Review Article

Biogeochemistry and biodiversity in a network of saline–alkaline lakes: Implications of ecohydrological connectivity in the Kenyan Rift Valley

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A B S T R A C T

The volcanic and tectonic lakes of the eastern branch of the African Great Rift Valley are exposed to multiple stressors and characterised by different levels of hydrological connectivity. Past volcanic activity generated endorheic basins, in which the nature of the bedrock, its connection with groundwater, and local climatic conditions, favoured the formation of highly alkaline soda waters. While little is known about their nutrient dynamics, most lakes in this area experience considerable microbial blooms and harbour diverse and specifically adapted microbial populations, some of which could embody novel biotechnological potential.

Here we review the geochemical and (micro)biological features of a cluster of lakes distributed within the East African Rift, ranging from fresh to hypersaline, under different levels of hydrological connectivity. Possibly no other location on Earth has a comparable range of lake types in close proximity to each other and representing such a remarkable microbial biodiversity. Environmental heterogeneity and habitat connectivity among adjacent aquatic ecosystems may have positive implications in terms of regional environmental stability by enhancing the overall carrying capacity, i.e. the resilience to various forms of impact, contributing to biodiversity protection.

Within these ecosystems, microbial processes encompass the entire basis of their primary production, in particular those driven by cyanobacteria. Combining a multi-disciplinary ecohydrological approach with a biogeochemical investigation of the principles underlying their functioning, our study can contribute to the development of appropriate environmental protection measures to effectively maintain their natural capital.

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1. Introduction

The interaction among bedrock, surface and ground waters, in aquifers and within deep lake sediments, is a major driver of ecosystem dynamics in lakes worldwide, and particularly in lakes affected by geogenic water inputs with high mineral content (Borch et al., 2009; Christenson et al., 2015). Water–bedrock interactions are further intensified in tropical areas, owing to high average annual temperatures, intense weathering, and frequent hydrological extremes (floods and droughts), which fundamentally contribute to environmental variability. In semi-arid and sub-humid tropical regions, aquatic ecosystems are threatened by intense anthropogenic impact because of urban waste disposal, discharge of industrial effluents, intensive agricultural practices employing fertilizers and pesticides, water abstraction for irrigation and human uses, and hydroelectric energy production. The combined and interacting influence of geogenic and anthropogenic drivers results in biodiversity decline and habitat reduction (Dudgeon et al., 2006); this situation has been recently exacerbated by climate change and demographic growth.

Understanding lake biogeochemical dynamics is essential for interpreting the specificity of human impact and for identifying adequate conservation measures (Vitousek et al., 1997); this is of great relevance for alkaline lakes where biogeochemical conditions represent a strong environmental filter in the selection of resident lake communities of micro-organisms (prokaryotes as well as algae and micro-crustaceans, Schagerl, 2016). Variable degrees of connectivity (defined as “the strength of interactions across ecotones”, Ward et al., 1999) between separate wetlands bear a significant influence on the composition of fish communities (Bouvier et al., 2009) as well as on aquatic bacteria (Peter and Sommaruga, 2016), thus impacting onto regional biodiversity. We propose that connectivity among adjacent environmentally heterogeneous aquatic ecosystems may have positive implications in terms of contributing to biodiversity protection and to resilience towards various forms of impact, thus enhancing regional environmental stability and overall carrying capacity. This reflects the urgency of collecting scientific data from water bodies at different levels of ecohydrological connectivity. It will support the understanding of ecosystem features and the design of adequate lake management tools for restoring biodiversity, improving water quality and enhancing ecosystem services for the benefit of lake-dependent communities.

Following the concept of ecohydrology, defined on the basis of the mutual interaction between hydrological drivers and biotic processes (sensu Zalewski, 2000), this paper reviews existing links between ecohydrological features, hydrological connectivity, and carrying capacity within a lake network. Overall, this review illustrates how environmental variability among lakes can support system stability and biodiversity dynamics at regional scale.

