The Ecology of East African Soda Lakes: Implications for lesser flamingo (*Phoeniconaias minor*) feeding behaviour

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By

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"…and flamingos are utterly unpredictable and supremely opportunistic. Anyone who tries over a long period of time to rationalize what they do, is asking for trouble."

"The mystery of the flamingos" - Leslie Brown, 1979

The ecology of East African soda lakes: implications for lesser flamingo (*Phoeniconaias minor*) feeding behaviours

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Abstract

This thesis investigates the feeding ecology of the lesser flamingo (*Phoeniconaias minor*). Studies took place at six endorheic alkaline-saline lakes within the East African Rift Valley, which varied in terms of taxonomic composition and biomass, both spatially and temporally. The lakes could be categorised as *Arthrospira fusiformis* dominated (lakes Bogoria and Sonachi), diatom dominated (Lakes Natron and Elementaita) or 'other' cyanobacteria dominated (lakes Oloidien and Nakuru). From 2009 to 2013, the lake levels were consistently rising with the average biomass reducing concurrently; maximum surface *A. fusiformis* recorded was > 800 mg L^{-1} in 2009 at Lake Bogoria, falling to < 50 mg L^{-1} in 2013. A reduction in average biomass was recorded at all lakes throughout the study period, with the exception of Lake Natron, where higher diatom abundance was recorded in 2011 than in 2009. This study identified 10 distinct feeding behaviours utilised by lesser flamingos at different times of day. Different behaviours were also employed to access different food resources from a variety of niches throughout the aquatic habitat: from the lake's edge, the open water and the lake-sediment interface. Deep water feeding was occurring in higher frequency than recorded previously, at Lake Bogoria where flamingos were exploiting a highly concentrated food resource of sedimented *A. fusiformis,* discovered during this study. This confirms that deep water feeding behaviours are more common than only being utilised to access diatoms as an emergency food source, as has been suggested. The time spent feeding was negatively correlated with food abundance across the six lakes with lower biomass requiring longer feeding duration, however, at Lake Bogoria a positive correlation was identified, suggesting re-stocking of energy reserves. A positive correlation was identified between the distribution of food resources within Lake Bogoria and lesser flamingo distribution across the lake. Finally, a significant difference was found between flock density when feeding on different food sources (more densely flocked when feeding on *A. fusiformis* than on diatoms) or through different feeding behaviours.

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Asante sana!

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Chapter 1   Introduction

The alkaline-saline[1] lakes of the East African Rift Valley are amongst the world's most productive ecosystems (Melack & Kilham, 1974) and are situated in an area currently undergoing significant environmental change, with both natural and anthropogenic causes (Anyamba *et al.*, 2002; Harper *et al.*, 2011). These lakes are defined as endorheic as they are closed basin lake systems with no surface outlet and because of this they are intrinsically linked to climate. Water chemistry and lake level result from the delicate balance between inputs from direct precipitation, surface runoff and groundwater flow and losses through evaporation and groundwater recharge (Mason *et al.*, 1994). The East African soda lakes are situated in the Intertropical Convergence Zone (ITCZ), therefore, climatic unpredictability can have significant effects on lake parameters, including their biota (Smol & Stoermer, 2010).

Characterised by their high pH and salinity (Na_2CO_3), endorheic alkaline-saline lakes experience both seasonal and long-term lake level fluctuations as a result of the subtle balance between precipitation and evaporation. The solute composition of the lakes is initially assimilated through chemical weathering of rocks and surface deposits (Smol & Stoermer, 2010). Subsequent epaporative water loss further concentrates the dissolved salts and maintains the alkaline-saline status.

Alkaline-saline lakes in East Africa are essential for the survival of the lesser flamingo (*Phoeniconaias minor* Geoffroy Saint-Hilaire, 1798) as they provide both vital food resources and a breeding ground for 75% of the global population of this 'Near-Threatened' species. This thesis will explore the variation in the ecology of six alkaline-saline lakes and examine how their composition influences the foraging duration and behaviour of these mysterious birds.

1.1   Lakes of the East African Rift Valley

The lakes studied in this thesis are situated in the East African Rift Valley, in arid (25-200 mm annual precipitation) and semi-arid (200-500 mm annual precipitation) climatic zones (Hammer, 1981). The East African Rift Valley was formed in the

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[1] Alkaline-saline lakes are often referred to as 'soda' lakes due to the high concentration of Sodium carbonate and bicarbonate ions; the two terms are used interchangeably throughout this thesis.

Cenozoic era (approximately 40 million years ago (Ma)); as a result of volcanic and tectonic activity. The current climate of alternating periods of high humidity and high aridity dates back 2.7-0.9 Ma (Trauth, 2005), after the onset of the glacial cycles in the Northern Hemisphere experienced in the Plio-pleistocene (de Menocal, 1995). There is much diatomite evidence to suggest the presence of very large lakes, exceeding 250m in depth, between 1.9-0.9 Ma, one of which was still in existence 9,200 years ago (Trauth *et al.*, 2010). This lake shrank over the following years, being considerably smaller 3,000 years ago (Richardson & Richardson, 1972) and the present lakes are all that remain.

The Eastern Rift Valley passes through Ethiopia, Kenya and Tanzania; it contains 14 lakes, of which only three are freshwater; the remaining 11 are soda lakes. The freshwater lakes support high biodiversity and economic activity, through horticulture, fisheries and tourism and have been the focus of extensive limnological studies (Harper *et al.*, 2011). Conversely, alkaline-saline lakes are less well studied, although they are unique in terms of their ecology. They are renowned for their high salinity and alkalinity with pH > 9.5 resulting from the high concentration of Na^+ trachyte lava in the surrounding volcanic highlands, which is dissolved by rainwater running into the lakes. There are low levels of Ca^{2+} ions in the water, so sodium-sesquicarbonate also known as 'trona' or 'soda ash', an alkaline salt $Na_2CO_2.NaHCO_3.2H_2O$, is the dominant compound (Grant, 2004). The lakes have no outlet; therefore this alkaline salt becomes concentrated to equilibrium through the evaporation of water.

All the lakes within the East African Rift Valley have undergone extreme and erratic fluctuations in both water level and environmental conditions over the last few hundred years (Verschuren, 2001). The lakes vary dramatically in terms of hydrology and ecology, ranging in depth from just 15cm in parts of Lake Natron to over 16m at Lake Bogoria's deepest point. The conductivity of the deeper lakes is characteristically high and semi-stable at around 70,000 μS cm^{-1} (Harper *et al.*, 2003; Schagerl & Odour, 2008) whilst the shallow lakes experience high variability, ranging from 11,000-160,000 μS cm^{-1} as their levels fluctuate (Verschuren, 2004). These soda lakes support some of the highest rates of aquatic primary production in the world and as a result their ecology is of significant interest (Talling *et al.*, 1973).

The phytoplankton is dominated by the cyanobacterium *Arthrospira fusiformis* (Voronichin) Komárek and Lund, with other cyanobacteria such as *Anabaena sp.* and *Anabaenopsis sp.* also being recorded, alongside the single-celled *Synecochoccus sp.*. The prevailing diatom genera consist of *Navicula, Cyclotella, Nitzschia, Anomoeoneis* and *Coscinodiscus* with different species favouring differing alkalinities (Hecky & Kilham, 1973). The diatoms found in these lakes also form characteristic groupings and are significant contributors to the algal community (ibid.).

The lesser flamingo is the most important consumer in these lake ecosystems, together with zooplankton dominated by rotifer species (principally *Brachionus dimidiatus, B. plicatilis* and *Hexartha jenkinae)* and many protozoan species. The foremost protozoan genera of these soda lakes are the small bacterivorous ciliates such as *Cyclidium* which are numerically dominant, the large ciliate *Condylostoma* which normally dominates in terms of biomass and the algivorous *Frontonia* which accounts for the majority of the ciliate productivity (Yasindi *et al.,* 2002).

1.2   Lesser flamingo classification

Six species of flamingo, within three genera *Phoenicopterus*, *Phoenicoparrus* and *Phoeniconaias* (Sibley *et al.*, 1969) make up the family Phoenicopteridae (Figure 1.1). All species are instantly recognisable due to their long slender legs, pink plumage and long flexible necks. They have evolved from microphagous, wading birds and their distribution is closely aligned with hypersaline lakes and great deserts (Bildstein *et al.*, 1993).

Two of the six species are Old World; the lesser flamingo (*Phoeniconaias minor*) and the greater flamingo (*Phoenicopterus roseus* Pallus, 1811) and four are New World; the Caribbean or American flamingo (*Phoenicopterus ruber* Linnaeus, 1758), Chilean flamingo (*Phoenicopterus ruber chilensis* Molina, 1782), Andean flamingo (*Phoenicoparrus andinus* Philippi, 1854) and James's flamingo (*Phoenicoparrus jamesi* Sclater, 1886).
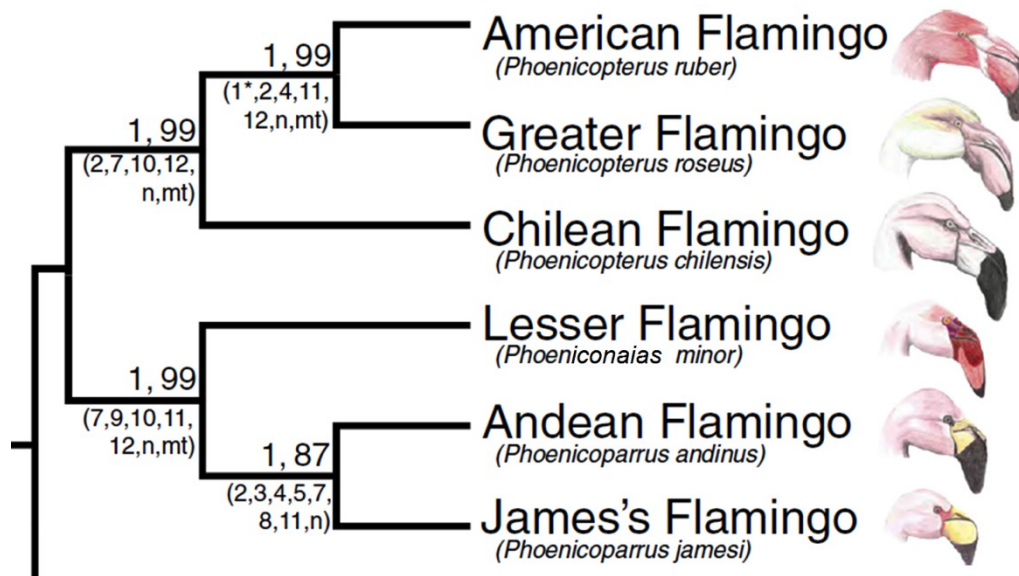
Figure 1.1: Cladogram displaying the relationship between the flamingo species, including posterior probabilities (Bayesian inference) and bootstrap values (maximum likelihood) above each node. The numbers and letters to the right of each node signify data subsets and individual genes. (Modified from Torres *et al.*, 2014)

1.3   Lesser flamingo populations, distribution, movements and conservation

The lesser flamingo is the smallest and most numerous of all the species, with an estimated global population of 2.2-3.2 million individuals (Birdlife International, 2012). In 1962, Leslie Brown reported the presence of 1,035,000 nests at Lake Magadi (Brown, 1973), where he counting nests. He stated that this represented over two million breeding adults; therefore with the addition of non-breeding adults, sub-adults and juveniles, he estimated a population of three million lesser flamingos at Magadi and Natron alone (ibid.). In the early 1970s there were a few counts carried out via aerial censuses over part of their natural range, which produced much lower estimates for the East African population but without carrying out a fully collaborative aerial consensus of all lesser flamingo populations, it is unlikely that a definitive population number will be reached. It cannot currently be proved whether the global population is in decline, stable or even increasing.

