Aquatic biodiversity and saline lakes: Lake Bogoria National Reserve, Kenya

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Abstract

Lake Bogoria, in the Rift Valley of Kenya is an extreme saline lake (conductivity 40–80 mS cm^{-1}, alkalinity 1500 m equ l^{-1}). It is hydrologically more stable than the other, endorheic lakes in Kenya, because it is deep – maximum depth at present just over 10 m in an area of 3000 ha – and so does not have periods when it is dry. It is ecologically simple, with only one species dominating the phytoplankton – the cyanobacterium 'spirulina', *Arthrospira fusiformis*. Its biomass and productivity were very high – biomass between 38 and 365 μg l^{-1} chlorophyll '*a*' and 3.4–21 $\times$ 10^3 coils ml^{-1} and net production between 0.24 and 1 gm C m^3 h, the latter in a narrow zone of less than a metre. There were no macro-zooplankton in the plankton and the only grazer of *A. fusiformis* was the lesser flamingo, *Phoeniconaias minor,* which occurred irregularly in very high concentrations (in excess of 1 $\times$ 10^6). Detritivory in the benthos was effected by a single chironomid species, *Paratendipes* sp., at a maximum density of 4 $\times$ 10^4 m^{-2}. The mean daily emergence of adult chironomids was estimated to be 1 $\times$ 10^3 m^{-2}, the maximum 3. There was no littoral plant community within the lake but 44 dicotyledonous and 31 monocotyledonous plant species in the drawn-down zone and adjacent to it. A diverse draw-down terrestrial invertebrate fauna, only superficially described here, processed the flamingo feathers and carcasses, with other detritus such as chironomid pupal exuviae and decaying *A. fusiformis* scum. About 50 bird species depended upon the chironomids, either as they emerged through the water column as flying adults or later on the shoreline as floating pupal exuvia and dead adults. The lake has high conservation value because of three bird species in particular – lesser flamingo, Cape teal and black-necked grebe. The former provides real economic value in a region otherwise impoverished, because of the spectacle of tens of thousands of flamingos set against the landscape of hot springs and fumaroles at the lake edge, which draws 15 000 visitors per annum. *P. minor* has experienced three periods during the past ten years when major mortalities have occurred, the last of which killed 700 birds day^{-1}. This could have involved as many as 200 000 birds (about 1/5th of the maximum population at this lake) if mortality was at a constant rate for the nine months it was observed. Causes of mortality have been suggested as avian tuberculosis, poisoning from cyanobacterial toxins or from heavy metal contamination at Lake Nakuru, but it is still not yet clear what contribution each makes to the problem.

Introduction

Biodiversity is a word with a short life history, even though Henri Dumont has been a practitioner of it for his long and productive professional life. Probably first used in 1984 at a conference in Washington DC, U.S.A. (Wilcox, 1984) and several times in quick succession thereafter (Wilson, 1987, 1988), the number of times it was used in the literature accelerated through the early 1990s (Harper & Hawksworth, 1994). Its entry into everyday English is a result of its widespread use at the 1992 Rio de Janeiro Conference on Environment & Development (popularly called the Earth Summit). This UN Conference helped to focus global attention on the rates of loss of biodiversity – extinction of species and populations – that are now considered so alarmingly high by many scientists as to threaten the life-support systems of our planet (Wilson, 2002). At best, deterioration of these life-support systems will be financially crippling (Constanza et al., 1997), at worst it will reduce the capacity of the planet to sustain humans (e.g. water resources; Vosmarty et al., 2000).

Henri's life has been devoted to improving our knowledge of aquatic biodiversity and limnology. On the one hand he has made considerable advances in taxonomy, particularly of crustacea, and on the other hand he has advanced our understanding of aquatic ecosystems and their processes through his development of *Hydrobiologia*. An aquatic ecosystem promoted extensively in this journal has been the saline lake, particularly through the inclusion of the edited conference proceedings of six scientific meetings devoted to it (e.g. Melack et al., 2001). Saline lakes present several interesting facets of aquatic biodiversity and Lake Bogoria, Kenya, illustrates these *par excellence*. There has been no previous publication specifically on this lake's limnology or biodiversity and it is appropriate therefore, that the first one appears in this volume.

Much of the knowledge of saline lakes in Africa has come from studies of their chemistry (e.g. Talling & Talling, 1965; Wood & Talling, 1988), biodiversity (e.g. Jones et al., 1994) and the magnitude of their primary production (e.g. Melack & Kilham, 1974; Melack, 1981). It is well understood that saline lakes have a limited species complement in macro-organisms in contrast to considerable biodiversity in micro-organisms (Beadle, 1981; Grant et al., 1990; Duckworth et al., 1996) and that production of the few species that dominate each trophic level is high

(Vareschi, 1987). Attention has now focussed on their temporal dynamics (Verschuren et al., 1999), because of the fundamental scientific interest but increasingly because of the applied value in understanding human interference with their hydrological balance [e.g. Mono lake, California (Jellison et al., 2001) and Lake Nakuru, Kenya (Anon, 2003)]. In African saline lakes, this applied value has a unique facet because these lakes have economic value to the local human population through tourism based almost entirely on one species – the lesser flamingo (*Phoeniconaias minor* Geoffroy).

P. minor is the major primary consumer in East African saline lakes in particular, but also in South Africa and parts of West Africa (Simmons, 2000), filtering the planktonic cyanobacterium 'spirulina' (Ridley et al., 1955), *Arthrospira fusiformis* (Voronichin) Komárek (Hindák, 1985) together with shallow littoral diatoms in lakes and a wider range of cyanobacteria and diatoms in temporary wetlands (McCullough et al., 2003) These flocks of *P. minor* give the term 'biodiversity value' an unusual slant, because it is elsewhere generally synonymous with species diversity. Lake Nakuru, the first protected area in Africa for birds alone (and Kenya's first Ramsar site), was primarily purchased and conserved for this one species; is the second most visited National Park in Kenya and was considered "the most fabulous bird spectacle in the world" by Roger Tory Petersen (Williams, 1967). Lakes Bogoria and Elmenteita are the other two Kenyan saline lakes used extensively by *P. minor* (Owino et al., 2001). The former is a protected National Reserve and Ramsar site; the latter privately owned but managed sympathetically. *P. minor* occurs in flocks of over a million individuals at these lakes (see below) but is considered to be a 'near-threatened' species (Hilton-Taylor, 2000), because the numbers are only about half of those formerly recorded [1.5 million Lake Nakuru (Vareschi, 1978), 2 million Lake Bogoria, (Brown, 1959)] and it only has one regular breeding site in East Africa and breeds there only intermittently – Lake Natron in Tanzania. Moreover, three large mortalities of *P. minor* have occurred in Kenya in the previous decade; both at lakes Bogoria and Nakuru in late 1993 and late 1995, at Lake Bogoria alone in late 1999. At least 40, 20 and 80×10^3 birds, respectively are estimated to have died in these three incidents (by subjective media reports at the time; no scientific numbers have been published). Two decades earlier, in late 1973 several hundred birds had died at Lake Nakuru, coincident with a

sharp decline in the biomass of their food (Vareschi, 1978) and avian tuberculosis was identified in post-mortems (Cooper et al., 1975; Sileo et al., 1979). The deaths during the 1990s, currently not convincingly explained, threaten *P. minor*'s economic value through depleting tourist income, as well as its conservation status.

P. minor is a nomadic species, moving between the lakes on which it feeds at irregular intervals in un-predictable numbers. Leslie Brown, the first biologist to study flamingos objectively in the 1950s and who discovered their breeding sites (Brown & Root, 1971) wrote "Personally, I hope that no one ever will fully rationalise flamingos, and that they will remain the supremely beautiful, elusive, opportunistic, unpredict-able beings I like to think they are" (Brown, 1979). Their nomadic behaviour has probably evolved as a response to the unpredictable dynamics of their food supply in the short-term and the unpredictable status of the lakes in the long-term.

Most of the Rift Valley lakes have shown major hydrological changes on a time scale of centuries and longer, their limnology alternating between saline and fresh, from the paleolimnological evidence in sedi-ment cores (e.g. Lake Abiyata, Ethiopia; Legesse et al., 2002; Chalié & Gasse, 2002). Lakes Elmenteita and Nakuru were once joined, forming a single large freshwater lake (Nilsson, 1932) but are currently sep-arate, shallow and saline. Nakuru has dried up 7 times in the past 70 years (Vareschi, 1978; Nasirwa, 2000) and Elmenteita also at least once per decade (I. Mar-shall, pers. comm.). Both lakes experienced an order of magnitude change in their alkalinities over 8 years in the 1960s, between 122 and 1440 meq 1^{-1} (Living-stone & Melack, 1984). Bogoria was also once part of a larger freshwater lake, joined with the current Baringo (Nilsson, 1932) but by contrast with the other two, it is currently still moderately deep, with a max-imum depth recorded as 12 m (Vareschi, 1978). It is thus likely to be both physically and chemically more stable than the other two in drought conditions.

