J. Phycol. **46,** 1088–1096 (2010)
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DOI: 10.1111/j.1529-8817.2010.00915.x

FLUCTUATING ALGAL FOOD POPULATIONS AND THE OCCURRENCE OF LESSER FLAMINGOS (*PHOENICONAIAS MINOR*) IN THREE KENYAN RIFT VALLEY LAKES[1]

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The last two decades have witnessed increasing episodes of lesser flamingo die-offs in East Africa. Based on data on phytoplankton composition, biomass, and flamingo population density in three alkaline-saline lakes of Kenya (Bogoria, Nakuru, and Oloidien) in 2001–2010, this study explored the link between sudden flamingo deaths and fluctuations in algal food quantity and quality. The phytoplankton biomass ranged from 13 to 768 mg · L^{-1}. Similarly, flamingo numbers varied widely from <1,000 to >500,000 individuals in the study lakes. The dominance of the cyanobacterium *Arthrospira fusiformis* (Woron.) Komárek et J. W. G. Lund was interrupted at irregular intervals in each lake and replaced partly by populations of different species of the nostocalean *Anabaenopsis* or by the picoplanktonic chlorophyte *Picocystis salinarum* Lewin. The populations of *Anabaenopsis* have the potential of blocking the flamingo food filtration system with their large and slimy colonies; moreover, they are able to produce cyanotoxins. Estimates of flamingo populations suggest that low flamingo numbers coincided with periods of low algal food quantity and/or poor quality. A food deficit can be theorized to have two effects on the flamingos: (i) it weakens them to the point of being susceptible to attacks of infective diseases, such as the ones caused by *Mycobacterium avium* and *Pseudomonas aeruginosa*, and (ii) it predisposes them to poisoning by cyanotoxins and pollutants, by reducing their capacity to handle toxic substances. This study therefore concludes that the challenges facing the flamingos are associated with changes in their environment, which affect food and water supply.

***Key index words: Anabaenopsis*; *Arthrospira*; food algae; lesser flamingo; *Phoeniconaias minor*; *Picocystis salinarum*; toxic cyanobacteria**

***Abbreviation:* DM, dry mass**

The lesser flamingo, *Phoeniconaias minor* Geoffroy (syn. *Phoenicopterus minor* Geoffroy), is a characteristic bird of alkaline-saline lakes and pans of Africa and India. The dense population of these pink birds at soda lakes of East Africa is rated as one of the most fascinating wildlife spectacles of the world (Jenkin 1929, Brown 1973, Mari and Collar 2000). Recent estimates of lesser flamingos at the main distribution areas are as follows: 1.5–2.5 million in eastern Africa; ~390,000 in northwestern India; 55,000–65,000 in southwestern Africa; and 15,000–25,000 in western Africa. The highest population densities have been observed in Kenya (~1.5 million) and Tanzania (~600,000) (Childress et al. 2008). Lesser flamingos are well adapted to the harsh conditions of their habitats, which include the high temperature of air and water, the extreme concentrations of salt (20–60 g · L^{-1}), and a high pH of ~10. They are able to migrate several hundreds of kilometers each day to access sites with suitable living conditions. The search for favorable conditions to breed and feed is thought to be the main reason for their itinerant habit.

Lesser flamingos have a highly specialized diet consisting almost entirely of microscopic cyanobacteria and benthic diatoms. Contrarily, the greater flamingos (*Phoenicopterus roseus* Pallas), which are found in the same habitat as the lessers (but with a population density of <10% of the total number of flamingos), are generalists consuming copepods, mollusks, and other small planktonic and benthic animals in addition to algae (Jenkin 1957, Childress et al. 2008). Because of its specialized diet, the lesser flamingo is more sensitive to fluctuations in food quality and quantity and therefore can be considered as an indicator of ecosystem health. The lesser flamingo is the main primary consumer at the soda lakes of East Africa (Vareschi 1978, Vareschi and Jacobs 1985, Harper et al. 2003). In a short and direct food chain from the phototrophic primary producers to the warm-blooded consumer birds, the lesser flamingo efficiently filters the major part of the daily algal production in these lakes. The main food resource of the lesser flamingo is *A. fusiformis* (often named as ''*Spirulina*''), a very fast-growing cyanobacterium. Vonshak (1997) reported doubling times of 11–20 h of *Arthrospira* in culture under saline conditions at 35°C. Unfortunately, the dense

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[1] Received 19 August 2009. Accepted 30 June 2010.

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populations of *Arthrospira* collapse irregularly and unpredictably (Vareschi 1978, Tuite 1981, Melack 1988). Alternatively, the lesser flamingos consume benthic diatoms. However, net primary productivity of benthic diatoms in East African soda lakes is one to two orders of magnitude lesser than that of *Arthrospira*, and the carrying capacity of the habitat with diatoms is lower in the same order (Tuite 2000). When feeding, the flamingos tilt their heads slightly upside down (Fig. 1a) and sweep their heads from side to side just below the surface. The piston-like tongue aids in sucking food-filled water past the lamellae located inside the curved bill. The lamellae retain food particles but exclude those particles that may be too large (Fig. 1, b and c). The lamellae are equipped with rows of fringed platelets (Jenkin 1957) (Fig. 1d) that have the perfect size to collect the coiled filaments of *Arthrospira*.

Fig. 1. Food uptake by lesser flamingos. (a) Flamingos in feeding position. (b–d) Inner side of the bill. (b) An overview of the inner part of the bill showing a row of tooth-shaped excluders at the outer margin of the bill (black arrow). Scale bar, 1 cm. (c) Excluders under a higher magnification. One excluder is covered by a slimy lump of *Anabaenopsis* (white star), which cannot pass through the space between the excluders. The much smaller spirals of *Arthrospira* (white double-headed arrow) can pass through the space between the excluders easily. The excluders are 800 μm from each other. Scale bar, 500 μm. (d) Inner lamellae (20 rows · mm^{-2}) with rows of fringed platelets partially clogged by slimy *Anabaenopsis*. Scale bar, 100 μm.