Lesser flamingos are classified as 'Near-Threatened' on the 2012 IUCN Red List of Threatened Species despite ambiguity surrounding the population size, due to a reliance on specific breeding conditions that occur rarely and at a limited number of unprotected locations, as well as a perceived decline in numbers (Childress *et al.*, 2008; Birdlife International, 2012). As a result, the lesser flamingo is the subject of a Single

Species Action Plan (SSAP) for conservation (Childress *et al.*, 2007). A gregarious species, large assemblies of lesser flamingo have often been recorded (Brown, 1979; Tuite, 1979; Bildstein *et al.*, 1993; Childress *et al.*, 2007), occasionally in excess of one million birds (Brown, 1973; Harper *et al.*, 2003), creating a vision that has been regarded as one of the most captivating spectacles of nature worldwide (Jenkin, 1929; Brown, 1973) and attracting considerable numbers of visitors to the East African Rift.

There are four permanent populations of lesser flamingo, the East African being the largest, accounting for over 75% of the global total (Tuite, 1979; Childress *et al.*, 2007; Delany & Scott, 2006); it is this population that forms the focus of this study. Smaller permanent populations can be found in the Rann of Kachchh in northwestern India, in southern Africa and in West Africa (Delany & Scott, 2006; Mlingwa & Baker, 2006). Vagrant lesser flamingos have been recorded in almost every sub-Saharan African country and coastal state from the Arabian Peninsula to Pakistan (Birdlife International, 2102). It was once thought that the four main populations were distinct, with little interaction between them, however satellite tracking and preliminary genetic studies have disproved this, detecting gene flow between the eastern and southern populations and Africa and India (Childress *et al.*, 2007; Zaccara *et al.*, 2008, Zaccara *et al.*, 2011).

The lesser flamingo is a long-lived species with a life span of over 40 years in the wild (Childress *et al.*, 2008). On 13th February 2013, a newly deceased lesser flamingo was found on the shores of Lake Bogoria, bearing a British Trust for Ornithology (BTO) ring. This identified the flamingo as one of 8,000 ringed after hatching at Lake Magadi in 1962. Colin Jackson reported that Leslie Brown was responsible for ringing this bird on 1st November 1962, making it 50 years, three months and 25 days old, the oldest ever recorded wild flamingo (Anon, 2013). Only ten of the 8,000 ringed have been recovered since 1962, one in West Africa on the edge of the Western Sahara, some 6,197km away from the shores of Magadi (Outerwater, 2013), suggesting transfer also between East and West African populations.

Lesser flamingos maintain a peripatetic lifestyle, unpredictably visiting lakes, determining the suitability of the feeding conditions and if they are found to be inadequate, moving on (Pennycuick & Bartholomew, 1973; Vareschi, 1978). The first

extensive studies of lesser flamingo behaviour were carried out in the 1950s and 1960s by Leslie Brown (Brown, 1959; 1971) and since then, there has been progress made on further understanding the basic ecology of lesser flamingos (Vareschi, 1978; Tuite 1979; 2000), although there are still many questions left unanswered.

Periodic mortalities have been reported since the 1950s and were initially attributed to large-scale phytoplankton crashes causing starvation (Brown, 1959). In 1974, a significant decline in *Arthrospira fusiformis* biomass of 75% resulted in extensive migration from Lake Nakuru (Tuite, 2000). The 10,000 birds left behind experienced a higher mortality rate than usual, 420 carcasses were collected over 19 days and 51 debilitated birds were analysed (Sileo *et al*., 1979). Nineteen of these had avian tuberculosis (*Mycobacterium avium* Type 1) (ibid.) with the rest, perhaps, afflicted by starvation and or parasites (Harper *et al*., 2003). Since then further die off events have been reported, an event in 1993, coinciding with an unusually high population, high temperatures and declining water levels, saw 18,500 birds die as a result of 'septicaemia, complicated in those afflicted, by mycobacteriosis' (Kock *et al*., 1999). The ingestion of cyanobacterial toxins has been suggested more recently as contributing factor, identified in hot springs at Lake Bogoria where the carcasses of dead flamingos were found (Krienitz *et al*., 2003). The likelihood is that mortality is caused by more than one factor (Haper *et al*., 2003). If food is not abundant within the lakes, lesser flamingos will become malnourished and certainly densely pack together at lakes that have the most food available. Avian tuberculosis is present within the population; however, it may only become lethal if they are already immuno-compromised and as such Harper *et al*. (2003) surmised that it may not be a coincidence that die off events have occurred towards the end of long droughts.

Figure 1.2 shows the network of lakes that were visited by lesser flamingos during a satellite tracking study (Childress *et al*., 2004). This is not a comprehensive list of all the important feeding lakes, but it does give an indication of the range of the species. Lesser flamingo movements are highly irregular, moving between various feeding sites throughout the East African Rift, often hundreds of kilometres apart. Fluctuations can be vast at a single lake, at Nakuru the population dropped from hundreds of thousands to a few thousand over a short period of time (Vareschi, 1978). In August 1956, Brown (1959) reported the departure of over 400,000 flamingos from Lake Bogoria in just

seven days. It is extremely difficult to quantify their movements as large-scale exoduses can occur overnight and over long distances (Childress *et al.*, 2008).

Figure 1.2: The lakes visited by lesser flamingos during a satellite tracking study (Modified from Childress *et al.*, 2004) (Latitude: 0°56'N - 6°30'S; Longitude: 33°24'E - 40°12'E)

The unpredictability of food availability at each lake within their network has meant that lesser flamingos have had to adapt in order to exploit their resources. They are able to double their body mass from lean to maximum, through the storage of fat and proteins in order to compensate for this variability and the long flight distance between lakes (Tuite, 2004). Assuming maximum reserves, lesser flamingos should be able to fly between 8,000 and 11,000 km, easily travelling to South Africa from East Africa or moving extensively within the East African Rift (Tuite, 2004). The satellite tracking survey revealed that lesser flamingos in East Africa were covering a range of 940 km from the Bahi Swamp in Tanzania to Lake Logipi in Kenya (Childress *et al.*, 2007).

The seemingly erratic movements are still not understood: Vareschi proposed five potential triggers for such movements in 1978. Firstly, changes in the quality and / or quantity of food; secondly, changes in the availability of freshwater for drinking and

bathing; thirdly, changes in lake water conductivity; fourthly, moving to breeding sites and finally, disturbance by humans or predators. At Lake Nakuru, significant correlations were found between the density of *A. fusiformis* and the number of flamingos on the lake; however, this has not been the case for all lakes. Momella Lake for example, in Tanzania, had a very high algal biomass but few flamingos (Vareschi, 1978).

1.4   Living in groups

In nature group living is extremely common with many animal species, across a range of taxa, displaying grouping behaviour during some stage of their lives (Krause & Ruxton, 2002). Two of the primary benefits of group living are increased foraging success and reduced risk of predation, with secondary benefits of reduced transport costs, accessibility to mates and a reduction in loss of body heat (Wilson, 1980; Herskin & Steffensen, 1998; Krause & Ruxton, 2002).

Individuals within groups potentially assume lower *per capita* predation risk than solitary individuals as they have the advantage of the 'many eyes' effect, whereby they are likely to detect approaching predators sooner (Krause & Ruxton, 2002). It is suggested that within groups there will be numerous vigilant individuals scanning for threats at any given time and when this is combined with the potential for increased rates of transmission of information, it allows individuals of groups to have lower investment in predator detection without increasing their risk (Krause & Ruxton, 2002). The risk to any one individual during an attack is inversely proportional to group size as a result of dilution effects, which is known as the flock effect (Powell, 1974; Wrona & Dixon, 1991). Active behavioural strategies such as predator swamping, where group members synchronise their flight responses, can help to increase this effect (Sweeney & Vannote, 1982).

The position of an individual within the flock also has an effect on vigilance; studies have shown that those located on the periphery dedicate more time to being vigilant than those located centrally (Underwood, 1982; Keys & Dugatkin, 1990; Bednekoff & Ritter, 1994). Those in the centre of the flock are able to dedicate more of their time to

efficient foraging therefore and as a result it is not uncommon to see a rotation with those on the periphery.

The acquisition of social information is beneficial for group foraging, as distribution of resources is not always uniform. Larger groups are able to cover a greater area, therefore locating the patches of resource with the greatest returns more readily (Valone, 1989). Social information is passed on both actively and passively from foragers to give information about the resource. Local enhancement is passive, drawing receivers to areas where foragers are already exploiting a food source but giving no information as to the quality of the resource. Conversely, public information is more specialised, conveying usable information concerning the quality of the food to the receiver (Valone, 1989; Valone & Templeton, 2002). By observing the foraging performance of individuals, receivers are able to identify the most profitable foraging areas to maximise their own fitness.

Members of groups are able to increase their individual foraging efficiency as a direct or indirect consequence of the presence of others. This is a result of a reduced individual investment in vigilance due to the 'many eyes' effect (previously mentioned), which allows them to allocate more of their time to foraging (Day *et al.,* 2001).

Group living is not without cost however, as the lower predation risk for individuals associated with group living, is offset by the possible risk that large groups have a greater initial attraction to predators (Krause & Ruxton, 2002). This may be due to the fact that groups are easier to detect or that predators may preferentially attack larger groups, to give them a greater chance of many successful incidents. A second cost is competition for resources, especially apparent in times of low resources. Indirect competition takes the form of exploitation whereby a resource is utilised by foragers, leaving it somewhat depleted for the remainder of the group who subsequently try to use the same area (Krause & Ruxton, 2002).

The delicate balance of these costs and benefits will vary over time and if an individual is to gain an advantage from group living it must engage in behavioural trade-offs. Lesser flamingos are unevenly distributed across soda lakes, aggregated around freshwater drinking sites, clumped in foraging groups on the lake edge or spread over

the open water feeding. Lesser flamingos have many predators including the marabou stork (*Leptoptilos cruminiferus*), olive baboon (*Papio anubis*), African fish eagle (*Haliaeetus vocifer*), spotted hyena (*Crocuta crocuta*) and African wild dog (*Lycaon pictus*). As a result vigilance is important and both the 'many eyes' and 'flock effect' seem to be applicable.

1.5   Lesser flamingo feeding

Optimal foraging theory is often applied to food selection, predicting a critical level of resource that determines how animals distribute themselves (Stephens & Krebs, 1986). Animals select a patch from which to feed, committing themselves to spending a period of time in that location and therefore utilising one of the four categories of foraging – optimal diet, patch choice, allocation of time to patches and the foraging path (Pyke *et al.,* 1977). The optimal diet is defined as that which maximises the rate of energy intake, so animals will preferentially select the food patch that has the highest profitability (Smith, 1970; Menge & Menge, 1974). It has been hypothesised that optimal behaviour would be to allocate all foraging time to the patch with the highest abundance of food (Pyke *et al.*, 1977). Studies using titmice (*Baeolophus* sp.) found that whilst the birds allocated most time to the highest density patch, as the patches became progressively poorer, the time birds invested in foraging decreased (Smith & Dawkins, 1971; Smith & Sweatman, 1974). It was suggested that this behaviour represented a long-term adaptation to a fluctuating food environment, as birds would expend less energy foraging in sparse areas to conserve energy for foraging in more fruitful patches (Smith & Sweatman, 1974). The subject of patch choice is discussed further in Chapters 5 and 6 of this thesis.

The optimal allocation of time to patches suggests that animals can estimate their average rate of food intake in any given patch and will therefore leave if inadequate volumes of food are encountered within a given time (Pyke *et al.*, 1977). The lesser-studied theory of the foraging path assumes that animal movements are restricted to a bounded foraging area and that they are unable to detect food at a distance, so this does not affect their movements (Pyke *et al.*, 1977). It was suggested that the optimal path was that which results in the least re-crossing of paths therefore accessing the most profitable patches without continually retracing their movements (Cody, 1971; 1974). It therefore follows that flamingos should be utilising the areas of the lakes with

the highest net rate of return in order to maximise their foraging efficiency. None of the soda lakes have a uniform distribution of food resources and therefore choosing where to forage within each lake may involve sampling more than one site.

