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Food algae for Lesser Flamingos: a stocktaking

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Abstract Lesser Flamingo, the flagship species of saline wetlands of Africa and India, is a specialised feeder subsisting on microscopic cyanobacteria and algae. To establish the relationship between flamingo occurrence and food algal abundance and quality, an extensive microphyte survey in more than 150 sampling trips to seven countries over a 15-years period (2001–2015) was carried out. The 44 habitat sites included the core soda lakes in eastern Africa (Bogoria, Nakuru, Elmentaita, Oloidien), where the highest numbers of flamingos were observed, and five breeding sites in eastern and southern Africa as well as in north-western India. A reference describing the diversity of microphytes was established including members of three orders of cyanobacteria and nine orders of eukaryotic algae that potentially could act as food source for Lesser Flamingos. Preferred food organisms consisted of filamentous cyanobacteria, mainly *Arthrospira*, as well as benthic diatoms. Further investigation on the suitability of other microphytes as alternative flamingo diet revealed the food potential of chlorophytes and euglenophytes. This paper discusses a phycological perspective in the feeding ecology of Lesser Flamingos. The survey findings can assist scientists and conservationists in evaluating

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the potential of wetlands to support flocks of this endangered bird.

Keywords *Arthrospira fusiformis* · Cyanobacteria · Benthic diatoms · Extreme habitats · Food web interaction · Saline wetlands · Tropical soda lakes

Introduction

Considered as an embodiment of the mythical firebird *Phoenix* (Mari & Collar, 2000; Reichholf, 2012), the Lesser Flamingo (*Phoeniconaias minor* Geoffroy Saint-Hilaire) (Fig. 1), is the flagship species of harsh saline-alkaline wetland and lake environments (Childress et al., 2008). This food specialist occurs on salt pans and soda lakes of Africa (Brown, 1959; Berry, 1972; Vareschi, 1978) and India (Parasharya, 2009; Parasharya et al., 2015), where it survives on microscopic cyanobacteria and algae that establish dense populations in water and mud under extreme conditions (Tuite, 1981; Vareschi & Jacobs, 1985). With specially developed lamellae in the bill, the Lesser Flamingo filters food organisms within a size range of between 15 and 800 μm (Jenkin, 1957). Large blooms of the spirally twisted filaments of the cyanobacterium *Arthrospira fusiformis* (Voronikhin) Komárek et Lund are the preferred diet (Vareschi, 1978; Tuite, 1981, 2000; Kaggwa et al., 2013a). However, this cyanobacterium is not always available in adequate quantities (Vareschi, 1978; Tuite, 1981; Burgis & Symoens, 1987; Schagerl et al., 2015). Hence, the Lesser Flamingo exhibits a nomadic behaviour as it searches for other suitable food sources (Tuite, 2000). The

Fig. 1 Lesser Flamingos at Lake Bogoria

itinerant behaviour of these flamingos (McCulloch et al., 2003; Childress et al., 2006) creates a complex distribution pattern characterised by strong fluctuations in population densities of the bird at a given site (Childress et al., 2008). According to contemporary reports, food scarcity has been aggravated by habitat degradation resulting in erratic changes in populations of cyanobacteria and algae (Ndetei & Muhandiki, 2005; Beangstrom, 2011; Zimmermann et al., 2011; BirdLife International, 2012; Krienitz et al., 2013a; Anderson, 2015). However, information on the alternative food algae that the Lesser Flamingos exploit if *Arthrospira* is not available is still missing and therefore particularly timely (Ridley et al., 1955; Krienitz & Kotut, 2010). The findings provided in this extensive microphyte survey attempts to fill this information gap.

Our study comprises findings from habitats of the core soda lakes in eastern Africa, where the highest numbers of flamingos were observed, four breeding sites in Africa and one breeding site in India. From the more than 150 sampling trips carried out, we sampled mostly planktonic but also benthic microphytes of 44 habitats in seven countries in a span of over 15 years (2001–2015). In this paper, we focus on the phycological perspective of the potential food and effort to contribute to the feeding ecology of the Lesser Flamingo. The paper also seeks to demonstrate the importance of microscopical surveys in identifying cyanobacteria and algae, which are suitable as food for these flamingos and their predominance among microphytes in soda lakes and salt pans. By giving an ecological outlook to this microscopical inquiry, the information provided will be of value to ecologists, ornithologists and stakeholders to identify suitable habitats that can support Lesser Flamingos and to manage protection of this endangered bird species.

Materials and methods

Sampling sites

The size and depth of saline waters in the tropics vary considerably as a result of the strong influence of climate and the hydrological regime (Beadle, 1974; Burgis & Morris, 1987; Mason et al., 1994; Verschuren, 2003). The extent of these fluctuations largely depends on the morphometry of the habitats,

and is greatest when margins are flat (MacIntyre & Melack, 1982; Harper et al., 2003). Some of the waters investigated during the study period alternated between nearly dried out to fully filled up phases (Krienitz & Kotut, 2010). Hence, the values given can only be considered as rough estimates. The sampling sites are listed and described in greater detail in the Electronic Supplementary Material (ESM_1).

Sampling and microscopy

Sampling was carried out over the period 2001–2015. Owing to logistic challenges, the sampling frequency varied widely among the sites. Whereas four soda lakes in the Kenyan part of the Great African Rift Valley were studied regularly each year, other sites were only accessed once (ESM_2). At each site, water samples for phytoplankton counting were scooped from a depth of about 10 cm below the water surface and preserved with Lugol's solution. Phytoplankton samples for morphological studies were concentrated with plankton nets of 10 or 25 μm mesh size and fixed with formalin. Benthic algae were scraped from stones or dead macrophytes with a spoon or skimmed off from the sediment surface. Salinity, conductivity and pH were measured at each sampling site using a WTW Multiline P4 meter (Wissenschaftlich-Technische Werkstätten Weilheim, Germany). All samples including main data measured are listed in ESM_2. Based on the salinity values recorded, all the wetlands studied were grouped into five salinity classes ranging from fresh (<0.5) to hypersaline (>50 ppt) using the classification scheme of Hammer (1986) (Table in ESM_1).

Phytoplankton and benthic algae were studied and photographically documented with a Nikon Eclipse E 600 light microscope using a Nikon digital camera DS-Fi1 and Nikon software NIS-Elements D (Nikon Corporation, Tokyo, Japan). Selected samples were deposited at the Botanical Museum at Berlin-Dahlem under the designation B 52 0000 161-231 (Table 2 in ESM_2). Diatoms samples were obtained from biofilms on stones and sediments of the selected lakes (ESM_3). The samples were prepared following the procedure described by Kalbe & Werner (1974). The permanent slides (Naphrax®) developed were examined under the light microscope using a ZEISS Axioplan (oil-immersion Plan-Apochromat objective, ×1,000 magnification, numerical aperture 1.4). The

sampled biofilms did not allow for the quantitative analyses of biomass per unit area or volume for the diatoms. Biofilm diatom frequency was therefore recorded on a scale of 1–3 (3—mass development or very numerous, 2—numerous, 1—seldom) and x for only single occurrence, as compared to other algae and cyanobacteria. For counting the sum of frequency, x was replaced by an arbitrary constant of 0.2 (ESM_3).

Scanning electron microscopy (SEM) studies were carried out using cleaned samples (Kalbe & Werner, 1974). The suspensions of algae were dropped and dried on aluminium stubs, coated with gold/palladium and investigated under a ZEISS-Merlin SEM (ZEISS, Oberkochen, Germany) 5–10 kV, 10 μA. Further SEM analyses were carried out with a Hitachi S-4500 (Hitachi Corporation, Tokyo, Japan).

To establish the phytoplankton biomass of water bodies, the Lugol iodine preserved samples were counted in sedimentation chambers (Hydro-Bios Apparatebau GmbH, Kiel, Germany) under an inverted microscope Eclipse TS 100 (Nikon Corporation, Tokyo, Japan) following the method of Utermöhl (1958). The phytoplankton biomass (fresh weight) was calculated by geometric approximations using the computerised counting programme OPTICOUNT (Opticount, 2008). The specific density of phytoplankton cells was taken as 1 g cm^{-3}.

Besides an assessment of flamingo food quantity, food quality was also evaluated in Lesser Flamingo habitats. We determined which cyanobacteria and algae other than the primary food *Arthrospira* match the ingestion requirements of Lesser Flamingos (in terms of cell size and other phycological characteristics such as the appearance as single cells or the formation of colonies with or without mucilaginous envelopes). All the taxa present were grouped into five categories that describe their suitability rating as food for the Lesser Flamingo (Table 1). It is important to note that each category of food suitability is based on microscopical observations of more than 170 individual samples taken during this extended microphyte survey. The categories of food suitability from Table 1 can be summarised as follows: 5—primary food *Arthrospira*, 4—alternate food of good suitability such as *Anabaenopsis* and many other filamentous cyanobacteria, diatoms and specific *Euglena* species, 3—moderate food suitability of specific chlorophytes as these species may form large aggregates depending

Table 1 Cyanobacteria and algae occurring in flamingo habitats and their food suitability

	Main occurrence	Salinity range (ppt)	Category of food suitability
Arthrospira fusiformis large size	Lakes Bogoria, Elmentaita, Nakuru, Simbi, Sonachi (Kenya),	High abundance 11–55	5
	Lake Big Momella (Tanzania),	Low abundance	
	Lake Sambhar area (India)	0–300	
Arthrospira fusiformis, small size	Lake Oloidien (Kenya),	11–4.1	5
	Sewage outfall ponds Walvis Bay (Namibia), Kamfers Dam (South Africa)		
Anabaenopsis abijatae	Lakes Bogoria, Elmentaita, Nakuru (Kenya)	10–30	4
Anabaenopsis arnoldii	Lakes Elmentaita, Nakuru (Kenya), Burunge (Tanzania)	10–30	4
Anabaenopsis elenkinii	Lake Oloidien (Kenya)	1–15	4
Anabaenopsis sp.	Etosha Pan, sewage outfall ponds (Namibia)	18–26	4
Cyanospira capsulata	Lakes Bogoria, Magadi (Kenya)	30–40	2
Cyanospira rippkae	Lake Nakuru (Kenya)	25–35	4
Haloleptolyngbya alcalis	Lakes Nakuru, Elmentaita (Kenya), Natron (Tanzania)	5–10	4
Oscillatoria div. spec., *Phormidium* div. spec.	Etosha Pan region (Namibia)	1–55	4
	Makgadikgadi Pan (Botswana)		
	Lake Sambhar region (India)		
Solitary picocyanobacteria, *Synechococcus* sp.	Lakes Elmentaita, Oloidien, Sewage oxidation ponds Nakuru, Hot Springs Bogoria (Kenya),	0–300	1
	Lakes Makat, Manyara (Tanzania)		
	Lakes Bagusa, Katwe (Uganda)		
Diatoms (Soda lakes)	Lakes Nakuru, Magadi (Kenya),	3–63	4
	Lake Natron (Tanzania)		
Diatoms (Marine mudflats)	Lagoon, Walvis Bay (Namibia)	35–36	4
Diatoms (Salt ponds)	Salt evaporation ponds (Namibia)	35–68	4
Diatoms (Salt pans)	Little Rann of Kutch (India)	1.7–37	4
Picocystis salinarum	Lakes Bogoria, Nakuru & Magadi (Kenya)	50–300	1
Coccoid chlorophytes	Lakes Nakuru, Elmentaita, Magadi, Oloidien, Sonachi (Kenya), Etosha Pan (Namibia), Makgadikgadi Pan (Botswana)	1–12–(40)	3
Microchloropsis salina	Salt evaporation ponds Swakopmund (Namibia)	60–70	1
Coccoid eustigmatophytes	Lakes Elmentaita, Nakuru (Kenya)	3–6	1
Dunaliella sp.	Lake Sambhar (India)	120–200	1
Tetraselmis sp. and other green flagellates	Sewage outfall ponds Walvis Bay (Namibia) Lake Nakuru (Kenya)	5–60	1
Euglena div. spec.	Lake Nakuru (Kenya),	1–6	4
	Sewage outfall ponds Walvis Bay (Namibia)		
Cryptomonas	Lake Nakuru (Kenya)	9–23	1

(Category of food suitability: *5* priority food of Lesser Flamingos, *4* suitable alternative food, *3* depending on aggregation size suitable or not, *2* too large for ingestion *1* too small for ingestion)

on the species and growth conditions, 2—not suitable food which might be avoided such as *Cyanospira* too large for ingestion and 1—not suitable food which cannot be retained because of the small size, in particular in case of single cells of picoplanktonic species and a number of small eukaryotic flagellates of various taxonomic affiliations.

During the low-salinity phase experienced in Lake Nakuru in January 2015, we encountered difficulties in our attempts to identify the organisms by microscopy. To overcome this challenge, we applied the molecular method of 454 pyrosequencing (see in ESM_4 for details) to determine phytoplankton composition. The application of molecular methods is part of ongoing investigations to gain a better insight into the biodiversity of saline lakes and wetlands in Africa.

At each site visited, a visual estimate of the number of flamingos was carried at strategic points along the shore or from the boat. These estimates were categorised by a semiquantitative ranking into four abundance groups ($+++$ = >100,000; $++$ = >10,000; $+$ = >1,000; O = <1,000). In many cases, it was possible to adjust our estimates by comparing our observed findings with those of the guides and wardens at the sampling sites.

Additional photos of microphytes and sampling sites are as compiled in ESM_5.