Lakes Nakuru and Elmenteita were intensively studied during the 1970s for several consecutive years (Vareschi, 1982; Melack, 1988). These authors recor-ded one longer period of stable, high photosynthesis and biomass in the early seventies and one short period of unstable, low photosynthesis and biomass in 1974. It was hypothesised then, that the changes were triggered by the rate of increase in salinity as water level declined in drought conditions (Melack, 1988). This decrease in primary producer biomass also resul-ted in decreases in *P. minor* at these lakes (Vareschi, 1978; Tuite, 2000). Lake Bogoria was sampled less often during this period of study in the 1970s (see be-low) and so the extent to which Bogoria is more stable than the two other lakes remains unclear.

The objectives of this study were to establish whether the chemical and biological parameters of Lake Bogoria are more stable than those of the two shallow lakes and what the consequences of chemical changes might be for lake ecology and biodiversity, particularly flamingo behaviour and biology.

Some preliminary measurements (not hitherto pub-lished) were recorded in the open water in the 1970s; an investigation of the microbial flora of lake water was undertaken over one year in 1988–9 and then five visits were made between February 2000 and February 2003 in which both limnology and biodiversity were investigated. This paper de-scribes the lake's limnology and its links to the Na-tional Reserve's biodiversity, from these three peri-ods. It forms a prelude to a longer multidisciplin-ary project, funded by the U.K. Darwin Initiative (http://www.darwin.gov.uk/projects.htm) which will make monthly visits from July 2003–June 2006.

Study site

The Eastern (Gregory) Rift Valley of Africa con-tains several dozen lakes ranging in size from Lake Turkana, 250 km long, in northern Kenya to many small (<1 km) volcanic crater lakes. All of them are endorheic in depressions on the valley floor or inside volcanic craters. Most of them, as a consequence, are saline to a greater or lesser degree (Talling & Talling, 1965). Lake Bogoria lies in a trough, created by tilt faulting which is characteristic of this area of the Rift in northern Kenya (Fig. 1). It is 16 km long and 1–4 km wide, on a north-south axis with three basins between two 'necks' formed by raised ground.

The rainfall pattern of this area is complicated by the topography of the Rift here, which widens in a triangular shape northwards with Bogoria close to the southern apex. Precipitation is influenced by both the Rift's escarpments and by mountain ranges rising from the widened Rift floor. The lake itself lies in a rel-atively low altitude (975 m), low rainfall area (mean 708 mm 1976–2001) and experiences two rainy peri-ods associated with the Inter Tropical Convergence Zone in April–May and October–November plus an additional July–August peak attributed to a westerly
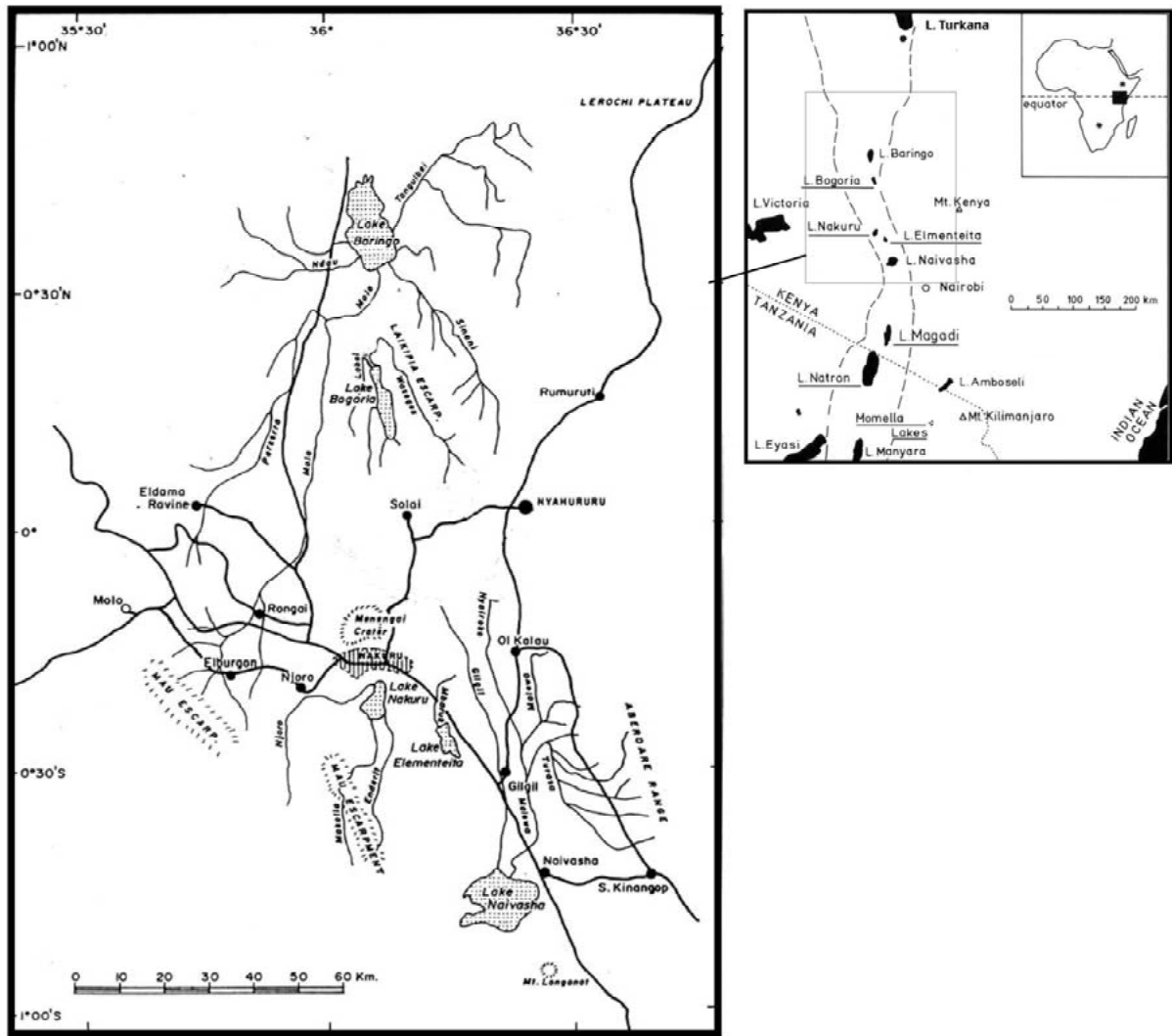
Figure 1. Saline lakes (names underlined) within the lake series in the floor of the Gregory Rift Valley of Kenya. Modified from Vareschi (1978).

air stream (Davies et al., 1985; LaVigne & Ashley, 2001). The hydrology of the lake is complicated by the inflow from numerous hot springs along its western and south-eastern shoreline in addition to its 5 river inflows. Three of these are permanent; two small freshwater streams, fed by springs, enter in the south while one river, the Ndolaita-Loboi, which formerly flowed northwards, has been diverted for irrigation and flows in the northern end of the lake. Two seasonal rivers, with substantial deltas, enter the north and west (Fig. 2).

The chemistry of the lake was initially studied by Jenkin (1936), Talling & Talling (1965), Vares-chi (1978) and Melack (1981). The latter two papers recorded that the lake had a temperature range of 24–31°C, conductivity of 72–77 mS cm^{-1}, alkalinity 1500 meq l^{-1}, and pH of 10.2–10.3 in 1974. Its general alkaline state is a result of strong equatorial evaporative concentration, which leaves a sodium- and carbonate- dominated solution (Livingstone & Melack, 1984; Grant et al, 1990).

Methods

The lake outline was taken from the 1:50 000 maps of the Survey of Kenya, 1973, which were based on aerial

photographs flown in January–February 1969. Bathymetry was measured from an inflatable dinghy during the period 16–26th August 2002 using a Lowrance X-15A chart recording echo-sounder with a 20° transducer beam. Positions of key depth readings were located with a Garmin 12 hand-held GPS receiver, enabling contours and maximum depths to be mapped.