Flamingos are filter feeders in shallow aquatic environments. Three of the six species are described as generalist feeders and three are specialist feeders as a result of the different mesh sizes within their bills (Jenkin, 1957). The greater flamingo, Caribbean flamingo and Chilean flamingo fall into the generalist category with a diet including crustaceans, small molluscs, insect larvae and worms, conversely the lesser flamingo, Andean flamingo and James' flamingo are specialists, with a diet consisting of single-celled colonial phytoplankton and benthic diatoms (Jenkin, 1957). The disparities in diet result from anatomical differences in the feeding apparatus as generalist feeders have shallow-keeled bills, leading to the mesh differences (Jenkin, 1957), and less restrictive diet (Brown & Root, 1971) whereas specialists have deep-keeled bills.

The lesser flamingo is a unique phytoplankton filter feeder, the primary consumer in an exceptionally productive ecosystem (Bartholomew & Pennycuick, 1973) where the principal food source is the alkaliphilic cyanobacterium *Arthrospira fusiformis* (formally *Spirulina platensis)* and a secondary source is benthic diatoms, which are also able to tolerate the fluctuating extreme abiotic conditions (Ndetei & Muhandiki, 2005). Lesser flamingos feed by either filtering *A. fusiformis* from the top few centimetres of the water column (either standing in the lake shallows or swimming on the open water) or by skimming the surface of wet mud for sedimented cyanobacteria and benthic diatoms (Tuite, 1981). These three well-documented feeding behaviours and a fourth, less commonly reported, were referred to by Tuite (2000) but not quantified. These are 'stand filter feeding', 'swim filter feeding', 'wet mud skim feeding' and the lesser studied, 'deep water feeding', whereby the whole head and neck are submerged to enable feeding at the bottom of the water column.

The deep keeled, angular bill of the lesser flamingo is well adapted to the size of *A. fusiformis* spirals, which average 40-200 μm x 20-50 μm (Vareschi, 1978) as well as to a diet of benthic diatoms (Figure 1.3). The bill is held parallel to and slightly submerged under the water's surface. Lesser flamingos are able to maintain such a position, with their heads bowed, due to their specially adapted lower mandibles, which hold air,

enabling the bill to float (Jenkin, 1957). The upper jaw is narrow, sinking below the rami of the lower jaw, only visible at the tip and above the bend (Figure 1.4A). It fits neatly into a groove within the lower jaw (Figure 1.4B), which gives it a characteristic triangular cross section (ibid.).
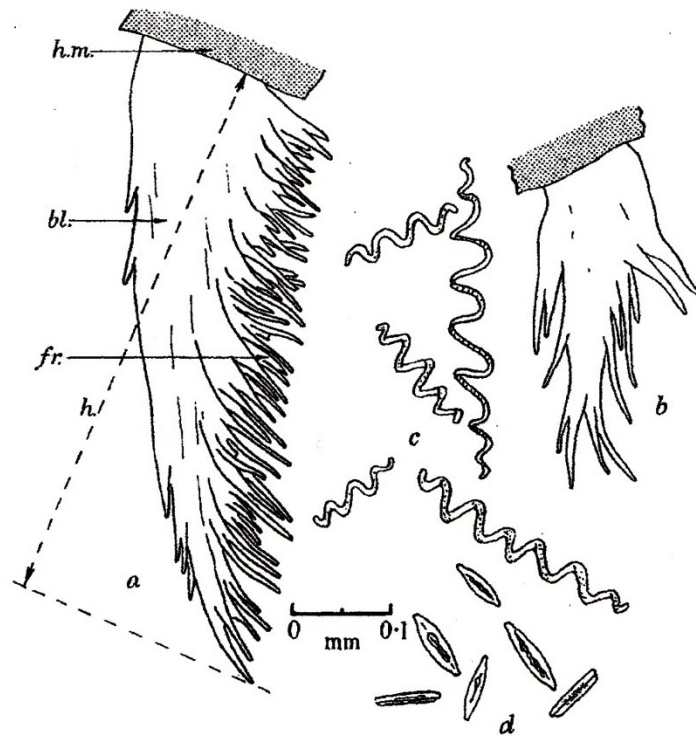
Figure 1.3: The platelets and food of *Phoeniconais minor*, enlarged to same extent. (a) a fringed inner platelet, (b) small proximal platelet, (c) coiled filaments of *Arthrospira fusiformis*, (d) diatom frustules (from Jenkin, 1957)

The area of contact between the two jaws is about 35 cm^2; nearly double that of the shallow-keeled greater flamingo. Both the upper and lower jaws contain low undivided ridges, the most distal of which are smooth, but proximally they begin to divide in to long low platelets, which, like all other platelets within the bill, acquire a fringed edge (Jenkin, 1957). A single undivided lamella forms a collecting trough in the lower jaw that runs longitudinally along the median edge, at right angles to all of the other lamellae (ibid.). The large lamellated areas of both jaws show little variance and are almost wholly covered in fringed platelets, which are viewed as a remarkably regular pattern of diagonal rows to the naked eye. Over 10,000 lamellae are contained within the bill in order to maximise feeding efficiency. These are small and tightly packed, with the platelets trapping microscopic food items as the water is filtered (ibid.). The marginal hooks and leaflets along the edge of the bill act as excluders as water is sucked

in along the whole length of the gape, to prevent any large particles from entering and blocking or damaging the delicate filtering mechanisms. The spacing of the inner lamellae ranges from 60 μm to 200 μm, with a mean size of 120 μm on the upper jaw and 105 μm on the lower jaw. The spacing of the excluders averages 130 μm at position D, increasing to 260 μm at BN (ibid.) (Figure 1.4).
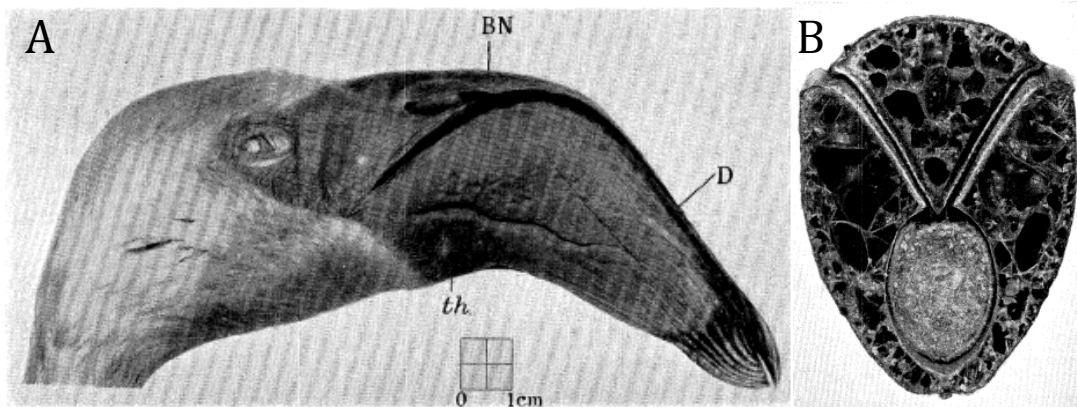
Figure 1.4: The deep-keeled bill of the lesser flamingo (*Phoeniconaias minor*) (a) with the upper mandible only visible at the tip and above the bend and (b) in cross section (taken from Jenkin, 1957)

The strong tongue functions as a pump, its downward action causes an influx of cyanobacteria rich water, flattening the smaller of the lamellae whilst the excluders prevent anything too large from entering and damaging the filter. The upward movement forces the water out and with it the smaller lamellae stand up and the platelets trap the food items from the exiting water. This process of filtering algae through rapid tongue pump action is repeated up to 20 times a second (Pennycuick & Bartholomew, 1973).

There is some uncertainty as to the amount that lesser flamingo need to consume within a day. Vareschi (1978) calculated it to be 72 $\pm$ 6.5 g of cyanobacteria (dry weight (DW)) per day whilst Pennycuick and Bartholomew (1973) calculated that 90 g DW day^{-1} is needed by a non-breeding flamingo and 250 g DW day^{-1} required by a breeding one. The feeding efficiency is dependent on the size of the food particles, which varies considerably. *A. fusiformis* size in different lakes is as follows: Nakuru 120 μm x 25 μm; Bogoria 200 μm x 55 μm; Big Momella 60 μm x 35 μm. Lake Elementaita is mainly diatoms 50 μm x 18 μm although there is occasional dominance by a diatom that is 130 μm (Vareschi, 1978). Pennycuick & Bartholomew, (1973) surmised that lesser flamingo needed to feed for 80% of their time, based on a dry weight availability of

0.125 Kg m^{-3} in order to meet the 90 g DW day^{-1} requirement. Vareschi's study of caged birds at lake Nakuru found that feeding stopped altogether if the concentration dropped below 100 g DW m^{-3} (Vareschi, 1978).

1.6   Food of the lesser flamingo

The planktonic filamentous cyanobacteria *Arthrospira fusiformis* is the primary food source of lesser flamingo with a secondary food source of shallow littoral, benthic diatoms and a potential third in the form of rotifer and protozoa zooplankton, which can always be filtered but may constitute a more important food source when they are present in dense blooms (Jenkin, 1957; Tuite, 1979; Vareschi, 1978).

The *Arthrospira* genus currently has 12 species accepted taxonomically, four of which have been studied in greater depth. *A. jenneri* and *A. platensis* are benthic species whilst *A. maxima* and *A. fusiformis* are planktonic species (Komárek & Lund, 1990). In addition, a small ecotype of *A. fusiformis* (*A. fusiformis var. minor*) was recorded occasionally at Lake Nakuru (Vareschi, 1978) and now dominates Lake Oloidien (Krienitz *et al.*, 2013). There are morphological differences between these, difficult to tell apart through microscopy alone and it is often assumed that the dominant species in the alkaline-saline lakes is *A. fusiformis*.

Arthrospira fusiformis is an obligate photoautotroph that appears as blue-green filaments composed of cylindrical cells arranged in unbranched helicoidal trichomes (Ciferri, 1983). *Arthrospira* can tolerate a number of difficult conditions including high concentrations of salts, high pH values and low irradiances during blooms. It is classified as thermotolerant, alkaliphilic and halotolerant, based on the definitions of differing extremophiles (Mesbah & Wiegel, 2004). *A. fusiformis* exists a three morphological variants: S-, C- and H-type trichomes; S- and C-types form loosely coiled helices (6-9 or 3-14 and 2-12 or 3-7 coils per filament respectively) whilst H-types form tightly coiled helices (3-30 or 5-30 coils per filament) (Jeeji Bai & Seshardi, 1980; Hindák, 1985).

Benthic diatoms are only able to grow where the light can penetrate and are therefore often located at the edges of deeper lakes on the wet mud and in shallow waters, in

shallow lakes they seem to have stable densities (Tuite, 1981). There has been little research done into how much of a role diatoms actually play in the diet of a lesser flamingo and they have previously been referred to as an 'emergency' food source (Tuite, 1981). The field studies conducted over the past five years, for this thesis, have indicated that in lakes that remain shallow for extended periods of time, or in shallow lagoons or deltas formed by inflowing streams, diatoms may play a much larger role (see Chapter 3). Three quarters of a million lesser flamingos were observed in November 2007, subsisting entirely on benthic diatoms within the lagoon formed at the delta of the Ewaso Ngiro as it enters Lake Natron (Harper, D.M., pers. comm.). Prior to this, Vareschi (1978) had observed lesser flamingo feeding on a film of diatoms and cyanobacteria growing on the wet mud at the edges of Lake Nakuru, at a time when the *A. fusiformis* density was decreasing within the lake.