We focused on a cluster of lakes aligned from North to South within the Kenyan portion of the East African Rift; they are subject to different levels of hydrological connectivity and represent a discontinuous gradient of water bodies, stretching from freshwater to hypersaline conditions (Schagerl, 2016). Knowledge of these lakes is limited to few accessible ones and research activities that were carried out typically achieved a lifespan no longer than a PhD thesis. Limited long-term studies exist except those few based on satellite image analysis (lake levels and chlorophyll concentrations; Tebbs et al., 2011, 2013) and those on cyanobacteria mass development over a 12-year period (Krienitz et al., 2013a,b,c) and a 15-year period (Krienitz et al., 2016a). This despite the fact that some lakes are under protected area management and could be regularly monitored by conservation management agencies. The harsh biogeochemical setting created conditions for the development of highly selected and diversified microbial communities; very few fish species persist, in particular some cichlids remarkably adapted to alkaline conditions. The target lake network offers a series of stepping stones for migratory birds as well as habitats for sedentary endemic populations, thus retaining a relevant value in terms of regional avian biodiversity.

2. Lakes in the Kenyan portion of the East African Rift Valley

The major 30 volcanic and tectonic lakes of the eastern branch of the African Great Rift Valley are characterised by different ranges of hydrological connectivity and are exposed to multiple natural and anthropogenic stressors. Within the Rift, all catchments, except that of Ewaso Ng’iro North (receiving tributaries from the Nyandarua mountains and from Mt. Kenya) have developed endorheic basins lacking surface outflow. All the lakes are situated in sub-humid to semi-arid savannahs (300–600 mm year$^{-1}$) subject to high potential evaporation rates (1300–2000 mm year$^{-1}$) and are fed by drainage from mountain blocks on either side of the Rift Valley. Drastic hydrological changes are rather frequent in the Rift Valley, owing to capricious precipitation patterns originating in distant geographical regions, which are dependent on the variable position of the Inter Tropical Convergence Zone, on the strength of the monsoons and on the temperature of the Indian Ocean. Lake water levels depend upon the balance between water output (e.g. evaporation) and input, controlled by the rate of rainfall that occurs in forested upland portions of the lake catchments. Water levels may vary also under the influence of groundwater pressure, which is connected to tectonic movements below the earth crust and to pressure forces that arise within the mantle. Unusual changes in the water levels of wells are considered common signs of volcanic activity (Tilling, 1989). De Carolis and Patricelli (2003) report that water level in wells had risen in occasion of the Vesuvius volcanic eruption of December 1631; similarly, water levels rose in Taal crater lake in the Philippines just before an eruption (Smith, 2013). Ephemeral streams, from lower altitudes of the catchments and underground springs at the bases of the mountains, can constitute a small proportion of the inflows significantly contributing to the water chemistry. Since 2010, most East African lakes are at high water level despite lacking evidence of an increase in rainfall (Odongo et al., 2015). Upper catchment deforestation and land cover degradation could be an important contributing factor, but
there is no clear understanding of the complex hydrology of this Region, where hydrological records disagree with IPCC climate change predictions based upon popular global circulation models, according to which higher rainfall should be expected (Klein et al., 2016; Odongo et al., 2015).

A cluster of these lakes (Table 1 and Fig. 1) forms a discontinuous gradient of water bodies, from freshwater (Baringo and Naivasha) to hypersaline (Bogoria, Nakuru, Elementeita, Sonachi, Natron). The latter are evaporative systems (pH from 9.0 to 12.0) representing extreme conditions, characterised by high salinity, high alkalinity and high primary productivity under constant high temperatures. While Nakuru is protected as a National Park, Lake Bogoria is a National Reserve (managed by the County of Baringo), and Lake Elementeita, a Wildlife Sanctuary, is largely within Soysambu Conservancy, a private conservation charity.

Most lakes are primarily of tectonic origin, having developed along linear faults stretching across a geologically ancient volcanic landscape reshaped by recent volcanic activity. Others, such as Sonachi Crater Lake, are entirely within a volcanic caldera and Naivasha, itself a tectonic lake, includes a number of in-filled volcanic craters. Early hydrological studies using stable isotopes highlighted deep water connections below the Rift Valley floor able to transfer groundwater over great distances (Eugster, 1970). In this way, it could be ascertained that water from Lake Naivasha reaches as far as Suswa and up to Lake Magadi, over 100 km South. Recent monitoring of the vertical profile in Lake Sonachi showed a distinct increase in temperature and alkalinity with depth (Pacini, unpublished), indicating that lake level increase in late 2016 (during a dry season) was due to feeding by underground alkaline springs. In some lakes, such as Nasikie Engida and Lake Magadi in southern Kenya, hot spring provide most of the recharge; in other lake basins, thermal springs are minor but sometimes important contributors (Schagerl and Renault, 2016).

