and Oloidien in Kenya and Lakes Lelu and Momera in Tanzania. These lakes are salty and some have high concentrations of fluoride and sodium carbonate salts. For a general overview, please refer to the Appendix.

8.1.1 The Ethiopian Soda Lakes

Many lakes in Ethiopia tend to concentrate salts due to evaporative concentration, hot springs and saline intrusions. However, the major lakes that concentrate carbonate-bicarbonate salts, mainly of the sodium type, are Arenguade, Abijata, Shala and Chitu (see Table 8.3). In Lake Abijata, the lake water has been withdrawn for industrial extraction of soda ash since 1985 with an annual production of 8500 tons. Ayenew (2002) documented that the water level of Lake Abijata has receded drastically since then, exposing dry bed of trona and posing a threat to the aquatic and bird life (Fig. 8.2). Lake Shala, one of the deepest lakes in Africa (Z_{max} = 266 m), has a rich reserve of carbonate-bicarbonate salts, despite the inflow of many small freshwater hot springs from its caldera rim (Fig. 8.3). Lake Chitu, a small lake near Lake Shala, has higher salinity and alkalinity than the other Ethiopian lakes and supports high populations of heterotrophic Bacteria, *Arthrospira fusiformis* and flamingos. The hypersaline lakes in the Afar Depression close to the Red Sea are brine solutions of NaCl and other salts such as K, Ca, Mg and SO_4; they accumulate very little carbonate salts. The geographical location, salinity and

Fig. 8.2 Lake Abijata (Ethiopia) in 2011—receding lake water and evaporative deposit of trona (photo: Steve Omondi)

Fig. 8.3 Lake Shala (Ethiopia)—fresh hot springs flowing into the lake (photo: Seyoum Mengistou)

carbonate-bicarbonate concentration of the four soda lakes in Ethiopia are given in the Appendix.

8.1.2 The Kenyan Soda Lakes

The major soda lakes in Kenya include Bogoria, Elmenteita, Oloidien (low in salinity with around 4), the well-studied Lake Nakuru and L. Sonachi and Lake Magadi, where industrial extraction of trona for the commercial production of soda ash has been taking place since 1924. The northern soda lakes include Lakes Logipi, Elmenteita, Nakuru and Bogoria, and some of which have lake water temperatures at about 40 °C (Hughes and Hughes 1992).

Lake Magadi It is at the southern end in the Kenya Rift Valley, and during the dry season, it is 80 % covered by trona and is well known for its wading birds, including flamingos. Lake Magadi is a saline, alkaline lake, approximately 100 km^2 in size. It is an example of a "saline pan", with some areas being up to 40 m thick with salt.

Lake Bogoria This is a moderately sized soda lake (area 30 km^2) with high salinity (conductivity 40–80 mS cm^{-1}), alkalinity (1500 meq L^{-1}) and pH 10.3. Hot fumaroles and springs fringe the lake shore and the deposited soda layers are evident from a long distance. The lake has a narrow and extended littoral zone, which is devoid of vegetation and harbours one of the largest Lesser Flamingo populations in the Rift Valley (Mutanga et al. 2000). Lake Bogoria is rich in concentrated carbonate-bicarbonate mixture, and the *Arthrospira* that thrives abundantly is restricted to certain parts of the lake, where large flocks of the Lesser Flamingo concentrate. The chironomid *Paratendipes* sp. dominates the invertebrate community; sometimes a mass emergence of Ephydridae can be observed (Figs. 8.4 and 8.5). Rotifers include *Brachionus dimidiatus* (Fig. 8.6), *B. plicatilis* and *Hexarthra jenkinae* (Burian et al. 2013). Ong'Ondo et al. (2013) also reported many ciliate species such as *Cyclidium*, *Rimaleptus*, *Halophyra*, *Acineria* and *Frontonia* spp., with the latter forming the dominant group.

Lake Nakuru It typically covers between 35 km^2 and 49 km^2 but occasionally dries out completely due to unknown reasons; this endorheic lake with a mean depth of 2.3 m is small for its large drainage area of 1760 km^2 (International Lake Environment Committee 2001) and as a result has high external loading of nutrients and sediment. The three major rivers feeding the lake are Njoro, Makalia and Nderit, and it also receives water from several alkaline springs. The lake was voted as a Ramsar site in 1990. Scientists estimated that the flamingo

Fig. 8.4 Mass emergence of Ephydridae at Lake Bogoria, 2010 (photo: Michael Schagerl)

Fig. 8.5 Exuviae of Ephydridae at shore of Lake Bogoria, 2010 (photo: Michael Schagerl)

population at Nakuru consumes about 250,000 kg of algae per hectare of surface area per year (International Lake Environment Committee 2001). The invertebrate community here has been comparatively well studied and is discussed under other sections.

Lake Sonachi It is a small (0.14 km^2), shallow (Z_{max} 4.25 m in 1993), alkaline-saline crater lake located 1884 m above sea level in the semiarid Rift Valley of central Kenya. Its water level is maintained against a strong moisture deficit by subsurface flow from nearby Lake Naivasha. The salt budget of Lake Sonachi is governed by rainfall and evaporation at the surface and dissolution of sedimentary evaporates by percolating groundwater. As in other African soda lakes, the ionic composition of lake water is dominated by sodium and bicarbonate, whereas pH values are very high (9.0–10.3; Melack 1976). Surface-

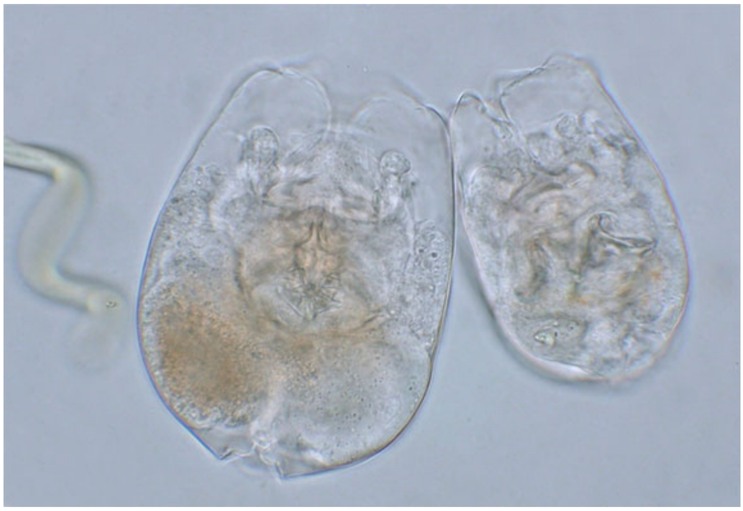

Fig. 8.6 *Brachionus dimidiatus* from Lake Nakuru (photo: Michael Schagerl)

water conductivity (K_{25}) since 1929 ranged from 3000 to 11,550 μS cm^{-1}, and years with good data coverage show seasonal fluctuations on the order of 1000–2000 μS cm^{-1} (Verschuren et al. 1999). The lake is rich in planktonic Cyanobacteria including *Arthrospira fusiformis*, whereas planktonic diatoms and green algae are scarce.

Lake Oloidien It is less saline and alkaline than the other Kenyan lakes (conductivity less than 5 mS cm^{-1}) and is situated at the southern tip of Lake Naivasha, with which it shares euryhaline zooplankton forms typically found in freshwater tropical lakes. These include the cyclopoid *Thermocyclops oblongatus*, the cladocerans *Ceriodaphnia cornuta* and *Diaphanosoma excisum* and the rotifers *Brachionus angularis* and *Hexarthra mira* (Uku and Mavuti 1994). The collected benthic macroinvertebrates included forms also present in other soda lakes such as oligochaetes (Tubificidae) and chironomids (Clark et al. 1989).