Lesser flamingos have a mesh size of 60-200 μm and therefore it cannot be assumed that they would be able to positively exclude rotifers and protozoans that fall into this size classification. Lesser flamingos were able to utilise this resource when rotifers were present at Lake Nakuru in densities of 19 mg DW L^{-1} and supplemented their diet by up to 20% (Vareschi, 1978).

1.7 Lesser flamingo breeding

Lesser flamingo breeding has been regularly recorded at five sites, spanning four countries, in recent years. These are Botswana, India, Namibia and Tanzania (Childress *et al.*, 2008). There are early reports of Lake Magadi in Kenya also being utilised for (unsuccessful) breeding and reports of isolated breeding events occurring in both Ethiopia and South Africa in 2005 and 2008 respectively.

Lake Natron, in northern Tanzania, is the most important breeding site as it is the only known active breeding site for the East African population, accounting for 75% of the global population. Whilst the exact details regarding breeding success are unknown, the unique hydrology found at Lake Natron allows 'trona' islands to form with receding water levels, creating remote nesting sites away from the shore edge (Brown, 1959; Tebbs *et al.*, 2012).

Breeding events do not occur annually in lesser flamingo populations; rather they are erratic and dependent on the seasonal rains, with the majority of breeding events occurring between November and February (Childress *et al.*, 2008). During periods of receding lake levels the lake is dilute enough to maintain the floating 'trona' islands that form at the surface, making them inaccessible to terrestrial predators (Tebbs *et al.*, 2012), although breeding birds are still vulnerable to aerial attacks by Egyptian vultures.

Lesser flamingos breed in large groups, with each pair building a nest and laying a single egg. The fledgling success rate is estimated to be around 42%, with the majority of mortalities occurring in the first three weeks as a result of predation, nest desertion or the chicks getting stuck in hot mud and salt, which crystallises, trapping them (Childress *et al.*, 2008). Breeding is the result of a delicate balance of conditions which all have to occur simultaneously in order to produce successful events. Earlier in this chapter it was mentioned that Pennycuick and Bartholomew (1973) had calculated that breeding flamingos require a much higher food intake than non-breeding birds (250 g DW d^{-1} compared to 90 g DW d^{-1}) as it is energetically expensive to produce an egg and parents also spend less time feeding whilst they are incubating their egg. It is therefore plausible that the capricious nature of breeding events is the result of irregular availability of high food concentrations (as shown in this study) alongside the meeting of highly specific hydrological conditions at Lake Natron (Brown, 1971; Tebbs *et al.*, 2012).

Lesser flamingos become a deeper shade of pink as a result of their increased food intake, specifically the resultant increase in carotenoids that is responsible for their colouration. They perform breeding displays that encompass large group dances, made up of characteristic moves and often make practice nests on the lakeshores of the lake at which they are feeding. These practice nests have been recorded at Elementaita, Bogoria, Oloidien and Nakuru throughout the duration of this study but no successful breeding occurred at any of these locations.

Lake Natron is currently under threat from two large industrial developments, as although it is a Ramsar site, it remains relatively unprotected. The development of both a large soda ash extraction factory and a multi-purpose dam on the Ewaso Ngiro River could prove to be extremely detrimental to the breeding success of lesser flamingos, as

they are likely to alter the hydrology of the lake. Therefore this construction could pose a serious threat to the survival of the species (Childress *et al.*, 2008).

1.8   Aim and justification

The lesser flamingo is a gregarious, long-lived, species that falls towards the 'K' end of the gradient in terms of the r-K life history strategies. The species has irregular breeding with relatively few offspring produced during the adult's individual life and only one at each reproductive event. Breeding is communal, providing greater individual protection and there is a large investment into parental care, both during incubation and once the chick has hatched. Many species have evolved to track high-quality food resources, often spatially and temporally separated; many seabirds have evolved to do so by predictable migrations. In Western India, the lesser flamingo migrates between summer feeding grounds and winter breeding in the Rann of Kachchh (Jadhav & Paracharya, 2004) but the population in East Africa does not migrate. The food resources in East African alkaline-saline lakes - sometimes limited - do not fluctuate in a predictable or seasonal fashion and therefore these birds can be described as nomadic rather than migratory (Brown, 1959).

This potentially disastrous evolutionary state invokes the following questions: 1) Is the feeding behaviour of the species plastic or is it as ecologically rigid as the requirement for colonial cyanobacteria in alkaline-saline lakes? 2) Is there any evidence of behavioural flexibility in adapting to fluctuating resources? 3) What is the periodicity of the fluctuation of resources over different time scales and is there any evidence that the birds can track and cope with the changes?

The lesser flamingo is a 'Near-Threatened' species that generates a large amount of income for both Kenya and Tanzania through tourism. The East African Rift experiences dramatic climactic changes, which potentially alter the ecology of the alkaline-saline lakes that lesser flamingos rely on for beeding and feeding. The importance of the lesser flamingo to East Africa inspired this thesis and the studies conducted sought to broaden the understanding of both soda lake ecology and lesser flamingo foraging behaviours. The aim of this thesis was to build on the earlier works of Vareschi and Tuite by further investigating the importance of diatoms as a food source; the ability of lesser flamingos to adapt their feeding behaviours when feeding

on differing food sources or different concentrations of food; the temporal and spatial differences in foraging behaviour; the relationship between food abundance and lesser flamingo distribution; the density of lesser flamingo flocks in relation to food source and feeding behaviour and finally investigating whether the proposed energy budget (Pennycuick and Bartholomew, 1973) is too simplistic for current feeding trends in lesser flamingos (is there a difference when feeding on *A. fusiformis* or diatoms?).

1.9   Specific objectives

The main questions that I sought to answer were:

- Are all soda lake ecosystems spatially and temporally uniform in both abundance and composition of food resources?
  - ➢ If not what are the implications for lesser flamingo diet?
- Do lesser flamingos have a broader feeding behavioural repertoire than previously reported?
  - ➢ Does feeding behaviour vary with food abundance, composition and distribution between and within lakes?
- Does time spent feeding vary at different lakes?
  - ➢ Do lesser flamingos always feed for the same amount of time at the same lake?
  - ➢ Do lesser flamingos spend more time feeding at night than during the day?
  - ➢ Does feeding time vary when feeding on different food sources?
- Do lesser flamingos distribute themselves across lakes in accordance with food availability?
  - ➢ Is there a difference in distribution when feeding on different food sources?
  - ➢ Does food source affect flock density?
  - ➢ Does feeding behaviour vary with flock density?

1.10   Thesis layout

This thesis begins by looking at the variation in soda lake ecosystems and the different photosynthetic communities that make up the diet of the lesser flamingo (Chapter 3). This leads to investigating the intricacies of the feeding behaviours and how behaviours adapt in relation to the type and distribution of food resources available (Chapter 4). This is followed by research into how long flamingos feed for within a 24 hour period

(Chapter 5) as well as how they distribute themselves in accordance with the differing food sources and behaviours (Chapter 6). Emphasis is then placed on drawing all this information together to revisit the energy budget proposed in the 1970s in the general discussion (Chapter 7). Specific predictions and hypotheses are made and tested on a chapter by chapter basis and the findings of the thesis are discussed in the context of existing knowledge and the current theory regarding East African soda lakes and lesser flamingo feeding habits.

Chapter 2

Chapter 2   Study sites and full methodology

2.1   Study Sites

The majority of the work contained within this thesis was conducted at Lakes Bogoria and Oloidien, however comparative observation and water samples were also taken from four other lakes supporting lesser flamingo populations; Lake Sonachi (Crater Lake), Lake Elementaita, Lake Nakuru and Lake Natron; the only breeding site within East Africa (Figure 2.1).
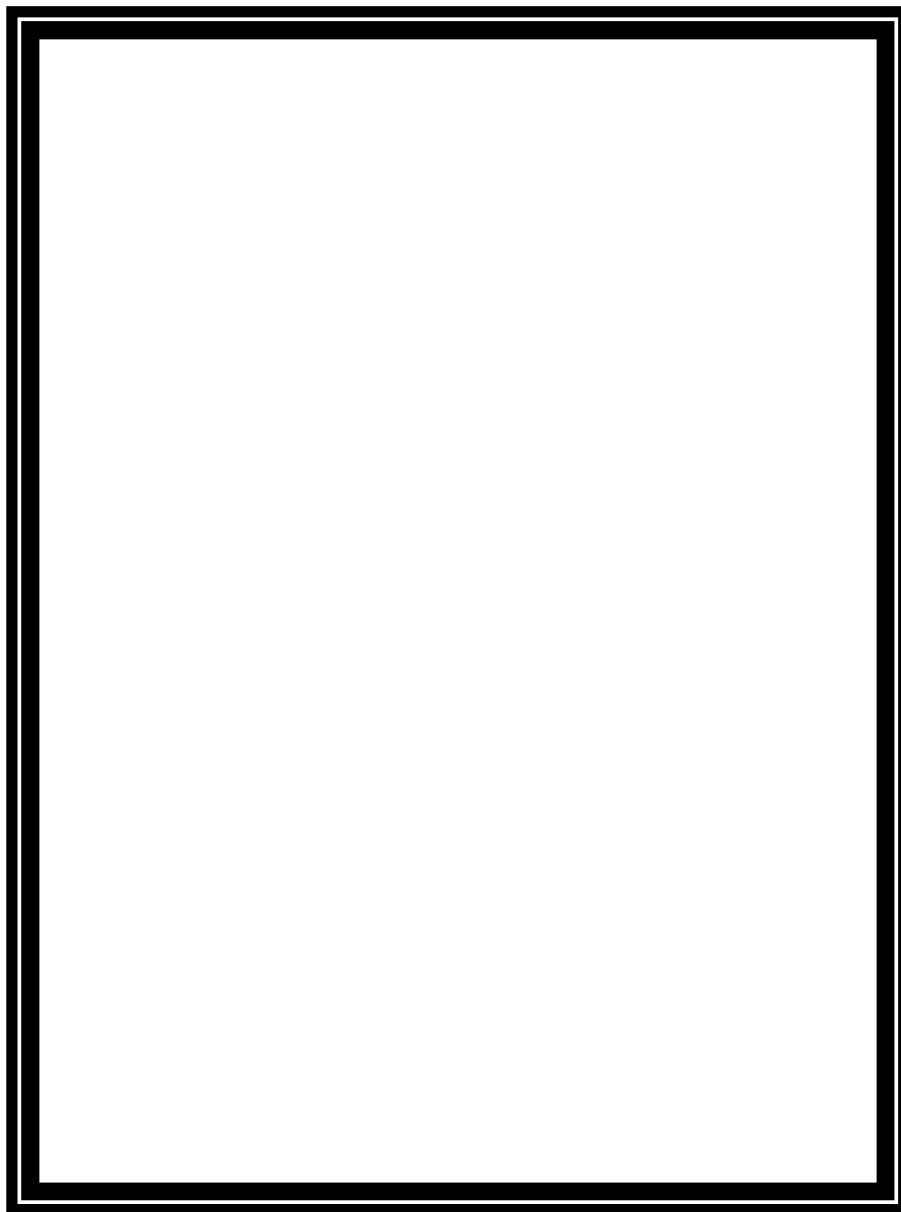
Figure 2.1: Alkaline-saline lakes of the East African Rift Valley utilised for this study (modified from Google maps)

2.1.1 Lake Bogoria

Lake Bogoria (00°11'-20'N 036°07'-08E), formerly known as Lake Hannington, has been a designated Ramsar site since 2001. It is located just north of the Equator, at the foot of the Laikipia escarpment within Lake Bogoria National Reserve (protected since 1973) at ~990 m above sea level (McCall, 2010). The lake is approximately 16 km in length, 1-4 km in width, with a surface area of around 34 km^2, experiencing fluctuating rainfall with a mean of approximately 500 mm yr^{-1}. Lake conductivity ranges between 25,000-77,000 μS cm^{-1} with a pH fluctuating around 10.2 (Vareschi, 1978; Harper *et al.*, 2003; this study). It has three basins, an average depth of 5.4 m and is recorded to be 10.2 m at its deepest; however, in August 2013 the depth was measured at 16 m after 3 years of continuous lake level rise.