No two lakes have the same limnological characteristics due to their different histories and degrees of hydrological connection within their catchment, and no one lake is stable enough to maintain a consistently high primary production. The most studied lakes have been: Naivasha (limnology, ecology, management), Magadi (microbiology and geochemistry) and Nakuru (ecology and management), whereas Bogoria, Sonachi, Elementeita and Oloidien lakes have been poorly investigated (Table 2).

Kenya’s saline–alkaline lakes offer highly prized cultural ecosystem services. They are renowned spots for bird and wildlife tourism, offer magnificent landscape views and include important paleontological sites. Bogoria is visited as much for its hot springs, around the western shore of the lake, as for its flamingos; these springs are reputed to be the most visually impressive and extensive in Africa. Both Bogoria and Elementeita have a spectacular scenery of escarpments and extinct craters. Elementeita was formerly part of a much larger prehistoric lake basin whose level was well above the present one, connected to both present day Nakuru to the North and Naivasha to the South. The lake shoreline was situated at the altitude of the nationally most important stone tool site attributable to Homo erectus, dated about 0.75 Ma, Kariandusi. Lake Magadi, in the South of the country, is in private ownership and extensively exploited on an industrial scale for its deposits of soda ash (i.e., trona) left after evaporation.

3. Processes controlling the chemical composition of lake waters

Endorheic basins formed by tectonic processes generate aquatic ecosystems affected by strong evaporation under the prevailing semi-arid climate and the intense equatorial radiation. The dominant lithology, consisting of recent volcanic rocks and volcanoclastic sediments (e.g., MacDon- nald, 2003; Dawson, 2008; Abbate et al., 2015) is rapidly weathered to produce highly soluble secondary minerals (e.g., nahcolite, trona, and thermonatrite). Soda lakes chemistry is associated with modern or past volcanic activity (Pecoraino et al., 2015). High pH and Na-HCO₃ dominance originate from the hydrolysis of the abundant silicate minerals, such as sodium-rich plagioclase feldspar, whose weathering is very effective under the prevailing high temperatures. This process consumes hydrogen ions from solution and release alkali cations, resulting in high pH and increase in dissolved Na⁺ concentrations. Once released, dissolved silicate is transported to lakes. A strong reduction in dissolved reactive silicate has been noticed in the last decades in freshwater lakes Victoria (Verschuren et al., 1998) and Naivasha (Pacini, unpublished data), a likely consequence of eutrophication and development of dense communities of colonial diatoms.

In alkaline lakes, high evaporation may lead to the precipitation of alkaline earth carbonates (e.g. calcite, Mg-calcite, smectite), which produces a decrease of Ca²⁺ and secondarily, Mg²⁺ in solution, as shown in South American evaporitic alkaline lakes (Furquim et al., 2008; Barbiero et al., 2017). Mg precipitation in alkaline lakes is frequently mediated by cyanobacteria (Shirokova et al., 2013). The occurrence of alkaline springs (e.g. Cioni et al., 1992) also significantly contributes to the formation of sodic lakes. Their peculiar geochemical features are reflected in the ratio between total dissolved inorganic carbon (TDIC) and Earth–alkaline elements reaching values much higher than 1.

The caustic nature of carbonatic brines further enhances bedrock dissolution causing a release of nutrients limiting primary production. Phosphate concentrations that are naturally extremely low in tropical freshwaters due to sustained primary production, are commonly found in alkaline lakes surrounded by rocks of volcanic origin, such as basalt, trachyte, phonolite, in which phosphorus tends to be moderately abundant. A further crucial limiting element is nitrogen; being primarily the product of bacterial fixation within surrounding soils and wetlands, its presence is biologically regulated and excess nitrate tends to inhibit the nitrogenase, i.e. the enzyme responsible for nitrogen fixation. Denitrification tends to reduce dissolved nitrogen in tropical wetlands at alkaline lake shores.