8.1.3 Tanzanian Soda Lakes

In the Tanzanian Rift Valley, the largest saline and soda lakes are Lakes Eyasi, Manyara and Natron, but many small saline alkaline lakes also exist (see appendix).

Lake Eyasi It is a seasonal shallow endorheic soda lake on the floor of the Great Rift Valley at the base of the Serengeti Plateau in the Crater Highlands of Tanzania. It is usually dry, but may occasionally flood up to a depth of 1 m (Hughes and Hughes 1992). The Sibiti River occasionally flows into the lake but its waters usually evaporate before reaching the dry lakebed. Even though permanent springs lie along the lakeshores, their waters evaporate quickly, leaving huge flakes of salt on the lake shore.

Lake Manyara It is a shallow lake (max depth 3.7 m) in the Natron-Manyara-Balangida branch of the Great Rift Valley in Tanzania. It was said by Ernest Hemingway to be the "loveliest [lake] . . . in Africa", with its huge flocks of flamingos that rely on the abundant *Arthrospira* and extensive dry out of soda salts during lake recession (Matagi 2004).

Lake Natron It lies to the north on the border between Kenya and Tanzania. Seasonal streams drain into Lake Natron from the Ngorongoro Highlands south of the lake (Hughes and Hughes 1992). About 28 springs, most of them saline, also feed into the lake. Despite these inflows, most of the lake's water is derived from direct precipitation. Evaporation exceeds precipitation, and the maximum depth is only 2 m. A large portion of the lake's bed is covered by a salt crust that dissolves during the rainy season. Lake Natron serves as an important breeding site for the Lesser Flamingo populations that fly over from other Rift Valley lakes as far away as Kenya and Ethiopia (Mutanga et al. 2000). Temperatures in the lake can reach 50 °C and, depending on rainfall, a pH of 9–10.5 can be reached (almost as alkaline as ammonia).

8.2 Invertebrate Species Composition in Ethiopian Soda Lakes

8.2.1 Zooplankton

Copepods are the dominant zooplankton in soda lakes. Cladocera are rare and Rotifera are represented by a few euryhaline salt-tolerant taxa such as *Brachionus dimidiatus*, *B. plicatilis*, *B. calyciflorus* and *B. angularis*.

Of the Copepoda, the calanoids are prominent in soda lakes and sometimes the sole zooplankton in small soda lakes such as Lake Arenguade in Ethiopia (pers. observation). The species most often encountered is *Lovenula africana* (*Paradiaptomus africanus*). This large calanoid (max length 1.48 mm) subsists on the rich cyanoprokaryote food resource in soda lakes, especially *Arthrospira fusiformis*. Fragments of *Arthrospira* sp. were often visible in the gut of this calanoid in Lake Arenguade (Afeworki Ghebrai, pers. comm.), and other large protozoans such as the ciliates belonging to genera *Strombidium*, *Strobilidium* and *Halteria* were observed to ingest large pieces of this cyanoprokaryote in East African lakes (Yasindi and Taylor 2006; see Yasindi and Taylor, Chap. 7).

Cyclopoids are less represented in soda lakes and often belong to a few euryhaline genera also common in freshwater lakes. *Mesocyclops* has wide range of tolerance to conductivity up to 5000 μS cm^{-1}, whereas *Afrocyclops* and *Thermocyclops* spp. extend to even higher conductivities close to 10,000 μS cm^{-1} (LaBarbera and Kilham 1974). *Mesocyclops* has occasionally been observed in Lake Abijata along with *Afrocyclops gibsoni* and *Eucyclops serrulatus*. These cyclopoids were present in low numbers and only at certain times of the year, especially when the lake became diluted during the rainy season (June–Sept.). Matagi (2004) reported two cyclopoids from Lake Shala—*Lytocyclops gibsoni* and *Cyclops agiloides*. Matagi (2004) did not state the source of the finding, and the present author has doubts as to the authenticity of the records. The *Lytocyclops gibsoni* probably refers to *Afrocyclops gibsoni*, which this author collected only from Lake Abijata and not Shala. The identity of the species identified as *Cyclops agiloides* remains unclear. Equally, there are no reports of any cladoceran from Lake Shala, and *Diaphanosoma excisum* was never recovered from this lake, even though it is abundant in other freshwater lakes in Ethiopia. A copepod parasite of fish, *Argulus africanus*, was regularly observed in the freshwater influx areas of Lake Shala, where fish are often present (see Fig. 8.3).

Of particular interest was the recording of a harpacticoid copepod in Lake Shala in 1983 (pers. observation). This harpacticoid (*Nitocra lacustris*) was the dominant and sole zooplankton in the lake during the survey. Tudorancea and Taylor (2002) also reported recovering this harpacticoid from the benthos of Lakes Abijata and Shala.

Cladocera are rare in soda lakes, mainly because of the high osmotic pressure, which they cannot withstand. The osmoregulatory mechanisms that calanoids have evolved to withstand the osmotic stress in soda lakes have apparently not been well developed in Cladocera. The rare species encountered in soda lakes include the ubiquitous *Moina* spp., *Alona* spp. and *Macrothrix triseralis*. *Moina belli* was encountered only in Lake Shala.

Rotifera are the most diverse zooplankton in soda lakes. The species most often encountered are the euryhaline, halophilic forms which can tolerate high salinity and are represented by *Brachionus* species—*B. dimidiatus*, *B. urceolaris*, *B. plicatilis*, *B. angularis* and

B. calyciflorus. Other rotifers encountered include: *Lecane bulla*, *L. luna* and *Trichocerca tetractis* in Lake Shala and *Hexarthra* sp. and *Asplanchna brightwelli* in Lake Chitu. Apparently, rotifers in the soda lakes face dual problems: they have to withstand the high ionic concentration and imbalance and must also subsist on detrital and bacterial food resources. This is because the large cyanoprokaryotes in the soda lakes, such as *Arthrospira* spp., *Anabaenopsis* spp. and *Synechococcus* spp., cannot be ingested by the small rotifers. *Oocystis*, a small chlorophyte, became the dominant planktonic algae in the soda Lake Abijata in 1961 (Wood and Talling 1988). Rotifers can potentially rely on such small primary producers (besides Bacteria and detritus) whenever they bloom in soda lakes.

In general, the zooplankton community of soda lakes is poor and restricted to a few halophilic and alkalophilic species, which is also true for the phytoplankton and microbial communities studied in these lakes (e.g. Grant et al. 1990). The list of the common zooplankton species encountered in the Ethiopian soda lakes is presented in Table 8.1.

8.2.2 Benthic Invertebrates

The list of benthic invertebrate species documented from the Ethiopian soda lakes is presented in Table 8.2; Table 8.3 provides a summary of invertebrates occurring in the EASL. The species diversity of benthic macroinvertebrates in soda lakes is low, with maximum of 20 taxa, and restricted to a few specialized taxa that have evolved mechanisms to tolerate the extreme alkalinity and salinity. From the limited studies done on the invertebrate composition and distribution in soda lakes, the dominant forms are from the Arthropoda, Order Hemiptera (bugs), the Nematoda (roundworms), Oligochaeta (aquatic earthworms) and Chelicerata. Two families are well represented in the Hemiptera, including the Families Corixidae (water boatmen) and Notonectidae (backswimmers). The Diptera are highly represented by the family Chironomidae, subfamily Chironominae (non-biting midges), which can reach enormous densities during emergence. Harrison (2002) published a detailed study of the Chironomidae in the soda lakes of Ethiopia and his records are included in Table 8.2.