Since the mid-1990s, an increased mortality of lesser flamingos has been observed in East Africa. In the years 1993, 1995, 1999, 2001, 2006, and 2008, massive deaths involving >10,000 birds in each episode were reported (Ndetei and Muhandiki 2005). The causes of these die-offs are far from being completely understood but appear to be related to the degradation of their habitats. A combination of factors, such as infective diseases (Sileo et al. 1979, Kock et al. 1999) and poisoning by pesticides and heavy metals (Greichus et al. 1978, Kairu 1996), are subjects of ongoing investigations. Nevertheless, the die-offs could also be linked to changes in food quantity (Sileo et al. 1979, Ton 2007) and quality (Motelin et al. 2000, Ndetei and Muhandiki 2005). Malnutrition resulting from a decline in *Arthrospira* food concentration is thought to have caused the birds to suffer from immunodeficiency leading to infection causing microbacteriosis (Sileo et al. 1979). The flamingos are also confronted with toxic cyanobacteria, which occasionally assume dominance displacing the previously healthy and nutritious populations of *Arthrospira* (Ballot et al. 2004a,b, Krienitz et al. 2005, Koenig 2006).

The data obtained over a period of 10 years (2001–2010) were interpreted in the context of recent mass die-offs of the lesser flamingos at the sites studied. We focused on two water bodies with the highest numbers of lesser flamingos all over the world, the soda lakes Nakuru and Bogoria located in the Kenyan Great Rift Valley. Additionally, we considered Lake Oloidien, which has in recent years started hosting lesser flamingos. Lake Oloidien is a former bay of the freshwater lake Naivasha. The aim of the study was to analyze the phytoplankton succession in each lake and to assess their suitability as food for the lesser flamingos.

MATERIALS AND METHODS

The three lakes were studied 15 times, at irregular intervals during the period 2001–2010. Conditions at the sampling sites are described by Harper et al. (2003) and Ballot et al. (2004a,b, 2009). Main characteristics are summarized in Table 1.

Conductivity, salinity, and pH were measured at each sampling date using a WTW Multiline P4 meter (Wissenschaftlich Technische Werkstätten, Weilheim, Germany). Total phosphorus, total nitrogen, and total alkalinity were measured during the period 2001–2002 for Nakuru and Bogoria, and from 2001 to 2005 for Oloidien (details are given in Ballot et al. 2004a,b, 2009).

Phytoplankton samples were obtained from a few centimeters below the water surface at a distance of ~10 m from the shoreline and immediately fixed with formaldehyde (final concentration 1%). The distance chosen was necessary in order to avoid the dense scums of cyanobacteria that establish directly at the shore as a result of wind-induced patchy distribution. Sampling points (Table 1) were located near the foot of the Baboon Cliffs on the lake's western side at Lake Nakuru; at the western shore in a relatively undisturbed part between the Loburo and Mawe Moto hot springs area at Lake Bogoria; and at the northern shore of Lake Oloidien, which is used as a water hole by high numbers of flamingos and livestock. Phytoplankton was counted according to Utermöhl (1958) and photographically documented in sedimentation chambers (Hydro-Bios Apparatebau GmbH, Kiel, Germany) under an inverted microscope Eclipse TS 100 (Nikon Corporation, Tokyo, Japan). The phytoplankton biomass was calculated by geometric approximations using the computerized counting programme Opticount (Sequentix 2006). The specific density of phytoplankton cells was taken as $1\ g \cdot cm^{-3}$.

A visual estimate of the number of flamingos was made at each site and sorted into three categories. For Nakuru and Bogoria, the categories were >500,000; 500,000–100,000; and <100,000 individuals. For Oloidien, the categories were >20,000; 20,000–10,000; and <1,000 individuals. These rough estimates were carried out at strategic points at each lake. In Nakuru, it was carried out from the viewpoint on the Baboon Cliffs, and directly from the shoreline near the main distribution areas around the lake. At the long but narrow Lake Bogoria, estimates were made directly from the western shoreline by driving along the ~20 km road that overlooks the lake to its eastern section. In most cases, it was possible to adjust our estimates by comparing our observed findings with those of the wardens at lakes Nakuru and Bogoria.

RESULTS

Lake Nakuru. The salinity of the shallow Lake Nakuru was highly variable, with values between 17 and 51 ppt. In the period 2001–2009, the phytoplankton community of the lake was dominated by cyanobacteria (Fig. 2; Fig. S1a in the supplementary

TABLE 1. Characteristics of the sampling sites (in physicochemical properties the minimum, median, and maximum values are given).

	Nakuru	Bogoria	Oloidien
Sampling point	00°21′88.70″ S, 36°03′46.50″ E	00°13′83.30″ N 36°05′55.60″ E	00°49′00.88″ S, 36°15′52.15″ E
Surface area (km^2)	40	34	6
Maximum depth (m)	4.5	10.3	4.0
TP[a] ($mg \cdot L^{-1}$)	4.4–7.4–40.0	5.4–9.5–33.6	0.4–0.5–1.0
TN[a] ($mg \cdot L^{-1}$)	1.1–4.3–11.3	0.1–1.7–8.2	0.9–3.4–6.3
pH	10.1–10.2–10.5	9.9–9.9–10.6	9.3–9.7–10.1
Conductivity ($mS \cdot cm^{-1}$)	20.70–43.70–68.80	43.00–66.80–75.20	3.89–5.27–7.41
Salinity (ppt)	17–25–51	39–48–55	1.7–2.5–5.5
Alkalinity[a] ($meq \cdot L^{-1}$)	438–812–1,480	702–1,390–1,760	39–55–65

TN, total nitrogen; TP, total phosphorus.

[a] For lakes Nakuru and Bogoria, from Ballot et al. (2004a,b); for Oloidien, from Ballot et al. (2009).