Water samples from 1972–78 and 2000–3 were collected in replicate from a dinghy in open water stations over the deepest point in each of the three basins; in 1988–9 from the western shore at two locations in 30 cm of water depth on 12 consecutive monthly occasions. Water samples were collected at predetermined depth intervals from Rutner bottle (1972–8) and either from a rubber tube and pump (from the upper half metre) (1972–78) or a plastic Van Dorn-type messenger-closed 1.25 l sampling bottle (from 1 m and below) (2000–3). Secchi disc transparency was measured using the extinction of a 20-cm diameter black and white quartered disc. Conductivity and temperature were measured using a WTW conductivity meter with Withney electronic thermometer (1972–8), Markson portable conductivity meter with automatic temperature correction (1988–9), YSI (Yellow Springs Electrode company) model 50 Conductivity meter (2000–2) and YSI 6600 Multiparameter Sonde (2003). pH was measured on WTH, Pye-Unicam Gingold, Hach and YSI instruments. Oxygen was measured by Winkler titration (1972–8) and YSI model 58 meter (2000–3). Alkalinity was titrated with 0.1N HCl using phenolphphalein and Bromocresol Green-Methyl Red indicators.

Viable counts of bacteria on the lake water collected in 1988–9 were made by Colony Forming Units (CFU) cultured on Horokishi medium modified by addition of 4% NaCl, for 48 h at 37 °C. Total counts were made using epifluorescence microscopy on a water sample with acridine orange stain, filtered through black Millipore filter (0.22 μ pore size). Immersion oil was placed on the filter paper and bacteria counted at 1000 × magnification on a Leitz microscope with blue epifluorescence light.

A. fusiformis was counted microscopically, a minimum of 4 times on each water sample, by mounting 1 ml of shaken sample in a plastic Sedgwick Rafter cell and then counting 20 squares at random under 40 or 100× magnification on a compound microscope. Numbers of colonies of *A. fusiformis* were counted and then number of coils calculated from a single determination of the mean number of coils per colony for each visit. Other phytoplankter species were searched for using a microscope at 100 and 400× magnification from a composite sample.

A fixed volume of each water sample was filtered through Whatman GFC filter paper to retain the phytoplankton. The papers were placed in the dark until all samples had been filtered for chlorophyll '*a*' determination. When filtering was complete, the papers were each cut into strips and then ground in a pestle and mortar in a small quantity of 90% alkaline acetone and a pinch of sand for 5 minutes. The contents were carefully washed using more acetone into a 15 ml centrifuge tube after no green flecks could be seen, the tube made up to the mark and then centrifuged for 5 min at maximum speed on a hand-operated centrifuge. The liquid was carefully decanted into matched glass tubes and read against acetone blank in a Hach DR 2000 portable spectrophotometer at 750 and 665 nm. Phytoplankton chlorophyll '*a*' pigment concentration was then determined using the approximate equation of Talling & Driver (1963).

Primary production was measured in water collected from 15 to 25 cm, enclosed in Winkler (1972–8) or 250 ml 'Pyrex' glass reagent bottles (2003) which were suspended at the same point in the lake in pairs horizontally and pairs in light-proof containers vertically, at fixed depths for a measured time. Oxygen concentrations were measured at beginning and end by Winkler determination (1972–8) or YSI Model 58 Oxygen meter with pre-calibrated BOD probe immersed in the bottles and mechanically-agitated (2003).

Benthic samples were taken from measured depth with an Ekman grab of 15 × 15 cm and the mud filtered through a 25 micron mesh sieve over the side of the boat. Invertebrates were sorted live and counted in the laboratory, then blotted with damp tissue paper and wet-weighed, before preservation in 70% alcohol.

Flowering plant species growing within the draw-down zone and within 100 m of the current lake edge were identified from Agnew & Agnew (1994), grasses from Weiss (1989), and sedges and rushes from Haines & Lye (1983). Coleoptera inhabiting this zone and the riparian *Acacia* scrub were sampled by beating and sweeping using a standard entomologist's sweep net and by hand searching under the stones, dead wood and litter. A Heath portable moth trap in conjunction with a white suspended sheet was used for flying individuals. A series of pitfall traps was also used to sample the ground active coleoptera on vertical transects from the water's edge into the draw-down zone.
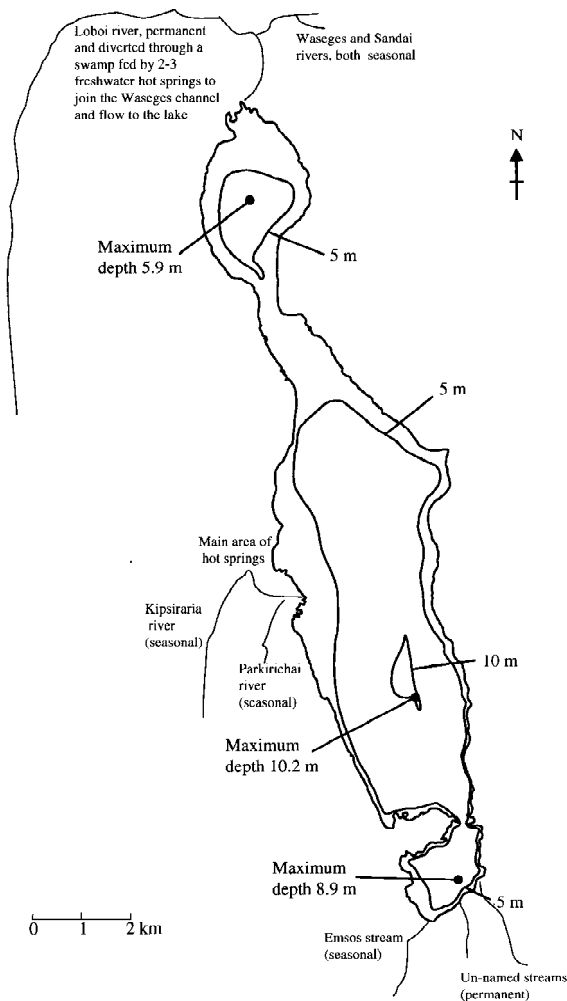
Figure 2. Details of Lake Bogoria showing inflows and bathymetry at August 2002 with 5 m depth contours and positions at which maximum depth was recorded in the three basins.

Bird species were identified using 10 × 42 binoculars and the Field Guide of Stephen & Fanshawe (2002) at all times during the visits 2000–3. Lesser flamingos on the lake were counted on each visit. Two–5 observers drove along the Reserve road from the south-west corner to the north-west. The vehicle stopped at every vantage point to divide the shore up into recognisable small sections, with one or more 'flocks' of birds. Each observer then recorded the numbers by counting 100 and estimating the number of 100-bird subgroups in the flock, using binoculars (10 × 42) or telescope (20–60 × zoom) to view the eastern shore. The observers worked independently; if their numbers were <5% of each other an average of

the group was taken; if it was greater the count was repeated by all. At the end of the day the numbers in the sections were summed.

In February and December 2000, and August 2001, the mortality of *P. minor* was calculated from daily censuses at dawn of 5, 1-km lengths along the north and western shoreline in each basin over 12 consecutive days. Dead birds were removed from the shoreline before the start of the exercise and each day as they were counted. On one day, in the middle of the counting period, in 2000, the eastern shores were walked in their entirety in order to quantify the carcasses that were there. On other dates in 2002 and 2003 mortality was estimated.

Results

The majority of the lake is deeper than 5 m (Fig. 2) with shallower areas associated with deposition from the inflowing rivers in the north and west and along the neck of the lake between the central and northern basins. The deepest point was 10.2 m in the central basin. Lake surface elevation is now regularly recorded at the southern shore of the lake (W. Kimosop, pers. comm.) and this shows that lake level decline has been about 2 m, continuous for the last 3 years, which accounts for the deeper maximum published for the 1970s by Vareschi (1978).

The main chemical parameters showed some variation between 1972 and 2003 (Table 1). The largest change was in conductivity, which was half the value in 1978 and in 1988/9 that it achieved in 1974 or 2000–2003. There are no figures of lake level available for this period, but the rainfall collected at the Reserve indicate that the two periods of low conductivity corresponded to high rainfall associated with 'El Niño' events (77–79 & 88–90). (The heavy rain commenced in April 1977; the conductivity was recorded in the first 2 months of that year). The limited range of parameters measured over this period nevertheless indicate that the lake water is well buffered against changes, with pH only changing between 0.7 units (bearing in mind each visit used different instruments) and alkalinity changing little between heavy rainfall periods (88–89) and drought periods (1974 and 2000–3).

Replicates taken either from the north and south basins in 1988–9 or from a boat in all three basins in 2002 and 2003, resulted in low variance, indicating spatial uniformity throughout the lake. In August 1978 however, the middle of the 'El Niño' event, clear

	pH	Conductivity mS cm^{-1}	Alkalinity meq l^{-1}
1972–3 ($n = 4$)	10.0	52.3	
1974 ($n = 2$)*	10.25	74.5	1500
1975–7 ($n = 3$)	10.3	59.0	
1978 ($n = 2$)	10.1	44.0	
1988/9 ($n = 24$)	10.7$^{+}/_{-}$0.2	36.8 $^{+}/_{-}$11.7	1160$^{+}/_{-}$14.2
2000–3 ($n = 12$)	10.3 $^{+}/_{-}$0.25	74.2 $^{+}/_{-}$ 2.6	1190 ($n = 1$)

*From Vareshi (1978) and Melack (1981); one measurement published in each.

chemical stratification was recorded in the south basin only, with the upper 5 m showing 60% of the conductivity of the deeper layers (Fig. 3a), which was not mirrored by pH differences (between 10.1 and 10.2 at all depths).