Table 8.1 List of the zooplankton in Ethiopian soda lakes

Taxon	L. Arenguade	L. Abijata	L. Shala	L. Chitu
Protozoa	*Strombidium*, *Strobilidium*			*Strombidium*
Cyclopoida (Copepoda)		*Mesocyclops* sp.* *Afrocyclops gibsoni** *Eucyclops serrulatus**		
Harpacticoida (Copepoda)			*Nitocra lacustris*	
Calanoida (Copepoda)	*Paradiaptomus africanus*	Nauplii		
Cladocera		*Alona rectangula*	*Moina belli*	
		*Macrothrix triseralis**		
Rotifera		*Brachionus dimidiatus*	*Lecane luna*	*B. calyciflorus**
		B. plicatilis	*L. bulla*	*B. plicatilis*
		B. urceolaris	*Trichocerca tetractis*	*B. urceolaris*
		B. angularis		*Hexarthra* sp.*

*Also found in other non-soda Ethiopian lakes

Table 8.2 Benthic invertebrate taxa documented from Ethiopian soda lakes

Taxon (common name)	L. Arenguade	L. Abijata	L. Shala	L. Chitu
Order Hemiptera (bugs) Fam. Corixidae (water boatmen)				
Micronecta jenkinae	+	++		
Sigara hieroglyphica	+	++		
Order Hemiptera Fam. Notonectidae (backswimmers)				
Anisops sp.				+
Class Crustacea				
Order Ostracoda (mussel shrimp)				
Limnocythere barosi	+	(44,922) ++	(14,836) ++	
Gomphocythere sp.			(40) +	
Darwinula stevensoni			(60) +	
Potamocypris mastigophora		+		
Order Diptera				
Fam. Chironomidae (midges)				
Subfamily Chironominae				
Kiefferulus dispersalis	+	(27,360) ++	(1) rare	+
Cladotanytarsus pseudomancus		(281) +	(1592) +	+
Microchironomus deribae		(10,644)	(412) +	+
M. lendlin		++	+	+
Tanytarsus minutipalpis		+	+	+
Chelicerata				
Hydracarina sp. (water mites)		+	+	
Nematoda		(10 species)	(3 species)	
Monohystera		(539) ++	(49) +	
Mesodorylaimus		(326) ++	(949) +	
Oligochaeta (aquatic earthworms)				
Tubificidae		(167) +	(1761) ++	

Relative occurrence recorded as + = common and ++ = very common
Numbers in brackets are densities in number m^{-2}

Nematode worms of the genera *Monohystera* and *Mesodorylaimus* are quite common in soda lakes, while the Oligochaeta, represented by the family Tubificidae, can reach high densities in the lake bottom. Other macroinvertebrates in soda lakes include the chelicerate *Hydracarina* (water mites) and crustaceans belonging to the class Ostracoda. Members of the genus *Limnocythere* can reach extremely high densities in soda lakes such as Lake Abijata (~ 45,000 m^{-2}).

Eyualem (2002) conducted an exhaustive study on the nematodes of the Ethiopian Rift Valley lakes, including the soda lakes Abijata and Shala. The genus *Monhystrella* of the family Nordidae dominated in soda lakes, represented by about four species—*M. parvellus*, *M. hoogewejisi*, *M. jacobsi* and *M. macrura* (Table 8.4). This is followed by the family Dorylaimidae with the genera *Dorylaimus* and *Mesodorylaimus*. *M. macrospiculum* is present in both soda lakes, whereas the other two species are lacking from Lake Abijata.

Hughes and Hughes (1992) reported the presence of the molluscs *Bellamya unicolor* and *Helicarion ruppellianum* in Lake Abijata, which were not collected from Lakes Shala and Chitu. Apparently, these molluscs tolerated the lower salinity of Lake Abijata but not the higher salinities of Lakes Shala and Chitu.

Table 8.3 Checklist of invertebrates in East African soda lakes (after various sources); number codes of the lakes are (1) Arenguade, (2) Abijata, (3) Shala, (4) Chitu, (5) Elmenteita, (6) Nakuru, (7) Bogoria, (8) Sonachi

Group	Genus species	Lake Code
Protozoa	*Strombidium* sp.	1,4
	Strobilidium sp.	1
	Condylostoma sp.	1,6
	Euplotes sp.	6
	Pleuronema sp.	6
	Lionatus sp.	6
	Frontonia sp.	6, 7
Copepoda		
Calanoida	*Paradiaptomus africanus*	1,6,7
Cyclopoida	*Mesocyclops* sp.	2
	Afrocyclops gibsoni	2,3
	Eucyclops serrulatus	2
Harpacticoida	*Nitocra lacustris*	3
Cladocera	*Alona* sp.	2,8
	Macrothrix triseralis	2
	Moina spp. *Ceriodaphnia cornuta*	2,3,6,8 12
	Diaphanosoma excisum	2, 7
Rotifera	*Brachionus dimidiatus*	2,6,8
	B. plicatilis	2,4,6
	B. urceolaris	2,4
	B. angularis	2
	Lecane luna	3
	L. bulla	3
	Trichocerca tetractis	3
	Hexarthra jenkinae	4,6
	Keratella tropica	6
	Filinia longiseta	6
Macroinvertebrates		
Order Hemiptera (bugs)		
Fam. Corixidae (water boatmen) Fam. Notonectidae (backswimmers)	*Micronecta* sp. *Sigara* sp. *Anisops* sp.	1,2,6 1,2,6 4
Order Coleoptera (beetles)	Dytiscidae	8
Dytiscidae (diving beetles)	Hydrophilidae	8
Class Crustacea		
Order Anostraca (fairy shrimp)	*Branchinella spinosa*	5
Order Ostracoda (mussel shrimp)	*Limnocythere barosi*	2,3
	Gomphocythere sp.	1,3
	Darwinula stevensoni	2,3
	Potamocypris mastigophora	2

(continued)

Table 8.3 (continued)

Group	Genus species	Lake Code
Order Diptera		
Fam. Chironomidae (midges)		
Subfamily Chironominae	*Kiefferulus dispersalis*	1,2,8
	Cladotanytarsus pseudomancus	2,3,8
	Microchironomus deribae	2,3,4,6,8
	M. lendlin *Tanytarsus minutipalpis*	2,3,4, 2,3,4,6
	Dicrotendipes septemmaculatus	8
	Cladotanytarsus pseudomancus	7, 8
	Paratendipes sp.	7, 8
	Microtendipes spp.	7,8
Subfamily Orthocladiinae		
	Smittia spp.	8
Chelicerata	*Hydracarina* sp. (water mites)	2,3
Nematoda		
Family Dorylaimidae	*Dorylaimus generi*	3
	Mesodorylaimus bainsi	3
	M. macrospiculum	2,3
Family Monhysteridae		
	Monhystrella parvellus	3
	M. hoogewejisi	2,3
	M. jacobsi	2,3
Family Aphelechoididae	*M. macrura*	3
Family Isolamidae	*Brenolobrilus graciloides*	2,3
Family Rhabdolaimidae	*Isolaminium africanum*	2,3
	Rhabdolaimus aequatorialis	3
Oligochaeta (aquatic earthworms)	Tubificidae	2,3,6