The lake is surrounded by about 30-40 hot springs and fumaroles, of varying salinity, which feed the lake, accounting for perhaps 25% of its hydrological input (Cioni *et al.*, 1992). The remaining water budget is maintained by three semi-/permanent rivers, the Waseges/Sandai in the North basin and the Emsos and Fig Tree in the South basin, as well as and the Loburu, a temporary river entering the Central basin. Chemically it is one of the most stable lakes, despite fluctuations in water level (Harper *et al.*, 2003; WWF/TNC, 2008).

Bogoria can support an extremely high cyanobacterial biomass of several hundred μm Chl-a l^{-1} (Odour & Schagerl, 2007b). *A. fusiformis* contributes around 98% of the phytoplankton biomass, dropping to 80% at times (Schagerl & Odour, 2008), with species such as *Synechocystis* sp. and *Navicula halophilia* making up the remainder. It supports near permanent blooms of cyanobacteria (of differing concentration) and is often considered to be a refuge for lesser flamingos when other lakes don't have favourable feeding conditions. This lake, therefore, maintains large numbers of lesser flamingos but also provides foraging for greater flamingos due to the abundance of the chironomid larvae *Paratendipes* sp. (Harper *et al.*, 2003). The riparian ecosystem includes *Acacia salvadora* woodland that provides a crucial habitat for the endangered greater kudu (*Tragelaphus strepsciseros)* amongst others (Ramsar, 2001).
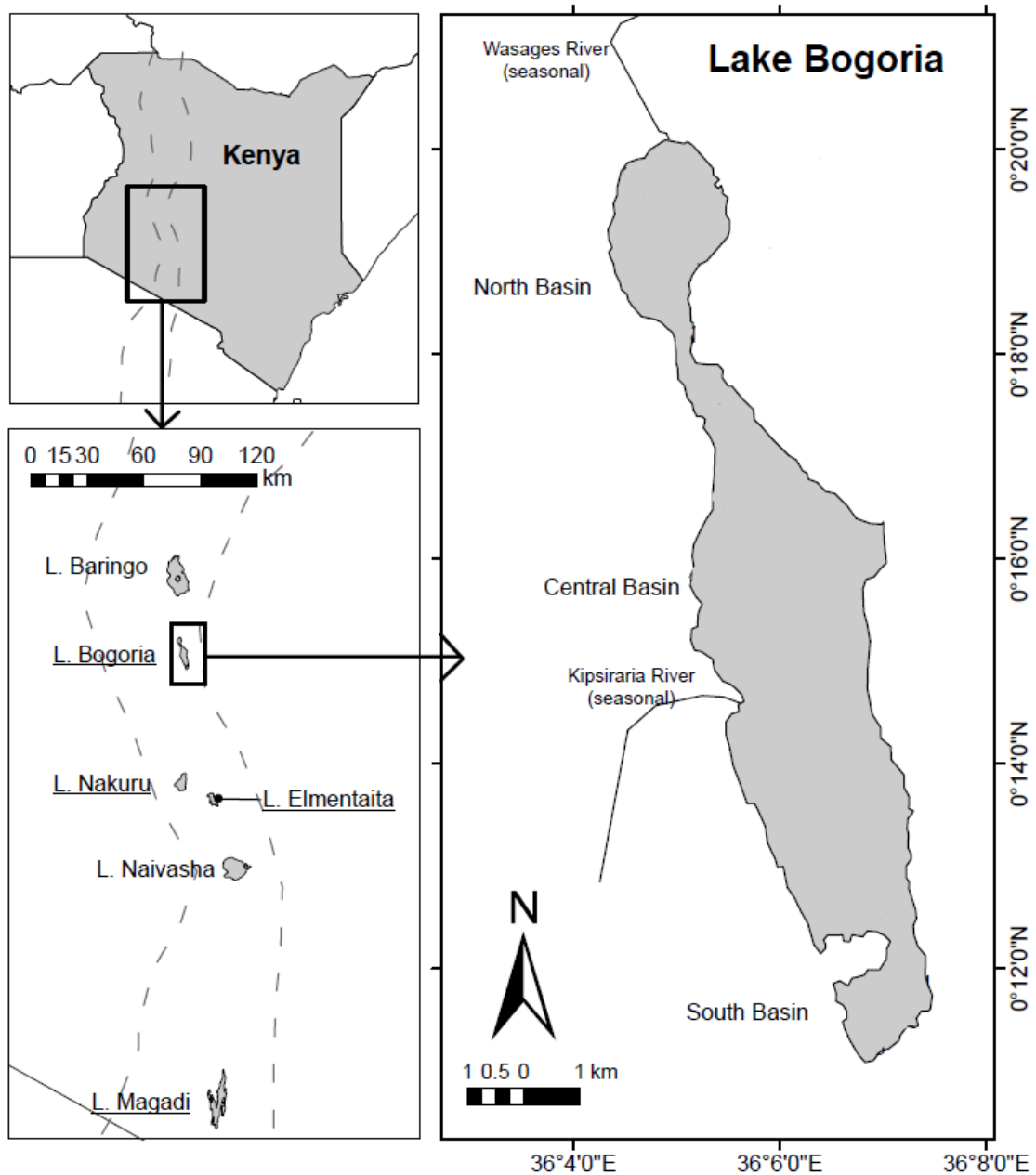
Figure 2.2: Map of Lake Bogoria and its location within the East African Rift Valley (From Tebbs *et al.,* 2013)

2.1.2   Lake Oloidien

Lake Oloidien (00°50'S 036°17' E) is situated immediately southwest of Lake Naivasha at an altitude of ~1885 m a.s.l., a shallow lake with a surface area of 5.1 km^2 and an average depth of 5.6 m (Verschuren *et al.*, 2000). The surrounding highlands intercept the majority of the rainfall, which averages 608 mm yr^{-1} although there is conservable inter-annual variation (Verschuren *et al.*, 2000).

Lake Oloidien used to be connected with Lake Naivasha, completely separating in 1984 (Lyngs, 1996); as a result the drainage basin of Oloidien is hydrologically closed with water loses attributed almost entirely to evaporation. There is no river inflow and with such limited run-off, the water levels are maintained through rainfall on the lake surface and subsurface inflow from Lake Naivasha (Verschuren *et al.*, 2000). Since Oloidien separated from Naivasha, it has gradually become more eutrophic, and alkaline-saline due to the evaporative concentration of salts.

The phytoplankton ecology of the lake has changed considerably as it has become more alkaline-saline. Prior to 2006 the dominant phytoplankton was coccoid Chlorophyceae, which gave way to *Arthrospira fusiformis* and *Anabaenopsis elenkinii* (Ballot, 2009). With the change in phytoplankton community, the lake became suitable as a feeding lake for lesser flamingos with 70,000 birds on the lake in 2006 (David Harper, pers. comm.) and reports of up to 500,000 on the lake in the years since (personal observation).

Figure 2.3: Map of Lake Oloidien (modified from Google maps)

2.1.3   Lake Elementaita

Lake Elementaita (00°25'-27'S, 036°15'-20'E) was designated a Ramsar site in 2005. Located 120 km northwest of Nairobi, it has an altitude of ~1800m a.s.l., lying between lakes Naivasha and Nakuru. It has a maximum depth of 2 m and a surface area fluctuating between 19 and 22 km^2. It has a drainage basin of about 500 km^2 with conductivity ranging between 11,900-25,000 mS cm^{-1} and pH around 9.8 (Vareschi, 1978). Three non-permanent rivers, the Chamuka, Mbaruk and Kariandusi, maintain the lake, along with hot springs on the south shore.

A. fusiformis is reported to contribute < 50% of the planktonic biomass, with the remainder being made up of species such as *Anabaenopsis arnoldii*, *Anabaena* sp. and *Synechococcus* sp. Diatoms are abundant at Lake Elementaita, with species such as *Navicula halophile*, *Navicula elkab*, *Nitzschia frustulum* and *Anomoeoneis sphaerophora* being part of the diverse community (Odour & Schagerl, 2008).

The majority of the shoreline is muddy and relatively open, with few rocky outcrops and little emergent vegetation (Owino *et al.,* 2001). Lesser flamingos have utilised this feeding lake for many years due to its ability to support them on either *A. fusiformis* or benthic diatoms.
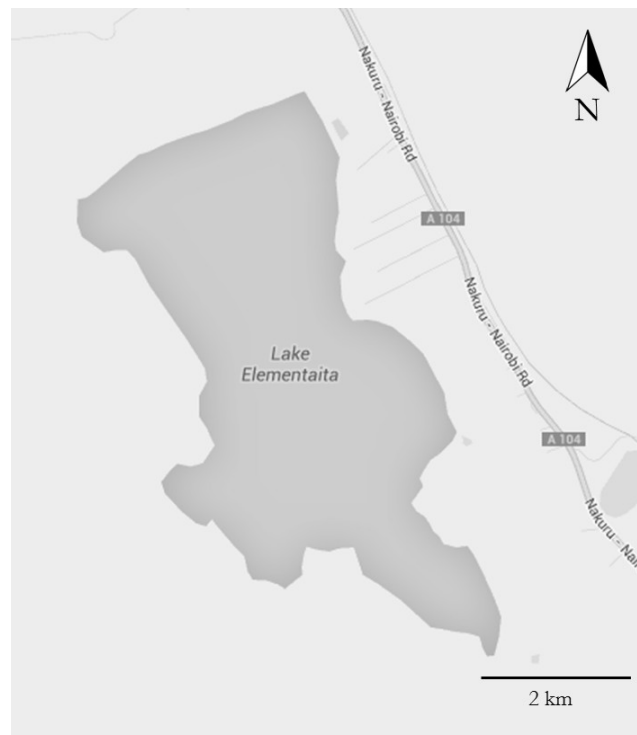
Figure 2.4: Map of Lake Elementaita (modified from Google maps)

2.1.4   Lake Nakuru

Lake Nakuru (00°24'S, 036°05'E) is situated within Lake Nakuru National Park at an altitude of ~1760 m a.s.l. It has a mean depth of 2.3 m and a fluctuating surface area of 5-45 km^2 (Ndetei & Muhandiki, 2005). Its conductivity is extremely variable, fluctuating between 11,000-160,000 µS cm-1 with pH about 10.5 (Vareschi, 1978; Verschuren, 2004). It is maintained by four seasonal rivers, the Njiro, Lomudioc, Nderit and Makalia with the Baharini and other perennial springs on the eastern shore; it has been known to completely dry up leaving isolated spring-pools. *A. fusiformis* contributes around 60% of phytoplanktonic biomass with the remainder coming from species similar to those found in nearby Lake Elementaita. These include *Anabaenopsis abijatae, Anabaenopsis arnoldii* and diatoms such as *Nitzschia sigma, Nitzschia frustulum,, Navicula halophila* and *Navicula elkab* (Vareschi, 1978).