Very clear vertical stratification of oxygen was recorded on every boat sampling occasion from 1972 to 2003. In the south basin (sheltered) the oxycline always occurred between 1 and 2 m (Fig. 3b), but in the north and central basin (more exposed to prevailing winds) it was replaced by a more gradual decline from super-saturation at the surface to anoxia below 5 m. The surface waters were always supersaturated with oxygen, up to to 300% during the daylight hours, with a daily maximum in the afternoon between 1500 and 1700 (Fig. 3c). The temperature, by contrast, varied relatively slightly. The water below 4 m was between 23 and 25 °C on every occasion the lake was studied between 1972 and 2003. Surface water was at the same temperature morning and evening, but rose as high as 32 °C in the upper metre (Fig 3d).

Biological characteristics indicated up to an order of magnitude variation between sampling occasions (Table 2), with biomass of chlorophyll '*a*' from 38 to 363 mg m^{-3}. The density of *A. fusiformis* and the chlorophyll biomass varied approximately five-fold between 2000 and 2003 (2.7–21 × 10^3 coils ml^{-1} and 38–165 mg m^{-3} chlorophyll '*a*') with a progressive rise through the four years. The low frequency of visits may give a deceptive air of stability, because a lake-wide *A. fusiformis* crash occurred in October 2001 (Nasirwa, pers. obs.), with aroma from the decay detectable several kilometres from the lakeshore (Kimosop, pers. comm.), although it is not known what the consequences were for succession

or primary production, and no adverse effects of *P. minor* occurred. In all years studied *A. fusiformis* was the overwhelmingly dominant phytoplankton species. It represented over 70% of the community sampled throughout 1988–9 when the sample was collected from the shallow littoral but 100% of the true plankton community in 1972–8 and 2000–3 with no other species entering the counts. Diatoms were occasionally seen in the plankton, but were most likely vagrants from the shallow mud and hot springs inflow streams, where 34 species have recently been recorded (Escuté-Gasulla et al., 2002) (see also Gasse, 1996). Other cyanobacteria were also common in the hot inflow streams.

Spatial differences in *A. fusiformis* density and biomass occurred between basins on any one day, of up to 2–3 times, but this was not great enough to show differences in transparency. Observations from the air and from lake-side vantage points, indicated that wind-generated slicks concentrated lines of *A. fusiformis*, which attracted feeding *P. minor*; this short-term spatial pattern will be the subject of another paper (Vareschi, Mills, pers. obs.). Vertical differences within slicks could however be extreme; in May 1972 biomass of *A. fusiformis* in the top 5 cm was 20 times greater than that in the upper 25 cm.

The primary production of phytoplankton was confined to the upper metre of water surface, in all years when measured – 1972, 1974 and 2003. Net production ranged between 0.8 and 3.3 gm 0^2 h^{-1}, or 0.2-1 gm C h^{-1}.

Six strains of mainly gram-negative alkaliphilic bacteria, such as *Vibrio* sp., were commonly recorded in the water of Lake Bogoria during the 12 months when its microbial community was studied, 1988-9. Three of them, which occurred every month, accounted for over half the density. Overall, the mean density expressed as CFU was 3.85 × 10^5 ml^{-1}, two orders of magnitude lower than the total epifluorescence count of planktonic bacteria. The taxonomy of these alkaliphiles is a poorly-understood area still being investigated (W.D.Grant, pers comm.).

There were no zooplankton above the size of protozoa in the water column at any time and only a single chironomid species of zoobenthos grazer/detritivore. This species, tentatively identified as *Paratendipes* sp., occurred in high densities throughout the lake above the anoxic depths (Fig. 4), with no difference between lake basins or between sampling date, 2000–2003. Maximum larval densities at 1–2 m depth were 3.9 × 10^4 m^{-2} (wet weight 65.3 g), with a mean for the lake
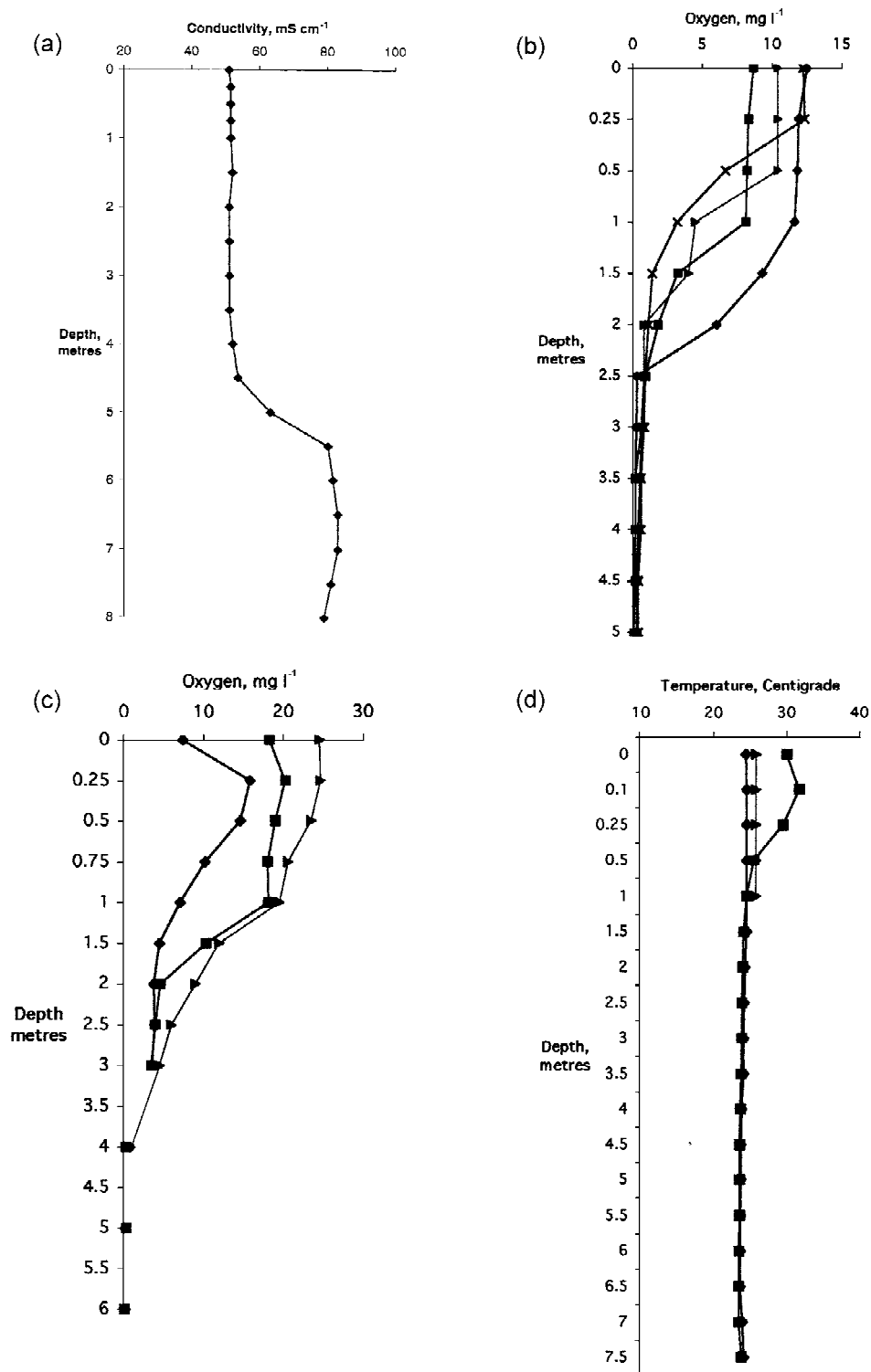
Figure 3. Vertical stratification of chemical parameters at Lake Bogoria, 1972–2003. (a) conductivity stratification in August 1978. (b) Oxygen stratification in February 2000 (diamonds), February 2001 (squares), October 2002 (triangles) and February 2003 (crosses). (c) Diurnal pattern of oxygen supersaturation in August 1978 between 1100 hrs (diamonds), 1500 hrs (square) and 1700 hrs (triangles). (d) Temperature stratification in February 1972 between 0800 hrs (diamonds), 1300 hrs (squares) and 1700 hrs (triangles).