Table 8.4 List of nematodes recovered from Ethiopian soda lakes (from Eyualem 2002) (Relative occurrence code same as for Table 8.2)

Taxon	Lake Abijata	Lake Shala
Family Aphelechoididae		
Brenolobrilus graciloides	+	+
Family Dorylaimidae		
Dorylaimus generi		+
Mesodorylaimus bainsi		+
M. macrospiculum	+	+
Family Isolamidae		
Isolaminium africanum		+
Family Nordidae		
Monhystrella parvellus		+
M. hoogewejisi	+	+
M. jacobsi	+	+
M. macrura		+
Family Rhabdolaimidae		
Rhabdolaimus aequatorialis		+
Total number of species	4	10

The ostracod taxa in the Ethiopian Rift Valley appear to show distinct segregation in saline and nonsaline lakes. Martens (2002) recorded that the freshwater Lakes Ziway, Langano and Awasa harboured the new subspecies *Limnocythere thomasi thomasi* (Ziway), *L. thomasi langanoensis* (Langano) and *L. thomasi awasensis* (Awasa), while the saline soda lakes Abijata and Shala harboured the subspecies *Limnocythere borisi borisi* (Abijata) and *L. borisi shalaensis* (Shala). Other ostracods present in the soda lakes were also represented in the freshwater lakes, such as *Potamocypris mastigophora*, *Gomphocythere angulata* and *Darwinula stevensoni*, the latter present almost in all Ethiopian Rift Valley lakes.

8.3 Invertebrates in Kenyan Soda Lakes

The main invertebrate taxa recorded from the Kenyan soda lakes (Table 8.5) closely resemble those from the Ethiopian soda lakes. Lake Nakuru was studied more extensively and more data are available for this lake (Burian et al. 2013, 2014; Matagi 2004; Oyoo-Okoth et al. 2011; Vareschi and Jacobs 1984, 1985).

The most abundant macroinvertebrates in the Kenyan soda lakes are the chironomids. In Lake Bogoria, chironomid dipterans have been recorded by Mutanga et al. (2000). In Lake Nakuru, *Culicinae* sp., the chironomid *Tanypus*, oligochaetes and *Microchironomus deribae* form the dominant species (Vareschi and Jacobs 1985). In Lake Elmenteita the anostracan *Branchinella spinosa* and the hemipterans *Micronecta* spp. were reported by Vareschi and Jacobs (1985). Four heteropterans, one notonectid and three corixids were identified in Lake Nakuru.

In Lake Nakuru, unsurprisingly, the same invertebrate species are present as those recorded from Ethiopian soda lakes. Two zooplankton groups, with a total of nine species, were reported by Matagi (2004) and Oyoo-Okoth et al. (2011). Rotifers were represented by *Brachionus dimidiatus*, *B. plicatilis*, *B. calyciflorus*, *Keratella*

Table 8.5 List of invertebrates reported from Lake Nakuru (Kenya)

	Taxon/species
Protozoa Ciliates	*Condylostoma* spp.
	Euplotes spp.
	Pleuronema spp.
	Lionatus spp.
	Frontonia spp.
Copepoda, Calanoida	*Paradiaptomus africanus*
Rotifera	*Brachionus dimidiatus*
	B. plicatilis
	B. calyciflorus
	Keratella tropica
	Filinia longiseta
	Hexarthra jenkinae
Heteroptera Notonectidae	*Anisops varia*
Corixidae	*Micronecta scutellaris*
	M. jenkinae
	Sigara hieroglyphica kilimanjaronis
Chironomidae	*Microchironomus deribae*
	Tanytarsus horni (=*T. minutipalpis*)
	Total number of taxa =17

tropica and *Filinia longiseta* (Burian et al. 2014), while ciliates were represented by *Condylostoma* spp., *Euplotes* spp., *Lionatus* spp. and *Pleuronema* spp. (Yasindi and Taylor 2006). In all the zooplankton samples, *B. dimidiatus* dominated, with a peak abundance (80–100,000 $\times 10^3$ individuals m^{-3}) and highest carbon biomass, and constituting about 80 % of the zooplankton samples (Chemoiwa et al. 2014). *Condylostoma* spp. dominated among the ciliates, although the ciliates were overall less abundant than the rotifers (Burian et al. 2013, 2014).

Macroinvertebrates in Lake Nakuru consist of three species of water bug (*Micronecta jenkinae*, *M. scutellaris* and *Sigara hieroglyphica kilimanjaronis*), which is typical of shallow, saline lakes and alkaline-saline lakes (Matagi 2004). The zooplankton included a copepod (*Paradiaptomus africanus*), beetle larvae, ceratopogonids, chironomid larvae (*Microchironomus deribae* and *Tanytarsus* spp.) and three species of rotifers (*Brachionus dimidiatus*, *B. plicatilis*, *Hexarthra jenkinae)*.

Lake Oloidien The zooplankton of Lake Oloidien consists of freshwater forms such as the cladocerans *Ceriodaphnia cornuta* and *Diaphanosoma excisum* and cyclopoid copepods such as *Thermocyclops oblongatus*. Rotifera was dominated by *Brachionus angularis* and *Hexarthra mira*, and the euryhaline forms of *Brachionus* (*B. dimidiatus and B. plicatilis*) are missing (Uku and Mavuti 1994). The chironomids, however, are also found in other soda lakes and include *Chironomus*, *Dicrotendipes*, *Cladotanytarsus* and *Nilodorus* species. Hemipterans include Notonectidae, Corixidae, Pleidae, Hebridae and Microvelidae. Molluscs of the family Physidae dominate the benthos in Lake Oloidien (Clark et al. 1989).

Lake Sonachi The zooplankton community of Lake Sonachi has a poor species assemblage which is similar to other northern Ethiopian and Kenyan soda lakes. Earlier, De Beauchamp (1932) recorded the rotifer *Brachionus dimidiatus* in 1929, and Beadle (1932) encountered the calanoid copepod *Paradiaptomus africanus* in 1931, but the zooplankton seems to have disappeared since then. The nearshore zoobenthos consisted of salt-tolerant chironomids (*Kiefferulus disparilis*, *Microtendipes* sp. and *Cladotanytarsus pseudomancus*), with a total density of 13,500 organisms m^2 (Clark et al. 1989). Other invertebrates reported from Lake Sonachi include coleopterans such as Dytiscidae (diving beetles) and Hydrophilidae along with hemipterans such as Notonectidae and Corixidae (Clark et al. 1989).

Verschuren et al. (1999) conducted a paleaolimnologial study on fossil invertebrate communities in Lake Sonachi and reported freshwater forms which do not exist in the lake at present. These included benthic cladoceran remains of *Bosmina longirostris*, *Euryalona orientalis*, *Alona pulchella*, *Chydorus sphaericus*, *C. parvus* and *Pseudochydorus globosus*. Planktonic cladocerans such as *Moina micrura* and *Alona rectangula* and one species of Orthocladiinae, eight of Chironomini and two of Tanytarsini chironomids were reported (Verschuren et al. 1999). The authors noted that the palaeofauna was dominated by two anoxia-tolerant halobiontic species, *Kiefferulus disparilis* and *Microtendipes* sp. *Tanytarsus minutipalpis* is also a halobiont but intolerant to anoxia.