Statistical analyses

The whole dataset of phytoplankton observations in seven countries comprised more than 170 samples (ESM_2), which were partly used for statistical analyses. In case of 143 samples, we quantified the phytoplankton composition microscopically as described before and used 142 of them to analyse the microphyte food pattern (one sample with a «milky» appearance was excluded as it had no microphytes). As many of these data referred to a sporadic sampling in lakes and wetlands, we further focused on a less-biased dataset that covers the four main lakes where samples were taken over 15 years ($n = 60$ with 15 values for each lake). According to the non-parametric Shapiro test (Dunn & Clark, 1974), none of the phytoplankton biomass parameters (biomass of taxonomic groups or single taxa) followed a normal distribution. To determine whether there was a significant difference in food availability among the four abundance groups of the Lesser Flamingo (ranked

ordinal data covering four flamingo abundance groups), we applied non-parametric tests using R (R i386 Version 2.15.2). We used Kruskal–Wallis Tests to determine differences between median values of the phytoplankton (*Arthrospira*, *Anabaenopsis* and «others») of the four flamingo abundance groups. For identifying homogeneous subsets when comparing these median values, we carried out pairwise Mann–Whitney U Tests with a Bonferroni correction. The phytoplankton biomass and the proportion of single taxa representing potential food for the Lesser Flamingo were here displayed as box-and-whisker plots using SigmaPlot 10 (SPSS Inc., Chicago, USA). The line inside the box indicates the median, both ends of the box the 25th and 75th percentile and the error bars the 10th and 90th percentile.

For graphical display of food pattern along the large range of phytoplankton biomass (0.9–3159 mg L^{-1}), we reduced the information of metric phytoplankton biomass to a binary set of presence and absence data. We divided the phytoplankton into five categories, which included the primary, alternative and not suitable food for the Lesser Flamingo (Table 1). In addition, the predominant food category for each phytoplankton sample was identified.

Results

Saline habitats and their microphyton flora

Over the 15-year-study period, a wide fluctuation in the annual mean values of salinity and phytoplankton biomass was recorded in the four core lakes in Kenya (Bogoria, Nakuru, Elmentaita and Oloidien, Fig. 2).

Bogoria (Fig. 2a) and hot springs. The period 2001–2005 was characterised by stable water level and a salinity ranging between 45 and 51 ppt. A nearly monospecific development of large-celled *Arthrospira fusiformis* (filaments diameter 10–15 μm) supported large numbers of Lesser Flamingos (ESM_5). In March 2003, for example, the total observed population of these birds reached numbers exceeding 500,000. In this phase, the biomass of *Arthrospira* ranged from 20 to 768 mg L^{-1}. In 2006, a critical increase of salinity to 55 ppt led to the establishment of the halophilic prasinophyte *Picocystis salinarum* Lewin. This tiny green alga (diameter about 2 μm only) was not a suitable food substitute as it was too

Fig. 2 Salinity, phytoplankton biomass and flamingo abundance in four saline-alkaline lakes of the Kenyan part of the Great African Rift Valley in the period of 2001–2015. **a** Lake Bogoria, **b** Lake Nakuru, **c** Lake Elmentaita, **d** Lake Oloidien. For years with more than one sampling date, the mean value was calculated. The circles above the phytoplankton columns indicate the flamingo abundance groups: *black* = >100,000, *dark grey* = >10,000, *pale grey* = >1,000, *white* = <1,000 flamingos
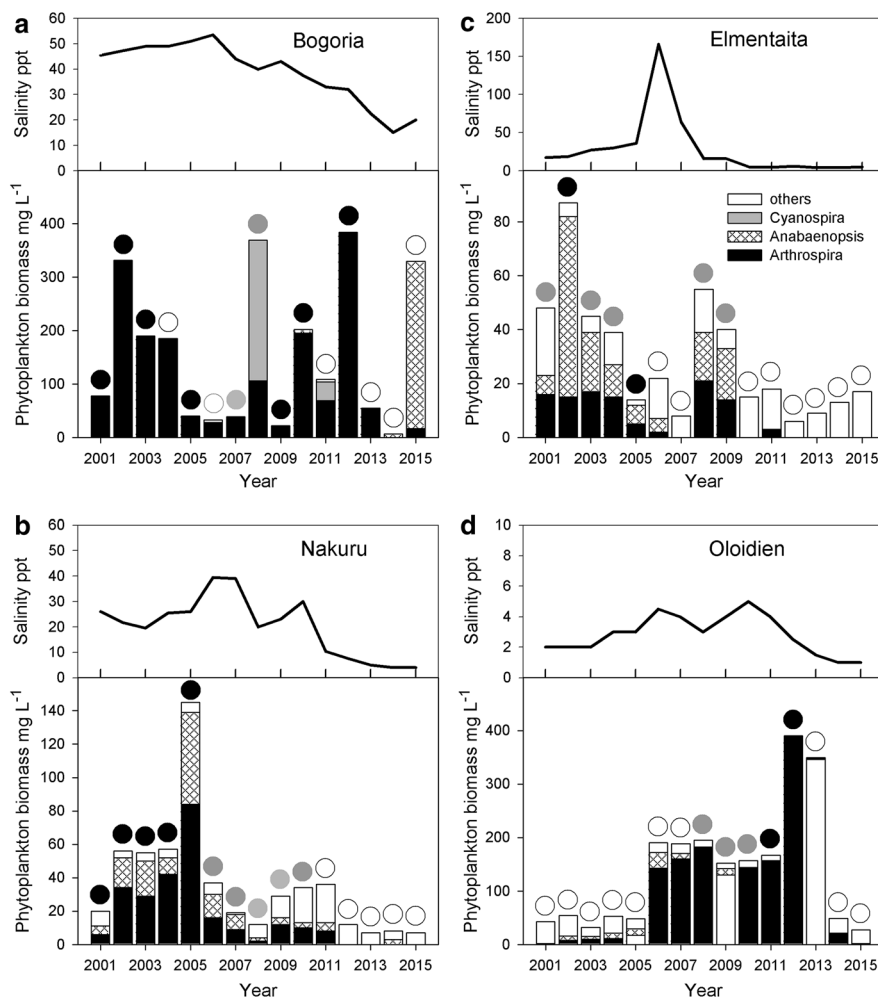
small to be retained by the flamingo food filter system (ESM_5). Hence the number of flamingos dramatically decreased to numbers below 1,000 birds. In 2008, *Arthrospira* reached an elevated biomass again. From this year onward to 2011, however, the water level and salinity (26–47 ppt) varied largely. During that period, the massive development of the colonial cyanobacterium *Cyanospira capsulata* Florenzano, Sili, Pelosi et Vincenzini was recorded twice. A notable morphological feature of this cyanobacterium was the possession of a thick mucilaginous coat covering the colonies, which were too large for ingestion by Lesser Flamingos (ESM_5).

A completely new phase started at the end of 2010, when heavy rains led to a steep rise in water levels in the lakes of the Kenyan part of the Rift Valley. After an intermediate bloom of *Arthrospira*, the population

of this cyanobacterium collapsed towards the end of 2013. During our sampling trip in December 2013, we found sections of the main road close to the shore flooded and impassable. Sampling sites near the submerged hot springs were therefore accessed via a new route passing through higher grounds on the surrounding hills. After reaching the lake shore, it became evident that the dense cyanobacterial bloom had disappeared and the Lesser Flamingos were not able to find food in the clear water body. Salinity decreased to 15.8 ppt while the phytoplankton biomass was <1 mg L^{-1}. The filtration of several litres of water through the plankton net yielded a small phytoplankton sample dominated by *Anabaenopsis abijatae* Kebede et Willén, a taxon never before reported in this lake. Only very few filaments of *Arthrospira* that would eventually serve as inoculum

for later phases of re-establishing flamingo food were recorded. In January 2014, the density of phytoplankton in the different parts of the lake varied widely. Whereas the phytoplankton biomass in the northern part, near the Loboi gate was <1 mg L^{-1}, a slightly higher biomass of 7 mg L^{-1} was measured at the central sampling point, that was about 14 km away from this gate. In the southern part of the lake (19 km from the gate), we estimated a huge biomass of 250 mg L^{-1}. Even in 2015, the recovery of *Arthrospira* did not occur due to the still elevated water levels and low values of salinity. In January 2015, we measured a salinity of 20.3 ppt. The distribution of phytoplankton was still very heterogeneous with low values in the clear water in the northern section of the lake (<1 mg L^{-1}) and higher values in the turbid water at the central part. At a 300-m broad sector of the lake, strong winds led to the accumulation of a dense bloom of *Anabaenopsis abijatae*. At this sampling point, there were about 3,000 Lesser Flamingos feeding on the blooms.

Compared to the lake water (~ 30°C, >20 ppt, pH < 10), water temperature in the hot springs at the Bogoria shoreline was considerably higher (40–90°C). The salinity (3.5 ppt) and pH (9.2), however, were much lower. These contrasting features of the two habitats were the reason for the survival of different microphytes at each site. Despite the close connection between these habitats, their cyanobacterial communities differed widely. In the hot springs, the dominant morphotypes belonged to thermophilic members of the cyanobacterial genera *Leptolyngbya*, *Phormidium*, *Spirulina* and *Synechococcus*. A few filaments belonging to *Arthrospira* were also detected. Due to the rising water levels that started in 2010, the geyser and hot spring area of Lake Bogoria were totally submerged by 2014. Sampling in January 2015 revealed that the flooded Chemurkeu area was inhabited by floating cyanobacterial mats on the water surface containing taxa from both habitats (ESM_5).

Nakuru (Fig. 2b) and sewage ponds. Between 2001 and 2005, three different cyanobacterial taxa dominated the phytoplankton: *Arthrospira fusiformis*, *Anabaenopsis abijatae* and *Anabaenopsis arnoldii* Aptekarj (ESM_5). In addition, *Cyanospira rippkae* Florenzano, Sili, Pelosi et Vincenzini also occurred in association with each of the abovementioned cyanobacteria. None of the species ever exhibited monospecific dominance. In this period, the salinity

with values ranging from 19 to 29 ppt was distinctly lower than in Bogoria. The phytoplankton biomass varied between 25 and 135 mg L^{-1}. Diatoms were also present during this period but in low numbers. Besides the dominance of the diatom species by *Nitzschia*, centric diatoms such as *Stephanodiscus aegyptiacus* Ehrenberg were present. After a dry phase in 2007, the lake maintained only a low biomass of *Arthrospira*, i.e. never exceeding values of 12 mg L^{-1}. Diatoms and cryptomonas dominated the phytoplankton and the flamingo numbers dropped as the only available food consisted mainly of diatoms. Due to the dry weather in January 2010, the water salinity increased to 50.7 ppt. This resulted in the establishment of small-celled *Picocystis salinarum*, which outcompeted the filamentous cyanobacteria. The scarcity of suitable food led to the emigration of the flamingos.

The onset of the rainy season in November 2010, led to a steady rise in the water level while salinity dropped from 10.4 ppt to 3.6 ppt in January 2015. The consequence of this was a reduction in phytoplankton biomass to values of less than 10 mg L^{-1}. The species present were made up of tiny coccoid green and eustigmatophycean algae as well as phytoflagellates. As a result of improved light penetration to the floor of the lake during this period, benthic biofilms dominated by diatoms were established (ESM_5). Mass developments of only three species dominated the diatom communities (*Anomoeoneis sphaerophora* Pfitzer, *Rhopalodia gibberula* (Ehrenberg) Müller and *Nitzschia palea* (Kützing) Grunow, co-dominated by different *Nitzschia* species and a few centric diatoms of the genera *Stephanodiscus* and *Cyclotella*. Most of the diatoms were typically freshwater species with high trophic values. Surprisingly, only three and two species (during cyanobacteria and non-cyanobacteria-dominance, respectively) were typical for inland saline waters. Of the remaining species, only *Rhopalodia gibberula* reached high dominances. The extremely few Lesser Flamingos that were remaining at the lake with its clear water, survived by consuming these diatoms from the sediment surface.

Microscopic examination of the sample from the low-salinity phase in January 2015 failed to provide an insight into the species composition as only very small or sensitive organisms were predominant in the sample. A molecular 454 pyrosequencing approach was therefore applied to determine the diversity of the sample at this phase of the lake (ESM_4). The

community of picoplanktonic cyanobacteria was dominated by genotypes that closely matched the different clones of *Synechococcus* and *Synechocystis*. Filamentous cyanobacteria belonging to the genera *Leptolyngbya, Haloleptolyngbya, Phormidium, Planktothricoides, Spirulina, Anabaenopsis* and *Nodularia* were also observed. A notable finding was the re-appearance of three cyanophycean taxa in the lake: *Synechocystis minuscula* Woronichin SAG 258.80, *Haloleptolyngbya alcalis* Dadheech, Mahoud, Kotut et Krienitz KR2005/106 and *Spirulina laxissima* G.S. West SAG 256.80 that had been reported in earlier studies and deposited in strain collections. The eukaryotic microphytes were dominated by picoplanktonic *Nannochloropsis limnetica* Krienitz, Hepperle, Stich et Weiler and *Picochloron* sp., as well as nanoplanktonic diatoms and dinoflagellates. The prymnesiophytan flagellate *Isochrysis* was also recovered. Other findings included the identification of the DNA of about ten taxa of zooplankton, six of them belonged to the rotifer group.

The sewage oxidation ponds of Nakuru town had very low salinity values ranging from 0.1 to 0.3 ppt. The ponds were phycologically rich with diverse groups comprising coccoid green algae, euglenophytes, picocyanobacteria and occasionally by a small-celled *Arthrospira* or blooms of *Microcystis* found in the plankton (ESM_5). Another characteristic feature of the sewage pond phytoplankton was a strong temporal fluctuation in phytoplankton composition with biomass values ranging from 27 to 136 mg L^{-1}. Inflows from the sewage ponds introduced phytoplankton species into the lake. Greatest influence of sewage pond taxa on the biocoenosis of Lake Nakuru was when lake salinity fell to a concentration below 4 ppt.