Table 2. Biological parameters recorded at Bogoria from 1972 to 2003

Month/Year	1972	1974*	1978	1988–9	02/2000	2001[1]	10/2002	03/2003
Secchi disc cm, mean	–	36.5	–	–	53	23	19	18
standard deviation or range		28–45			5.7	3.7	2.3	1.1
n		2			9	18	22	18
Chlorophyll mg m^{-3}, mean	163	350	276	363.3	37.9	56.8	142.1	165.2
standard deviation or range	74	150–800	60	487.7	4.8	24.4	24.3	79.4
n	12	2	4	24	20	12	9	10
A. fusiformis coils ml^{-1}	2773	–		–	3375	11 639	14 520	20 826
standard deviation	750				1652	2152	1325	1151
n	15				23	12	11	15

*From Melack (1981).

[1]*A. fusiformis* counted March–June, but chlorophyll measured in March & August.

under 5 m of 1.4×10^4 m^{-2}, (wet weight 20.4 g). Adult emergence appeared to be continuous; with an estimated life cycle of 2 weeks (given the adult size and lake temperature), so the maximum daily production could be 3000 adults m^{-2}, mean 1000 m^{-2}. A conservative wet weight biomass is in the order of 3 tonnes, with a daily emergence of 210 kg, for the whole lake. This sustains several thousand individual avian predators; the most numerous are swifts and swallows and the most important for biodiversity conservation are the Cape teal and black-necked grebe (see below).

The density of *P. minor*, major grazer of the phytoplankton in the lake Bogoria ecosystem, varied rapidly, doubling or halving during the two and a half weeks of a sampling campaign, so the interpretation of numbers over a short time scale without substantial accompanying environmental data would be misleading. Its minimum numbers were 30 000 in February 2003, its maximum 510 000 in August 2001.

The most recent and the largest mortality of this species is believed to have commenced in July 1999 (Gough, 2000) and petered out in March 2000 (W. Kimosop, pers. comm.). The average daily mortality on the western side of the lake in late February 2000, was 28.8 $^+/-$ 5 individuals km^{-1}, with no evidence of either temporal (over 12 days) or spatial (between basin) differences. On the single count of south and eastern shores, only 25 flamingo carcasses, of all stages of decay, were recorded, which indicated that prevailing winds brought almost all carcasses to the western shore. Extrapolating the western shore counts to the length of shoreline exposed (west and north), gives a daily mortality for the lake of approximately 700 birds. This leads to a speculative mortality

of 2×10^5 deceased birds for the nine months of the event, equivalent to about 20% of the late-1990s observed population (Owino et al., 2001). Comparison of this with mortality estimates subsequently made, in December 2000, August 2001, October 2002 and February 2003, suggest that smaller peaks of mortality occur on top of a base mortality (approximately 0.01% would be an average daily mortality of a bird with lifespan estimated at between 35 and 50 years). In December 2000–January 2001, when the number of *P. minor* went from 40 000 to 297 000 in 3 weeks, average mortality was measured as 9 $^+/-$ 4 birds day^{-1}. In August 2001, however, when between 510 000 and 325 000 birds were counted at the lake, 113.5 day^{-1} died. In October 2002 and February 2003, fewer birds were present – 92–94 $\times 10^3$ and 40–20 $\times 10^3$, respectively. Whole-lake mortality was estimated (not counted) as no higher than 10 per day, but at this low number it was difficult to distinguish between birds healthy but predated (by marabou stork, fish eagle or steppe eagle) and birds which had been close to death and were scavenged. Visual examination of the weak birds – between 20 and 50 – in a sub-population of circa 5000 on each of 12 days in February 2003, showed that less than 1 in 20 of weak birds was 'sick' (characteristic staggering and head-drooping): the remainder had visible damage to limbs (and occasionally wings) but held necks up, so were 'injured'.

In 2002 and 2003, over 50% of the population at the lake consisted of birds under 2 years old (white-grey plumage), which indicate that breeding had replaced the 2000 mortality. Breeding was still in evidence by March 2003, with an estimated 20 000
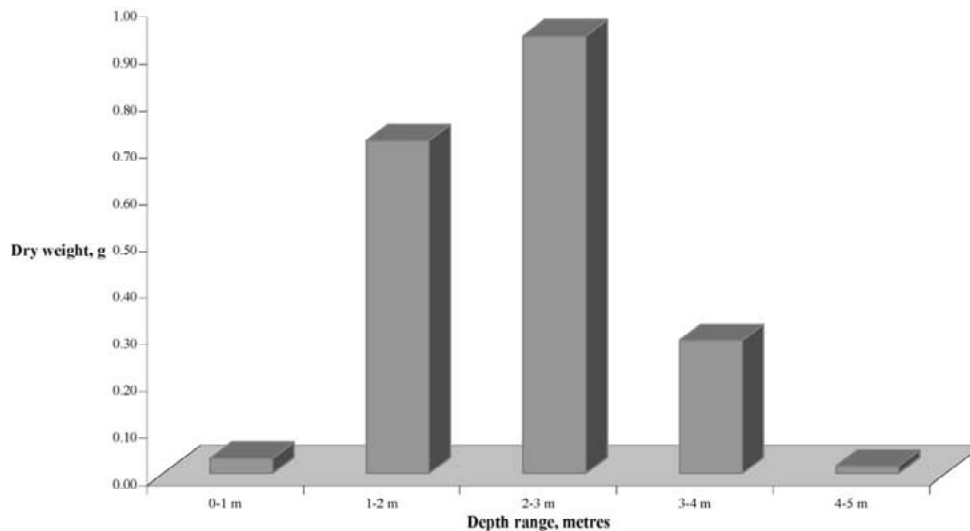
Figure 4. Mean distribution of wet weight of larvae of the midge *Paratendipes* sp. from 36 Ekman grab samples in February 2002. The standard deviations are not shown because the variances were very high (SD =/> mean) due to extensive density variation under 2 m depth.

chicks visible on Lake Natron (DMH, MMH, EV & A. Simpson, pers obs.).

No aquatic higher plants occurred in the lake. However, a diversity of plants have colonised the draw-down zone. Twenty-three families and 27 species of herbs and low-growing shrubs were recorded close to the shore (Table 3). Plant densities, although not necessarily species richness, were low in all areas other than around freshwater inflows. Adaptions to water stress, salt stress and removal by herbivores appeared to be more important in shaping the plant community than competitive interactions between individuals or closely related species. The high plant taxonomic diversity at family level is consistent with the wide range of habitats that are created by different substrate, salinity and water table depths and with a considerable breadth of plant adaptations to environmental stress. Selection appears restricted to the level of genus with typically only one or two species in each genus. The shoreline was rich in grass species, with 27 species. Of these, only *Sporobolus spicatus* and *Cyperus laevigatus* are true halophytes. The ratio of monocots to dicots in the ground flora was 1:1.3, which is much closer to the ratio expected in aquatic plant communities than the ratio of 1:4 more typical for terrestrial plants. Only three herbaceous species; the two lilies and the *Commelina* sp., are monocotyledons. The Liliiflorae are likely to have been under-represented, as bulbs and tuberous roots

sometimes uncovered in dry and stony areas, had no evidence of aerial growth.

The water's edge consisted of a marginal 'drift' of flamingo feathers, remains of flamingo carcasses, bird droppings and vegetation debris, overlying rock-strewn gritty mud. This attracted high numbers of coleoptera, particularly tenebrionids, such as *Gonocephalum* sp., *Sepidium* spp. *Vietomorpha* spp., and *Rhytinota praelonga* Koch to nocturnally scavenge 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), commonly 'hawking' and running over the mud and bare sands. 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), *Myriochile vicina pseudovicina* (Mandl). In wetter periods Scarabaeidae dominated light trap catches, particularly rutelids and melolonthids. Elaterids (click beetles) were common, including the 6–7 cm long *Tetralobus* spp.