The freshwater chironomids recorded with varying degrees of tolerance to the high salinities typical of African soda lakes include *Dicrotendipes septemmaculatus*, *Cladotanytarsus pseudomancus*, *Chironomus formosipennis*, *C. alluaudi*, *Nilodorum brevipalpis* and the Orthocladiinae *Smittia* (Verschuren et al. 1999).

Lake Bogoria It had no zooplankton larger than the size of protozoa and only a single chironomid species was recorded. The latter was tentatively designated as *Paratendipes* sp. and occurred in high densities throughout the lake, with an enormous wet weight biomass in the order of 3 tons and a daily emergence of 210 kg for the whole lake (Harper et al. 2003). This sustained several thousand individual avian predators, the most numerous being swifts and swallows and the most important for biodiversity conservation being the Cape Teal and Black-necked Grebe. Several insects were also recorded from the shores of Lake Bogoria including Coleoptera, particularly tenebrionids such as *Gonocephalum* spp., *Sepidium* spp., *Vietomorpha* spp. and *Rhytinota praelonga*, which scavenge nocturnally and shelter by day under stones. During the day, the lake margin was dominated by *Zophosis* spp. and the predatory cicindelid (Tiger Beetle) *Lophyra boreodilatata* (Horn). The lake edge scrub supported many cerambycids (Longhorn Beetles), including the large prionids *Tithoes confinis* Castelnau and the ubiquitous *Macrotoma palmata* (Fabricius), which are primary agents in breaking down dead wood. Tiger Beetles caught in light traps were *Prothyma methneri methneri* (Horn), *Cylindera rectangularis* (Klug) and *Myriochile vicina pseudovicina* (Mandl). In wetter periods, Scarabaeidae dominated light trap catches, particularly rutelids and melolonthids. Elaterids were common, including the 6–7 cm long *Tetralobus* spp. (Harper et al. 2003).

Lake Magadi It is located 610 m below sea level and has an area of 100 km^2 and a depth range from 1 to 5 m (Grant et al. 1990). The lake has no zooplankton or other aquatic invertebrates and is dominated by heterotrophic Bacteria. The alkaline lake niche limits diversity in microbial life due to high pH and high salinity. The large presence of trona causes the lake water to form a sodium carbonate brine and an extremely high fluoride concentration. Nonetheless, this hostile environment hosts extremophile Bacteria, the Magadi Tilapia *Alcolapia grahami* Boulenger and flamingos, herons, pelicans and spoonbills. These animals have developed unique physiological mechanisms to withstand the extreme salinity, alkalinity and fluoride content.

8.4 Invertebrates in Tanzanian Soda Lakes

Less information is available on the invertebrate fauna of the Tanzanian soda lakes. The invertebrate composition of some Tanzanian lakes has been discussed in relation to lake protection and conservation (Sarunday 1999). Because many endangered birds depend on the invertebrates as a food source, it is argued that conservation of the larger avifauna must be planned in conjunction with reducing the threats to the invertebrate fauna. In Africa as a whole, however, the protection of invertebrate diversity has been accorded less status and attention compared with the issue of fish diversity extinction by Nile Perch piscivory in Lake Victoria, for example.

8.5 Secondary Production of Invertebrates in Soda Lakes

8.5.1 Zooplankton Secondary Production

The only extensive study done on secondary production rates in soda lakes is the work of Vareschi and Jacobs (1984, 1985) in Lake Nakuru, Kenya. They studied production, consumption and energy flow of the dominant consumer organisms in the lake from 1972 to 1976. In general, Vareschi and Jacobs (1985) estimated secondary production rates for the zooplankton from field abundance data and laboratory experiments on growth and filtration rates. They did not include detrital food chains in their study, making it difficult to extrapolate the relative contribution of energy provided by live algal food versus the detrital component for the grazers in the food chain. The major food source believed to be grazed by zooplankton was the dominant cyanoprokaryote *Arthrospira fusiformis* (therein called *Spirulina platensis*) and an unknown fraction of food contributed by Bacteria and detritus. Besides the zooplankton, the other important grazers on *Arthrospira* were the Lesser Flamingo (*Phoeniconaias minor*) and the cichlid fish *Alcolapia grahami*. Of the zooplankton, the major grazers on *Arthrospira* were the calanoid *Paradiaptomus africanus* and the three dominant rotifers—*Brachionus dimidiatus*, *B. plicatilis* and *Hexarthra jenkinae*.

8.5.1.1 Calanoida: *Paradiaptomus africanus*

Laboratory cultures were used to obtain data on the stage duration and dry mass (DM) of this large calanoid (Vareschi and Jacobs 1985). Field data were used to determine the abundance of each stage. Egg production (adult) was estimated from the field egg ratio. The daily production of each stage, nauplii, copepodites and eggs (adults) was estimated by the discrete-step method (growth summation method) of Winberg et al. (1971). Daily secondary production of *P. africanus* was highly variable from year to year. Total production of all stages (eggs, nauplii and copepodites) was 80, 55 and 30 mg $m^{-3}day^{-1}$ DM during 1972, 1973 and 1974, respectively. This calanoid had a prodigious abundance and very high production in Lake Nakuru when compared with other calanoids in large, freshwater Lake Tana (Wondie and Mengistou 2006). *Thermodiaptomus galebi*, the dominant calanoid in Lake Tana, had a mean daily production of only 1.04 mg m^{-3} day^{-1} DM.

The mean biomass of *P. africanus* was about 1.81 g m^{-3} DM (Vareschi and Jacobs 1985); this high value apparently reflects the lack of competition by other zooplankton and surplus food sources in soda lakes, which result in enormous numbers of the calanoids, even in the presence of fish predators such as *Alcolapia grahami*.

Daily biomass turnover rates (P/B ratio) of the calanoids in Lakes Nakuru and Tana were similar at about 0.05 day^{-1}, or 5 % of the biomass turnover every day. This indicates that although the biomass and production of calanoids can be extremely high in soda lakes, the productivity or daily biomass turnover rate is not correspondingly high. This could be because of few predators or higher consumers to remove the high biomass in soda lakes or because the excess food does not contribute to biomass production beyond threshold levels in soda lakes. These are interesting research questions to follow up.

What does the calanoid *Paradiaptomus africanus* feed on? Vareschi and Jacobs (1985) tackled this question by conducting feeding (clearance rate) experiments on live *Arthrospira* in laboratory cultures and noting the algal mortality with time. They found that consumption rates were highest for copepodites, followed by adults and nauplii, and that this calanoid consumed only about 15–25 % of the net primary production, the rest being consumed by the Lesser Flamingo and fish. This food source is probably insufficient to support such high calanoid production, and the copepods apparently supplement their additional energy needs with live Bacteria and detritus. Literature data on calanoid secondary production from different types of aquatic ecosystems were compiled (Table 8.6), with an effort to show the

Table 8.6 Biomass (*B*), daily production (*P*) and daily *P*/*B* ratio of selected calanoids from different tropical aquatic ecosystems (sources included)

Lake/country	Calanoid species	*B* (mg m^{-3})	*P* (mg DM m^{-3} day^{-1})	*P*/*B* (day^{-1})	Reference
Nakuru/Kenya	*Paradiaptomus africanus*	1165	67.20	0.05	Vareshi and Jacobs (1984, 1985)
Tana/Ethiopia	*Thermodiaptomus galebi*	21	1.04	0.05	Wondie and Mengistou (2006)
Brazil Reservoir	*Notodiaptomus iheringi*		8.08 mean 13.67 highest value		Santos-Wisniewski and Rocha (2007)

performance of soda lakes versus other systems. It can be concluded that calanoid daily production is highest in soda lakes but the *P*/*B* ratio is not. Introducing consumers such as fish could increase the productivity of the system, but apparently very few fish are adapted to survive in the harsh soda lake environment. This is one of the dilemmas of soda lakes!