Lake Nakuru was extensively studied in the 1970s and whilst the lake has been known to support over a million birds, there are times when lake Nakuru exists in an alternative state, dominated by the single celled cyanobacteria, fed upon by calanoid crustacea and the cichlid fish *Sarotherodon alkalicus graham,* which itself supports a population of pelicans *Pelecanus onocrotalus.*
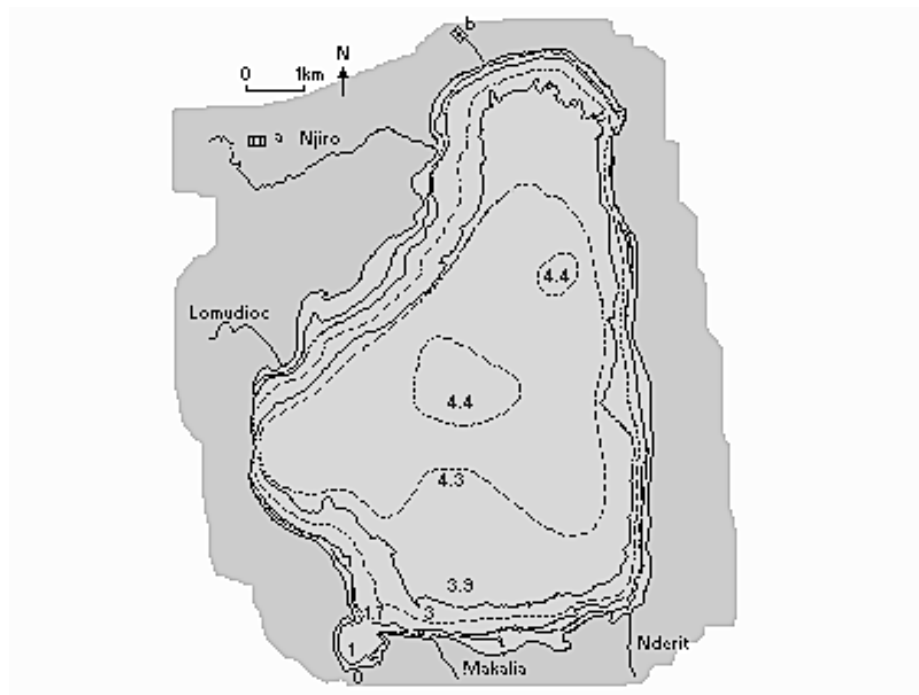
Figure 2.5: Bathymethric map of Lake Nakuru (Modified from Vareschi, 1982). Depth in metres; solid isopleths indicate actual shorelines at different lake levels; a & b are sewage treatment works

2.1.5 Lake Sonachi

Lake Sonachi (00°47'S 036°16'E), also called Crater Lake, is a small lake situated in a volcanic crater, 3km from Lake Naivasha at an altitude of ~1885 m a.s.l. A shallow lake with a depth of around 4 m and a surface area of ca. 0.18 km^2, the water level is maintained through rainfall and subsurface flow from Naivasha, as there are no rivers flowing into the lake.

The phytoplankton community is dominated by *Synechococcus bacillaris*, contributing 50% of the algal biomass, the remainder being constituted of *Lyngbya limnetica, Spirulina laxissima, Arthrospira fusiformis* and *Synechocystis aquatilis* (Melack, 1981). Diatom species such as *Anomoeoneis sphaerophora, Navicula cryptocephala* and *Craticula eklab* have also been recorded alongside the rotifer species *Brachionus dimidatus* and *Brachionus plicatilis* (Verschuren *et al.*, 1999).

Figure 2.6: Map of Lake Sonachi (modified from Google maps)

2.1.6   Lake Natron

Lake Natron (02°09'-36'S 035°54'-036°06'E) is located on the border of Kenya and Tanzania at an altitude of ~600 m a.s.l. A large, shallow alkaline-saline lake with a pH of around 10, it is the world's most caustic water body, with a surface area of 1040 km^2 and a depth ranging from a few centimetres to 2m at its deepest point (Kasule *et al.*, 1993). At the centre of the lake, it appears red due to the presence of extremophile bacteria and as the lake level falls, a characteristic alkaline 'trona' forms. Due to the inaccessibility of the lake, the hydrology and ecology of Natron is poorly understood relative to other lakes.

Lake Natron is of great significance as it the breeding site responsible for over 75% of the global lesser flamingo population and the only known current breeding site in East Africa. It is maintained by two permanent rivers; the Ewaso Ngiro that rises in the Mau escarpment in Kenya and the Penini from the Loliondo escarpment of Tanzania. There are also seasonal rivers from the Ngorongoro highlands, and Loita hills surrounding the lake. The remaining 25% of the water budget is contributed by the *c.* 30 hot springs that are present all around the lake.
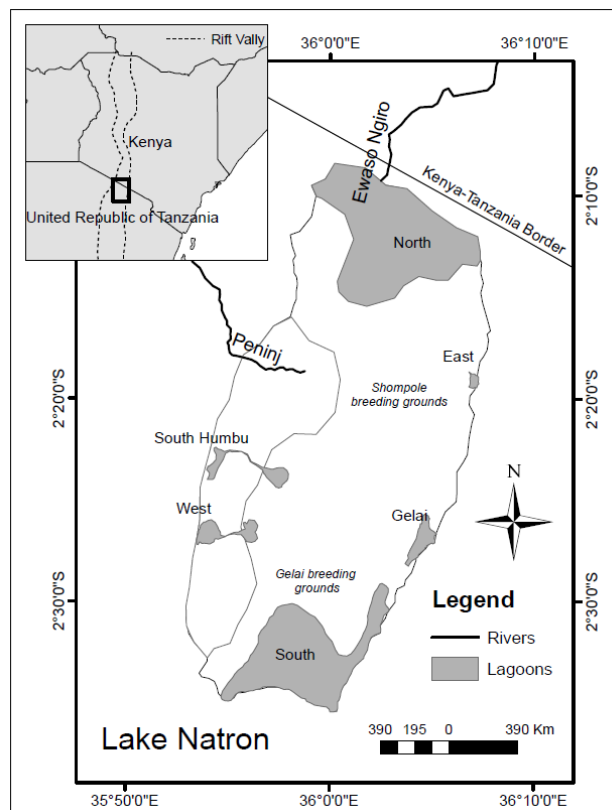
Figure 2.7: Map of Lake Natron (from Tebbs *et al.*, 2013)

2.2   Methodology

2.2.1   Behavioural observations

Observations were made at the six alkaline-saline lakes described (Figures 2.2 – 2.7), all known to be important sites for lesser flamingo feeding. Studies were concentrated at lakes Bogoria and Oloidien, with observations being made at the other lakes when it was logistically feasible to do so.

Preliminary observations were by focal animal samples at Lake Bogoria, over 2 days, in order to ascertain the repertoire of feeding behaviours as well as to assess a suitable interval and method for subpopulation scan sampling. Instantaneous scan sampling was then used, as there were many individuals displaying relatively few, easily discernable behaviours (Altmann, 1974; Lehner, 1996). There was a focus on the feeding behaviours (Plate 2.1) being exhibited, with all other behaviours being recorded as 'other'. The subpopulation was also described in terms of adults, sub-adults and juveniles (Plate 2.2) alongside the behaviours, to allow for comparison between age groups on occasion.

Scans were conducted over a full 24-hour period using a 6 x 90 mm night-vision telescope where possible or throughout the daylight hours where it was not feasible to obtain this. Observation periods varied between four and six hours with scans carried out every 15 minutes. The 24-hour period was divided into dawn (0600-0900), morning (0915-1200), afternoon (1215-1545), evening (1600-1900), pre-midnight (1915-0000) and post-midnight (0015-0545) for the purpose of reporting,

Monitoring was carried out using a 20-60 x 80 mm zoom telescope mounted on a tripod, a 6 x 90 mm night vision telescope or 10.5 x 28 binoculars, with the behaviour of each individual being recorded on to a voice recorder and then transcribed between scan samples. The scan was completed within 30 seconds to reduce inaccuracies and provide as detailed a snapshot as possible. Daylight observations were accompanied by photographs, taken every 15 minutes, from a mounted Nikon D90 with either a 17-55 mm or a 80-300mm Tamron lens which was set up to take photos of the same subpopulation that was being monitored during the scan samples. The photo was immediately succeeded by a one-minute video, which could subsequently be used in

case of ambiguity of behaviours. Night observations were more difficult but after two nights of acclimitisation (to ensure precision), all 10 feeding behaviours were discernible using the night vision scope to make accurate comparisons with the daylight hours.

There was a freshwater source at all of the sites and the subpopulation being monitored included birds along the shoreline as well as on the open water to try and ensure that it was as indicative of the whole population as possible. As far as possible, repeat visits were made to the same sites, however it was not always possible to gain access to the same sites due to lake level rise, in which case the same area was monitored from an alternative vantage point.

Continuous qualitative monitoring was carried out simultaneously to the scan samples at each site to ensure that any interesting observations were not missed. A sketch of each site was made to detect whether there was any apparent zonation to the behaviours. Photos were analysed in Adobe Photoshop Lightroom 5, behaviours were identified from the position of the head and their position in the water, using a series of reference images taken during the preliminary observations. Once the behaviour was recorded the individual within the image was marked with a symbol to prevent double counting and video was referred to where it was not possible to identify the behaviour from the still image alone. The photos were compared with the voice-recorded transcripts to ensure the most accurate representation of the behaviours being carried out.

It was necessary to collate the behaviours into four categories dependent on where within the lake lesser flamingos were foraging, when linking feeding behaviours to the availability of food; these were: stand filter feeding (STF1, STF2, WF1 and WF2), wet mud feeding (WMF and SWMF), swim filtering (SWF1 and SWF2) and deep water feeding (DWF and DWKF).

The subpopulation size sampled differed at each of the lakes, therefore, results were standardised to allow statistical tests to be carried out. Human interference and the presence of predators were recorded in the qualitative observations to assess their impact on lesser flamingo behaviours.
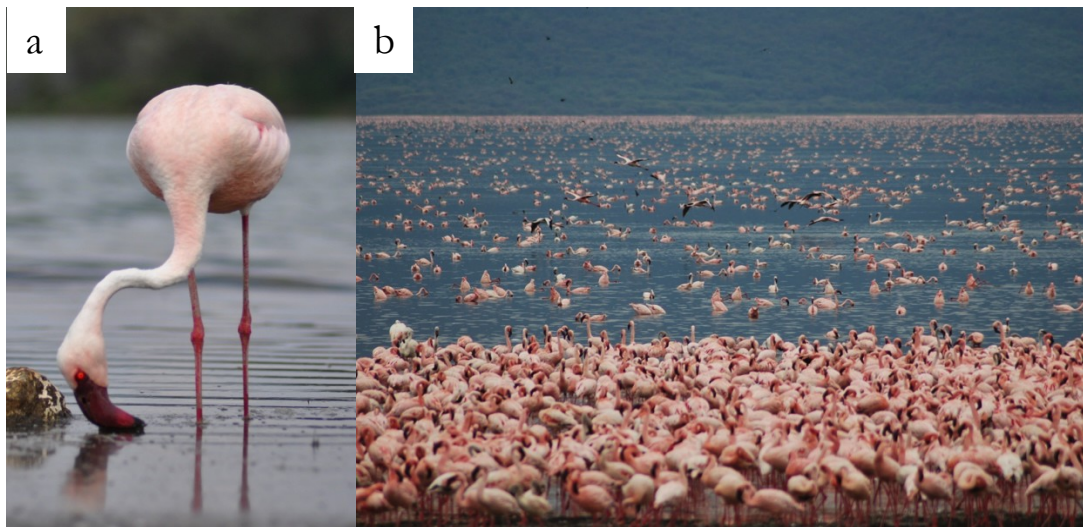
Plate 2.1: Lesser flamingo feeding: (a) an adult lesser flamingo engaging in stand filter 1; (b) lesser flamingos engaging in deep water feeding (middle) and swim feeding (distance)
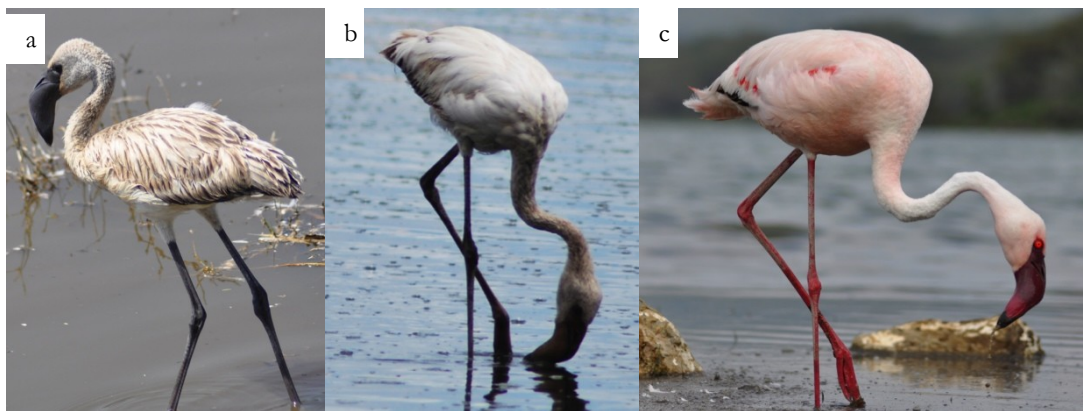
Plate 2.2: Lesser flamingo age classes: (a) Juvenile with fluffy brown plumage, short legs and neck and dark bill; (b) Sub-adult, same size as adult but with white plumage, dark bill and legs; (c) Adult with pink plumage, pink legs and maroon and pink bill