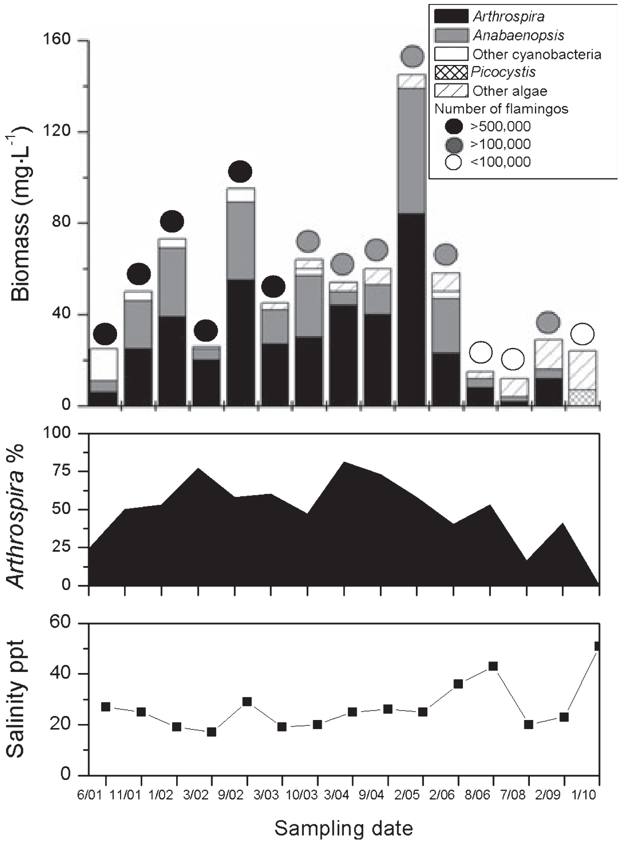

FIG. 2. Changes in total phytoplankton biomass, biomass contribution of the dominant phytoplankton species, number of flamingos, percentage contribution of *Arthrospira* to total phytoplankton biomass, and salinity in Lake Nakuru during the period 2001–2010.

material). *Arthrospira* never exhibited monospecific dominance but was usually accompanied by dense populations of *Anabaenopsis* or *Synechococcus*. *Anabaenopsis* was represented by two species, the coiled *Anabaenopsis arnoldii* (Aptekarj) and the lumpy *Anabaenopsis abijatae* (Kebede et Willén) (Fig. S1a). The biomass contribution of the accompanying taxa was usually between one-third and two-thirds of the total phytoplankton biomass. The highest biomass contribution by *Arthrospira* (81%) was observed in March 2004 when flamingo numbers were ~400,000. Phytoplankton biomass varied between 25 and 145 mg · L^{-1}. However, during the refilling phase after the lake nearly dried out in 2007, the phytoplankton biomass dropped down below 20 mg · L^{-1} and was mostly due to flagellates from different taxonomic groups, especially cryptomonads. Additionally, a few pennate diatoms (most of them belonging to the genus *Nitzschia*) whirled up from the sediment were found in the samples. In January 2010, the cyanobacteria disappeared completely from the phytoplankton and were replaced by the chlorophyte *P. salinarum*, cryptomonads (*Cryptomonas* sp., *Rhodomonas* sp.), and diatoms [*Nitzschia* spp., *Anomoeoneis sphaerophora* (Ehrenb.) Pfitz.] (Fig. S1b).

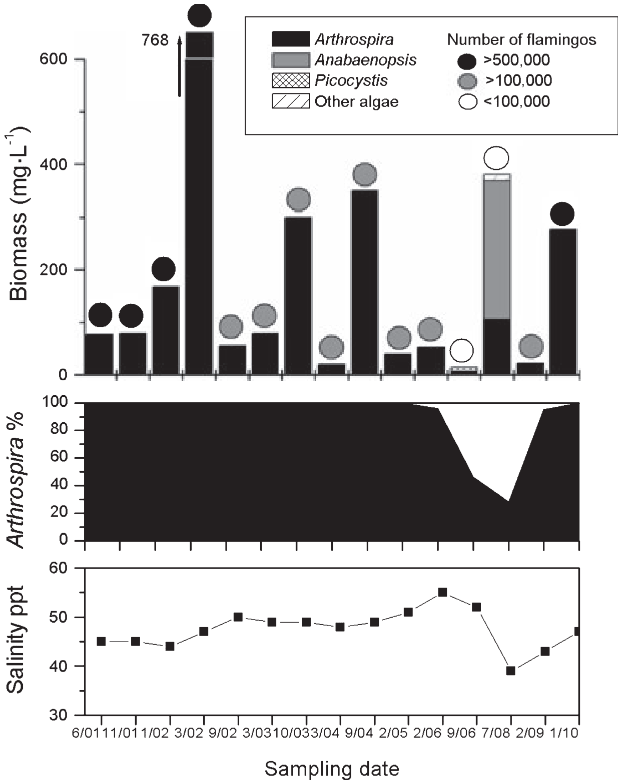

FIG. 3. Changes in phytoplankton biomass, biomass contribution of the dominant phytoplankton species, number of flamingos, percentage contribution of *Arthrospira* to total biomass, and salinity in Lake Bogoria during the period 2001–2010.

The population densities of flamingos at Nakuru from 2001 to March 2003 were relatively high, with numbers of up to one half of a million. In the following years, the numbers fluctuated between 200,000 and 400,000. In 2006, low concentrations of food and prevalence of a disease decimated the flamingos. In July/August 2006, the highest mortality of ~30,000 flamingos was observed at Lake Nakuru. In 2007, the lake almost dried up but was subsequently refilled. During this period, the number of flamingos dropped to <100,000. A slight increase was noticed in 2009, but in January 2010, the number was reduced again to <100,000.

Lake Bogoria. In Lake Bogoria, salinity was higher than that in the other lakes investigated and was relatively stable, varying between 39 and 55 ppt. A wide fluctuation in phytoplankton biomass ranging from 13 to 768 mg · L^{-1} was observed during the study period (Fig. 3). In the years 2001–2005, a nearly monospecific dominance of *A. fusiformis* was observed (Fig. S2a in the supplementary material). In 2006, *Arthrospira* was replaced by the fast-growing (4-fold per day in cultures, L. Krienitz, unpublished results) green picoplankton *P. salinarum* (Fig. 3; Fig. S2, b and c), which overall had a low biomass (2 mg · L^{-1} in February and 7 mg · L^{-1} in September 2006). The cyanobacteria recovered to reestablish dominance in

2008. However, *Arthrospira* contributed only one-third to the overall biomass with the remaining two-thirds (263 mg · L^{-1}) being due to big lumps of *Anabaenopsis* sp. (Fig. S2d). This *Anabaenopsis*, whose species identity could not be determined, exhibited a different morphology compared to *A. arnoldii*, *A. abijatae* (in Lake Nakuru), and *Anabaenopsis elenkinii* V. V. Mill. (in Lake Oloidien). In 2009, *Anabaenopsis* disappeared completely, and *Arthrospira* recovered but produced only a small amount of biomass (21 mg · L^{-1}). In 2010, a monoculture (100% of the biomass) of *Arthrospira* with a high biomass content of 277 mg · L^{-1} was recorded.