Elmentaita (Fig. 2c). In Lake Elmentaita, *Arthrospira* was associated with *Anabaenopsis arnoldii, A. abijatae* or *A. elenkinii* Miller. In 2002, *Arthrospira* and *Anabaenopsis* produced nearly 100 mg L^{-1} biomass. This was the only time in the 15-year sampling period when more than 100,000 Lesser Flamingos found sufficient food in the plankton. In 2005, again same high numbers of this bird were recorded at the lake, however, the phytoplankton biomass with 14 mg L^{-1} was very low. This cyanobacterial assortment dominated the phytoplankton until 2009 and was interrupted in 2006 when the lake nearly dried out and the salinity reached extreme values of more than 150 ppt. After 2010, the lake was refilled and the salinity dropped below 10 ppt. *Arthrospira* and *Anabaenopsis* vanished and were replaced by coccoid cyanobacteria and small green and eustigmatophycean algae which were not suitable as flamingo food. *Haloleptolyngbya alcalis* was found as temporary and locally available alternative flamingo food (ESM_5).

Oloidien (Fig. 2d), *Naivasha* During the 25 sampling trips to Lake Oloidien, the lake underwent a full circle of very remarkable changes. As a result of the progressive changes in hydrology and salinity, the phytoplankton community responded with gradual changes in species composition and biomass levels. At its peak season in 2012, the lake attracted a population of about >200,000 Lesser Flamingos. Between 2001 and 2005, the water had a low salinity of 2 ppt. During this low-salinity phase, the phytoplankton was dominated by coccoid green algae as well as coccoid, filamentous and colonial cyanobacteria. In 2006, the salinity level reached a value of more than 3 ppt leading to massive growth of *Arthrospira fusiformis*. The nostocalean cyanobacterium *Anabaenopsis elenkinii* was subdominant and reached its maximum in 2006 with densities of 50–60 mg L^{-1}. Because of long dry seasons in subsequent years, salinity increased to a maximum value of 5.5 ppt in January 2010.

Heavy rains starting falling at the end of 2010 and diluted the water again to salinity values of 3 ppt. However, *Arthrospira* development remained on high biomass level of more than 150 mg L^{-1}. Even in November 2012 and January 2013, when further heavy rains resulted in a drop in salinity to values of 2.2 ppt, phytoplankton dominance by *Arthrospira* remained at 100%. The *Arthrospira* biomass in Lake Oloidien rose to a maximum of 623 mg L^{-1} and was entirely made of small filamentous forms. The majority of filaments were 4–5 μm wide with a few being 6–8 μm wide. Finally, by the end of 2013, when the salinity dropped to around 1 ppt, the dominance by *Arthrospira* broke down and was replaced by coccoid green algae, a situation similar to the observation made at the beginning of this flamingo-episode in 2001 (ESM_5).

Lesser Flamingos responded promptly to the development of *Arthrospira*. Whereas between 2001 and 2005, when *Arthrospira* was absent, the number of flamingos at Oloidien was very low and did never exceed 1,000 individuals. In 2006, the situation changed considerably. The number of flamingos

increased to more than 20,000 in September 2006. In the following years, the flamingo numbers fluctuated between 10,000 and 20,000. Towards the end of 2010, the flamingos established a stable population of up to 50,000. By April 2012, between 150,000 and 250,000 flamingos were recorded in Oloidien. In November 2012 and January 2013, the number of flamingos decreased dramatically to about 1,000. It was interesting to observe that the *Arthrospira* biomass rose to maximum values of around 600 mg L^{-1} just after the flamingos left the lake and their grazing pressure turned out.

The freshwater lake *Naivasha* was characterised by a high diversity of phytoplankton dominated by coccoid cyanobacteria and green algae, desmids and diatoms. Only very few filaments of *Arthrospira* were occasionally found. According to our observations, flamingos never visited the lake.

Magadi The patchy appearance of the lagoons in this lake was evident during the seven sampling trips to the lake. Dry flats, shallow plains filled with red-coloured brine and bubbling springs created a mosaic of different habitats. The floor of the wet areas was often covered by cyanobacterial mats or layers of benthic diatoms. Planktonic microphytes only occured in areas with a water level of >20 cm. Our study focused on a more or less watered lagoon located on the route to the hot spring area in the southern part of the lake (ESM_5). However, even at this site salinity exhibited a high degree of fluctuation ranging from 29.7 to 80.9 ppt. The sample with the highest salinity, which was collected in January 2010 had the highest diversity of planktonic cyanobacteria. However, the cyanobacteria cells present, which comprised *Aphanothece* sp., *Myxobactron* sp. and *Synechocystis* cf. *salina* Wislouch were too small for ingestion by Lesser Flamingos, which generally visited the lakes only in lower numbers of 1,000–2,000 birds.

Sonachi At the beginning of our sampling exercise, this crater lake was found to harbour the most dense bloom of *Arthrospira*, which was never found in any other site within the frame of our study. An *Arthrospira* biomass of 3,159 mg L^{-1} was recorded in March 2002. The number of flamingos in this period was more than 1,000 individuals, a condition that was maintained until 2008. The relatively low number of birds at Sonachi, which probably harvested only a small proportion of the total yield of the fast-growing cyanobacterium, contributed to the high phytoplankton

fresh weight recorded. The high accumulation of phytoplankton gave the lake a dark-jade colour. In February 2009, the lake appeared to have experienced an overturn resulting in a phytoplankton crash that was replaced by a milky suspension of bacteria. The phytoplankton biomass declined to undetectable levels. In the subsequent years, *Arthrospira* never recovered to the high biomass levels measured before. Only a low concentration of *Arthrospira* of below 10 mg L^{-1}, which occurred in association with dinoflagellates, colonial picocyanobacteria and solitary eukaryotic picoplankton such as *Microchloropsis*, remained. The number of flamingos dropped to numbers below one hundred.

Simbi The lake was surveyed three times during which blooms of *Arthrospira fusiformis* were observed alongside *Anabaenopsis abijatae*. A maximum phytoplankton biomass of 348 mg L^{-1} was measured in November 2001. During the sampling trip, a flamingo population of >10,000 birds were observed feeding on the cyanobacterial bloom on the shallow waters near the lake shore.

Turkana Sampling was carried out once in January 2005 at the shore of the Ferguson's Gulf. The study revealed a low fresh weight of phytoplankton of 5 mg L^{-1} made up of diatoms and filamentous cyanobacteria. Flamingos were not observed at this time.

In October 2002, and 2015, we sampled soda lakes in North Tanzania during dry season.

Big Momella In 2002, a monospecific bloom of *Arthrospira* (119 mg L^{-1}) formed a food suspension for about 30,000 flamingos (ESM_5). In 2015, a dense *Arthrospira* bloom was established with 549 mg L^{-1}, however, only about 1,000 flamingos occurred. Salinity values of 27.2 (2002) and 24.6 ppt (2015) were measured. Two other lakes of the Arusha National Park, lakes Tulasia and Small Momella were also sampled in 2015 for comparison. Lake Tulasia (salinity 21.3 ppt) hosted about 100 flamingos that observed feeding on the *Arthrospira* suspension. Flamingos were, however, absent in Small Momella (salinity 5.1 ppt) whose phytoplankton was dominated by coccoid green algae with only few filaments of small-celled *Arthrospira*.

Manyara This lake was nearly dried out when it was visited in October 2002. However, in shallow water-holes picocyanobacteria, *Anabaenopsis*, *Arthrospira* and coccoid green algae built a relatively diverse phytoplankton community with a low biomass of

7 mg L^{-1} which did not attract flamingos. A similar situation was observed at the lake in 2015, however, the algal community was dominated by Oscillatoriales and pennate diatoms.

Burunge In October 2015, the phytoplankton community was dominated by *Anabaenopsis arnoldii*. Although no flamingos were observed during the sampling visit, the shoreline was full of pink flamingo feathers indicating a recent massive presence of the birds (ESM_5).

Makat When this lake was visited in 2002, the shallow pan was inhabited by picocyanobacterial phytoplankton. Few Lesser and some hundreds of Greater Flamingos grazed on benthic diatoms. During the second visit in October 2015, the lake was found to have completely dried out.

Natron The northern shoreline of this important flamingo lake was visited in October 2002. Pennate diatoms and filamentous cyanobacteria (*Phormidium* spp.) were found growing on the mud. Loose groups of flamingos in hundreds searched for food in the morass. In October 2015, in the southern lagoon was sampled. Oscillatoriales, *Haloleptolynbya* and pennate diatoms, dominated by *Anomoeoneis sphaerophora*, formed a poor diet for masses of flamingos (ESM_5). It was impossible to count the flamingo flocks that were difficult to access on the ground, however, their number was enormous high and consisted probably in several hundreds of thousands. We suspected that the flamingos were waiting to attempt breeding in the central region of the lake after the short rainy season (November–December) which creates the best breeding conditions.

Three crater lakes near the Queen Elizabeth National Park in Uganda (Katwe, Nyamanyuka and Bagusa) were sampled in February 2002, while Lake Katwe was visited again in January 2005. At this time, only some hundreds of flamingos were around in this crater lake area.

Katwe The extremely high salinity at levels near the saturation point did not allow a dense algal establishment on the brine. Among the species present in small numbers, the establishment included *Synechococcus*, *Arthrospira* and *Picocystis* (ESM_5).

Nyamanyuka The lake had an optimum salinity of 36.9 ppt. However, *Arthrospira* and *Anabaenopsis* occurred in low concentration of 8 mg L^{-1}.

Bagusa At a salinity of 49.1 ppt *Synechococcus*, *Picocystis* and pennate diatoms occurred in low concentrations.

Makgadikgadi The water of this large salt pan in Botswana had a salinity of 39.1 ppt when studied in February 2007. Microscopic examination of the phytoplankton samples revealed a diverse mix of phytoplankton consisting of Oscillatoriales, Nostocales, pennate diatoms and coccoid green algae with a low biomass of 11 mg L^{-1}. About two thousand flamingos occurred near the observation tower of Nata Bird Sanctuary.

Etosha National Park During our sampling trips in 2007, 2008 and 2014, the main parts of the Etosha Pan, Namibia, had dried out. We therefore only sampled the smaller water bodies and springs within the park. In November 2008, we visited two shallow and adjacent small pans in north-western Etosha with a salinity of 19 ppt. Blooms of *Anabaenopsis* sp. with a wet weight biomass of 50 mg L^{-1} and supporting about 3,000 flamingos were recorded. The water in the Pan had a characteristic strong smell of hydrogen sulphide, possibly owing to the presence of sulphur bacteria (ESM_5).

Ekuma mouth A delta of the ephemeral Ekuma River that empties into the Etosha pan from the north originates from the human settlements in the Ovambo area of northern Namibia. It was sampled twice at two different water levels and salinity. At a salinity of 11.2 ppt recorded in November 2008, the phytoplankton was characterised by a number of green algal species dominated by *Desmodesmus opoliensis* (Richter) E. Hegewald. In 2014, when salinity rose to a value of 29 ppt, dense mats of filamentous cyanobacteria were recorded. Light microscopy revealed a dominance of a species of *Phormidium* which differed from *P. etoshii* Dadheech, Casamatta, Casper et Krienitz by the shape of cells (longer than broad) and with a grey brownish colour. Other associated cyanobacteria taxa such as *Cyanospira*, *Oscillatoria* and narrowly filamented Oscillatoriales occurred in lower abundance. Additionally, pennate diatoms were also observed (ESM_5). The sample collected in 2014 was suitable as flamingo food, however, no flamingo was present at this time.

Okondeka This contact spring was covered completely by a monospecific mat of the filamentous cyanobacterium *Phormidium etoshii* (ESM_5).

Springbokfontein The dominant taxon in cyanobacterial mats in this contact spring was *Phormidium etoshii*. Besides this species, several other filamentous cyanobacteria that included *Spirulina* spec., *Oscillatoria* spec., *Pseudanabaena* spec. and a heterocytous cyanobacterium of the genus *Cronbergia* were also detected (ESM_5).

Walvis Bay, Sewage outfall ponds, Bird Paradise A number of shallow ponds had established in the dunes during our sampling visit in March 2014. Each pond had a different water colour brought about by a difference in the dominant phytoplankton group. Depending on the algal composition, each pond attracted different numbers of flamingos. The phytoplankton of the main pond (Pond 1), which was the largest in the area, was dominated by *Arthrospira fusiformis* with a moderate filament size with diameter from 6 to 9 µm. The associated species occurring at subdominant levels consisted of *Euglena* sp., and *Oocystis* sp. (green algae). Water salinity was 4.1 ppt and the total algal biomass was 41 mg L^{-1}. This pond hosted more than 2,000 flamingos. The second pond (Pond 2), which was characterised by a dark greyish blue algal bloom, had a salinity of 25.8 ppt, and a phytoplankton biomass of 67 mg L^{-1}. This pond was dominated by *Cyanospira* sp. and *Arthrospira fusiformis*. Subdominant species consisted of *Euglena* spec. and the marine diatom *Chaetoceros* sp. The third pond (Pond 3) had a yellow green bloom that was dominated by a green flagellate *Tetraselmis* sp. (ESM_5).