The vegetated riparian zones, which run down to the lake, contain quite mature *Acacia tortilis* and *A. seyal*, often overgrown with *Salvadora persica* and *Capparis* spp., in groves close to freshwater inflows and springs and *A. mellifera* in the drier areas. The

Table 3. Taxonomic list for ground-layer and low-growing shrub vegetation within 100 m of the lakeshore in Lake Bogoria National Reserve, August 2001 & 2002. Nomenclature follows Agnew & Agnew (1994). Grasses not found in this study but recorded by Onkware (1996) are marked with an asterisk

Acanthaceae
    Hypoestes aristata (Vahl) Roem. & Schultes
    Crossandra mucronata Lindau
    Barleria spinisepala E.A. Bruce
Aizoaceae
    Mollugo nudicaulis Lam.
Amaranthaceae
    Achyranthes aspera L.
    Sericocomopsis hildebrandtii Schinz
Asclepiadaceae
    Calotropis procera (Ait.) Ait.f.
Boranginaceae
    Heliotropium steudneri var. *steudneri*
Capparaceae
    Maerua decumbens (Brongn.) De Wolf
    Capparis tomentosa Lam.
Commelinaceae
    Commelina petersii Hassk.
Compositae (Asteraceae)
    Kleinia squarrosa Cuf.
Euphorbiaceae
    Acalypha fruticosa Forsk.
    A. psilostachya Hochst.
    A. racemosa Baill.
    Ricinus communis L.
Labiatae
    Leonotis nepetifolia (L.) Ait.f. var. africana
    Leucas sp.
Liliiflorae (Amaryllidaceae)
    Scilla hyacinthia (Roth.) Alston
Liliiflorae (Asparagaceae)
    Asparagus racemosus Willd.
Malvaceae
    Abutilon fruticosum Guill. & Perr.
    A. mauritianum (Jacq.) Medic.
    Hibiscus meyeri Harv.
    H. vitifolius L.
    Pavonia patens (Andr.) Chiov.
Orobanchaceae
    Orobanche minor Smith
Papilionaceae
    Indigofera volkensii Taub.
    Vigna schimperi Bak.
Pedaliaceae
    Sesamum latifolium Gillett
Plumbaginaceae
    Plumbago zeylanica L.

Table 3. Continued

Portulacaceae
    Portulaca foliosa Ker-Gawl.
    P. kermesina N.E.Br.
    P. quadrifida L.
Scrophulariaceae
    Cycnium tubulosum (L.f) Engl.
    Striga gesnerioides (willd.) Vatke
Solanaceae
    Lycium europaeum L.
    Solanum incanum L.
    S. nigrum L.
    S. renschii Vatke
Vitaceae
    Cissus quadrangularis L.
    C. rotundifolia (Forsk.) Vahl
Verbinaceae
    Lantana camara (exotic)
Zygophyllaceae
    Tribulus terrestris L.
    Tribulus cistoides L.
Poaceae (grasses)
    Andropogon sp.*
    Aristida dimuta
    *A. keniensis**
    A. somalensis
    A. stenostachya
    Bouteloua sp.
    Brachiaria sp.*
    *Chenchrus ciliaris**
    Chloris gayana
    C. virgata
    Cynodon dactylon
    *Cynodon nlemfuensis**
    Dactyloctenium australe
    *D. bogdanii**
    Elusine sp.
    *Enteropogon rupestris**
    Eragrostis sp.
    Heteropogon contortus
    Paspalum sp.
    Pennisetum sp.
    *Rhynchelytrum repens**
    Sporobolus consimilis
    *S. keutrophyllus**
    S. spicatus
    *Tragus berteronianus**
    Typha domingensis
    Urochloa raceme
Cyperaceae (sedges)
    Cyperus cyperoides L. Kuntze
    C. laevigatus L.
    C. rubicundus Vahl
    Schoenoplectus corymbosus (Roth. ex Roem.
        & Schult.) J. Raynal var. *brachyceras*
        (A. Rich.) K. Lye Rottb

acacias had a distinct coleopteran fauna in which the Buprestidae, Chrysomelidae and Curculionidae predominated. Some species infested the trees in population outbreaks, such as occurred in February 2000, when the eumolpine chrysomelid *Malegia affinis* Jacoby was the most abundant insect on the lake shore acacias.

The bird fauna consisted of 223 species recorded on the reserve between 2000 and 2003 and although most are not associated directly with the aquatic ecosystem, just over 50 species are directly dependent upon the lake and its associated mudflats, springs, streams, seepages and wetlands (Table 4). Up to another 50 terrestrial insectivorous species feed, in part, on the adult *Paratendipes* sp. when they settle on lakeshore scrub. Two aquatic species, are wholly also dependent upon the *Paratendipes* sp. and are more abundant at this lake than any other in Kenya; Cape teal *Anas capensis* and black-necked grebe *Podiceps nigricollis*. Both feed on the emerging pupae (grebe dive for them as they rise) and adults (teal dabble on the surface film collecting adults and shed pupal exuviae). The numbers of these species fluctuated considerably, but in August 2001, 2084 *P. nigricollis* and 663 *A. capensis* were counted. The families Apodidae (swifts) and Hirundinidae (swallows and martins), which have five and seven species respectively, fed extensively on emerging adults over the water. Conservative estimates, made in February 2000 and in February 2003, suggested the numbers of these two families over the lake at least matched those of *P. minor* on it. The lake is an important feeding station for four Palaearctic migrants, in both directions, being at the southern edge of Kenya's extensive northern arid district, particularly *Hirundo rustica, Riparia riparia* and *Apus apus*.

Discussion

The lake's chemical data suggest a more stable environment than has been recorded for the other saline, more shallow, lakes in Kenya, with no evidence for the major changes recorded in Elmenteita (Melack, 1988) and Nakuru (Vareschi, 1982) caused by drying-out. A 50% change in conductivity accompanied by little pH or alkalinity variations suggests that the measured fluctuations of an order of magnitude in *A. fusiformis* is more due to biological regulation rather than environmental effects, and it is close to its theoretical maximum, as has been recorded for deep crater lakes

Table 4. Taxonomic list of birds recorded at Lake Bogoria National Reserve, 2000-3, Family, scientific and English names

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Struthionidae: Ostriches
    Common Ostrich *Struthio camelus*
Podicipedidae: Grebes
    Little Grebe *Tachybaptus ruficollis*
    Black-necked Grebe *Podiceps nigricollis*
Pelicanidae: Pelicans
    Great White Pelican *Pelecanus onocrotalus*
Phalacrocoracidae: Cormorants
    Long-tailed Cormorant *Phalacrocorax africanus*
Ardeidae: Herons and Egrets
    Cattle Egret *Bubulcus ibis*
    Yellow-billed Egret *Mesophoyx intermedia*
    Little Egret *Egretta garzetta*
    Great Egret *Casmerodius albus*
    Striated (Green-backed) Heron *Butorides striatus*
    Grey Heron *Ardea cinerea*
    Black-headed Heron *Ardea melanocephala*
Scopidae: Hamerkop
    Hamerkop *Scopus umbretta*
Ciconiidae: Storks
    Yellow-billed Stork *Mycteria ibis*
    Wooly-necked Stork *Ciconia episcopus*
    Marabou Stork *Leptoptilos crumeniferus*
    White stork *Ciconia ciconia*
Threskiornithidae: Ibises and Spoonbills
    Sacred Ibis *Threskiornis aethiopicus*
    Hadada Ibis *Bostrychia hagedash*
    Glossy Ibis *Plegadis falcinellus*
    African Spoonbill *Platalea alba*
Phoenicopteridae: Flamingos
    Greater Flamingo *Phoenicopterus ruber*
    Lesser Flamingo *Phoeniconaias minor*
Anatidae: Ducks & Geese
    Egyptian Goose *Alopochen aegyptiacus*
    Spur-winged Goose *Plectropterus gambensis*
    Knob-billed Duck *Sarkidiornis melanotos*
    White-faced Whistling Duck *Dendrocygna viduata*
    Cape Teal *Anas capensis*
Accipitridae: Kites, Vultures, Eagles and Hawks
    Yellow-billed Kite *Milvus parasiticus*
    White backed vulture *Gyps africanus*
    African Fish Eagle *Haliaeetus vocifer*
    African Marsh Harrier *Circus ranivorus*
    Montagu's Harrier *Circus pygargus*
    Eurasian Marsh Harrier *Circus aeruginosus*
    Pallid Harrier *Circus macrourus*
    Dark Chanting Goshawk *Melierax metabates*
    Gabar Goshawk *Micronisus gabar*