Detailed descriptions and interpretations of the biogeochemical properties of Kenyan soda lakes are poorly developed. The closest to this topic is the research published in 2008.
<table>
<thead>
<tr>
<th>Lake</th>
<th>Latitude</th>
<th>Altitude</th>
<th>Tributaries</th>
<th>Outflow</th>
<th>Surface (km²)</th>
<th>Max Depth (m)</th>
<th>Alkalinity</th>
<th>Salinity</th>
<th>pH</th>
<th>Dominant salt</th>
<th>Hot springs</th>
<th>Fish</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lake Natron</td>
<td>2° 25’ S</td>
<td>675</td>
<td>Southern Ewaso Ng’iro</td>
<td>None</td>
<td>930</td>
<td>9</td>
<td>–</td>
<td>ca. 35%</td>
<td>11–12</td>
<td>Na carbonate</td>
<td>Yes</td>
<td>Alcolapia latilabris (end.), A. dalalani (end.), A. alcalica (introd.)</td>
</tr>
<tr>
<td>Lake Magadi</td>
<td>1° 52’ S</td>
<td>580</td>
<td>None</td>
<td>None</td>
<td>108</td>
<td>5</td>
<td>380 meq L⁻¹</td>
<td>ca. 35%</td>
<td>10.5</td>
<td>Na carbonate</td>
<td>Yes</td>
<td>Alcolapia grahami (end.)</td>
</tr>
<tr>
<td>Lake Nasikie Engida</td>
<td>1° 42’ S</td>
<td>613</td>
<td>None</td>
<td>None</td>
<td>35</td>
<td>1.5</td>
<td>–</td>
<td>ca. 30%</td>
<td>10.5</td>
<td>Na carbonate</td>
<td>Yes</td>
<td>Alcolapia grahami (end.)</td>
</tr>
<tr>
<td>Lake Oloidien</td>
<td>0° 48’ S</td>
<td>1890</td>
<td>None (fed by Lake Naivasha)</td>
<td>None</td>
<td>4.5</td>
<td>6</td>
<td>200 mg as CaCO₃ L⁻¹</td>
<td>Low</td>
<td>10</td>
<td>Na carbonate</td>
<td>No</td>
<td>Tilapia</td>
</tr>
<tr>
<td>Lake Naivasha</td>
<td>0° 48’ S</td>
<td>1888</td>
<td>Gilgil, Malewa</td>
<td>Underground</td>
<td>150</td>
<td>17</td>
<td>190 mg as CaCO₃ L⁻¹</td>
<td>&lt;1%</td>
<td>8–8.5</td>
<td>Na carbonate</td>
<td>No</td>
<td>Tilapia, carp, blackbass, catfish, barb</td>
</tr>
<tr>
<td>Lake Sonachi (Crater Lake)</td>
<td>0° 47’ S</td>
<td>1870</td>
<td>None</td>
<td>None</td>
<td>0.8</td>
<td>7</td>
<td>–</td>
<td>ca. 5%</td>
<td>10.5</td>
<td>Na carbonate</td>
<td>Underground</td>
<td>No</td>
</tr>
<tr>
<td>Lake Elementeita</td>
<td>0° 27’ S</td>
<td>1670</td>
<td>Mereroni Kariandusi, Mbaruk</td>
<td>None</td>
<td>18</td>
<td>2</td>
<td>130 meq L⁻¹</td>
<td>ca. 5%</td>
<td>10.5</td>
<td>Na carbonate</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>Lake Nakuru</td>
<td>0° 22’ S</td>
<td>1754</td>
<td>Njoro, Makalia, Nderit, Baharini Springs Waiseges, Emsos, Fig Tree</td>
<td>None</td>
<td>50</td>
<td>2</td>
<td>110 meq L⁻¹</td>
<td>ca. 5%</td>
<td>11</td>
<td>Na carbonate</td>
<td>Yes</td>
<td>Alcolapia grahami (introd.)</td>
</tr>
<tr>
<td>Lake Bogoria</td>
<td>0° 15’ N</td>
<td>1000</td>
<td>None</td>
<td>None</td>
<td>100</td>
<td>10</td>
<td>25 g as CaCO₃ L⁻¹</td>
<td>&gt;30%</td>
<td>10–11</td>
<td>Na carbonate</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>Lake Baringo</td>
<td>0° 45’ N</td>
<td>975</td>
<td>Perkerra, Molo Omo, Kerio, Turkwell</td>
<td>None</td>
<td>160</td>
<td>9</td>
<td>0.2–1 meq L⁻¹</td>
<td>ca. 2.4%</td>
<td>9.15</td>
<td>Na carbonate</td>
<td>Yes</td>
<td>&gt;50 spp. (at least 11 end.)</td>
</tr>
<tr>
<td>Lake Turkana</td>
<td>3° 35’ N</td>
<td>360</td>
<td>None</td>
<td>None</td>
<td>6405</td>
<td>106</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>
conducted by MacIntyre and Melack (1982) (Table 1). Attention has been mainly given to inorganic carbon, although dissolved organic matter (DOM) often represents the main carbon and energy source for aquatic heterotrophic communities as well as an important alternative source of nitrogen and phosphorus. The quantitative and qualitative characterisation of DOM including composition, structure, molecular weight and bioavailability, remains an important missing gap in the understanding of carbon cycling within the lakes of the Kenyan Rift.