Walvis Bay Lagoon Different diatom species were recorded on the mudflats of the lagoon. This attracted about 2,000 Lesser and 1,000 Greater Flamingos during both sampling times in 2007 and 2014 (ESM_5). The diatom biofilms were dominated by *Opephora* sp. with more than 90% of the diatom community. In addition, we found 13 other diatom species that occurred in low abundance. The diatom diversity in the Walvis Bay Lagoon was lower than in the salt evaporation ponds in Walvis Bay and in Swakopmund where several marine diatom taxa and diatoms with preferences for inland saline waters were associated with the dominant *Opephora* sp. (e.g. *Opephora olsenii* Møller and *Halamphora coffeaeformis* (Agardh) Levkov, and the centric *Auliscus sculptus* (W. Smith) Brightwell, *Paralia sulcata* (Ehrenberg) Cleve and *Actinoptychus senarius* (Ehrenberg) Ehrenberg). In the salt ponds of Walvis

Bay, the marine diatom *Parlibellus* sp., a member of the former *Navicula microstigmaticae* (Cox 1988) reached a frequency of ∼5%. The sum of frequency of marine and inland saltwater species was higher in the salt ponds than in the mudflats of the lagoon (ESM_3). However, the community was more diverse in 2014 as compared to 2007. Nearly 70% of the diatom frustules belonged to *Navicula* cf. *halinae* Witkowski, but compared with the sampling in 2007 due to occurrence of marine species.

Salt evaporation ponds of the Guano & Salt Company Swakopmund At this site, ditches transported water from the sea into different evaporation ponds. The physical and chemical characteristics of the water in the ponds were typical of seawater with a salinity >30 g L^{-1}. Depending on the stage of evaporation, the salinity of water differed in the different ponds. We selected two ponds with salinities of 68.0 and 38.1 ppt. The pond with the higher salinity exhibited a green colour while the water in the less saline pond was clear. Whereas no flamingo was observed in the green pond, several dozens of Greater and Lesser Flamingos trying to collect diatoms (dominant *Opephora* sp., and abundant *Opephora olsenii*) from the sediment on the clear water pond were spotted. Other diatom species present in the clear pond included *Actinoptychus senarius* and *Auliscus sculptus*. The pond with a salinity of 68 ppt exhibited a green vegetation colour induced by a dense bloom of *Microchloropsis salina* (Hibberd) M.W. Fawley, Jameson et K.P. Fawley (syn. *Nannochloropsis salina* Hibberd), a picoplanktonic eustigmatophycean alga (ESM_5).

Kamfers Dam The dominant taxon in this dam in Kimberley, South Africa, was *Arthrospira fusiformis*, which contributed more than 95% of the biomass near the sewage plant and more than 99% near the breeding island. We found few colonies of *Microcystis* and filaments of the genera *Anabaenopsis* and *Anabaena* as well as few cells of the euglenophytes *Lepocinclis* sp., *Euglena* spp. and *Phacus* spp., dinoflagellates and pennate diatoms. The *Arthrospira* observed at this site was similar to the small ecotype from Lake Oloidien, which was characterised by smaller (5–6 µm) filaments wider than the «normal» form of *Arthrospira* (8–15 µm) filaments (ESM_5).

River Vaal The phytoplankton was dominated by the potentially toxin-producing cyanobacteria of the genus *Microcystis* and coccoid green algae. Further,

we found euglenoid algae such as *Euglena* and *Phacus*, which are indicative of organic contamination. These taxa regularly invade the Kamfers Dam where they have the potential to disrupt the dominance of *Arthrospira*.

Little Rann of Kutch In October 2006, the plain of this wetland in north-western India had almost completely dried out with only a few shallow water ponds remaining. We sampled four sites with salinities ranging from 2.7 to 37.1 ppt. In all samples collected, we identified few species of filamentous cyanobacteria, mostly Oscillatoriales, and several diatoms dominated by *Diploneis subovalis* Cleve, and less numerous *Nitzschia dissipata* (Kützing) Grunow and *N. sigma* (Kützing) W. Smith. In addition, members of marine diatom flora such as *N. scalpelliformis* Grunow and *Campylodiscus bicostatus* W. Smith ex Roper were observed. At the nesting site, we counted about 150 nests with eggs. However, because of the low water level and insufficient algal food, all the eggs had been abandoned by the parent birds (ESM_5).

Lake Sambhar was sampled in November 2006 and May 2014. The salinity was extremely high and reached values of 121–200 ppt. The phytoplankton was dominated by *Dunaliella* sp., with only a few filaments of *Arthrospira* being recorded in the samples collected (ESM_5). The best site for flamingos was a dam near the lake shore where more than 1,000 flamingos were observed. The dam water had a lower salinity of 34.9 ppt, and was covered by dense mats of *Oscillatoria*, *Phormidium* and *Arthrospira.*

River Ganga was sampled once in November 2013 during a phase of dense algal growth. The phytoplankton community of the river had a high biodiversity, typical of river plankton. More than a hundred species of coccoid and filamentous cyanobacteria, green algae, diatoms and euglenophytes were recorded. Also present were few filaments of *Arthrospira*. This phytoplankton community reflects the diversity of waters in the flood plain and their potential to act as refugium for food algae of flamingos.

Statistical evaluation

The annual mean biomass data of the four core lakes depicted as Box-and-Whisker plots in Fig. 3 revealed that the highest abundance of flamingos (+++) occurred at lakes with the highest biomass of *Arthrospira* (Fig. 3a). Furthermore, an elevated

biomass of *Anabaenopsis* was found at sites with more than 1,000 flamingos (+) and an intermediate peak abundance when more than 10,000 flamingos (++) were observed (Fig. 3b, range of the abundance ranks see method). In turn, peak abundances of flamingos (+++) coincided with plankton observations where the biomass of other phytoplankton was particularly low and vice versa (Fig. 3c). These significant differences in the phytoplankton composition between the four flamingo abundance groups were even more pronounced when looking at the relative contribution of *Arthrospira* and others. While median values of more than 90% *Arthrospira* significantly corresponded to peak abundances of the Lesser Flamingo (Fig. 3d), a peak abundance of more than 90% of «others» referred to the group of the lowest flamingo abundance (Fig. 3f). Beside the phytoplankton groups, also the total biomass observed for these four lakes as well as for the whole dataset of individual samples ($n = 142$) showed significant differences in the median between the flamingo abundance groups ($P < 0.001$, Kruskal–Wallis Test, graphs not displayed).

The distribution pattern of the food displayed for individual samples of the whole dataset is shown for four flamingo abundance groups in Fig. 4. In case of observations of more than 100,000 flamingos (+++), the phytoplankton was often predominated by the primary food of the Lesser Flamingo *Arthrospira* (food category 5, Fig. 4a). Even if *Arthrospira* was not dominant in all samples, it was the most frequently occurring species (see the many dots for food category 5 in Fig. 4a). In addition, food category 4 was also quite frequent among these sampling sites. In two cases, species of food category 4 comprising *Anabaenopsis* (see upward bars in Fig. 4a) was the dominant food. Other suitable food of category 4, such as diatoms, other cyanobacteria or *Euglena*, did not play an important role as a food source (missing downward bars in Fig. 4a). Except on four observations, no other category of food was found when highest numbers of Lesser Flamingos were observed.

In case of samplings with a lower abundance of the Lesser Flamingo (++), the food categories 5 (*Arthrospira*) and 4 (mainly *Anabaenopsis*) were again often detected (many dots for food categories 5 and 4 in Fig. 4b) but the frequency of predominance by these taxa was not that high when found at the

Fig. 3 Biomass of *Arthrospira*, *Anabaenopsis* and other phytoplankton among the four flamingo abundance groups ranked from to <1,000 (o) to >100,000 (+++). The *Box-and-Whisker plots* **a–c** show the original biomass data; **d–f** the relative biomass contribution to total phytoplankton biomass (%). According to Kruskal–Wallis tests, statistical differences in the median were found among the flamingo abundance groups for *Arthrospira* and others with $P < 0.001$, and for *Anabaenopsis* with $P < 0.01$. Further, statistically significant differences between homogeneous subsets within each phytoplankton group are represented by *letters* above each *box* as determined by pairwise Mann–Whitney U Tests with a Bonferroni correction. *Data* are annual averages ($n = 60$) from the four lakes shown in Fig. 2
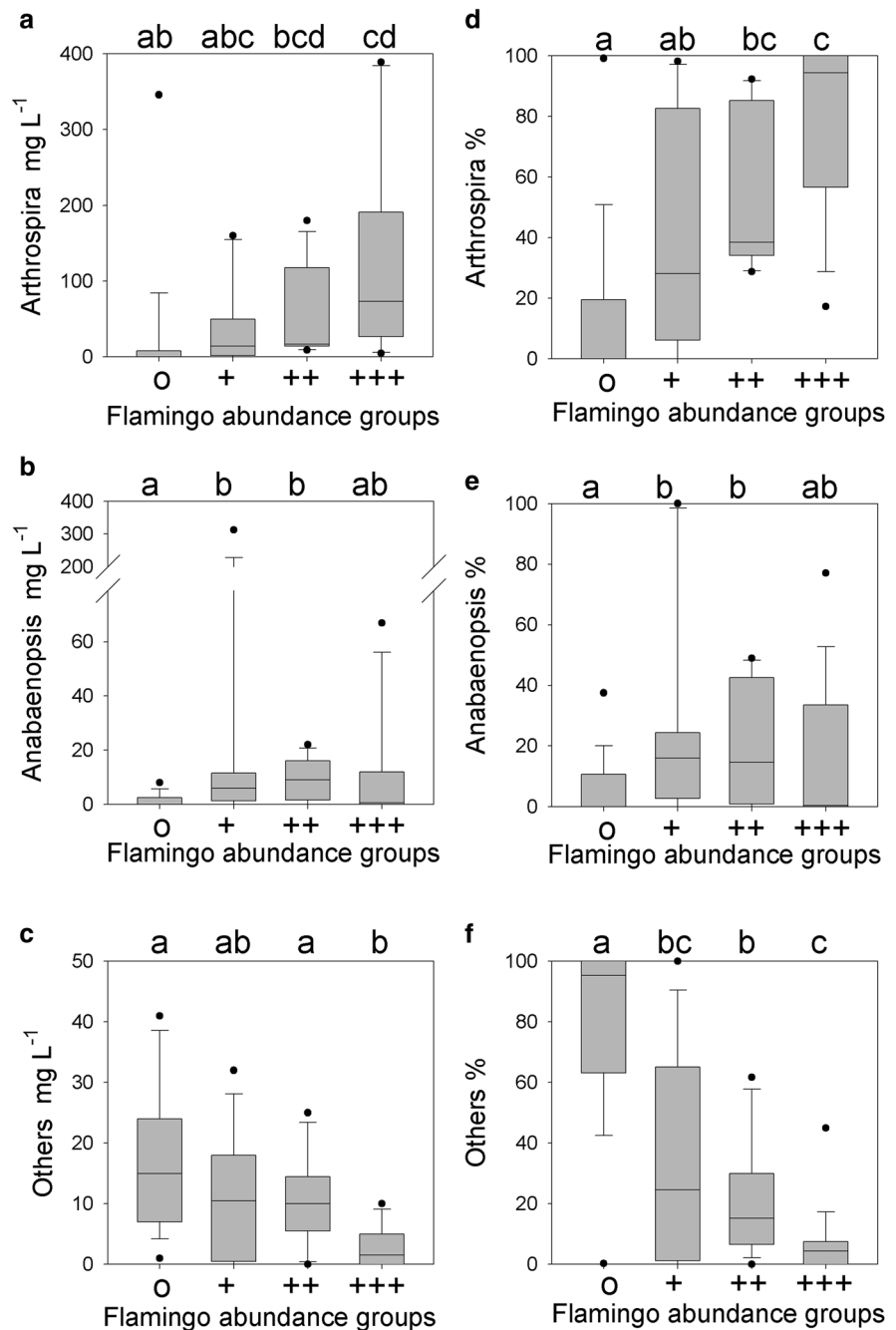
highest flamingo abundances. Phytoplankton composed of diatoms and other good alternative food reached a dominance status in three samples (see downward bars for food category 4 in Fig. 4b). Microphytes that were not suitable as food were quite common (many dots for category 1 in Fig. 4b).

Samples plotted in Fig. 4a, b were mainly from the four core lakes of our study and are indicated by black dots. 53% of the data points in Fig. 4a referred to individual samples taken from Lake Bogoria, while 50% of the data points in Fig. 4b referred to those from Lake Elmenteita.