Table 4. Continued

    Black-chested snake eagle *Circaetus pectoralis*
    African Harrier-Hawk *Polyboroides typus*
    Augur Buzzard *Buteo augur*
    Common Buzzard *Buteo buteo*
    Tawny Eagle *Aquila rapax*
    Steppe Eagle *Aquila nipalensis orientalis*
    Verreaux's Eagle *Aquila verreauxii*
    Martial Eagle *Polemaetus bellicosus*
Falconidae: Falcons
    Pygmy Falcon *Polihierax semitorquatus*
    Peregrine Falcon *Falco peregrinus*
    Lanner falcon *Falco biarmicus*
    Eurasian Hobby *Falco subbuteo*
Numididae: Guineafowls
    Helmeted Guineafowl *Numida meleagris*
Phasianidae: Quails and Francolins
    Jackson's Francolin *Francolinus jacksoni*
    Crested Francolin *Francolinus sephaena*
    Common Quail *Coturnix coturnix*
Rallidae: Crakes and Rails
    Black Crake *Amaurornis flavirostris*
Gruidae: Cranes
    Grey-crowned Crane *Balearica regulorum*
Recurvirostridae: Avocets and Stilts
    Black-winged Stilt *Himantopus himantopus*
    Pied Avocet *Recurvirostra avosetta*
Charadridae: Plovers
    Grey plover *Pluvialis squatarola*
    Spur-winged Lapwing *Vanellus spinosus*
    Crowned Lapwing *Vanellus coronatus*
    Black-headed Lapwing *Vanellus tectus*
    Kittlitz's Plover *Charadrius pecuarius*
    Three-banded Plover *Charadrius tricollaris*
    Common Ringed Plover *Charadrius hiaticula*
    Chestnut banded plover *Charadrius pallidus*
Scolapacidae: Sandpipers and Snipes
    Lesser Sandpiper *Charadrius mongolus*
    Common Sandpiper *Actitis hypoleucos*
    Ruff *Philomachus pugnax*
    Wood Sandpiper *Tringa glareola*
    Green Sandpiper *Tringa ochropus*
    Common Greenshank *Tringa nebularia*
    Marsh Sandpiper *Tringa stagnatilis*
    Spotted Redshank *Tringa erythropus*
    Little Stint *Calidris minuta*
    Curlew Sandpiper *Calidris ferruginea*
    Common Snipe *Gallinago gallinago*
    Broad-billed sandpiper *Limicola falcinellus*
Pteroclidae: Sandgrouse
    Lichtenstein's Sandgrouse *Pterocles lichtensteinii*

Table 4. Continued

Columbidae: Pigeons and Doves
    African Green-Pigeon *Treron calva*
    Speckled Pigeon *Columba guinea*
    Emerald-spotted Wood-Dove *Turtur chalcospilos*
    Namaqua Dove *Oena capensis*
    Ring-necked Dove *Streptopelia capicola*
    Red-eyed Dove *Streptopelia semitorquata*
    African Mourning Dove *Streptopelia decipiens*
    Laughing Dove *Streptopelia senegalensis*
Musophagidae: Turacos
    White-bellied Go-away-bird *Corythaixoides leucogaster*
Cuculidae: Cuckoos and Coucals
    Klaas's cuckoo *Chrysococcx klaas*
    White-browed Coucal *Centropus superciliosus*
Strigidae: Owls
    African Scops-Owl *Otus senegalensis*
    Verreaux's Eagle-Owl *Bubo lacteus*
    Pearl-spotted Owlet *Glaucidium perlatum*
Caprimulgidae: Nightjars
    Slender-tailed nightjar *Caprimulgus clarus*
Apodidae: Swifts
    Little Swift *Apus affinis*
    White-rumped Swift *Apus caffer*
    Mottled Swift *Apus aequatorialis*
    Nyanza Swift *Apus niansae*
    Eurasian Swift *Apus apus*
Coliidae: Mousebirds
    Speckled Mousebird *Colius striatus*
    Blue-naped Mousebird *Urocolius macrourus*
    Red-faced Mousebird *Urocolius indicus*
Alcedinidae: Kingfishers
    Grey-headed Kingfisher *Halcyon leucocephala*
    Woodland Kingfisher *Halcyon senegalensis*
    Malachite Kingfisher *Alcedo cristata*
    African Pigmy Kingfisher *Ispidina picta*
Meropidae: Bee Eaters
    Little Bee eater *Merops pusillius*
    Cinnamon-chested Bee eater *Merops oreobates*
    European Bee eater *Merops apiaster*
    Madagascar Bee eater *Merops superciliosus*
    White-fronted Bee eater *Merops bullockoides*
Coraciidae: Rollers
    Lilac-breasted Roller *Coracias caudate*
    Rufous-crowned Roller *Coracias naevia*
Upupidae: Hoopoes
    African Hoopoe *Upupa africana*
Phoenuculidae: Wood-hoopoes
    Green Wood-hoopoe *Phoeniculus purpureus*

Table 4. Continued

Bucerotidae: Hornbills
    Red-billed Hornbill *Tockus erythrorhynchus*
    Von der Decken's Hornbill *Tockus deckeni*
    Jackson's Hornbill *Tockus jacksoni*
    African Grey Hornbill *Tockus nasutus*
Captionidae: Barbets and Tinkerbirds
    Red-fronted Tinkerbird *Pogoniulus pusillus*
    Red-fronted Barbet *Tricholaema diademata*
    Black-throated Barbet *Tricholaema melanocephala*
    White-headed Barbet *Lybius leucocephalus*
    d'Arnaud's Barbet *Trachyphonus darnaudii*
    Red and yellow Barbet *Trachyphonus erythrocephalus*
Indicatoridae: Honeyguides:
    Lesser Honeyguide *Indicator minor*
Picidae: Woodpeckers
    Nubian Woodpecker *Campethera nubica*
    Cardinal Woodpecker *Dendropicos fuscescns*
    Bearded Woodpecker *Dendropicos namaquus*
    Grey Woodpecker *Dendropicos goertae*
Alaudidae: Larks
    Fischer's Sparrow-Lark *Eremopterix leucopareia*
Hirundinidae: Swallows and martins
    Rock Martin *Hirundo fuligula*
    Plain Martin *Riparia paludicola*
    Sand Martin *Riparia riparia*
    Red-rumped Swallow *Hirundo daurica*
    Lesser Striped Swallow *Hirundo abyssinica*
    Barn Swallow *Hirundo rustica*
    Wire-tailed Swallow *Hirundo smithii*
    Mosque Swallow *Hiundo senegalensis*
Motacillidae: Pipits and Wagtails
    African Pied Wagtail *Motacilla aguimp*
    Yellow-headed Wagtail *Motacilla lutea*
    Yellow wagtail *Motacilla flava*
    White wagtail *Motacilla alba*
Pycnonotidae: Bulbuls
    Common Bulbul *Pycnonotus barbatus*
Turdidae: Thrushes
    African Thrush *Turdus pelios*
    Olive Thrush *Turdus olivaceous*
    Spotted Morning Thrush *Cichladusa guttata*
    White-browed Scrub Robin *Cercotrichas guttata*
    Isabelline Wheatear *Oenanthe isabellina*
    Pied Wheatear *Oenanthe pleschanka*
    Northern Wheatear *Oenanthe oenanthe*
Sylvidae:Warblers
    Olivaceous Warbler *Hippolais pallida*
    Barred Warbler *Sylvia nisoria*

Table 4. Continued

    Willow Warbler *Phylloscopus trochilus*
    Yellow-breasted Apalis *Apalis flavidus*
    Red-face Cromec *Sylvieta whytii*
    Grey-backed Camaroptera *Camaroptera brachyura*
Muscicapidae: Flycatchers
    Southern Black Flycatcher *Melaenornis pammelaina*
    African Grey Flycatcher *Bradornis microrhynchus*
    Spotted Flycatcher *Muscicapa striata*
    Silverbird *Empidornis semipartitus*
Platysteiridae: Batises
    Pygmy Batis *Batis perkeo*
Monarchidae: monarch flycatchers
    African Paradise-flycatcher *Terpsiphone viridis*
Timaliidae: Chatterers and Babblers
    Rufus Chatterer *Turdoides rubiginosus*
    Northern Pied Babbler *Turdoides hypoleucus*
Paridae: Tits
    White-bellied Tit *Parus albiventris*
    Northern Grey Tit *Parus thruppi*
    Red-throated Tit *Parus fringillinus*
Nectariniidae: Sunbirds
    Beautiful Sunbird *Cinnyris pulchella*
    Eastern Violet-backed Sunbird *Anthreptes orientalis*
Laniidae: Shrikes
    Common Fiscal *Lanius collaris*
    Long-tailed Fiscal *Lanius cabanisi*
    Grey-backed Fiscal *Lanius excubitoroides*
Malaconotidae: Bush Shrikes
    Tropical Boubou *Laniarius aethiopicus*
    Slate-coloured Boubou *Laniarius funebris*
    Brubru *Nilaus afer*
    Black-backed Puffback *Dryoscopus cubla*
    Northern Puffback *Dryoscopus gambensis*
Prionopidae: Helmet-shrikes
    Northern White-crowned Shrike *Eurocephalus rueppelli*
Dicruridae: Drongos
    Fork-tailed Drongo *Dicrurus adsimilis*
Corvidae: Crows
    Pied Crow *Corvus albus*
Oriolidae: Orioles
    African Black-headed Oriole *Oriolus larvatus*
    African Golden Oriole *Oriolus auratus*
Sturnidae: Starlings and Oxpeckers
    Rüppell's Long-tailed Starling *Lamprotornis purpuropterus*
    Supurb Starling *Lamprotornis superbus*
    Greater Blue-eared Starling *Lamprotornis chalybaeus*
    Abbot's Starling *Cinnyricinclus femoralis*
    Ashy Starling *Cosmopsarus unicolor*
    Magpie Starling *Speculipastor bicolour*