4. Aquatic biodiversity, including microbiology

The East African Rift Valley is a cradle of mammalian and avian biodiversity. Over millennia, its high mountains served as freshwater refuges at times of drought, while the floor of the Rift Valley constituted a preferential corridor for latitudinal migration, as an adaptation to extreme conditions dictated by periodical climate changes. Still today, the Rift Valley shelters a high density of threatened fauna (i.e., ungulates, primates, rodents and birds). Alkaline lakes are part of a mosaic of diverse biotopes that contribute to landscape diversity as well as to local biodiversity. The aquatic organisms, which survive within the lakes themselves, are restricted to few species of tilapia (Alcolapia grahami, A. alcalica, A. latilabris), and to a small number of invertebrates (in alkaline lakes often a single species tends to dominate) belonging to Cladocera and Copepoda.

The water column of most soda lakes tends to be dominated by the planktonic Arthrospira fusiformis, commonly known as “Spirulina”, a colony forming rod-shaped bluegreen bacteria (cyanobacteria) that develops into macroscopic spirals of about 0.2–0.3 mm in length, visible as tiny flakes by the naked eye. Over the years, due to its highly nutritious properties coupled to its high productivity, commercial cultures of A. fusiformis developed in tropical regions of the world. Early assessments from Lake Sonachi indicated that A. fusiformis can achieve rates of primary productivity that place it among the fastest growing planktonic organisms in the world (Melack, 1979a,b). Overall, saline–alkaline lakes dominated by A. fusiformis colonies are characterised by high pH and strong light inhibition through self-shading, but no lake remains consistently highly productive. The onset and the crash of cyanobacterial blooms seem to be disconnected from the availability of elements that commonly limit primary production. One cause may be changes in hydrology that affect lake alkalinity, causing a disruption of the monoculture of A. fusiformis in favour of more complex assemblages typically dominated by colonial diatoms (Aulacoseira, Achnanthes) and other cyanobacteria (e.g. Microcystis). Another may be the wax and wane of cyanophages, known to be abundant in these waters (Junaideen, 2010; Foster, 2013; Peduzzi et al., 2014) (Fig. 2).

Few organisms have developed adaptations to feed on A. fusiformis, the most renown being the Lesser Flamingo, (Phoeniconaias minor). These large birds are entirely dependent on their A. fusiformis diet and have to feed during most of their waking hours. The long-term survival of their population depends upon the preservation of the regional network of lakes, enabling them to move away from lakes whose food supply unexpectedly drops in search of an alkaline lake with adequate A. fusiformis blooms (Harper et al., 2016). Flamingo movements support lake connectivity along the Rift Valley and contribute to the dispersal of microorganisms and invertebrates that remain attached to their feathers (Fig. 3).

Details about factors controlling the main A. fusiformis–P. minor food chain have not improved significantly since early studies carried out in Nakuru during the 1970s (e.g. Vareschi, 1978). Studies on A. fusiformis are frequent, addressing either a wide context (phytoplankton community) or focussing on the physiology and ecomorphology of the species (e.g. Schagerl, 2016 and references therein). A. fusiformis can synthesise tryptophan, an amino acid with well-known fluorescent properties in water. However, the availability of DOM-associated tryptophane has been largely disregarded, as well as the potential impact of large-scale DOM-tryptophan leaching on the diversity and production of bacterial plankton. Monitoring the availability and the fate of DOM-tryptophan by detecting fluorescence could reveal microbial loop interactions among primary and secondary producers in soda lakes (Suksomjit et al., 2009).