Fig. 4 Presence of phytoplankton food for the Lesser Flamingo displayed along the gradient of total phytoplankton biomass ranging from 0.9 to 3,159 mg L^{-1} ($n = 142$). **a–d** corresponds to decreasing flamingo abundances which ranked from >100,000 (+++) to <1,000 (o). The categories of food suitability comprise phytoplankton from the most suitable food (5) to phytoplankton that is not suitable as food (2 and 1; details see Table 1). A food category is displayed as present if the contribution to the total phytoplankton biomass exceeds 5%. Note that each phytoplankton sample can be represented by all five food categories. *Black dots* stand for the four core lakes, *white dots* for the remaining sampling sites. A *bar* indicates the predominant food category for each sample. In case of food category 4, *upward bars* indicate *Anabaenopsis* only, *downward bars* diatoms together with the remaining phytoplankton taxa of this food category
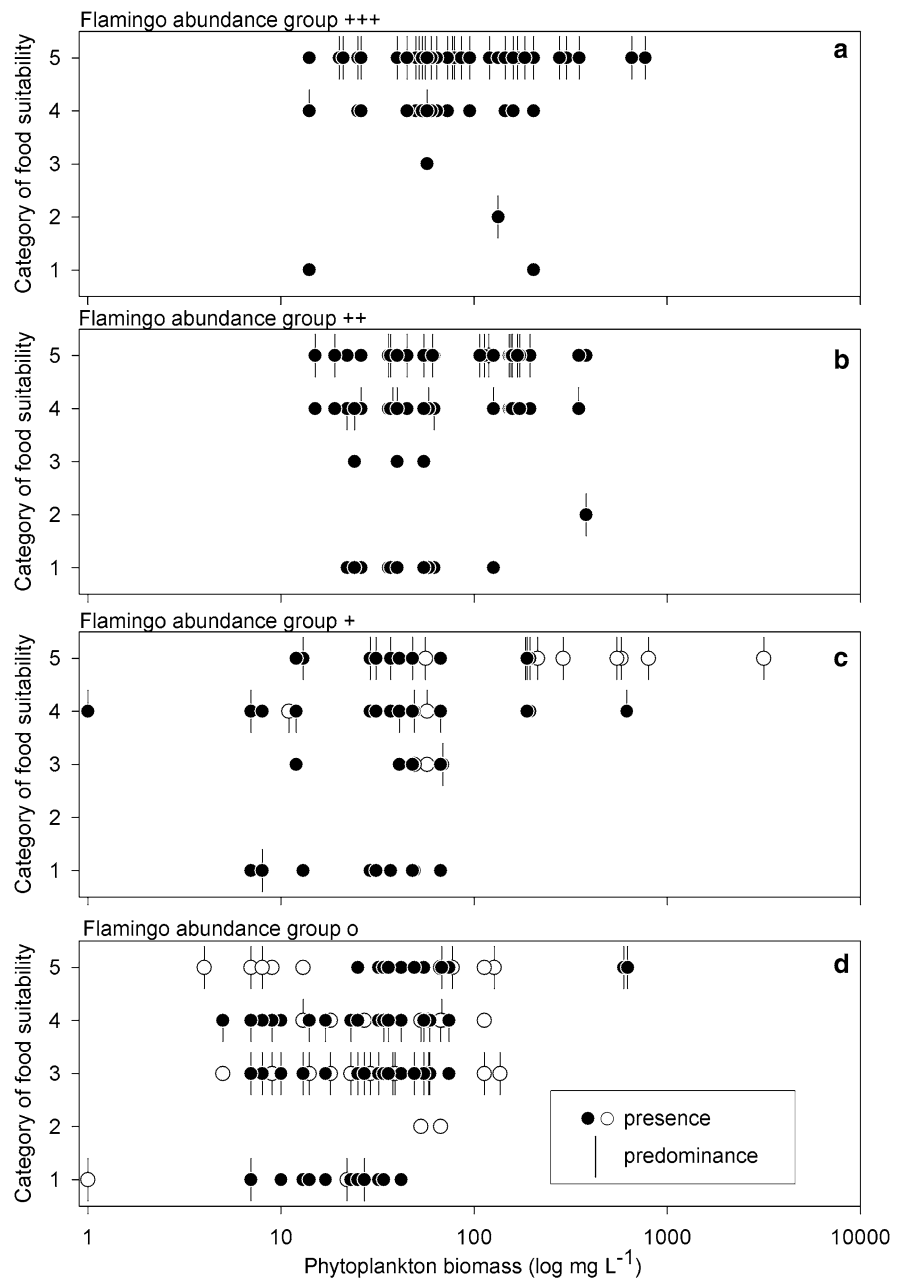
Lower flamingo abundances (+ and o) were recorded in the majority of samples from the rest of the lakes other than the core lakes (see many white dots in Fig. 4c, d). The contribution of the four core lakes (see black dots in Fig. 4c) was here modest and ranged from 12% (Lake Elmenteita) to 35% (Lake Oloidien). For habitats with lowest flamingo abundance, i.e. less than 1,000 birds, a distinct food pattern was found when compared with the three other flamingo abundance groups. While food of category 4 was observed in many samples owing to diatoms and other food suitable for the birds (downward bars for food category 4 in Fig. 4d), the number of samples dominated by algae that were only partly suitable or not suitable increased (majority of dots and bars indicated food category 3 and 1 in Fig. 4d). A high

portion of samples representing the four core lakes refers here to Lake Oloidien (44% of the black dots).

## Cyanobacteria and algae and their suitability as flamingo food

Based on our extensive microscopical observations, the following is a summary of the microphytes with different values as food for Lesser Flamingos, including members of three orders of cyanobacteria and nine orders of eukaryotic algae (Figs. 5, 6; Table 1, ESM_5).

Arthrospira fusiformis, a filamentous, spirally coiled cyanobacterium of the order Oscillatoriales exhibited different phenotypes. The size of the commonly observed types was as follows: filaments diameter 10–15 µm, filaments length up to 700 µm, spiral diameter up to ∼100 µm, number of coils up to 20 (Fig. 5a). During the present sampling survey, mass developments of *Arthrospira fusiformis* were

found under salinities between 26 and 55 ppt as it was observed, for example, in lakes Bogoria, Nakuru, Big Momella and Sonachi. Moderate developments as subdominants in the phytoplankton community were abundant down to salinity of 11 ppt. Single filaments were able to survive under extreme conditions both in fresh waters (e.g. Lake Naivasha, rivers Ganga and Vaal) as well as salt waters near saturation point (e.g. Lakes Katwe, Sambhar). High concentrations of monospecific *Arthrospira* attracted very high numbers of Lesser Flamingos. Similarly, an association of *Arthrospira* and *Anabaenopsis* as found in lakes Elmentaita, Nakuru and Simbi was also an important food source for flamingos.

Beside the large types of *Arthrospira fusiformis*, a smaller type with the following characteristics was found at some sites: filaments diameter 4-5-(8) µm, filaments length up to 100 µm, spiral diameter up to 35 µm, number of coils 2–4 (Fig. 5b). This small ecotype was only prevalent under low-salinity

Fig. 5 Cyanobacteria and algae of different food suitabilities for Lesser Flamingos. Categories of food suitability according to Table 1 are given in squared brackets. **a** *Arthrospira fusiformis*, large form [5], **b** *Arthrospira fusiformis*, small form [5], **c** *Anabaenopsis abijatae* [4], **d** *Cyanospira capsulata* [2], Indian ink at the *right margin* indicates the edge of mucilaginous envelope of the colony, **e** *Phormidium etoshii* [4], **f** tight spiral of *Arthrospira fusiformis* [5] attached to a flock of pennate diatoms (*Nitzschia* sp.) [4], **g** *Picocystis salinarum* [1], **h** *Microchloropsis salina* [1], **i** *Euglena* sp. [4] associated with *Oocystis* sp. [4], a thin oscillatorialean cyanobacterium [4] and a pennate diatom [4]. *Scale bar* = 10 µm (**e**, **g**, **h**), 20 µm (**a–c**, **i**), 30 µm (**d**, **f**)
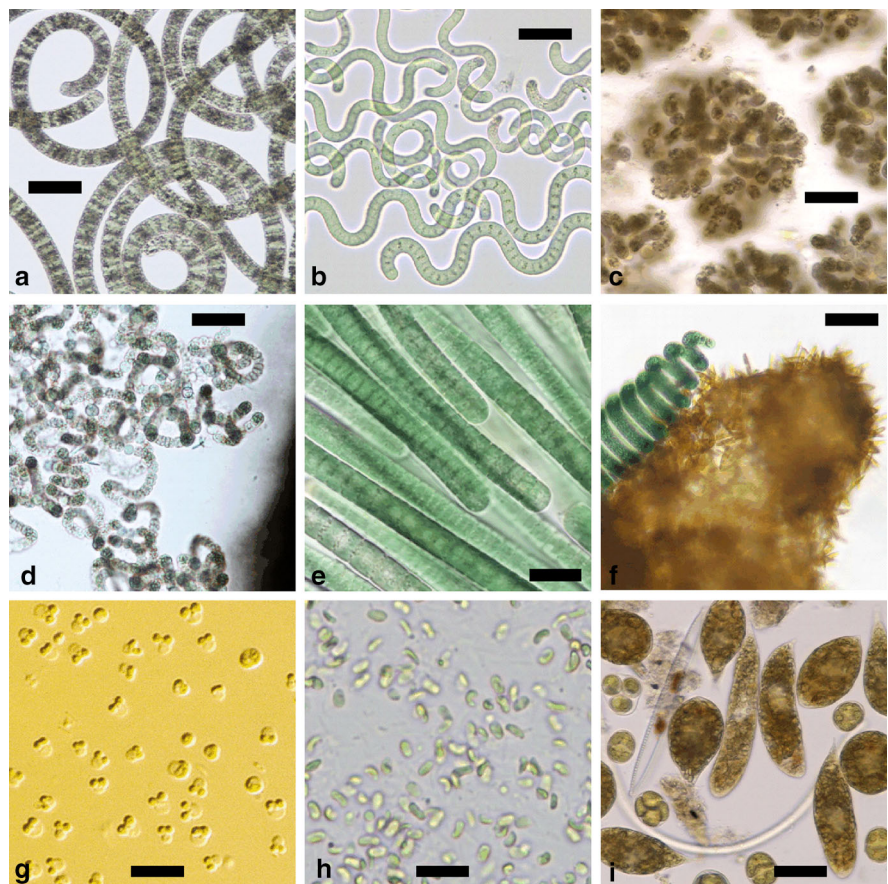
Fig. 6 Pennate diatoms from diatom-dominated benthic biofilms. **a, b** *Rhopalodia gibberula*, **c** *Nitzschia liebetruthii*, **d** *Nitzschia palea*, **e** *Anomoeoneis sphaerophora* (**a–e** Lake Nakuru); **f** *Halamphora coffeaeformis*; **g** *Nitzschia scalpelliformis* (**f, g** Walvis Bay, Lagoon); **h** *Navicula* cf. *halinae*, **i–k** *Opephora* sp., **l** *Parlibellus* sp. (**h–l** Walvis Bay, salt evaporation ponds); **m** *Actinoptychus senarius*, **n** *Auliscus sculptus* (**m, n** Swakopmund, salt evaporation ponds); **o, p** *Campylodiscus bicostatus*, **q** *Diploneis subovalis*, (**o–q** Little Rann of Kutch). *Scale bar* = 5 μm (**a–l, q**), 20 μm (**m–p**)
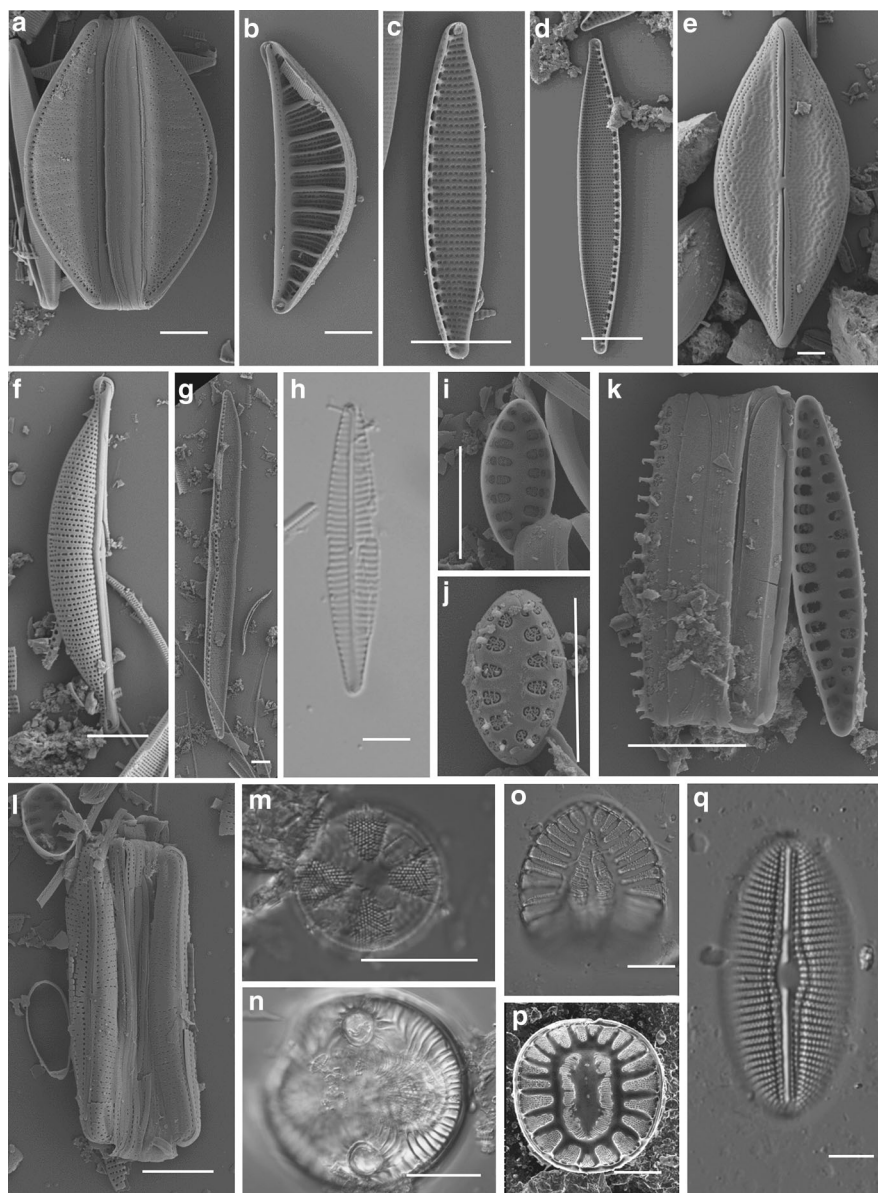
conditions of 1.1–4.4 ppt as measured in Lake Oloidien, Kamfers Dam and sewage outfall ponds Walvis Bay. Notwithstanding the small size of the filaments, high numbers of Lesser Flamingos were attracted to these sites whenever the concentration of filaments was high enough in the waters.