Table 4. Continued

Wattled Starling *Creatophora cinerea*
Red-billed Oxpecker *Buphagus erythrorhynchus*
Passeridae: Sparrows
    House Sparrow *Passer domesticus*
    Chestnut Sparrow *Passer eminibey*
    Grey-headed Sparrow *Passer griseus*
    Rufous Sparrow *Passer rufocinctus*
    Yellow-spotted Petronia *Petronia pyrgitta*
Ploceidae: Weavers
    White-headed Buffalo-Weaver *Dinemellia dinemelli*
    Speckle-fronted Weaver *Sporopipes frontalis*
    Red-headed Weaver *Anaplectes rubriceps*
    White-billed Buffalo-Weaver *Bubalornis albirostris*
    Red-billed Buffalo Weaver *Bubalornis niger*
    White-browed Sparrow-Weaver *Plocepasser mahali*
    Northern Masked Weaver *Ploceus taeniopterus*
    Vitelline Masked Weaver *Ploceus velatus*
    Reichenow's Weaver *Ploceus baglafecht*
    Speke's Weaver *Ploceus spekei*
    Golden-backed Weaver *Ploceus jacksoni*
    Black-headed Weaver *Ploceus cucullatus*
    Little Weaver *Ploceus luteolus*
Emberizidae: Waxbills and Whydahs
    Green-winged Pytilia *Pytilia melba*
    Red-cheeked Cordon-bleu *Uraeginthus bengalus*
    Blue-capped Cordon-bleu *Uraeginthus cyanocephalus*
    Purple Grenadier *Uraeginthus ianthinogaster*
    Red-billed Firefinch *Lagonosticta senegala*
    Black-cheeked Waxbill *Estrilda charmosyna*
    Pin-tailed Whydah *Vidua macroura*
    Straw-tailed Whydah *Vidua fischeri*
    Steel-blue Whydah *Vidua hypocherina*
    Village Indigobird *Vidua chalybeata*
Fringillidae: canaries and seadeaters
    African Citril *Serinus citrinelloides*
    Streaky Seedeater *Serinus striolatus*
    White-bellied Canary *Serinus dorsostriatus*

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in Ethiopia such as Lake Aranguadi (Talling et al., 1973).

The monoculture of *A. fusiformis* in the phytoplankton, the absence of any macro-zooplankton, and a single species in the benthos, reflect the extreme saline environment. This implies instability, using the 'simple-unstable, diverse-stable' concept of ecology espoused in the 1970s. The initial data presented here however, indicates that a hydro-chemical stability confers an ecological stability on an extremely simple limnological food-web. The greatest instability in the lake was the outbreak of mortality of *P. minor*. Periodic large-scale die-offs have been reported for the past 40 years. Initially, these die-offs were attributed to starvation, due to sudden crashes of phytoplankton and other unknown causes (Brown, 1959). At Lake Nakuru, during the first three months of 1974, the 75% decline in the standing crop of *A. fusiformis*, was followed by a subsequent massive emigration of lesser flamingos from > one million birds in January to < 10 000 by August–September (Tuite, 2000). Amongst the approximately 10 000 birds remaining during July and August, there was unusually high mortality, 420 carcasses being collected in 19 days (Sileo et al., 1979). In April, 51 debilitated birds (26 adults and 25 immature birds) were collected for analysis. Ten adults (38%) and nine immature birds (36%) had avian tuberculosis *Mycobacterium avium* Type 1 (Sileo et al., 1979). The rest perhaps were debilitated from a combination of starvation and the effects of parasites.

There have been three notable die-offs within the past decade, in 1993, 1995, and again in 1999–2000. The 1993 die-off, which was first noticed at Lake Bogoria and then a month later at Lake Nakuru, resulted in an estimated 18 500 deaths on the two lakes. Zimbabwe veterinarians Nancy and Richard Kock studied this die-off, which occurred at a time when the population was unusually high, water levels declining, and ambient air temperatures high (Nasirwa & Bennun, 1994; Kock et al., 1999). They concluded that the primary cause of death was "septicemia, complicated in those affected, by mycobacteriosis", or avian tuberculosis (Kock et al., 1999).

M. avium Type 1 was first isolated in a *P. minor* in Kenya at Lake Nakuru in 1970 by Koeman et al. (1972). The African fish eagle *Haliaeetus vocifer* feeds largely on *P. minor* there (Cooper et al., 1975) and in 1972, an *H. vocifer* at Lake Nakuru was also found infected with the disease (Kaliner & Cooper, 1973). In 1973, Cooper et al. (1975) had found *M. avium* Type 1 in two of four debilitated *P. minor* also collected at Lake Nakuru. The species had been shown not to be very susceptible to avian TB in captive flocks held within avian collections where avian TB was otherwise prevalent (Wood, 1975), so it was not clear why they seemed so susceptible at Lake Nakuru, or how the disease was introduced there.

One hypothesis is that the bacterium might have been introduced to Lake Nakuru as an effect of ecological changes following the introduction of *Tilapia grahami* in the early 1960s and the immigration of fish eating birds such as the pelican (Cooper et al.,

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1975). Its spread to other lakes could then have been accomplished by the flamingos themselves through their constant vagrancy. In humans, susceptibility to tuberculosis increases amongst underweight and undernourished individuals living in overcrowded conditions (Evans & Feldman, 1982; Benenson, 1990). Ratcliffe (1946) studied data from 3000 avian postmortems performed over a 20-year period at the Philadelphia Zoological Garden and concluded that resistance of birds to tuberculosis was influenced by nutritional factors. Perhaps, the dense flocks of hungry *P. minor* at lakes Nakuru and Bogoria following a phytoplankton decline, provide the conditions for *M. avium* to become epizootic; at Bogoria the number of birds reached nearly a million just prior to each of the three mortalities (Owino et al., 2001). On the other hand, in some humans and laboratory animals, genetic factors have been shown to influence resistance to the disease (Evans & Feldman, 1982). Wood (1975) suggested that similar factors might operate in flamingos, based on his observations of captive birds.

A second hypothesis to explain the mass lesser flamingo die-offs is that they are the result of toxicosis. A joint study by the World Wide Fund for Nature and Egerton University found substantial amounts of hepatoxic algae and toxic metals, particularly chromium, in Lake Nakuru that appears to have originated from industries surrounding the lake. Web-site claims were made for high levels in bird tissues although these have not yet been supported by scientific publication. A linked experimental study predicted increased metal exposure rates through increased absorption by birds as the population of *A. fusiformis* declined (Nelson et al., 1998), which provided a possible explanation for the die-offs observed at Lake Nakuru. Toxicosis is not yet clearly a cause of flamingo deaths at Lake Nakuru without hard evidence, but cannot be ruled out. In Lake Bogoria however, where the 1993 die-off was first noticed and the 1999–2000 was almost entirely confined, there is no polluting industry in its catchment.

The pathological role of algal toxins in flamingos has also been suggested as a contributing factor at Bogoria (Krienitz et al., 2003), where toxin-secreting species were identified in hot-spring streams and in two flamingo carcasses in 2001, the period of the lower mortality-peak (see above). In greater flamingos, cyanobacterial toxins from planktonic species known to be toxin-generating – *Microcystis aeruginosa* and *Anabaena flos-aquae* – have been identified as the causative agents for a mortality of 60%

of *Phoenicopterus ruber* chicks in Doñana National Park, southern Spain, in 2001. At Bogoria, the water of hot spring streams is potable if its salinity is substantially lower than lake water (conductivity by up to one-third lower, pers. obs. DMH). Lines of birds may be seen drinking from such streams (e.g. Fig. 1E in Krienitz et al., 2003). However, the water represents a small proportion of the available drinking water at Bogoria and hot spring sources are primarily located along the middle of the western shore. In the north, the Sandai river brings a small permanent flow of the diverted Loboi river and in the south, two freshwater springs supply permanent streams; all three are used extensively for drinking (DMH, RBC, MMH, pers. obs.).

In all probability there are multiple causes of the mortality. Avian tuberculosis may be endemic in the population but not lethal to individuals unless their immunity has been compromised by another factor. It is perhaps not an accident that all three mortalities in the 1990s occurred towards the end of long droughts (LaVigne & Ashley, 2001) as well as at a time when the number of birds at Bogoria peaked at close to 1 $\times$ 10^6 (Owino et al., 2001), both factors which would have increased stress on individuals. The population in 2000 might also have been undernourished, since the quantity of *A. fusiformis* was low and the filtering demands of *P. minor* are high (Vareschi, 1978).

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