2.2.2   Biomass calculations

Water samples were collected at all sites immediately after behavioural observations in order to ensure that there was no disruption to the observed flamingo behaviours. Samples were collected in order to assess the phytoplankton and zooplankton within the lakes that were being utilised by lesser flamingos for food. Where possible, the samples were collected at the same distances from the shore, to ensure uniformity when comparing, these were: edge, shallow water (top and bottom), 1 m from shore (top, middle and bottom), 10 m from shore (top, middle and bottom), 20 m from shore (top, middle and bottom) and an open water samples from as far out as it was possible to wade. These distances were chosen as they corresponded to areas where

different feeding behaviours had been observed and therefore 13 water samples were collected after each behavioural observation block.

Cores of water from surface to mud were collected using a Gilson corer (Duncan & Associates, Cumbria, UK) by pushing it into the substrate, inserting a hand under the lower opening and lifting it out of the water vertically. The majority of the mud was then released from the bottom of the core by slow transverse rotation of the hand at the base. The top 5 cm of the water column were decanted into one container (top sample), the majority of the remaining water column was transferred into a second container (middle; including planktonic or suspended epipelic food resources), whilst the final 2 cm of water above the substrate was swilled and decanted into a third container to quantify the epipelic community (bottom). If an obvious aggregation of sedimented *A. fusiformis* was present above the mud (Figure 2.8b) (ranging from 2 cm to 6 cm above the lakebed) and the dense sunken *A. fusiformis* was treated the same as the epipelic community, measuring the entire volume of sedimented *A. fusiformis* by decanting into a separate container.

The samples were then taken back to the lab, shaken and diluted where necessary, with the dilution noted, to enable taxonomic identification and quantification. The taxa were identified using established keys: Barber & Haworth, 1994; Bellinger, 1992; Boney, 1989; Ilits, 1980; Schubert, 2003 as well as Hecky & Kilham, 1973. 1 ml of each sample was transferred to a Sedgwick Rafter cell (1 ml volume, 20x50 mm^3 grid) and when *A. fusiformis* or *A fusiformis var minor* was present, the number of colonies present in 250 cells was counted, using an inverted Nikon microscope at 100x and 200x magnification. In all the samples, 100 randomly selected colonies of *A. fusiformis* (or all if less than 100 were present) were used to calculate the percentage of S-/C- (loosely coiled) and H-type (tightly coiled) colonies (Figure 2.8a) and width, length and cross-section measurements were made to allow geometric volume calculations before using the volume of the entire sample to calculate the average biomass in mg L^{-1} (as per Vareschi, 1978). The number of diatoms, other cyanobacteria, rotifers and protozoans were also recorded and their volumes quantified when in abundance. If diatoms dominated the samples, then the shapes and sizes of 100 were noted to enable accurate biovolume calculations. For each individual water sample, three repeat Sedgewick Rafter cells were analysed and the average was considered representative.

Samples were fixed using 5 drops Lugol's iodine where it was not possible to analyse all samples in the lab in Kenya, and returned to Leicester for analysis (the volume before and after addition of Lugol's was noted to correct for dilution on return). In order to estimate the biovolume of the various taxa, geometric formulae were used according to the methods set out in Hillebrand *et al.* (1999) and McCauley (1984). To convert cell volume (mm^3) into cell biomass (mg) a conversion factor of 1 was used (Wetzel & Likens, 1991) allowing for the calculation of volume in 1 ml and then in mg L^{-1} as per Vareschi (1978).

If a single species of cyanobacteria accounted for over 50% of the biomass at a lake at any given time during the study it was recorded as dominant (a score of 3 in Table 3.3). A species, which accounted for 20% or more, was abundant (score of 2) and eanything else was recorded as present (score of 1). The micro-zooplankton was recorded with a similar system; if a species was present in all water samples for that lake it received a 3; 1 in every 5 samples (or more), a 2 and if it was present but not in high abundance, a 1.
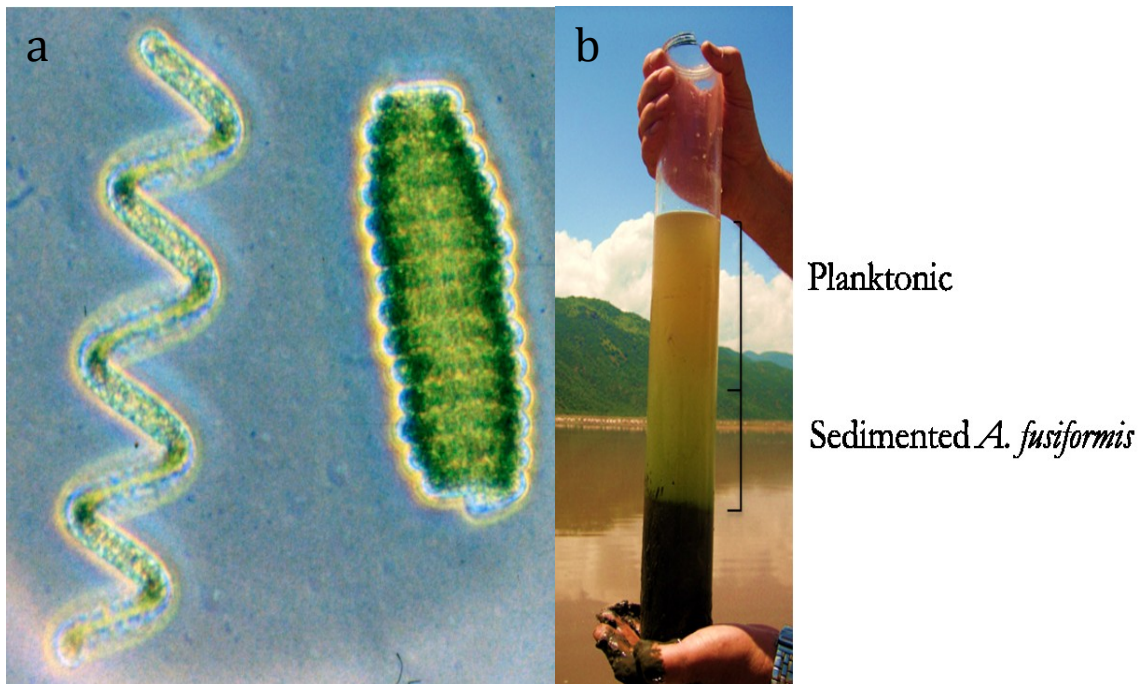
Figure 2.8: (a) Phase contrast image of *Arthrospira fusiformis*; loosely coiled S-type variant on the left and tightly coiled H-type on the right (used with permission of Dr S. Mills). (b) A core of water showing the distinct difference in colouration from the water at the top of the lake and the greener water at the bottom, referred to as the sedimented *A. fusiformis*

2.2.3   Spatial variation in biomass

All three basins of Lake Bogoria were sampled for spatial variation in 2009, 2010, 2012 and 2013. Additionally, in 2009 and 2013, surface transects were conducted from a boat in Lake Bogoria and water samples were collected from 16 GPS locations at depths of 0, 5, 15, 25 and 50 cm. In 2012, water samples were collected from the shore of Lake Bogoria at the edge, 10 m, 20 m and 50 m out into the lake (open) from eight sites (Figure 2.9). In 2012, four sites were studied at Lake Oloidien with surface and substrate samples taken at each site (Figure 2.9).
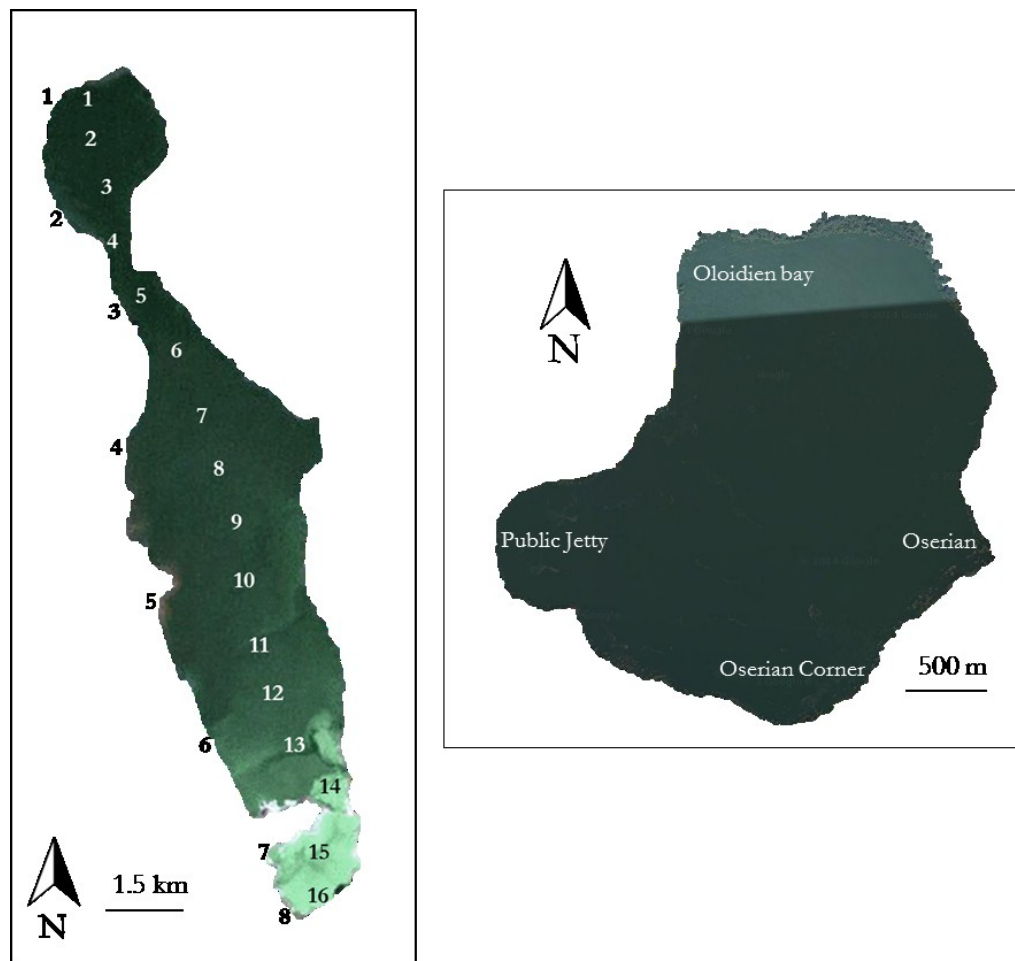
Figure 2.9: Map of surface and shoreline transect locations at Lake Bogoria (modified from a Lansat image); map of the four sample sites at Lake Oloidien (modified from Google maps)

2.2.4 Crop samples

Crop samples were collected from 11 dead flamingos over the course of this study, the contents was examined for the presence of protozoans and rotifers through dilution and microscopy using a Sedgewick Rafter cell. Where present, the species were noted and relative abundances of each were calculated.