Anabaenopsis, a cyanobacterial genus of heterocyte bearing Nostocales occurred with four different species establishing barrel-shaped cells arranged in filaments which were more or less spirally twisted or condensed to lumpy colonies. Their cell size ranged

between 4 and 12 μm. Pairwise and intercalary spherical heterocytes of 6–12 μm in diameter usually developed and later disintegrated, thus bringing them to a position at the ends of trichomes. Solitary or pairwise akinetes were usually formed. *Anabaenopsis abijatae* (Fig. 5c) exhibited dense botryoid-shaped colonies found in a salinity range of 10–30 ppt. *A. arnoldii,* which occurred within the same salinity range as *A. abijatae,* formed trichomes in wide helices. *A. elenkinii* normally had 1–2 coils, however, in Oloidien with a salinity range of 0–15 ppt, it had 3–5

coils. A morphotype of *Anabaenopsis* with loose spirals was found in saline waters of Namibia (18–26 ppt). This morphotype was distinct from all the known taxa of *Anabaenopsis* and should therefore be described as a new species after culture and genetic analyses. All the four *Anabaenopsis* species occurred at dominant or subdominant positions in phytoplankton communities often together with *Arthrospira* and were ingested by the Lesser Flamingos. On average, the biomass of *Anabaenopsis*, which serves as alternate food to *Arthrospira*, was almost the same as the remaining phytoplankton (see «others», Fig. 3c–f).

Closely related to *Anabaenopsis* were species of *Cyanospira*. The most striking morphological difference was the ability of *Cyanospira* to produce long chains of akinetes. These long strings of brownish akinetes developed in an apoheterocytic mode, i.e. by transformation of all vegetative cells between two heterocytes into akinetes. *Cyanospira rippkae* was found in association with *Arthrospira* in Lake Nakuru when salinity was in the range of 25–35 ppt, and was normally ingested by flamingos. *C. capsulata* (Fig. 5d) produced dense scums in Lake Bogoria in July 2008 when salinity was in the range of 30–40 ppt. Unlike *C. rippkae*, this cyanobacterium could not be ingested by Lesser Flamingos because of the large size of colonies and the prominent mucilaginous envelopes. The macroscopic colonies were 1–2 mm in size and clogged the lamellae of the bills of the birds.

Haloleptolyngbya alcalis, a thin filamented species of the family Leptolyngbyaceae of the order Synechococcales, occurred as solitary filaments or in floating mats. The small cylindric cells had a parietal oriented chromoplasma and a fine mucilaginous envelope. The trichomes had a diameter of 1.2–9 μm and were constricted at the cross walls. This species occurred in phases of low *Arthrospira* abundance in lakes Nakuru and Elmenteita and was suspected to be an alternative food source for Lesser Flamingos. This species was probably a common taxon in saline lakes but frequently confused with *Pseudanabaena* and related taxa.

Oscillatoria spp. and *Phormidium* spp. were common at all flamingo habitats mostly living on the sediments or on the mud at the rim of shallow waters. These simple filamentous morphotypes were very difficult to identify. Most impressive were the huge mats of *Phormidium etoshii* (Fig. 5e) in the Etosha Pan National Park. The significance of Oscillatoriales

as food for Lesser Flamingos depended on the population of the whole microphytean community. In cases, when *Arthrospira* was absent, their importance was high depending on the ease of transfer from felted mats into ingestible suspensions. This was found at the salt pans of southern Africa and at Lake Sambhar region where the oscillatorialean mats easily could be suspended by generating suction pressure (experimentally with a pipette) like that generated by the bill of flamingos during food intake.

Colonial coccoid cyanobacteria belonging to the orders Chroococcales and Synechococcales occurred in all types of water. Dominant members were from the genera *Aphanothece* and *Aphanocapsa*. Their ingestibility depended on the size of colonies with larger colonies being more ingestible. Solitary picocyanobacteria such as members of the polyphyletic genus *Synechococcus* were found always and everywhere. Nevertheless, these ubiquitous morphotypes, which belong to many different phylogenetic lineages, were too small for ingestion.

Pennate diatoms (Fig. 6) were always present at all sampling sites. However, their density on the mud or in the tychoplankton varied widely over time and in space. The main taxa of different habitats were as follows: (i) in the soda lakes Nakuru and Natron—*Anomoeneis sphaerophora*, *Nitzschia* spp., *Rhopalodia gibberula* (only Nakuru) and *Craticula* spp. (only Natron), (ii) in the marine mudflats at the Namibian coast and salt evaporation ponds—*Opephora* sp., *Navicula* cf. *halinae*, *Hantzschia amphioxus* (Ehrenberg) Grunow and *Parlibellus* sp., (iii) at the salt pan Little Rann of Kutch—*Diploneis subovalis*. With the exception of *Opehora* sp., which was too small in most cases, most of the species found had sizes large enough to be retained by the filter lamellae of flamingo bills.

Coccoid chlorophytes of the classes Chlorophyceae and Trebouxiophyceae assumed dominance in the soda lakes at low-salinity levels (1–12 ppt). Taxa with a thick mucilaginous envelope such as Oocystaceae were found to occur under high salinity conditions of up to 40 ppt at the Makgadikgadi pan. Generally, the species diversity of these green alga groups was very high. Whereas some taxa had cells or colonies that were large enough to be eaten by the flamingos, there were also taxa, mostly the solitary forms that were too small for ingestion. Edible forms belonged to the families of Pediastraceae, Scenedesmaceae, Oocystaceae and colonial forms of Chlorellaceae and

Selenastraceae. Non-edible forms were mostly members of solitary living Chlorellaceae, Selenastraceae and Mychonastaceae.

Picocystis salinarum (Fig. 5g), a picoplanktonic (~ 2 μm in diameter) prasinophyte occurred in the soda lakes as solitary spheres with or without two lobate apices containing the chloroplasts. *Picocystis* emerged as a strong competitor against *Arthrospira* at elevated salinity levels of >50 ppt. For the flamingos, the dominance of *Picocystis* had fatal consequences, because this green alga was too small to be ingested by the birds. This picoplankton was found in lakes Bogoria, Magadi, Nakuru and crater lakes in Uganda.

Coccoid eustigmatophytes mostly occurred as solitary living forms and were extremely small as in the case of *Microchloropsis salina* (Fig. 5h) ($3–4 \times 1.5–2.5$ μm) and could not be filtered by flamingos. Mass development of *Microchloropsis* was observed in a salt evaporation pond (68 ppt) at Swakopmund producing an impressive water bloom that did not attract any flamingo. Other eustigmatophytes were observed under low-salinity conditions (3–6 ppt) in the flooded soda lakes Elmenteita and Nakuru.

Diverse flagellates of different taxonomic affiliations played varying roles in the food web of saline waters. The halophilic green algal flagellate *Dunaliella* sp. was observed at Lake Sambhar under high salinity conditions of between 120 and 200 ppt. However, its cells were so tiny that they did not attract flamingo feeding. The same was with a bloom of *Tetraselmis* sp. in a sewage outfall pond in Walvis Bay. Other small size, green chlamydomonas flagellates and cryptomonas occurred in Lake Nakuru under the low water salinity phase. In contrast, members of the genus *Euglena* (Fig. 5i) were large enough to serve as an alternative food resource for Lesser Flamingos in Lake Nakuru and at main sewage outfall pond in Walvis Bay.

Discussion

The analyses of algal communities can enable researchers and naturalists to predict the potential of a given saline wetland in tropical Africa or India to serve as a feeding ground of Lesser Flamingos. By studying algal availability, it is possible to compute a rough estimate of the order of magnitude of flamingos

that can be supported by a habitat (Vareschi, 1978; Tuite, 1981). Projects or studies on the distribution patterns of flamingos can benefit from considering the microscopic world, which is behind the bird abundance. There have been different reasons for avoidance of microscopical observations. Often flamingo sites are inaccessible or accessible via long walks under strenuous conditions. In the study of flamingo sites, among the currently promising options is the use of aerial surveys. Recently, the application of remote sensing (Landsat) in the evaluation of food supply and flamingo numbers in saline-alkaline lakes has given some encouraging results (Groom et al., 2011; Bakó et al., 2014; Tebbs et al., 2013b, 2015). Field sampling and working with the microscope attract much less enthusiasts than flying in an airplane and observing the stunning pink swarms with the naked eye. Undoubtedly, the most efficient way would be to combine the approaches from the air and from the ground. In this paper, an overview of the results generated through microscopy is presented. Cyanobacteria and algae and their food potential were evaluated to encourage environmentalists to combine this experience with their «macroscopic» strategy.

Soda lakes when under the cover of dense assemblages of Lesser Flamingos are overwhelming spectacles of nature, which from a casual observation appears to have been in existence for eons. Indeed, it is important to realise that what is being seen is a snapshot in time. This apparent stable stage driven by the primary producer *Arthrospira* and its primary consumer Lesser Flamingo is only one of the phases that occurs in these archaic ecosystems.

Melack (1979) and Burgis & Symoens (1987) described the wide amplitude of temporal variation of phytoplankton in tropical lakes. Vareschi & Jacobs (1985) demonstrated using the example of Lake Nakuru, the best studied tropical soda lake, that the trophic structure has no predictable long-term continuity, and consequently there is no «normal» or «typical» stage of a soda lake. In their 5-year study (1972–1976) they observed three different stages, (i) the «*Spirulina*» (*Arthrospira*) stage, (ii) the stage of low algal densities and (iii) transitional stages. The conductivity in this study phase varied between 14 and 26 mS cm^{-1}. In our sampling covering a span of 15 years, we were able to observe much lower and higher ranges in conductivity values ranging to 6.5 and 70 mS cm^{-1} at Nakuru. We established additional

stages in the phases of extreme conductivity values: under hyposaline conditions (>3 ppt) the phytoplankton was characterised by an extraordinary diversity of chlorophytes, chromophytes and euglenophytes (also shown by pyrosequencing), whereas under hypersaline conditions (>50 ppt) the prasinophyte *Picocystis* was the only dominant species in the phytoplankton (Krienitz et al., 2012). According to Verschuren (2013) and Schagerl et al. (2015), an interplay between the hydrological regime, the physical and chemical characteristics of the water and the diversity of primary producers largely influences the structure of consumer populations. It is important to realise that only one stage, the *Arthrospira* stage, is characterised by involvement of Lesser Flamingos in the food web. Another example of wetlands with strong changes in succession patterns of biota is the well-studied crater lake Sonachi, where *Arthrospira* has not always been predominant. *Arthrospira* was replaced by coccoid cyanobacteria between the 1930s and 1970s (Verschuren et al., 1999), it was available only in low numbers in the 1980s when it was replaced by cyanobacterial and eukaryotic picoplankton (mainly *Microchloropsis salina,* syn. *Monallanthus salina, Nannochloropsis salina*) (Melack et al., 1982; Njuguna, 1988) and declined again in 2009 (this study).

Melack (1988) has discussed eight possible reasons of the breakdowns of *Arthrospira*. This includes the following: changes in salinity, nutrient concentrations and water level; competitive displacement by coccoid or flagellated plankton and attacks by cyanophages or autolysis. More recently, a study by Peduzzi et al. (2014) demonstrated the role of infections by viruses in the breakdown of *Arthrospira* populations.

Our microphyte observations allowed a screening of food availability for the Lesser Flamingo in wetlands across the main distribution range of Lesser Flamingos in seven countries over 15 years. Owing to sampling logistics, this large survey dataset was mainly carried out in non-regular intervals in space and time and thus comprises snapshot information of the Lesser Flamingo habitats. Despite the sporadic sampling, the consistency in the sampling procedure over many sites and the long study period allowed inferring valuable insights in the diversity of microphytes. The a priori ranking of the flamingo densities in four abundance groups turned out to be a powerful descriptor of the match between birds and the bird's food availability across a large spatial and temporal

scale. Such semiquantitative ranking by scores is commonly applied studying the structure of biotic communities as, e.g. by vegetation surveys or water quality assessments (Wikum & Shanholtzer, 1978; Ramakrishnan, 2003). With our flamingo dataset, we could show that snapshot surveys, which are rarely applied in ecology (e.g. Grayson et al., 1997; Wiegand et al., 2000), can satisfy rules of statistical data evaluation. Here, our main finding that flamingos were most abundant when *Arthrospira* or other cyanobacteria and algae, which are most suitable as food, were amply available extends results from previous work (Tuite 1981, 2000). Nevertheless, we are aware that sampling in regular time intervals is needed to provide information about intra-annual changes of abiotic and biotic interactions in soda lakes. Because of logistic challenges such studies have only been realised a few times: at Lake Nakuru monthly sampling in 1972–1974 (Vareschi, 1982), at Lake Elmenteita from February 1973 to August 1974 with a bi-weekly to bi-monthly sampling regime (Melack, 1988), at Bogoria, Elmenteita and Nakuru monthly from November 2003 to February 2005 (Oduor & Schagerl, 2007; Schagerl & Oduor, 2008) and at Bogoria and Nakuru in weekly intervals from July 2008 to October 2009 (Kaggwa et al., 2013a).

Dense suspensions of *Arthrospira fusiformis* are the main and preferred food for Lesser Flamingos (Jenkin, 1957; Vareschi, 1978; Kaggwa et al., 2013a). This alkaliphilic cyanobacterium, which grows well even at pH > 10 (Grant et al., 1990), is the key primary producer in soda lakes (Melack & Kilham, 1974; Schagerl et al., 2015). It is an alkaliphilic cyanobacterium and grows well even at pH > 10 (Grant et al., 1990). Optimal growth performance was reported at salinities of 22–62 ppt (Iltis, 1968). It can tolerate temperatures of >35°C (Vonshak, 1997). *Arthrospira* is able to exist in a wide range of conditions even if under low number of filaments or hormogonia: from freshwater to hypersaline waters (Ciferri, 1983; Dadheech et al., 2010), from standing to running waters (Oxa et al., 2012; this study) and hot springs (Dadheech et al., 2013). The nutritional quality of *Arthrospira* is very high (Mühling et al., 2005). With a protein content up to 70%, it is one of the richest sources of this major nutrient of plant origin, and it is easily digestible by animals (Ciferri, 1983).