8.5.1.2 Rotifera

The dominant rotifer species in the East African soda lakes are invariably *Brachionus dimidiatus*, *B. calyciflorus*, *B. angularis*, *B. urceolaris*, *Keratella tropica*, *Hexarthra jenkinae* and *Filinia longiseta* (Appendix). Recent studies on Rotifera from East Africa have focused on their feeding behaviour and their role in the food webs using stable isotope analyses (Burian et al. 2013, 2014).

More intensive studies on secondary production estimates were done earlier for two very abundant rotifer species in Lake Nakuru by Vareschi and Jacobs (1984, 1985). The growth increment method (Winberg et al. 1971) was used to estimate production of rotifer eggs and juveniles separately. Egg production was determined according to the equation $P = DM\text{e} \times N\text{e} \times D\text{e}^{-1}$ (mg DW m^{-3} day^{-1}), where *DM*e is the dry mass of eggs in mg, *N*e is the number of eggs per m^3 and *D*e is the duration of egg development in days. The authors determined De in laboratory experiments and obtained Ne from field data. Production of juvenile rotifers was calculated from $P\text{j} = DM\text{j} \times N\text{f} \times D\text{f}^{-1}$ (mg m^{-3} day^{-1} DM), where *DM*j is the dry mass of juveniles, *N*f is the number of females per m^3 and *D*f is an estimated life span. Rotifer life span was computed as the half-life of the mortality (d) of rotifers ($= Ln2/d$) between two successive time intervals, $t1$ and $t2$, which was obtained from the difference between the birth rate (b) and rate of population change (r). b was calculated as $b = \ln(1 + N\text{e} \times D\text{e}^{-1} \times N\text{f}^{-1})$ and r as $(\ln N_2 - \ln N_1)/t2\text{–}t1$. It is unclear whether the growth increment method over- or underestimated secondary production, but it has recently been shown that the recruitment method of estimating secondary production is more appropriate for small species with small difference in biomass between eggs and adults, such as rotifers (Rodriguez and Tundisi 2002; Wondie and Mengistou 2014).

Results for daily production rates of *B. dimidiatus* and *B. plicatilis* were highly variable between the five years of investigation of Vareschi and Jacobs (1985; Table 8.7), indicating the dynamic nature of rotifer secondary production, which fluctuates erratically depending on temporal and spatial variations of food, temperature and biotic conditions. Overall, the larger species, *B. plicatilis*, was 3× more productive during the five study years. In recent studies using isotopic labelling, Burian et al. (2014) showed that *B. plicatilis* obtained almost half (48 %) of its diet from fragments of *A. fusiformis*, whereas *B. dimidiatus* mainly ingested particles < 2 μm. In other tropical freshwater lakes, we observed that rotifer production often peaks after some time lag of decomposition of cyanoprokaryote blooms, and we attributed this to their grazing on detrital particles and Bacteria (Assefa and Mengistou 2011; Wondie and Mengistou 2014). The poor quality of this detrital food was suggested as a possible factor for the low secondary production of rotifers in these freshwater lakes.

When compared with freshwater lakes, rotifer secondary production is clearly higher in soda lakes, even comparable to, and at times exceeding, production by calanoids and other grazers in the system. Vareschi and Jacobs (1985) argued that the main reasons for the high rotifer production are the large egg sizes and the short development times of eggs and juveniles. The latter are features common to many tropical rotifers, and perhaps a more plausible explanation for the high secondary production of large rotifers in soda lakes is the conducive high temperature and excess cyanoprokaryote food supply.

In general, secondary production by rotifers in soda lakes is higher by two orders of magnitude when compared with values in freshwater lakes, even taking computational differences into consideration (see Table 8.7). For example, comparing the secondary production of the smaller *B. dimidiatus* in Lake Nakuru with that of other brachionids in Lake Tana and Lake Kuriftu (both

Table 8.7 Daily production and mean biomass of Rotifera in Lake Nakuru during 1972 and 1976 and some other tropical African lakes (sources included)

Species/year/lake	Mean biomass (*B*) (mg DW m^{-3})	Daily *P* (mg DW m^{-3} day^{-1})	*P*/*B* (day^{-1})	Reference
B. dimidiatus				
1972	65	34	0.53	
1973	230	90	0.40	
1974	232	76	0.44	
1975	346	133	0.42	
1976	585	210	0.48	Vareschi and Jacobs (1985)
B. plicatilis				
1973	58	45	0.70	
1974	1 592	674	0.49	
1975	1 010	316	0.43	
1976	425	118	0.65	Vareschi and Jacobs (1985)
Brachionus spp.				
Lake Tana/Eth 2005	1.09	0.34	0.03	Wondie and Mengistou (2014)
B. calyciflorus				
Lake Kuriftu/Eth 2009	0.63	0.18	0.29	Assefa and Mengistou (2011)
Filinia pejleri				
Brazilian reservoir 2002	0.11	0.04	0.42	Rodriguez and Tundisi (2002)
Keratella americana				
Brazilian reservoir 2002	0.27	0.08	0.30	Rodriguez and Tundisi (2002)

Ethiopia) indicates that daily production in the freshwater lakes is < 1.00 mg, whereas an average of 100 mg m^{-3} day^{-1} DM was documented for the former in Lake Nakuru over a period of five years. Some of the reasons for the low rotifer production in the Ethiopian lakes were the low primary production in Lakes Tana and Kuriftu, and the low quality of the detrital food available for rotifers during the productive post-rainy months in these lakes (Assefa and Mengistou 2011; Wondie and Mengistou 2014). Rodriguez and Tundisi (2002) did not discuss the reasons for the extremely low rotifer production they calculated in a Brazilian reservoir.

Perhaps the daily biomass turnover rate (*P*/*B* ratio) is more insightful to explain the high daily production of rotifers in soda lakes. Close to 50 % of the rotifer biomass was replaced every day according to the 5-year study done by Vareschi and Jacobs (1985). This implies that half of the biomass is replaced daily due to the synergistic effects of food and temperature and lack of important rotifer predators. This is incredibly high when compared to a turnover rate of just 3 % in Lake Tana, which was attributed to factors mentioned above, such as poor food quality and low water temperature. A higher daily turnover rate of 30 % was documented in the small shallow Lake Kuriftu in Ethiopia (Assefa and Mengistou 2011). This reflected high primary production and water temperature, even though the food quality was still poor. In a tropical Brazilian reservoir, Rodriguez and Tundisi (2002) calculated quite high daily biomass turnover rates, closer to the values obtained in soda lakes (40 % per day) and higher than the values recorded for the Ethiopian shallow lakes. In general, the factors governing rates of secondary production and productivity (*P*/*B*) of rotifers in soda lakes need to be investigated in greater detail in the future.

8.5.2 Secondary Production of Macroinvertebrates in Soda Lakes

In view of the low species diversity of macroinvertebrates in soda lakes, less attention was paid to secondary production in this group. Nevertheless, the high seasonal biomass of some benthic macroinvertebrates during emergence has been noted by ecologists and others for centuries, most notably because of the spectacular impressions formed when millions or billions of insects emerge from lakes and literally "conquer" the surrounding environment for a short period.