The numbers of flamingos in the years 2001 and 2002 were >500,000. In the period between 2003 and 2006, the numbers fluctuated between 200,000 and 400,000. A dramatic collapse of the flamingo population to <100,000 was experienced at Bogoria in September 2006 and again in July 2008 when the phytoplankton was dominated by *Picocystis* and *Anabaenopsis* (Fig. 3). In July 2008, the number of flamingos was further reduced by a die-off that resulted in ~30,000 carcasses accumulating along the shoreline. In January 2010, a large and healthy population of lesser flamingos was observed reaching numbers of >1 million birds.

Lake Oloidien. During the study period, Lake Oloiden was characterized by a gradual increase in salinity from 1.5 (in 2001) to 5.5 ppt (in 2010) (Fig. 4). Phytoplankton community changes that followed the increase in salinity can be divided into three distinct dominance phases (Fig. 4). The first phase, which was recorded in June 2001, was dominated by coccoid green algae (Fig. S3a in the supplementary material). The second phase was characterized by the dominance of coccoid cyanobacteria, with subdominant populations of *A. fusiformis* and *A. elenkinii* from the end of 2001 until 2005 (Fig. S3b). The third phase, which lasted between 2006 and 2010, was dominated by *Arthrospira* with high biomass levels of ~200 mg · L^{-1} (Fig. S3c). The size of the *Arthrospira* in Lake Oloidien was considerably smaller (filaments 10–150 μm long, 4–7 μm broad) (Fig. S3c) than that of the *Arthrospira* from the highly saline lakes Nakuru and Bogoria (100–500 μm long, 8–15 μm broad).

During the early years of our study (2001–2005), the numbers of flamingos never reached 1,000 individuals. However, with the beginning of mass development of *Arthrospira* and accompanying cyanobacteria species, the number of flamingos increased and reached its maximum in September 2006 when more than 20,000 flamingos were observed on the lake. Over the period 2007–2010, a steady flamingo population density of ~15,000 birds was recorded.

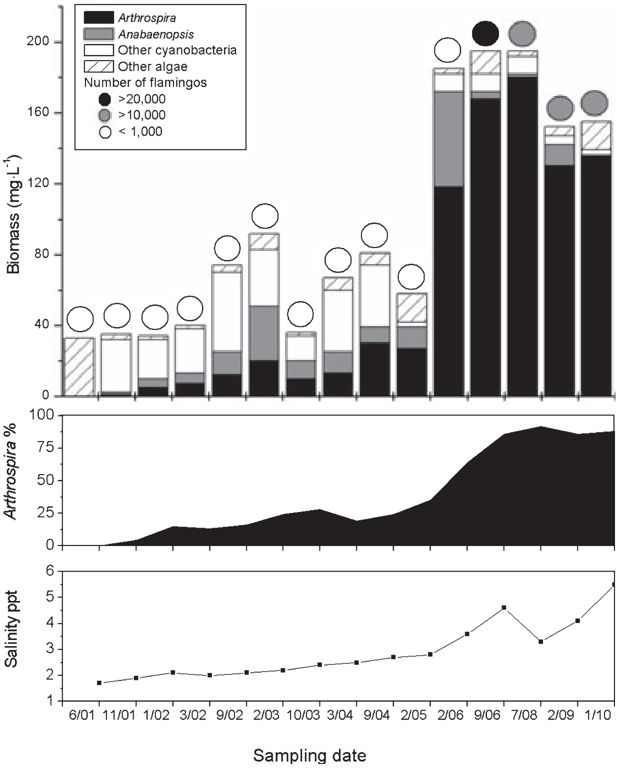

FIG. 4. Changes in total phytoplankton biomass, biomass contribution of the dominant species, number of flamingos, percentage contribution of *Arthrospira* to total phytoplankton biomass, and salinity in Lake Oloidien during the period 2001–2010.

DISCUSSION

Food algal production in the study lakes. The soda lakes of East Africa are often characterized by a dense bloom of the primary producer *Arthrospira* and large populations of the consumer bird *Phoeniconaias*. To maintain a balance between the members of the food web, the lake ecosystem has to provide a huge amount of food algae. In an experiment with caged lesser flamingos at Lake Nakuru, Vareschi (1978) established that an adult bird is able to filter ~30 L of lake water and to ingest 5.6 g dry mass (DM) of *Arthrospira* per hour, which equals to 70 g · d^{-1} DM. The whole flamingo population of ~1 million birds therefore extracts ~60 t · d^{-1} of food algal DM, representing 50%–94% of the daily primary production of the lake. The maximum phytoplankton biomass data of 145 mg · L^{-1} measured in the course of this study were slightly lower than that of >200 mg · L^{-1} recorded by Vareschi (1978) in 1972/1973 and were considerably lower than a maximum of 350–768 mg · L^{-1} recorded in Lake Bogoria over the period 2002–2004. Lake Oloidien, which was recently colonized by lesser flamingos and has a much lower salinity, was found to have a higher biomass of ~200 mg · L^{-1}. The main reason for lower phytoplankton biomass in Nakuru could be the stronger grazing pressure caused by higher numbers of lesser flamingos. Interestingly, the size of *Arthrospira* in Oloidien was remarkably smaller than in the more saline waters. Nevertheless, the length of the *Arthrospira* filaments (~100 μm) is large enough to be filtered by the flamingos. Occurrence of small filaments was also observed in two wastewater treatment ponds in Mozambique (Mussagy et al. 2006) and a sewage pond in Nakuru town (Kotut et al. 2010). Molecular phylogenetic studies have shown that the larger *Arthrospira* strains collected between Bogoria and Nakuru are genetically similar to the smaller strain from Oloidien (Dadheech et al. 2010).