Diatoms are the second important source of food for Lesser Flamingos. They are more widely

distributed than *Arthrospira*. However, the net primary production and carrying capacity of benthic diatoms in soda lakes are one or two orders of magnitude lower than that of *Arthrospira* (Tuite, 1981, 2000). In our study, we found 104 diatom taxa at the flamingo habitats. Despite this relatively high number of species most of which fell within the size class of flamingo food algae, only few of them attained predominance. These species originated from the sediment or from periphyton and could be distributed as tychoplankton. All the dominant taxa were pennate diatoms while centric diatoms were rarely found. With regard to salinity preferences, fresh, brackish/marine and saline inland waters taxa were detected. In the soda lakes Nakuru and Natron, most abundant diatom species are typically for highly polluted freshwater habitats and not necessarily for inland salt waters. For example *Anomoeoneis sphaerophora*, the dominant species in both lakes, is an eutraphent species, common in littoral zones of different habitats, from limnic to brackish water, but also in inland salt lakes (Krammer & Lange-Bertalot, 1986). *Rhopalodia gibberula* is characteristic of inland waters of high temperature and high conductivity values, so that the mass developments in these soda lakes are not surprising. Detections of *R. gibberula* in marine habitats are based on misinterpretation of the closely related species, such as *R. musculus* (Kützing) Müller or *R. acuminata* Krammer (Krammer & Lange-Bertalot, 1988). *Nitzschia palea* is an eutraphent species with a cosmopolitan distribution in mainly polluted lakes and rivers. However, it is also common in brackish water estuaries and inland salt lakes, and has also been detected in many African water supplies (Schoemann & Archibald, 1976). *N. palea* established high densities in the benthic biofilms of lakes Nakuru and Natron, mostly co-dominated by many other eutrophic *Nitzschia* species (*N. intermedia* Hantzsch, *N. liebetruthii* Rabenhorst, *N. supralitorea* Lange-Bertalot, *Nitzschia pusilla* Grunow) typical in habitats with highly fluctuating osmotic values (Krammer & Lange-Bertalot, 1988). Surprisingly, we did not find any *Nitzschia frustulum*, which according to Hecky & Kilham (1973) is one of the most abundant benthic diatoms in East African lakes. It is important to note at this stage that the taxonomic concept of *N. frustulum* has since changed: « Excluded from current diagnose (of *N. liebetruthii*) are all associations showing features of *N. frustulum*. Included (to *N. liebetruthii*)

are similar associations, but without central nodule.» (loc. cit. Krammer & Lange-Bertalot, 1988, p. 96). We found only frustules with continuously equidistant fibulae characteristic for *N. liebetruthii*, wide spread on different marine coasts (Krammer & Lange-Bertalot, 1988). *Diploneis subovalis*, the dominating diatom in Little Rann of Kutch, is one of the most abundant pennate diatoms in inland waters of tropic regions (Hustedt, 1937). Gasse (1986) localised this species mainly on aerophytic habitats near hot springs in Africa. *D. subovalis* can morphologically be distinguished from the very similar marine *D. smithii* (Brébisson) Cleve by a slightly lateral raphe (Krammer & Lange-Bertalot, 1986). The dominant *Opephora* sp. seems to be an unknown marine species (A. Witkowski, University of Szczecin, Poland has it as a clone culture from Namibian origin; personal communication).

We found a more balanced relation between marine, brackish and freshwater species in the salt ponds of Swakopmund and Walvis Bay and lagoons of the latter station. Although most taxa are freshwater species, the most abundant are of marine origin. The samples contained elements of the diatom flora described from the Redford Bay, Namibia, by Witkowski et al. (2000). The sum of the frequency of freshwater and marine species is nearly balanced (ESM_3). The greater abundance of marine species (*Navicula* cf. *halinae*, *Halamphora coffeaeformis, Opephora olsenii, O.* sp*., Parlibellus* sp.) can be explained by the water exchange with the open ocean resulting from the flooding of evaporation ponds with sea water.

Beside the diatoms, other planktonic and benthic microphytes also serve as flamingo food. These include both cyanobacteria, especially filamentous taxa such as *Oscillatoria*, *Phormidium*, *Haloleptolyngbya* and the heterocytous *Anabaenopsis*, as well as eukaryotic algae such as chloro- and euglenophytes (Berry, 1972; Krienitz, 2009; Dadheech et al., 2012; Krienitz et al., 2013a). Experimental studies on zooplankton and invertebrates have revealed the complexity of evaluating the food quality of natural algal communities. Microalgae normally contain 30–40% proteins, 10–20% lipids and 5–15% carbohydrates (Brown et al., 1997). High food quality is driven, for example, by amino acid and fatty acid content and composition (Müller-Navarra, 1995; Ferrão-Filho et al., 2003). However, the chemical

composition of nutritional components highly depends on the environmental conditions (Leonardes & Lucas, 2000). Often, a mix of different taxa can compensate food quality deficits of a monospecific diet (Brown, 2002; Jones & Flynn, 2005). Unfortunately, such a study looking at the interaction between Lesser Flamingos or other waders and their food sources is yet to be carried out and should therefore be urgently attempted.

A further limiting factor is the size of the food particles. To obtain food from its environment, the Lesser Flamingos employ a filter system to trap all particles which are available in the plankton or on the sediments of the supporting habitats (Burgis & Morris, 1987). However, not all the cyanobacteria and algae fit into the optimum size of the filter lamellae; some of them are too small while others are too large to be ingested (Jenkin, 1957; Krienitz & Kotut, 2010). Analyses of stomach contents of Lesser Flamingos revealed that the smallest particles ingested were pennate diatoms with a size range of 15–70 μm, while the main food was *Arthrospira* with a size of 40–800 μm (Jenkin, 1957). Despite the high variability of size and shape of the filaments of *Arthrospira fusiformis* (Vareschi, 1978; Kaggwa et al., 2013b; Krienitz et al., 2013b; Ogato & Kifle, 2014), all of these morphotypes are ingestible by the Lesser Flamingos. The maximum size class of up to 800 μm offers a further option for the birds to feed also on members of the zooplankton such as ciliates and rotifers. However, this is highly speculative. The main role of rotifers for example is the grazing on phytoplankton hence influencing the food availability for flamingos indirectly (Burian et al., 2014).

Examples of microphytes that do not fit into the edible size classes of Lesser Flamingos were found several times. The most spectacular were the large colonies of *Cyanospira capsulata* which were macroscopic with a visible size of 1–2 mm in Lake Bogoria distracting the Lesser Flamingos. The lamellae of the bill of Lesser Flamingos are equipped with rows of fringed platelets which have a distance of 120 μm (Jenkin, 1957). These narrow rows were clogged by the colonies of *Cyanospira*. Apart from the too large plankton forms, the extremely small cells (diameter ∼2 μm) of *Picocystis salinarum* (Lewin et al., 2000) also could not serve as food as these particles cannot be retained by Lesser Flamingos lamellae. The dominance of *Picocystis* in lakes Bogoria, Nakuru or

Magadi during phases of elevated salinity makes it to a strong competitor against *Arthrospira* (Krienitz et al., 2012). Another picoplankton, *Microchloropsis salina*, known mainly from marine habitats (Andersen et al., 1998), developed green coloured blooms in salt evaporation ponds, however, Lesser Flamingos were not attracted to feed on those because of their tiny size. The main diatom taxon of mudflats and salt ponds in Walvis Bay and Swakopmund, the pennate *Opephora* sp. with a size of 4.2–18.5 × 2.7–3.8 μm was in most cases not ingestible. This is because only cells >15 μm can be retained by the filter lamellae of Lesser Flamingo. Hence it is possible that this alga performs well under these conditions because individual cells are not affected by flamingo feeding. This combined with a fast reproduction rate allows them to accumulate to a large number of cells.

A particular plankton composition of Lake Nakuru was found during the phase of very low salinity in January 2015. The 454 pyrosequencing revealed a mixture of tiny coccoid or filamentous cyanobacteria which are usually found in freshwater reservoirs, tropical ponds or geothermal springs (see ESM_4). This demonstrates the struggle by the plankton community to adapt to the new conditions. Verschuren (2003) indicated that organisms adapted to different conditions can occur in an habitat in the presence of a transition between the different phases of salinity. Different genotypes of *Arthrospira* were not discovered in this study. Alternative food resources revealed by molecular data were (i) the confirmation of the existence of a genotype of *Haloleptolyngbya alcalis* (Dadheech et al., 2012), (ii) other filamentous taxa of the Oscillatoriales and Nostocales and (iii) the diatom *Anomoeoneis sphaerophora*, a well-known food alga for flamingos (Tuite, 1981). Further, it was interesting to note the occurrence of the marine prymnesiophycean flagellate *Isochrysis*, which is a known food organism in aquaculture (Wacker et al., 2002). *Isochrysis*, however, it is too tiny to be ingested by Lesser Flamingos. This also applies to the picoplanktonic *Nannochloropsis limnetica*, previously known only from inland freshwaters of Europe, North America and Asia, and recorded for the first time on the African continent during this study (Krienitz & Wirth, 2006). The pyrosequencing investigations serve as a bridge to the pioneering work of Vareschi (1978, 1982) in Lake Nakuru. Ekkehard Vareschi sent a living algal sample collected in 1976 to the German

phycologist Eberhard Hegewald who isolated two strains (*Synechocystis minuscula* SAG 258.80 and *Spirulina laxissima* SAG 256.80), and deposited them in the algal culture collection of the University of Göttingen (SAG) (E. Hegewald, pers. comm.). The modern DNA-based analyses have now allowed us to re-discover these cyanobacteria.

Experimental studies on feeding behaviour of caged Lesser Flamingos at Lake Nakuru in the early 1970s revealed that an adult bird requires 72 ± 6.5 g dry weight of *Arthrospira* per day (Vareschi, 1978). It was further postulated that a critical food concentration of about 100 ± 5 mg L^{-1} dry weight is necessary for activating feeding of Lesser Flamingos. Later phytoplankton analyses, however, established that *Arthrospira* biomass has only reached this critical level in Lake Bogoria only on a few occasions (Kaggwa et al., 2013a; Ballot et al., 2004). In most cases, the algal food concentration in the habitats investigated was considerably lower. Hence, the question that is yet to be answered is whether the Lesser Flamingos change their feeding behaviour in response to the lower food availability. No further experiments on the feeding behaviour of flamingos have been conducted since the 1970s. Therefore, there is an urgent need to carry out follow-up experiments so as to provide a better insight into the birds' preferred feeding requirements.

The possible content of toxins in the cyanobacterial food of Lesser Flamingos presents a new dimension to the discussion (Koenig, 2006). Generally, flamingos are susceptible to poisoning through feeding on toxic cyanobacteria (Codd et al., 2003). Studies on the occurrence of microcystins and anatoxin-a in the phytoplankton samples from the Kenyan flamingo lakes confirmed the presence of the toxins (Ballot et al., 2004, 2005; Ndetei & Muhandiki, 2005). Cyanotoxins were also found in cyanobacterial mats and fish from the hot springs at lakes Bogoria and Magadi (Krienitz et al., 2003). A low concentration of cyanotoxins was also recorded in three strains of *Arthrospira* (Ballot et al., 2004, 2005). Furthermore, microcystins and anatoxin-a were detected in tissue-samples of dead Lesser Flamingos (Krienitz et al., 2003) and in sediments of Kenyan soda lakes (Dadheech et al., 2009). A similar worrying finding has been reported from the soda lakes in Tanzania (Lugomela et al., 2006; Fyumagwa et al., 2013). In 2004, Lesser Flamingos die-offs of between 1050 and

43850 were reported during the Momella and Manyara die-offs, respectively. Neurotoxins and hepatotoxins were detected together with bacterial infections (Nonga et al., 2011; Fyumagwa et al., 2013). The toxicity of crude extracts of *Arthrospira*, the dominant phytoplankton from Big Momella was confirmed by mouse tests (Lugomela et al., 2006).

In contrast, Mussagy et al. (2006) did not detect cyanotoxins in strains of *Arthrospira*. Straubinger-Gansberger et al. (2014) conducted a thorough search for cyanotoxins from Lakes Nakuru and Bogoria in weekly phytoplankton samples from July 2008 to November 2009. In this period, three die-off events of Lesser Flamingos were observed at Bogoria. The examination of 20 carcasses of the birds did not reveal any cyanotoxins in their tissues.

During the mass die-offs of 2001, the examination of Lesser Flamingo feathers at lakes Nakuru and Bogoria detected the presence of microcystins and anatoxin-a (Metcalf et al., 2006). Furthermore, neurotoxic amino acids (β-*N*-methylamino-L-alanine [BMAA], and 2,4-diaminobutyric acid [DAB]) were later found in the same feather samples collected in 2001 (Metcalf et al., 2013). Based on these results, it was opined that under natural conditions, the toxins are sequestered in the feathers of Lesser Flamingos. However, due to the increasing environmental stress, sequestration mechanism in the weakened birds may not be effective enough to protect them against cyanotoxicosis. All these contrasting results show the urgent need for further studies on the contribution of cyanotoxins to the food quality challenges facing the Lesser Flamingos.