8.5.2.1 Hemiptera (Bugs)

The best example of an extensive study on secondary production of macroinvertebrates is that of Vareschi and Jacobs (1985). They considered two families and three species for their study on secondary production and consumption rates in Lake Nakuru (Kenya). The species studied belonged to the phylum Arthropoda, class Insecta, order Hemiptera (bugs), family Corixidae (water boatmen) and family Notonectidae (backswimmers). Two corixid species were considered—*Micronecta scutellaris* and *Sigara hieroglyphica kilimanjaronis*—along with *Anisops varia* of the Notonectidae. Biomass and daily production were estimated for each species based on culturing animals in aquaria and noting weight increment with age (Mavuti 1975). Egg production was estimated from the egg ratio and sex ratio (1:1 assumed). The results indicated that the three macroinvertebrates had a very low daily secondary production of < 1.00 mg m^{-3} day^{-1} DM (Table 8.8) and made up no more than 1 % of the total consumer production in the lake. The daily biomass turnover rates of all three species were very low—less than 4 % of the biomass was replaced every day, reflecting very slow growth rates for all macroinvertebrates. This is in contrast to some chironomids, which can replace 15 % of their biomass per day and achieve annual biomass turnover rates of over 50 times, whereas the heteropterans could achieve a maximum annual P/B ratio of only 15 times (Benke 1998).

The low production and biomass turnover rate of these macroinvertebrates probably reflect the seasonally limited food supply. The notonectid *Anisops* is predatory and feeds on calanoids and even fish, and the corixids feed on *Spirulina*, other zooplankton and algae, which are highly seasonal, as well as on detritus in the lake.

8.5.2.2 Chironomidae (Non-biting Midges)

The most common observation in soda lakes is the phenomenal emergence of millions of flies from the lake at certain times of the year. They are feast for birds and other predators and fortunately do not transmit disease or act as vectors themselves. Several studies on the secondary production of chironomids have treated

Table 8.8 Biomass, daily production and *P*/*B* ratio of macroinvertebrates in Lake Nakuru during 1972 and 1973 (after Vareschi and Jacobs 1985)

Family/species/year	Biomass (mg DM m^{-3})	Daily production (mg DM m^{-3} day^{-1})	*P*/*B* ratio (day^{-1})
Notonectidae, *Anisops*			
1972	24.9	0.29	0.012
1973	13.8	0.07	0.005
Corixidae, *Micronecta*			
1972	7.9	0.30	0.038
1973	6.3	0.14	0.022
Corixidae, *Sigara*			
1972	0.22	0.01	0.014
1973	1.05	0.02	0.019

non-soda lakes (e.g. Benke 1998) because of the ubiquitous distribution of chironomids in lakes of different water chemistry and trophic status.

The highest secondary production of chironomids, and indeed of any inland benthic community, was reported from the saline Australian Lake Werowrap by Paterson and Walker (1974): 182 mg m^{-2} day^{-1} DM. The chironomid biomass and production in soda lakes are lower, with a maximum value of 120 mg m^{-2} day^{-1} DM and a minimum value of 1 mg m^{-2} day^{-1} DM for the dominant chironomid *Microchironomus deribae* in Lake Nakuru (Vareschi and Jacobs 1985). The authors cultured the chironomid in the laboratory and estimated its production based on growth increments of stages and size-frequency field data. They reported that, in general, chironomid production in the soda Lake Nakuru was high compared with temperate lakes but still lower than the peak values reported in the saline Australian lake. In very saline but less alkaline lakes, brine flies are quite common and can reach incredible numbers seasonally. In the soda lakes, chironomids did not reach such numbers, even though the detrital organic food in the lake sediment was by no means limiting. Benke (1998) reported that chironomids can reach extremely high biomass turnover rates in snag habitats of rivers, even as high as 15 % daily. Vareschi and Jacobs (1985) recorded a mean of 8.4 % daily P/B ratio for the chironomid in Lake Nakuru. In general, high secondary production and biomass turnover rates of chironomids have been documented from saline and soda lakes. It is thus interesting to investigate what factor(s) cause such differences. Could the salt difference contribute to this because food levels are apparently high in both cases?

8.6 Conclusions

- Soda lakes are populated by a few, yet highly specialized group of invertebrates which can assume high seasonal biomass. The species diversity of the invertebrate fauna is generally poor.
- The zooplankton is dominated by Rotifera. Especially the species *Brachionus dimidiatus* can attain incredibly high biomass (800 million m^{-3}) at favourable times.
- The macroinvertebrate community is dominated by corixids (genera *Micronecta* and *Sigara*) and notonectids (genus *Anisops*). The chironomid *Microchironomus deribae* is very abundant in many soda lakes.
- Vertebrates such as birds either feed directly on the benthic macroinvertebrates (Greater Flamingo) or filter the *Arthrospira* biomass in soda lakes. The ecotourism potential of soda lakes is extremely high because of the spectacular numbers of birds at the lakes at any one time.
- The secondary production of chironomids in alkaline soda lakes is much lower than that of saline Australian lakes, indicating some limitation for invertebrate production in the former.
- Soda lakes have simple food chains and are ideal as natural experimental models to study food web dynamics and energy flow using stable isotopes.
- The inclination to extract biological and chemical resources from soda lakes should be discouraged at best or should be exercised with extreme caution at worst.

References

Assefa E, Mengistou S (2011) Seasonal variation of biomass and secondary production of *Thermocyclops* (Cyclopoida) and *Brachionus* (Rotifera) spp. in a shallow tropical Lake Kuriftu, Ethiopia. SINET Ethiop J Sci 34(2):73–88

Ayenew T (2002) Recent changes in the level of Lake Abijata, central main Ethiopian Rift. Hydrol Sci J 47:493–503

Beadle LC (1932) Scientific results of the Cambridge expedition to the East African lakes. 1930–31. 4. The waters of some East African lakes in relation to their fauna and flora. J Linn Soc Zool 38:157–211

Benke W (1998) Production dynamics of riverine chironomids: extremely high biomass turnover rates of primary consumers. Ecology 79:899–910

Burian A, Schagerl M, Yasindi A (2013) Microzooplankton feeding behavior: grazing on the microbial