Studies in the 1970s revealed an unusually high instability of the producer populations in the East African soda lakes (Vareschi 1978, Tuite 1981). Occasionally, blooms of the dominant *Arthrospira* were replaced by coccoid cyanobacteria, green algae, heterocytous cyanobacteria such as *Anabaenopsis*, diatoms and/or cryptomonads, a condition that could last for several months (Vareschi 1982). Melack (1988) has discussed eight possible causes of the abrupt switch from one phytoplankton assemblage to another in lakes Elmenteita and Nakuru, which include the following: changes in salinity, nutrient concentrations, and water level; outcompeting of filamentous cyanobacteria by coccoid or flagellated plankton; and attacks by cyanophages or autolysis. Nevertheless, the actual key factors still remain a subject of speculation. Studies by Oduor and Schagerl (2007) and Schagerl and Oduor (2008) focusing on lakes Nakuru, Bogoria, and Elmenteita over the period 2003–2005 also observed a wide variation in phytoplankton primary production rates and community composition, which did not fit into the general patterns of plankton successions.

Contribution of food algae quality and quantity to lesser flamingos' malnutrition. During our long-term study, a dramatic collapse of dominant cyanobacterial populations that did not follow any predictable pattern was observed in lakes Bogoria and Nakuru. In Lake Bogoria, after a long phase (2001–2005) of nearly monospecific dominance by *Arthrospira*, the tiny picoplanktonic green alga *P. salinarum* gained dominance in 2006. We also observed a prevalence of *Picocystis* in Lake Nakuru in 2010. These observations are the first evidence of the occurrence of this unique alga in the African continent that had previously been reported in extreme saline waters of North America and China (Lewin et al. 2000). This alga, which is ~2 μm in diameter, is too small to be retained by lamellae during feeding and produces only a small amount of biomass. Hence, flamingos suffer from starvation when this alga is dominant. Occasions of malnutrition of lesser flamingos accessing only <10% of their minimum daily food requirements have recently been reported at the Kenyan Rift Valley lakes, and the dead flamingos weighed only 63% of their usual body weight (Ton 2007). In March 2004, the phytoplankton of the final sewage pond of Nakuru town, which is situated in the Nakuru National Park, was dominated by small-sized *A. fusiformis* (60 $\mathrm{mg \cdot L^{-1}}$) (Kotut et al. 2010). Flocks of lesser flamingos were observed feeding on the algal food suspension. Obviously, during this period, the concentration of *Arthrospira* in Lake Nakuru was lower (44 $\mathrm{mg \cdot L^{-1}}$) than that in the sewage pond and not sufficient to feed the higher number of flamingos. In July 2006, when the lowest phytoplankton biomass (12 $\mathrm{mg \cdot L^{-1}}$) of the decade was recorded, we observed exhausted, underweight lesser flamingos feeding on neustonic skins of *Euglena* in small freshwater puddles situated several hundreds of meters from the lake shore (Krienitz 2009).

Starvation may also have contributed to the mass die-off at Lake Bogoria in July 2008. After the invasion of *Picocystis* in 2006, measurements carried out revealed that although *Arthrospira* had reestablished, it did not attain its usual dominance. Two-thirds of the phytoplankton was due to *Anabaenopsis* sp. Coincidentally, the deaths of ~30,000 flamingos occurred at the same time with the mass development of *Anabaenopsis* in July 2008. Since no disease infection or cyanotoxins were detected, it is possible that malnutrition could have been the cause of deaths. Large, slimy lumps of *Anabaenopsis* (300–2,000 μm in diameter) clogging the excluders and lamellae (Fig. 1, c and d) could have blocked the food uptake. The excluders are at ~800 μm distance each, while the lamellae of the bills possess 50 μm gaps. In comparison, the filaments of *Arthrospira* are 100–500 μm long, and the coils are 20–60 μm broad.

Possible intoxication of lesser flamingos by food algae. In addition to the problem of reduced food supply, another problem facing the flamingos is associated with the quality of the food algae. The birds are susceptible to poisoning by cyanobacterial toxins, which are usually taken up during feeding (Codd et al. 2003). In soda lakes, the possible sources of the toxins are the phytoplankton (Nostocales) and benthic cyanobacteria (Oscillatoriales) occurring in hot springs on the shoreline of Lake Bogoria (Krienitz et al. 2003, 2005, Ballot et al. 2004a,b, 2005, Kotut et al. 2006). Ndetei and Muhandiki (2005) reported the frequent occurrence of the microcystin-producing *Microcystis flos-aquae* in Lake Nakuru. However, our microscopic observations of samples from Lake Nakuru never revealed any *Microcystis* species but always *A. abijatae*, a nostocalean cyanobacterium that was first recorded in the alkaline Ethiopian lake Abijata by Kebede and Willén (1996). *A. abijatae* is filamentous; however, the filaments are coiled up in very dense lumps, which can easily be confused with *Microcystis* colonies (Ballot et al. 2008). We observed *Microcystis* taxa only in Kenyan freshwaters (lakes Victoria, Naivasha, and Baringo and several smaller reservoirs and ponds) (Krienitz et al. 2002, Ballot et al. 2003, 2009), and never in the soda lakes. Generally, *Microcystis* occurs in both freshwater and saline waters (salt concentration >50 $\mathrm{mg \cdot L^{-1}}$). However, they only survive in waters with low alkalinity (Hammer et al. 1983, Wood and Talling 1988, Kebede and Willén 1998).