Besides the risk posed by cyanobacterial toxins, Lesser Flamingos are also threatened by heavy metal and pesticide pollutants that are mostly from anthropogenic sources. The type of toxic substance in the lake largely depends on the industrial or agricultural activities in the catchment areas. Initial reports on heavy metal and pesticide presence in Lake Nakuru date back to studies by Kairu (1996) and Greichus et al. (1978). Burger & Gochfield (2001) compared the level of heavy metal contamination in feathers of cormorants, gulls and flamingos collected at the Namibian coast near the saltworks in Swakopmund. Their field survey showed that Lesser Flamingos had the least contamination depending on their algal food which is on the lowest trophic level as primary producers. Other threats are from infective diseases

such as mycobacteriosis (avian tuberculosis), avian cholera, botulism and inflammations caused by opportunistic bacteria (Anderson et al., 2005). However, further subsequent studies should be done to confirm the pathways of the different threats (Cooper, 1990; Cooper et al., 2014). According to Harper et al. (2003), the mass mortalities of Lesser Flamingos have multiple and complex causes.

Studies focusing on the natural breeding sites of the Lesser Flamingo have never reported on the occurrence of dense *Arthrospira*-blooms at these sites. Tebbs et al. (2013a) noted that *Arthrospira* at Lake Natron is very limited and the adult flamingos have to look for food at other lakes of Tanzania or southern Kenya. Only at the artificial breeding site of Kamfers Dam were the *Arthrospira* counts found to occur in sufficient concentrations to feed Lesser Flamingos in the stage of breeding business (Hill et al., 2013; LK, unpubl. data). At other breeding areas such as the large salt pans of south-western Africa and India, the most common species and therefore the main food source for the flamingos were different filamentous cyanobacteria such as *Phormidium*, *Oscillatoria*, *Leptolyngbya* and diverse diatoms. The occasionally reported high numbers of Lesser Flamingos breeding may suggest the existence of highly nutritive food sources such as *Arthrospira*. However, given that salinity at the breeding sites may be extremely high, it is not likely that *Arthrospira* can form a dense population. Consequently, the adult birds have to fly from the breeding site to nearby lakes for food.

Using an amphibious six-wheel-vehicle, it was possible to access the breeding site at Etosha Pan for a pioneering study on the breeding events in 1971 (Berry, 1972). Microscopic analysis of food algae samples collected by the research team revealed the presence of among others *Anabaena*, *Nodularia*, *Oscillatoria* and *Navicula* (Berry, 1972). In the context of a controversial proposal to establish an artificial breeding site for Lesser Flamingos in the Etosha Pan, Ekuma mouth was considered as a good option because of the relatively safe water and food availability (Simmons, 1996). Our visit to this site revealed the presence of *Phormidium* sp., *Leptolyngbya* sp., *Cyanospira* sp., coccoid green algae and pennate diatoms. We did not detect the main flamingo food, *Arthrospira fusiformis*, in waters of the Etosha National Park. The dominant filamentous cyanobacteria belong to the genus *Phormidium*, which occur

mostly in dense mats that cannot easily be taken up by the birds. However, at the early stages of their developmental, these cyanobacteria are able to live in suspension and can therefore be filtered by the flamingos. *Phormidium etoshii* was prevalent in the springs and nearby flooded waters. The findings from Etosha and Makgadikgadi showed that probably several other species of *Phormidium* can grow and become dominant in the salt pans. Hence more work on culture material and phylogenetic analyses of the cultures should be done to provide a better insight into the species diversity of the salt pans.

To study the flight-paths of Lesser Flamingos in their search for food and remote breeding sites, two modern tools were recently applied: satellite tracking and genetic analysis. The aim of the study was to establish whether there are interchanges between the populations of the birds in eastern, western and southern regions of the African continent as suggested by Tuite (1981), Simmons (2000) and other naturalists. Using satellite transmitters installed on five Lesser Flamingos in southern Africa and 19 in eastern Africa, the active inter-lake flights on the subcontinents were confirmed, however, no birds were reported to have flown out of their core area (McCulloch et al., 2003; Childress et al., 2006; Salewski et al., 2009). The record holder was a flamingo that started its journey at Lake Bogoria and flew for a total of 7870 km in 70 stages, visiting 11 different lakes in East Africa. Arguments for possible interchanges between eastern and southern Africa populations were based on the following facts; the coincidental increase in bird numbers in southern Africa at a time of reported decline in numbers in eastern Africa, the ability of well-fed flamingos to fly the minimum distance of 2200 km (from Lake Natron to Sua Pan) in one step, or the option to fly along the coastline of Tanzania and Mocambique with some stop-overs (Simmons, 2000).

Genetic comparison between a population of Lesser Flamingo in southern Africa (Makgadikgadi Pan) and eastern Africa (Lake Bogoria) revealed that despite the high similarity, there exists a moderate gene flow between the two populations (Zaccara et al., 2011). The estimated number of migrants was 3–4 per generation (10 years correspond with three generations). Furthermore, genetic studies on Indian Lesser Flamingos from Rann of Kutch revealed a number of two to three migrants between Kenya and Gujarat (Parasharya et al., 2015). This exchange between the

populations bridging long distances, presuppose the existence of shallow saline waters on the flightway which could act as stop-over for rest and food. At a time when the continent is faced with loss and degradation of wetlands, this presents a strong argument in support of activities aimed at protecting such areas that bridge the Lesser Flamingo migration.

The condition of flamingo habitats in the different countries, the activities for protection of Lesser Flamingos and the actual priorities for environmental groups and agencies in the areas of distribution of this bird vary considerably. In Kenya, when the main lakes in the Rift Valley became flooded, the flamingos left (Onywere et al., 2013). Due to the absence of reliable data on flamingo abundance in the region, the destination of the birds remains largely speculative. Several ephemeral lakes hidden in remote areas that are difficult to approach such as Lake Logipi in northern Kenya were found to support high numbers of flamingos in times when the core lakes were flooded (Tebbs et al., 2015).

Tanzania is coming into focus because of the high diversity of potential flamingo habitats. Counts of Lesser Flamingos density in 13 different soda lakes carried out between 1969 and 2004 revealed an extremely wide fluctuation in bird numbers (Mlingwa & Baker, 2006). The lowest number of 68163 was recorded in 1969, while the highest number of 2759026 was counted in 1995. Unfortunately, the actual research on the soda lakes in the country is very limited. From the few publications on Tanzanian wetlands, it is evident that they together with the Kenyan soda lakes represent the most important habitats for Lesser Flamingos in East Africa (Mlingwa & Baker, 2006; Flamingo, 2011). Based on the high numbers of flamingos, it can be hypothesised that the majority of the soda lakes host *Arthrospira* temporarily. However, this has not been investigated in great detail. Ekkehard Vareschi and his wife Angelika had planned to start a multiannual study of the ecology of Tanzanian soda lakes. In July 2005, they reported to their new field laboratory, the Endala Research Camp in the Manyara National Park. Sadly, two months afterwards, they suddenly died in an accident in the Arusha National Park (Tins, 2005).

The increase of vulnerability to extinction turns out as many habitats with high potential to host flamingos are located outside protected areas and are endangered due to increased siltation and chemical pollution (Yanda & Madula, 2005; Mlingwa & Baker, 2006). Lake Natron, the only breeding site of Lesser Flamingos in East Africa should arguably receive the highest protection priority (Clamsen et al., 2011). However, on the contrary it is under a serious threat from industrial and transportation projects (Baker, 2011; BirdLife International; 2012, Kadigi et al.; 2014).

Other countries of East Africa also have habitats with the capacity to shelter Lesser Flamingos. Uganda harbours a number of magnificent saline-alkaline crater lakes in the western part of the country (Pomeroy et al., 2003). In Ethiopia, the Lesser Flamingos are common at the crater lakes Chitu (Ogato & Kifle, 2014) and Arenguade (Girma et al., 2012) as well as at Lake Abijata (Kumssa & Bekele, 2014). However, because of human activities such as settlements, irrigation and industrial uses of the lakes at the floor of the Rift Valley, these valuable habitats are facing many threats (Gebre-Mariam, 2002; Willén et al., 2011). In the case of Lake Abijata, the type locality of *Anabaenopsis abijatae* (Kebede & Willén, 1996, 1998) and a shelter for Lesser Flamingos, the negative effects of irrigation on hydrology, chemistry and ecology are very evident. The water level has since declined, salinity has increased and *Arthrospira* has been outcompeted (Kebede & Willén, 1996). The main food for the reduced number of flamingos mainly consists of pennate diatoms (Kumssa & Bekele, 2014). In the 1980s, a soda ash factory was built at the shore of Lake Abijata. Its negative impact on the ecology of the lake is presently the subject of intense discussion (Esa, 2011; Getaneh et al., 2015). Presently, the flamingo feeding habitats in Ethiopia are not under any legal protection.

In eastern Africa, a reduction in flamingo population by 30% within the next 10 years has been predicted (Zaccara et al., 2011). The main reasons for the anticipated decline in population are the loss or degradation of habitats brought about by drought and human pressure. The recent phase of lake flooding in the East Africa Rift Valley suggests that both flooding and drought can result in habitat degradation.

In southern Africa, besides the huge flamingo habitats in Botswana (Makgadikgadi Pan) and Namibia (Etosha Pan), there are also a wide range of smaller wetlands and water bodies exist that act as food sources and resting places of the nomadic birds and are of great value in the protection of the flamingos. Some

of these sites, especially the Kamfers Dam, which has become famous as an artificial breeding place for Lesser Flamingo, have a great potential for research and conservation (Anderson, 2015). The artificial breeding site provides valuable experiences for birders and naturalist planning to set up such areas elsewhere in the flamingo countries. Other wetlands are more or less unrecognised and must be exploited as potential flamingo shelters and food stations. The highest diversity of flamingo habitats in southern Africa occurs in Namibia which has both natural (protected salt pans with springs and water hollows in the heartlands, as well as intertidal mudflats at the sea shore) and artificial wetlands (salt evaporation ponds, sewage outfall ponds). The detection of *Arthrospira fusiformis* in the sewage outfall ponds of Walvis Bay demonstrates the high value of these artificial waters for the survival of the flamingos in a phase were the population of Lesser Flamingo is declining in southern Africa (Simmons, 1996, 2000).

The extreme diversity of saline waters in a relatively small space provides an excellent opportunity to learn more about the food requirements of flamingos and the integration of the different approaches of research from the airplane to field studies. Using the example of salt evaporation and sewage outfall ponds in Swakopmund and Walvis Bay, we can learn how differences in the phytoplankton blooms originate and how they can be evaluated as flamingo food. Due to the extreme variations in salinity, the community structure of phytoplankton in these waters varied widely. The occurrence of dense blooms of the picoplanktonic algae such as *Microchloropsis*, for example, serves to demonstrate that dense blooms are not always an indication of food availability for flamingos. This lesson learned from ground field studies can be applied as a form of in situ validation of pigment spectra obtained from remote sensing from the airspace. Another example of difficult food interpretation provided by our microphyte survey is that cyanobacteria seem to be not always the suitable food source for the Lesser Flamingo. Here it becomes even trickier to track good food as blooms belong to the same taxonomic affiliations as the preferred flamingo food (cyanobacterium *Arthrospira*) but do not fit in by their size: it is too small (picocyanobacteria) or too large (cyanobacterium *Cyanospira*) for the filter feeding flamingos. Estimates of food algae retrieved from the pigment

pattern via airborne or satellite data can thus lead to substantial misinterpretations as all these species are phycobiline-rich cyanobacteria. To reduce these uncertainties, we recommend validation by microscopy.

India provides Lesser Flamingo hot spots on the Asian continent with two large habitats, sampled by us, which differ in origin, flooding regime and protection status. The Little Rann of Kutch, which is a protected flamingo refuge offers unique options to address the decline and threats to the birds. The diversity of saline wetlands in Lake Sambhar area could be a perfect experimental observatory under field conditions for study of the behaviour of the flamingos. A further challenge is the field of flamingo genetics. The ability of these birds to carry out intercontinental movements between Africa and India was convincingly demonstrated through genetic studies (Parasharya et al., 2015). In all areas of distribution of Lesser Flamingos at both continents, it is necessary to come up with a more accurate way of flamingo counting and tracking in order to compare the situation in different lakes at a given time. Such possibilities of reality mining of animal social systems are discussed generally by Sardà-Palomera et al. (2012) and Krause et al. (2013) and could also be applied to nomadic birds.

Recommendations for further protective works of the Lesser Flamingo

– Substantial efforts in research and protection of Lesser Flamingos demand the creation of bridges between many disciplines and specialisations, and collaboration between ornithologists, ecologists, hydrobiologists, phycologists, veterinarians, geneticists and conservationists.
– Modern methods such as remote sensing and advanced techniques of reality mining used to study migration of Lesser Flamingos in the search for food and breeding habitats should be incorporated into flamingo research and aligned to the uniqueness of flamingo behaviour and habitat conditions.
– Holistic approaches combining aerial surveys with physical, chemical and food web analyses on site should be intensified.

- Home universities of the flamingo countries should establish regular monitoring regimes and implement research and management of soda lakes in their educational «routine» work.
- The experimental approach established by E. Varschi in the 1970s at Lake Nakuru with caged birds should be carried out again to study food behaviour of Lesser Flamingos. In such experiments, focus should be on the following topics: food preferences, ingestion of microphytes in comparison to *Arthrospira*, comparison of the diet quality of monospecific and mixed taxa and validity of the concept of critical food concentration in time and space.
- Experimental field observations should be established in habitats which offer water bodies of different salt contents in close neighbourhood such as the evaporation ponds at Lake Sambhar and the salt ponds in Swakopmund and Walvis Bay.
- Creation of new flamingo habitats such as Kamfers Dam in Kimberley and the sewage outfall ponds in Walvis Bay should be carefully planned so as to provide stable food sources within the vicinity of flamingo sites.
- Deliberate efforts aimed at protecting lakes and wetlands which have the potential to act as shelter, feeding and breeding ground for the Lesser Flamingos should be made. Effective protection measures of the priority waters for survival and propagation of this endangered character bird of soda lakes, especially Lake Natron, have to be enforced by the policies of the flamingo countries.

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