Recent work has quantified the high dynamics of natural populations (Tebbs, 2014) and provided support for the hypothesis that infection by cyanophages could represent an important factor controlling their growth next to nutrient and/or light limitation. Marine research showed that Cyanobacterial viruses tend to be tightly linked to their hosts, to the extent that they are able to acquire from them a large number of genes (e.g., Clokie et al., 2006); these can be used to sustain host physiology during infection, in order to ensure that cells are ‘healthy’ and can maintain an energy source to produce more viruses. It is also known that the diversity of the cyanoviruses may drive bacterial diversity; this indicates that viruses are important for bacterial population

Fig. 1. Location of the selected lakes within the Kenyan Rift Valley – World Imagery.
Table 2

Relevant published studies on the ecology of the lakes within the Kenyan Rift Valley.

<table>
<thead>
<tr>
<th>Lakes</th>
<th>Bacteria isolates</th>
<th>Bacterial phylogeny genomics</th>
<th>Phytoplankton community physiology</th>
<th>Rotifers and ciliates</th>
<th>Vertebrates</th>
<th>Physico-chemical characteristics</th>
<th>Palaeoecology</th>
</tr>
</thead>
<tbody>
<tr>
<td>Natron</td>
<td>van Zyl et al., 2016; Zavarzina et al., 2013; Ghauri et al., 2006; Kevbrin et al., 1998; Grant and Jones, 2016</td>
<td>Kambura et al., 2016; Foti et al., 2006; Grant et al., 1999</td>
<td>Mikhodiu et al., 2008; Kotut and Krienitz, 2011; Krienitz et al., 2012; Krienitz and Schagerl, 2016</td>
<td>Zaccara et al., 2014; Kavembe et al., 2016b; Krienitz et al., 2016b</td>
<td>Seegers et al., 1999; Seegers and Tichy, 1999; Zaccara et al., 2014; Kavembe et al., 2016a,b; Krienitz et al., 2016b</td>
<td>Bettinetti et al., 2011</td>
<td>Jenks et al., 1977; Renaut, 2011; Deocampo and Renaut, 2016</td>
</tr>
<tr>
<td>Magadi</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nasikie Engida</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oloidien</td>
<td>Dadheech et al., 2009; Luo et al., 2017</td>
<td>Krienitz et al., 2013a,c</td>
<td>Yasindi and Taylor, 2016</td>
<td>Krienitz et al., 2016b</td>
<td>Owino et al., 2001</td>
<td>Olago et al., 2009</td>
<td>Verschuren et al., 2000</td>
</tr>
<tr>
<td>Naivasha</td>
<td></td>
<td>Krienitz et al., 2013b,c</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sonachi</td>
<td>Grant and Jones, 2016</td>
<td>Melack, 1982; Melack et al., 1982; Kotut and Krienitz, 2011; Ballot et al., 2005; Krienitz and Schagerl, 2016</td>
<td>Epp et al., 2010; Yasindi and Taylor, 2016</td>
<td>Krienitz et al., 2016b</td>
<td>Owino et al., 2001</td>
<td>Olago et al., 2009</td>
<td>De Cort et al., 2013</td>
</tr>
<tr>
<td>Elmenteita</td>