Practically each of the main cyanobacterial producers in the study lakes has, according to literature surveys, the potential to produce toxins (Carmichael et al. 2001, Codd et al. 2005). Even the main food of the lesser flamingos, *Arthrospira*, is suspected to act as a possible intoxicant. Although several studies have revealed the high nutritional and pharmaceutical value as well as the nontoxic nature of this cyanobacterium (Cifferi 1983, Belay et al. 1993, Fox 1996, Salazar et al. 1998), a few reports have commented on its potential toxicity. Iwasa et al. (2002) report on the hepatotoxic symptoms of a patient after treatment with *Arthrospira*-based tablets. Recently, neurotoxic effects of beta-*N*-methylamino-L-alanin (BMAA) from *Arthrospira*-based dietary supplements or pharmaceuticals were reported (Papapetropoulos 2007, Mazokopakis et al. 2008). Of a total of 40 *Arthrospira* strains isolated from Kenyas waters, two potentially toxic strains containing low concentrations of microcystins and anatoxin-a have been identified (Ballot et al. 2004a,b, 2005), but a survey on three other *Arthrospira* strains (two from a sewage pond in Mozambique, and one from Lake Nakuru, Kenya) did not reveal toxicity under test conditions (Mussagy et al. 2006). Mouse bioassays using crude extracts of monospecific, dense *Arthrospira* blooms from the soda lake Big Momella (Tanzania) revealed the potential toxicity of these natural cyanobacterial populations to lesser flamingos (Lugomela et al. 2006). Further evidence pointing to the potential exposure of flamingos to cyanotoxins was provided by the detection of aminotransferase domains for cyanotoxin production in sediments of the East African alkaline lakes (Dadheech et al. 2009). Metcalf et al. (2006) detected microcystins and anatoxin-a in extracts of basal wing feathers of lesser flamingos. The study hypothesized that under natural conditions, the toxins are sequestered in the feathers of lesser flamingos. However, due to the growing environmental stress, sequestration mechanism in the weakened flamingos may not be effective enough to protect the birds against cyanotoxicosis. All these results, which to some extent are debatable, show the urgent need for further studies to clarify the contribution of toxic cyanobacteria to sudden flamingo deaths in general and of *Arthrospira* in particular.

General outcome. Our results clearly indicate that the problems of food algae quantity and quality facing the lesser flamingos are complex. The available food algae might be inadequate or too small (*Picocystis*) or too large (*Anabaenopsis*) for uptake. At other times, the food can be toxic. These combined challenges related to food algae weaken the birds, leading to mass die-offs. The first well-documented case of massive lesser flamingo die-offs was reported from Lake Nakuru in 1974 (Sileo et al. 1979). The reason given to explain the die-off was an interaction of two different factors—starvation induced by a sudden reduction of *Arthrospira* population and the infection of the weakened birds by *M. avium* Chester (avian tuberculosis). The highest mortality of ~30,000 flamingos was observed at Lake Nakuru in July/August 2006. This mortality was mainly caused by an infection by *P. aeruginosa*, a common opportunistic bacterium that causes inflammation of inner organs of animals with weakened immune system. The weakening of birds was probably caused by a complex of stress factors including cyanotoxins, agrochemicals, and water stress (Njuguna and Owuor 2006). The lake is surrounded by densely populated hills, and hence it is greatly affected by the adverse environmental changes associated with human population increase, such as deforestation, intensive agricultural activities, and water discharge (Mathooko 2001, Kotut et al. 2010).

Lesser flamingos can respond to the fluctuations of algal food supply by migrating to other lakes. Compared to other water birds, flamingos show the highest variation of individual numbers at Kenyan lakes studied (Owino et al. 2001). Migration may also be for the purpose of accessing breeding sites. Worldwide, only six sites are used for breeding by the lesser flamingos: Lake Natron (Tanzania), Etosha Pan (Namibia), Makgadikgadi-Pan (Botswana), Kamfers Dam (South Africa), as well as two pans in the ''Little Rann of Kachchh'' (India) (Childress et al. 2008). Our study shows the importance of protecting the habitats of lesser flamingos, a species classified as nearly threatened in the red list of the International Union for the Conservation of Nature (IUCN). The major threats to the survival of the lesser flamingo are the loss and/or the degradation of its specialized habitat. *An International Single Species Action Plan for Conservation of the Lesser Flamingo* that was commissioned by IUCN-SSC/Wetlands International Flamingo Specialist Group and Wildfowl & Wetlands Trust has been adopted (Childress et al. 2008). The action plan aims at addressing the threats facing the lesser flamingos.

We thank the Government of Kenya for permission to carry out this research (No. MOEST 13/001/31 C 90). We are grateful to the German Federal Ministry of Education and Research for its financial support (grant no. 01LC0001). Our sincere appreciation is also due to the county councils of Koibatek and Baringo districts and the Kenya Wildlife Service for granting us access to lakes Bogoria and Nakuru. Our gratitude is also due to Andreas Ballot, Christina Bock, Peter Casper, Geoffrey A. Codd, Stephen M. Gichobi, William Kimosop, Oliver Nasirwa, Stephan Pflugmacher, Ekkehard Vareschi (†), and Claudia Wiegand for their assistance in the field and/or useful discussions. We thank two anonymous reviewers for valuable suggestions and advice.

Ballot, A., Dadheech, P. K., Haande, S. & Krienitz, L. 2008. Morphological and phylogenetic analysis of *Anabaenopsis abijatae* and *Anabaenopsis elenkinii* (Nostocales, Cyanobacteria) from tropical inland water bodies. *Microb. Ecol.* 55:608–18.

Ballot, A., Dadheech, P. & Krienitz, L. 2004a. Phylogenetic relationship of *Arthrospira*, *Phormidium* and *Spirulina* strains from Kenyan and Indian waterbodies. *Algol. Stud.* 113:37–56.

Ballot, A., Kotut, K., Novelo, E. & Krienitz, L. 2009. Changes of phytoplankton communities in Lakes Naivasha and Oloidien, examples of degradation and salinization of lakes in the Kenyan Rift Valley. *Hydrobiologia* 632:359–63.

Ballot, A., Krienitz, L., Kotut, K., Wiegand, C., Metcalf, J. S., Codd, G. A. & Pflugmacher, S. 2004b. Cyanobacteria and cyanobacterial toxins in three alkaline Rift Valley lakes of Kenya – Lakes Bogoria, Nakuru and Elmenteita. *J. Plankton Res.* 26: 925–35.

Ballot, A., Krienitz, L., Kotut, K., Wiegand, C. & Pflugmacher, S. 2005. Cyanobacteria and cyanobacterial toxins in the alkaline crater lakes Sonachi and Simbi, Kenya. *Harmful Algae* 4: 139–50.

Ballot, A., Pflugmacher, S., Wiegand, C., Kotut, K. & Krienitz, L. 2003. Cyanobacterial toxins in Lake Baringo, Kenya. *Limnologica* 33:2–9.

Belay, A., Ota, Y., Miyakawa, K. & Shimamatsu, H. 1993. Current knowledge on potential health benefits of *Spirulina*. *J. Appl. Phycol.* 5:235–41.