and the classical food web of African soda lakes. Hydrobiologia 710:61–72
Burian A, Kainz MJ, Schagerl M, Yasindi A (2014) The role of rotifers in the food web of the saline-alkaline, hypereutrophic Kenyan Rift Valley Lake Nakuru: a snapshot-analysis of micro- and mesoplankton communities. Freshw Biol 59:1257–1265
Chemoiwa EJ, Oyoo-Okoth E, Mugo-Bundi J, Njerga EW, Matary EC, Korir RT, Njugi CC (2014) Elemental ratio (C:N) and stable isotope composition of dominant rotifer species in a tropical eutrophic alkaline-saline Lake Nakuru (Kenya). Hydrobiologia. doi:10.1007/s10750-014-2123-y
Clark F, Beeby A, Kirry P (1989) A study of macro-invertebrates of lakes Naivasha, Oloidien and Sonachi, Kenya. Rev Hydriobiol Trop 22(1):21–33
De Beauchamp P (1932) XIX. Reports on the Percy Sladen expedition to some Rift Valley lakes in Kenya in 1929. III. Rotifieres des lacs de la valee du Rift. Annu Nat Hist Ser 10 9(50):158–165
Eyualem A (2002) Free-living aquatic nematodes of the Ethiopian Rift Valley. In: Tudorancea C, Taylor WD (eds) Ethiopian Rift valley lakes. Backhuys Publishers, Leiden, pp 143–156
Grant WD (2006) Alkaline environments and biodiversity in extremophiles. UNESCO/Ecles Publishers, Oxford
Grant WD, Mwatha WE, Jones BE (1990) Alkaliphiles: ecology, diversity and applications. FEMS Microbiol Rev 75:255–270
Hammer TU (1986) Saline Lake ecosystems of the world. Dr. W. Junk, Dordrecht
Harper DM, Brooks Childress R, Harper MM, Boar RR, Hickley P, Mills SC, Otieno N, Drane T, Vareschi E, Nasirwa O, Mwatha WE, Darlington JPEC, Gasulla X (2003) Aquatic biodiversity and saline lakes: Lake Bogoria National Reserve, Kenya. Hydrobiologia 500:259–276
Harrison AD (2002) A general view on the communities of the Chironomidae adults in the Ethiopian Rift Valley. In: Tudorancea C, Taylor WD (eds) Ethiopian Rift valley lakes. Backhuys Publishers, Leiden, pp 157–162
Hecky RE, Kilham P (1973) Diatoms in alkaline, saline lakes: ecology and geochemical implications. Limnol Oceanogr 18:53–71
Hughes RH, Hughes JS (1992) A directory of African wetlands. IUCN, Gland
Jirsa F, Gruber M, Stojanovic A, Odour SO, Mader D, Körner W, Schagerl M (2013) Major and trace element geochemistry of Lake Bogoria and Lake Nakuru, Kenya, during extreme drought. Chem Erde-Geochem 73:275–282
LaBarbera MC, Kilham P (1974) The chemical ecology of copepod distribution in the lakes of East and Central Africa. Limnol Oceanogr 19:459–465
Martens K (2002) Ostracoda in the Ziway-Shala-Awasa basin. In: Tudorancea C, Taylor WD (eds) Ethiopian Rift valley lakes. Backhuys Publishers, Leiden, pp 163–166
Matagi SV (2004) A biodiversity assessment of the flamingo lakes of eastern Africa. Biodiversity 5(1):13–26
Mavuti K (1975) Some aspects of the biology of the genera *Sigara* and *Micronectes* from Lake Nakuru. M.Sc. Thesis, University of Nairobi
McClanahan TR, Young TP, McClanahan T (1996) East African ecosystems and their conservation. Oxford University Press, Oxford
Melack JM (1976) Saline and freshwater lakes of the Kenyan Rift Valley. In: McClanahan TR, Young TP (eds) East African ecosystems and their conservation. Oxford University Press, Oxford, pp 171–190
Melack JM, Kilham P (1974) Photosynthetic rates of phytoplankton in East African Alkaline, saline lakes. Limnol Oceanogr 19:743–755
Mutanga JG, Mwatha W, Nasirwa O, Gichuru N (2000) Status and trends in the biodiversity of Eastern Rift Valley lakes in Kenya. In: Bennun LA, Ndede H, Gichuki NN (eds) Conservation and sustainable use of biodiversity in Eastern Rift Valley lakes, Kenya, GEF/UNDP Consultancy Report. National Museums of Kenya, Nairobi, pp 6–34
Mwatha WE (1991) Microbial ecology of Kenyan Soda Lakes. Dissertation, University of Leicester, UK
Oduor SO, Schagerl M (2007) Phytoplankton photosynthetic characteristics in three Kenyan Rift Valley saline-alkaline lakes. J Plankton Res 29:1041–1050
Ong'Ondo GO, Yasindi AW, Oduor SO, Jost S, Schagerl M, Sonntag B, Boenig J (2013) Ecology and community structure of ciliated protists in two alkaline, saline rift valley lakes in Kenya, with emphasis on Frontonia. J Plankton Res 35:759–771
Oyoo-Okoth EM, Muchiri M, Ngugi CC, Njenga EW, Ngure V, Orina PS, Chemoiiwa EC, Wanjohi BK (2011) Zooplankton partitioning in a tropical alkaline-saline endorheic Lake Nakuru, Kenya. Spatial and temporal trends in relation to the environment. Lake Reserv Res Manage 16:35–47
Paterson CG, Walker KF (1974) Seasonal dynamics and productivity of *Tanytarsus barbitarsis* Freeman (Diptera: Chironomidae) in the benthos of a shallow, saline lake. Aust J Mar Freshw Res 25:151–165
Rodriguez MA, Tundisi T (2002) Rotifer production in a shallow artificial lake (Lobo-Broa reservoir, Brazil). Braz J Biol 62:509–516
Santos-Wisniewski MJ, Rocha O (2007) Spatial distribution and secondary production of Copepoda in a tropical reservoir: Barra Bonita, SP, Brazil Distribuição espacial e produção secundária de Copepoda em um reservatório tropical em Barra Bonita, SP, Brasil. Braz J Biol 67:223–233
Sarunday WN (1999) Conservation and sustainable use of biodiversity in Eastern Rift Valley lakes in Tanzania. National Environment Management Council, Dar es Salaam, Tanzania

Talling JF (1992) Environmental regulation in African shallow lakes and wetlands. Rev Hydrobiol Trop 25:87–144

Talling JF, Wood RB, Prosser MV, Baxter RM (1973) The upper limit of primary productivity by phytoplankton: evidence from Ethiopian soda lakes. Freshw Biol 3:53–76

Tudorancea C, Taylor WD (2002) Ethiopian Rift Valley Lakes. Backhuys Publishers, Leiden

Uku JN, Mavuti KM (1994) Comparative limnology, species diversity and biomass relationship of zooplankton and phytoplankton in five freshwater lakes in Kenya. Hydrobiologia 272:251–258

Vareschi E, Jacobs J (1984) The ecology of lake Nakuru (Kenya) V. Production and consumption of consumer organisms. Oecologia 61:83–98

Vareschi E, Jacobs J (1985) The ecology of Lake Nakuru (Kenya) VI. Synopsis of production and energy flow. Oecologia 65:412–424

Vareschi E, Vareschi A (1984) The ecology of Lake Nakuru (Kenya) IV. Biomass and distribution of consumer organisms. Oecologia 61:70–82

Verschuren D, Cocquyt C, Tibby J, Roberts CN, Leavitt PR (1999) Long-term dynamics of algal and invertebrate communities in a small, fluctuating, tropical soda lake. Limnol Oceanogr 44:1216–1231

Winberg GG, Patalas K, Wright JC, Hillbricht-Ilkowska-A, Cooper WE, Mann KH (1971) Methods for calculating productivity. In: Edmondson WT, Winberg GG (eds) A manual on methods for the assessment of secondary productivity in fresh waters, IBP handbook no. 17. Blackwell Scientific Publications, Edinburgh, pp 296–317

Wondie A, Mengistou S (2006) Duration of development, biomass and rate of production of the dominant copepods (calanoida and cyclopoida) in Lake Tana, Ethiopia. SINET Ethiop J Sci 29(2):107–122

Wondie A, Mengistou S (2014) Seasonal variability of secondary production of Cladocerans and Rotifers and their trophic role in a large, turbid, tropical highland lake (Lake Tana, Ethiopia). Afr J Aquat Sci 39 (4):403–416

Wood RB, Talling JF (1988) Chemical and algal relationships in a salinity series of Ethiopian inland waters. Hydrobiologia 158:29–67

Yasindi AW, Taylor WD (2006) The trophic position of planktonic ciliate populations in the food web of some East African lakes. Afr J Aquat Sci 3(1):53–62