<td>Akhwale et al., 2015; Marquez et al., 2011; Mwirichia et al., 2010; Mwirichia et al., 2011; Grant and Jones, 2016</td>
<td>Foti et al., 2006; Dadheech et al., 2009; Melack &amp; Kilham, 1974; Ballot et al., 2004; Krienitz et al., 2013a; Kotut and Krienitz, 2011; Krienitz and Schagerl, 2016</td>
<td>Yasindi and Taylor, 2016</td>
<td>Krienitz et al., 2016b</td>
<td>Owino et al., 2001; Kavembe et al., 2016b; Krienitz et al., 2016b</td>
<td>Olago et al., 2009</td>
<td>Olago et al., 2009</td>
</tr>
<tr>
<td>Nakuru</td>
<td>Dadheech et al., 2012; Grant and Jones, 2016</td>
<td>Foti et al., 2006; Dadheech et al., 2009; Melack &amp; Kilham, 1974; Vareschi, 1982; Vareschi and Jacobs, 1985; Ballot et al., 2004; Kaggwa et al., 2013; Luo et al., 2013; Krienitz et al., 2012; Krienitz et al., 2013a; Kotut and Krienitz, 2011; Krienitz and Schagerl, 2016</td>
<td>Vareschi and Jacobs, 1984, 1985; Vareschi &amp; Vareschi, 1984; Burian et al., 2016; Chemoiwia et al., 2015; Burian et al., 2013; Ong‘ondo et al., 2013; Yasindi and Taylor, 2016</td>
<td>Vareschi, 1978, 1979; Vareschi and Jacobs, 1984, 1985; Vareschi &amp; Vareschi, 1984; Owino et al., 2001; Kavembe et al., 2016b; Krienitz et al., 2016b</td>
<td>Olago et al., 2009</td>
<td>Olago et al., 2009</td>
<td>De Cort et al., 2013</td>
</tr>
<tr>
<td>Bogoria</td>
<td>Vargas et al., 2005; Sorokin et al., 2001; Grant and Jones, 2016</td>
<td>Foti et al., 2006; Dadheech et al., 2009; Ballot et al., 2004; Kaggwa et al., 2013; Luo et al., 2013; Krienitz et al., 2012; Krienitz et al., 2013a; Dadheech et al., 2013; Krienitz et al., 2012; Kotut and Krienitz, 2011; Krienitz and Schagerl, 2016</td>
<td>Ong‘ondo et al., 2013; Yasindi and Taylor, 2016</td>
<td>Harper et al., 2003; Owino et al., 2001; Wecuwi et al., 2016; Kavembe et al., 2016b; Krienitz et al., 2016b</td>
<td>Olago et al., 2009; Jirsa et al., 2013; De Cort et al., 2016; De Cort, 2013; De Cort et al., 2013; Renaut et al., 2017</td>
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<td>Baringo</td>
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Fig. 2. Changes in hydrology affect lake alkalinity and disrupt *A. fusiformis* monocultures in favour of more complex microbial assemblages. When this occurs, overall productivity decreases and flamingos are forced to move in search of further “spirulina” lakes. Under different eco-hydrological conditions, *A. fusiformis* blooms occur at different times in different lakes. The lake network is able to offer a permanent food supply for the East African lesser flamingo population. Flamingo movements support lake connectivity along the Rift Valley and contribute to the dispersal of microorganisms and invertebrates supporting regional biodiversity.