Brown, L. H. 1973. *The Mystery of the Flamingos*. East African Publishing House, Nairobi, Kenya, 116 pp.

Carmichael, W. W., Azevedo, S. M. F. O., An, J. S., Molica, J. R., Jochimsen, E. M., Lau, S., Rinehart, K. L., Shaw, G. R. & Eaglesham, G. K. 2001. Human fatalities from cyanobacteria: chemical and biological evidence for cyanotoxins. *Environ. Health Perspect.* 109:663–8.

Childress, B., Nagy, S. & Hughes, B. 2008. *International Single Species Action Plan for Conservation of the Lesser Flamingo (Phoenicopterus minor)*. CMS Technical Series No. 18, AEWA Technical Series No. 34, Bonn, Germany, 59 pp.

Cifferi, O. 1983. *Spirulina,* the edible microorganism. *Microbiol. Rev.* 47:551–78.

Codd, G. A., Metcalf, J. S., Morrison, L. F., Krienitz, L., Ballot, A., Pflugmacher, S., Wiegand, C. & Kotut, K. 2003. Susceptibility of flamingos to cyanobacterial toxins via feeding. *Vet. Rec.* 152:722–3.

Codd, G. A., Morrison, L. F. & Metcalf, J. S. 2005. Cyanobacterial toxins: risk management for health protection. *Toxicol. Appl. Pharmacol.* 203:264–72.

Dadheech, P. K., Ballot, A., Casper, P., Kotut, K., Novelo, E., Lemma, B., Pröschold, T. & Krienitz, L. 2010. Phylogenetic relationship and divergence among planktonic strains of *Arthrospira* (Oscillatoriales, Cyanobacteria) of African, Asian and American origin deduced by 16S-23S ITS and phycocyanin operon sequences. *Phycologia* 49:361–72.

Dadheech, P. K., Krienitz, L., Kotut, K., Ballot, A. & Casper, P. 2009. Molecular detection of uncultured cyanobacteria and aminotransferase domains for cyanotoxin production in sediments. *FEMS Microbiol. Ecol.* 68:340–50.

Fox, R. D. 1996. *Spirulina: Production & Potential*. EDISUD, Aix-en-Provence, France, 232 pp.

Greichus, Y. A., Greichus, A., Amman, B. B. & Hopcraft, J. 1978. Insecticides, polychlorinated biphenyls and metals in African lake ecosystems. III. Lake Nakuru, Kenya. *Bull. Environ. Contam. Toxicol.* 19:454–61.

Hammer, U. T., Shamess, J. & Haynes, R. C. 1983. The distribution and the abundance of algae in saline lakes of Saskatchewan, Canada. *Hydrobiologia* 105:1–26.

Harper, D. M., Childress, R. B., Harper, M. M., Boar, R. R., Hickley, P. H., Mills, S. C., Otieno, N., et al. 2003. Aquatic biodiversity and saline lakes: Lake Bogoria National Reserve, Kenya. *Hydrobiologia* 500:259–76.

Iwasa, M., Yamamoto, M., Tanaka, Y., Kaito, M. & Adach, Y. 2002. *Spirulina*-associated hepatotoxicity. *Am. J. Gastroenterol.* 97: 3212–3.

Jenkin, P. M. 1929. Biology of lakes in Kenya. *Nature* 124:574.

Jenkin, P. M. 1957. The filter feeding and food of flamingoes (Phoenicopteri). *Philos. Trans. R. Soc. B* 240:401–93.

Kairu, J. K. 1996. Heavy metals residues in birds of Lake Nakuru, Kenya. *Afr. J. Ecol.* 34:397–400.

Kebede, E. & Willén, E. 1996. *Anabaenopsis abijatae*, a new cyanophyte from Lake Abijata, an alkaline, saline lake in the Ethiopian Rift Valley. *Algol. Stud.* 80:1–8.

Kebede, E. & Willén, E. 1998. Phytoplankton in a salinity-alkalinity series of lakes in the Ethiopian Rift Valley. *Algol. Stud.* 89:63–96.

Kock, N. D., Kock, R. A., Wambua, J., Kamau, G. J. & Mohan, K. 1999. *Mycobacterium avium*-related epizootic in free ranging Lesser Flamingos in Kenya. *J. Wildl. Dis.* 35:297–300.

Koenig, R. 2006. The pink death: die-offs of the Lesser Flamingo raise concern. *Science* 313:1724–5.

Kotut, K., Ballot, A. & Krienitz, L. 2006. Toxic cyanobacteria and their toxins in standing waters of Kenya: implications for water resource use. *J. Water Health* 4:233–45.

Kotut, K., Ballot, A., Wiegand, C. & Krienitz, L. 2010. Toxic cyanobacteria at Nakuru sewage oxidation ponds – a potential threat to wildlife. *Limnologica* 40:47–53.

Krienitz, L. 2009. Die Nahrungsprobleme des Zwergflamingos. *BiuZ* 39:258–66.

Krienitz, L., Ballot, A., Casper, P., Codd, G. A., Kotut, K., Metcalf, J. S., Morrison, L. F., Pflugmacher, S. & Wiegand, C. 2005. Contribution of toxic cyanobacteria to massive deaths of Lesser Flamingos at saline-alkaline lakes of Kenya. *Verh. Int. Ver. Limnol.* 29:783–6.

Krienitz, L., Ballot, A., Kotut, K., Wiegand, C., Pütz, S., Metcalf, J. S., Codd, G. A. & Pflugmacher, S. 2003. Contribution of hot spring cyanobacteria to the mysterious deaths of Lesser Flamingos at Lake Bogoria, Kenya. *FEMS Microbiol. Ecol.* 1437:141–8.

Krienitz, L., Ballot, A., Wiegand, C., Kotut, K., Codd, G. A. & Pflugmacher, S. 2002. Cyanotoxin producing bloom of *Anabaena flos-aquae*, *Anabaena discoidea* and *Microcystis aeruginosa* (Cyanobacteria) in Nyanza Gulf of Lake Victoria, Kenya. *J. Appl. Botany* 76:179–83.