Fig. 3. Schematic conceptual model of the Rift Valley lake network focussing on interactions between hydrological and ecological features. Impacts on water quality are represented in the lower part of the scheme. Lakes represented in green are dominated by *A. fusiformis* monocultures; in brown by complex microbial assemblages. East African lesser flamingo population only nest in Natron Lake.

dynamics as well as their long-term horizontal evolution (Parsons et al., 2012). These relationships have been far less studied in lake systems than in the ocean but are likely to be important here also and are likely to become a key to our understanding of lake microbiology. Virus–bacteria dynamics may change under climate change or other anthropogenic factors, with implications for species reliant on *A. fusiformis*. A serious limitation to our understanding of *Arthrospira* virus dynamics has been represented by the difficulty involved in isolating them. This is due to the fact that *Arthrospira* does not grow well on a plate, and typical virus isolation assays cannot be applied. Recently Peduzzi and co-workers (2014) provided strong evidence for the role of viruses in population crashes. They showed that virus-like particles accumulated inside *Arthrospira*, just before the population contracted and concomitantly flamingos departed. Other organisms of the *A. fusiformis* food chain have also received attention. Rotifers, who are able to consume *A. fusiformis*, have been the object of a few papers focusing on grazing, community diversity and genetics (Table 2).

The East African saline–alkaline lakes are renowned as the kingdom of prokaryotes, and in this respect, they represent biodiversity foci of global relevance. Dense
communities of cyanobacteria, archaea and microalgae, often forming mats and biofilms, grow upon bottom or littoral substrata of each lake along natural alkalinity and temperature gradients that develop as a result of inflowing freshwater tributaries, presence of brackish riparian swamps, hot springs and geysers. Bacterial communities in alkaline lakes have fascinated biologists all over the world as they host diverse microbial populations adapted to chemolithotrophic modes of energy conversion. The study of East African extremophiles, their metabolism, biology and ability to thrive in a range of extreme chemical and physical conditions has promoted a deeper fundamental understanding of bacterial physiology (Grant and Jones, 2016). Relatively little work on strain isolation has actually been carried out in this region, but data assembled so far suggest that the extant biological diversity provides options for huge biotechnological potential (as reviewed in Grant and Jones, 2016). Important applications can result from the characterisation of novel genes encoded within microbes, in particular those encoding proteins that are resistant to high temperatures, high alkalinity and salinity. Such proteins are used in pharmaceutical industries but also in wood processing and in biotechnology. It should be expected that bacterial and archaeal communities encode for genes whose proteins could host precursors of novel antimicrobial and other therapeutic properties (Cragg and Newman, 2013).

5. Open issues and information gaps

The main topic of published researches addressed structure and characterisation of microbial communities, especially cyanobacteria, including the genomic code of a restricted number of species. New species of bacteria have been isolated and described. Taking a food web perspective, however, there are several key gaps in our understanding of how the geochemistry may promote such a large microbial biodiversity, and yet despite this, the energy derived from microbial production enters very short low diversity food chains. It is probable that, given the moderate lake volume, hydrological processes have a much stronger influence upon ecosystem structure and function in alkaline lakes than in larger freshwater lakes because of radical changes that may occur following lake level rise and dilution. As an example, the only planktonic invertebrate consumers in Lake Bogoria up to 2010 were rotifers and protozoa (Burian et al., 2013; Ong’ondo et al., 2013). Since that time, lake levels have risen throughout the Rift Valley (2011–2016) and salinity became diluted by half (Amer, unpublished data). Since 2013 at least, the plankton has been invaded by Moïna sp., a cladoceran crustacean never previously recorded from alkaline-soda lakes. Concomitantly, rotifera and protozoa have become irrelevant, probably being out-competed by the large-sized filter-feeder, while the population of A. fusiiformis remained at about half the density of the previous 20 years (Tebbs, 2014).

A further gap in our understanding concerns the range of energy transfer mechanisms that sustain microbial communities. There is weak evidence that inorganic energy-rich compounds can be reduced by unique microbial assemblages, in a parallel situation to deep-sea vents. The composition of the microbial loop has been approached by recent studies (e.g., Burian et al., 2013; Ong’ondo et al., 2013), but nothing is known about the detailed structure and dynamics of these communities. We do not understand, how much A. fusiiformis is consumed by planktonic invertebrates, as opposed to how much enters the decomposer chain in different lakes. We do not know how much of the cyanobacterial turnover is caused by viral predation, which has been shown to be a key driver in ocean systems dominated by cyanobacteria (Sepulveda et al., 2016). We do not know the extent to which the microbial loop is able to regenerate inorganic phosphate, as opposed to its continuous regeneration from geochemical sources.

6. Concluding remarks

Future climate changes could cause unpredictable ecohydrological changes within lake basins throughout East Africa. At the same time, local impacts are pervasive with rampant deforestation, land use intensification, water abstraction for irrigation and inter-basin transfer. The high lake level phase that started in 2011 and continued until present does not seem to match higher rainfall and probably could be ascribed to higher runoff:rainfall ratio caused by basin degradation (Odongo et al., 2015). Interpreting and predicting the factors that rule lake hydrology represent an increasingly urgent challenge. Dilution engendered by increased runoff is tied to changes in lake biogeochemistry with cascading effects onto bacterial communities and the food chains they support, up to flamingos. Greater research effort is needed to investigate the highly diverse bacterial communities that develop in the Rift Valley lakes whose biodiversity is yet to be revealed. This can be highly beneficial for our understanding of bacterial ecology and dynamics in general, as well as for the development of new biotechnologies that can be supported by new enzymes isolated from natural bacterial communities.

Academic research should provide a coherent interdisciplinary perspective of the overall value of the ecosystems services offered by these lakes. These include cultural services linked to tourism that need to be preserved through adequate conservation measures, as well as enhanced by tourism development strategies. The management of these lakes will require a multi-disciplinary ecohydrological approach combined with a bio-geochemical understanding of the principles underlying their functioning.

Conflict of interest

None declared.

Ethical statement

Authors state that the research was conducted according to ethical standards.
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