Lewin, R. A., Krienitz, L., Goericke, R., Takeda, H. & Hepperle, D. 2000. *Picocystis salinarum* gen. et sp. nov. (Chlorophyta) – a new picoplanktonic green alga. *Phycologia* 39:560–5.

Lugomela, C., Pratap, H. B. & Mgaya, Y. D. 2006. Cyanobacteria blooms – a possible cause of mass mortality of Lesser Flamingos in Lake Manyara and Lake Big Momela, Tanzania. *Harmful Algae* 5:534–41.

Mari, C. & Collar, C. 2000. *Pink Africa*. The Harvill Press, London, 207 pp.

Mathooko, J. M. 2001. Disturbance of a Kenya Rift Valley stream by the daily activities of local people and their livestock. *Hydrobiologia* 458:131–9.

Mazokopakis, E. E., Karefilakis, C. M., Tsartsalis, A. N., Milkas, A. N. & Ganotakis, E. S. 2008. Acute rhabdomyolysis caused by *Spirulina* (*Arthrospira platensis*). *Phytomedicine* 15:525–7.

Melack, J. M. 1988. Primary producer dynamics associated with evaporative concentration in a shallow, equatorial soda lake (Lake Elmenteita, Kenya). *Hydrobiologia* 158:1–14.

Metcalf, J. S., Morrison, L. F., Krienitz, L., Ballot, A., Krause, E., Kotut, K., Pütz, S., Wiegand, C., Pflugmacher, S. & Codd, G. A. 2006. Analysis of cyanotoxins anatoxin-a and microcystins in Lesser Flamingo feathers. *Toxicol. Environ. Chem.* 88:159–67.

Motelin, G., Thampy, R. & Doros, D. 2000. An ecotoxicological study of the potential roles of metals, pesticides and algal toxins on the 1993/5 Lesser Flamingo mass die-offs in Lake Bogoria and Nakuru, Kenya; and the health status of the same species of birds in the Rift Valley Lakes during the 1990s. *In: Proceedings of the East African Environmental Forum, Nairobi, May 2000*, pp. 11–2.

Mussagy, A., Annadotter, H. & Cronberg, G. 2006. An experimental study of toxin production in *Arthrospira fusiformis* (Cyanophyceae) isolated from African waters. *Toxicon* 48:1027–34.

Ndetei, R. & Muhandiki, V. S. 2005. Mortalities of lesser flamingos in Kenyan Rift Valley saline lakes and the implications for sustainable management of the lakes. *Lakes Reserv. Res. Manag.* 10:51–8.

Njuguna, M. & Owuor, O. 2006. Lake Nakuru: flamingo death camp. *Daily Nation Nairobi, Horizons*, Sep. 7, 2006, pp. 1–2.

Oduor, S. O. & Schagerl, M. 2007. Phytoplankton photosynthetic characteristics in three Kenyan Rift Valley saline-alkaline lakes. *J. Plankton Res.* 29:1041–50.

Owino, A. O., Oyugi, J. O., Nasirwa, O. O. & Bennun, L. A. 2001. Patterns of variation in waterbird numbers on four Rift Valley lakes in Kenya, 1991–1999. *Hydrobiologia* 458:45–53.

Papapetropoulos, S. 2007. Is there a role for naturally occurring cyanobacterial toxins in neurodegeneration? The beta-N-methylamino-L-alanine (BMAA) paradigm. *Neurochem. Int.* 50:998–1003.

Salazar, M., Martinez, E., Madrigal, E., Ruiz, L. E. & Chamorro, G. A. 1998. Subchronic toxicity study in mice fed *Spirulina maxima*. *J. Ethnopharmacol.* 62:235–41.

Schagerl, M. & Oduor, S. O. 2008. Phytoplankton community relationship to environmental variables in three Kenyan Rift Valley saline-alkaline lakes. *Mar. Freshw. Res.* 59:125–36.

Sequentix. 2006. *Opticount*. Available at: http://www.sequentix.de (last accessed 27 September 2010).

Sileo, L., Grootenhuise, J. G., Tuite, G. H. & Hopcraft, H. D. 1979. Microbacteriosis in the lesser flamingo of Lake Nakuru, Kenya. *J. Wildl. Dis.* 15:387–90.

Ton, T. 2007. Pink starvation: flamingos in Africa malnourished. *Epoch Times*. Available at: http://en.epochtimes.com/news/7-1-23/50812.html (last accessed 27 September 2010).

Tuite, C. H. 1981. Standing crop densities and distribution of *Spirulina* and benthic diatoms in East African alkaline saline lakes. *Freshw. Biol.* 11:345–60.

Tuite, C. H. 2000. The distribution and density of Lesser Flamingos in East Africa in relation to food availability and productivity. *Waterbirds (Spec. Publ.)* 23:52–63.

Utermöhl, H. 1958. Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. *Mitt. Int. Ver. Limnol.* 9:1–38.

Vareschi, E. 1978. The ecology of Lake Nakuru (Kenya) I. Abundance and feeding of the Lesser Flamingo. *Oecologia* 32:11–35.

Vareschi, E. 1982. The ecology of Lake Nakuru (Kenya) III. Abiotic factors and primary production. *Oecologia* 55:81–101.

Vareschi, E. & Jacobs, J. 1985. The ecology of Lake Nakuru VI. Synopsis of production and energy flow. *Oecologia* 65:412–24.

Vonshak, A. 1997. *Spirulina*: growth, physiology and biochemistry. *In* Vonshak, A. [Ed.] Spirulina platensis (Arthrospira*) Physiology, Cell Biology and Biotechnology*. Taylor & Francis, London, pp. 43–65.

Wood, R. B. & Talling, J. F. 1988. Chemical and algal relationships in a salinity series of Ethiopian inland water. *Hydrobiologia* 158:29–67.

Supplementary Material

The following supplementary material is available for this article:

Figure S1. Phytoplankton from Lake Nakuru sampled on February 2005 (a) and January 2010 (b) in sedimentation chambers.

Figure S2. Phytoplankton from Lake Bogoria sampled in October 2003 (a), September 2006 (b and c), and July 2008 (d) in sedimentation chambers.

Figure S3. Phytoplankton from Lake Oloidien sampled in June 2001 (a), March 2002 (b), and February 2009 (c) in sedimentation chambers.

This material is available as part of the online article.