2.2.5 Chlorophyll and carotenoid analysis

A known volume of each sample was filtered through a Whatmann GF/C paper 45mm diameter as soon as it was returned to the lab. Filter papers were then wrapped in tin foil and frozen for 24 hours. After 24 hours the filter papers were each ground with a pinch of sand and 10 ml of 90% acetone using a pestle and mortar. Samples were then decanted into a blackened out 15 ml centrifuge tube and hand centrifuged at maximum speed (ca. 5,000 r.p.m) for five minutes. The supernatant was carefully pipetted into a 1 cm glass cuvette and the absorbance was measured against a 90% acetone blank in a Hach spectrophotometer at 480, 665, 663 and 750 nm, with the value at 750 correcting for any fine colloidal matter, using a 1cm thick chamber of optical glass.

The concentration of Chlorophyll *a* was then calculated using the following equation:

$$26.7*(A_{663}v)/Vd \text{ mg chlorophyll } a \text{ per litre of water}$$

Where:

A = absorbance at 663;

v = volume (ml) of 90% acetone used for extraction;

V= volume filtered (L);

d= path length of spectrophotometer cell.

The value 26.7 is derived from the specific absorbance (absorbance per mole) of chlorophyll *a* (Talling & Driver, 1963)

The carotenoid concentration was then calculated using the equation $m = 10A_{480}v/Vd$. Where

m Specific Pigment Unit (mSPU), which is roughly equivalent to 1mg per litre.

2.2.6 Electron microscopy

Electron microspopy was used for some diatom identification. Diatoms were first cleaned by placing 0.1g of wet sediment in a test tube and adding 5 ml of 30% hydrogen peroxide (H_2O_2). Test tubes were then placed in a water bath within a fume cupboard and heated for 2-4 hours at 80°C or until all organic material had been digested; the tubes were then removed from the bath. 1-2 drops of Hydrochloric acid (HCl) were added to each of the tubes to eliminate any remaining H_2O_2 along with any carbonates. The test tubes were then topped up with distilled water before being left in the cold room overnight to settle at 4°C. The resulting supernatant liquid was decanted off and the diatoms were re-suspended in further distilled water. This washing was repeated four times, with NH_3 being added to the final wash to prevent clumping and retain clays in suspension. Once, the samples were washed they were carefully applied to slides and coated with gold for electron microscopy.

2.2.7 Physical & chemical parameters

Physical and chemical parameters of the lake were monitored Where possible using a YSI 6600 multi-parameter sonde (Yellow Springs Electrode Company), to measure conductivity, water temperature and pH. A Secchi disk was used to measure visibility and a weighted line was used for water depth.

2.2.8 Density and distribution

Two methods were used to calculate the density and distribution of lesser flamingos. Flamingos were counted and mapped over the whole lake using 10.5 x 28 binoculars, by driving the length of lake Bogoria and stopping periodically. Open water, edge and a single water core, 1 m from the shore, were also collected along the entire length of the lake (in areas both with and without flamingos present) to assess whether flamingos distributed themselves according to food availability.

Secondly, an "octocopter" (Figure 2.10) was used with a Canon 5D mounted on it (50 mm lens) and associated GPS, over the flock being observed and photographs taken which corresponded to behavioural observations. This enabled analysis of distribution

in relation to food source and abundance and also feeding behaviours being engaged in. The photographs were analysed in Adobe Photoshop Lightroom 5 and the average density per m^2 was calculated.

Figure 2.10: Octocopter with GPS and Canon 5D (50 mm lens) mounted

2.2.9 Flamingo numbers

Visual estimations were made or the flamingo population on each lake every time they were visited. If the population was too large to be individually counted, each observer counted a group of 50 birds and estimated the number of 50-bird subgroups in the flock using binoculars (10 x 42) or a spotting scope (20-60 x zoom). At least three counts were made and as long as the counts did not have a discrepancy of more than 10%, an average was taken. If the variability between the counts was too large, the count was repeated

2.2.10 Statistical analysis and sample sizes

For statistical analysis, each single scan was treated at a datapoint and therefore when analysing feeding behaviours (Chapter 4) the overall sample size for Lake Bogoria is 10 x 685 as there were 10 feeding behaviours and 685 scans conducted overall (n = 6,850); for Lake Oloidien there were 8 feeding behaviours and 396 scans (n = 3,168); Lake

Nakuru recorded 8 feeding behaviours in 82 scans (n = 656); Lake Sonachi (n=164 (41 x 4)); Lake Natron (n = 291 (97 x 3)) and Lake Elementaita (n = 126 (42 x 3)). The sample size reduced when analysing subsets of data or when looking at time spent feeding rather than individual feeding behaviours (Chapter 5). Each of the 1,383 water samples collected and analysed was also treated as a single datapoint, therefore when comparing all lakes in terms of cyanobacteria, bacillariophyceae, rotifera and protozoans the sample size is 4 x 1,383 (n = 5,532). The sample size is reduced when analysisng subsets of data.

Results were tabulated in Microsoft Excel before being imported into SPSS 21.0 to test for variance, correlations or divergence from the expected. Normally distributed data were analysed using parametric tests and non–parametric tests were used in all other cases. The following tests were used throughout this thesis:

1) One-way between groups multivariate analysis of variance MANOVA (Bonferroni), Kruskal-Wallis (with Games-Howell Post hoc tests) and Mann-Whitney U tests to analyse the difference between variables such as different lakes, years, times of day or site.

2) Pearson product-moment correlation and Spearman's rank correlation coefficient to test positive or negative correlations between variables such as available biomass vs. time spent feeding; Chlorophyll a vs. carotenoid concentration vs. biomass; percentage of birds feeding vs. available biomass or a correlation in biomass along a lake surface transect.

3) Principle Component Analysis with a Varimax (Orthoganal) rotation whereby a linear combination (rotation) of the factors, is searched for, so that the variance of the loadings is maximised. Each factor has limited large loadings, therefore each variable is associated with one, or few, factors and each factor represents a small number of variables (Abdi, 2003). This was used to analyse groups of behaviour at each of the lakes.

4) Sorenson's Quotient to analyse similarity or difference between the taxonomic composition of the lakes

5) Autocorrelations to analyse whether time series data are stationary or non-stationary. This allows for patterns in feeding behaviour to be examined over a period of time, identifiying whether feeding is cyclic or random and whether there are different patterns of feeding over the course of the day at different lakes.

Chapter 3

Chapter 3 Variation in East African alkaline-saline lakes: alternative food resources of the lesser flamingo (*Phoeniconaias minor*)

Abstract

The East African alkaline-saline lakes vary considerably in terms of their phytoplankton and micro-zooplankton communities. It is often reputed that all of the East African soda lakes are dominated by the helicoid photoautotrophic cyanobacterium *Arthrospira fusiformis*. This study included six lakes (Bogoria, Oloidien, Elementaita, Nakuru, Natron and Sonachi), of which only two were dominated by *A. fusiformis* (lakes Bogoria and Sonachi). The remaining lakes where either dominated by bacillariophyceae or other cyanobacteria (*A. fusiformis var. minor* or *Anabaena arnoldii* and *Anabaenopsis magna*). The contribution of both epipelic and planktonic resources to the standing crop (biomass) was quantified, revealing the importance of including epipelic food resources (which are often excluded) into the average standing crop for a lake (Nakuru in 2009: epipelic = 239 mg L^{-1}; planktonic 102 mg L^{-1}). A new food source of dense sedimented aggregations of *A. fusiformis* was identified at Lake Bogoria where, in 2009, these accumulations had an average concentration of 526.8 mg L^{-1} compared to 142.05 mg L^{-1} of planktonic *A. fusiformis*. Between 2009 and 2013 all lakes experience large influxes of fresh water and the conductivity of Lake Bogoria reduced from 50,000 mS cm^{-1} to 25,000 mS cm^{-1}. Average phytoplankton standing crop varied both spatially (within and between lakes) as well as temporally and all lakes (except Lake Natron) experienced a reduction in standing crop between 2009 and 2013. Linear relationships were identified between Chl *a*, carotenoid and biomass in all cases, however the gradient of the correlation differed greatly indicating a complex relationship which could give and indication of the health of the phytoplankton.

3.1 Introduction

The specialised diet of lesser flamingos (*Phoeniconaias minor*) means that they are highly susceptible to fluctuations in food quality and quantity, therefore making them good indicators of ecosystem status (Krienitz & Kotut, 2010). Declines in food availability can cause malnutrition and therefore leave lesser flamingos with compromised immunity making them more vulnerable to infection (Sileo *et al.,* 1999).

In the 1970s and 80s, prolonged periods of drought led to a decrease in lake levels with concomitant increases in lake salinity which may have indirectly led to decreased *Arthrospira fusiformis* biomass (Melack, 1988). *A. fusiformis* standing crop densities are extremely variable both temporally and spatially; large-scale changes have been observed over short periods of time, at Lake Nakuru a 10-fold decrease in biomass was observed over three years (Vareschi, 1982) and changes such as this have been proposed to trigger extensive lesser flamingo movements (Pennycuick & Bartholomew, 1973). Periods of low cyanobacterial density have been linked to lower numbers of lesser flamingos on certain lakes (Vareschi, 1978; Tuite 2000); however no overall correlation has been identified between lesser flamingo movements and food abundance within the Rift Valley lakes (Brown, 1973; Vareschi, 1978; Krienitz & Kotut, 2010).

Temporal changes in phytoplankton biomass were observed in lakes Nakuru and Bogoria between July 2008 and October 2009 (Kaggwa *et al.*, 2013). At Lake Nakuru the fluctuation in biomass was much greater than at Bogoria, *A. fusiformis* contributed over 80% of the total during the wet season (August-November 2008 & April-August 2009) but experienced notable biomass crashes where it contributed less than 5% in May and September 2009. During these crashes, *A. fusiformis* was superseded by "a monospecific dominance of filamentous cyanobacterium (c.f. *P. acicularis*)" (Kaggwa *et al.*, 2013). Lake Bogoria experienced fluctuations in phytoplankton biomass over the same period, ranging from a maximum of 153.5 mg L^{-1} to a minimum of 21.4 mg L^{-1}; however, *A. fusiformis* maintained a mainly mono-specific dominance, consistently contributing upwards of 80% of the total phytoplankton biomass (unlike the crashes observed at Lake Nakuru) (ibid.).

Large-scale changes in the physico-chemical parameters of an alkaline-saline lake can consequently bring about changes in the taxonomic composition. Reduction in conductivity has been correlated with a shift from *A. fusiformis* dominating to other single-celled cyanobacteria becoming dominant (Vareschi, 1978). Therefore, dilution of all East African alkaline-saline lakes simultaneously could further result in a reduction of suitable food sources for lesser flamingos to utilise.

This chapter analyses the change in physico-chemical parameters at Lake Bogoria between 2009 and 2013 and also looks at the composition of phytoplankton and zooplankton within six East African soda lakes, quantifies the available biomass and explores all available food sources for lesser flamingos by addressing the following questions:

- Are all East African soda lakes uniform in terms of phytoplankton and zooplankton composition?
  - Do protozoans and rotifers play an important role in flamingo feeding?
- Is there a difference between planktonic and epipelic biomass?
  - Do the lakes differ in terms of their primary productivity?
- Do East African soda lakes show spatial and temporal variation in biomass?
  - Has lake level rise altered phytoplankton composition/abundance?
- Does *Arthrospira fusiformis* migrate through the water column throughout the day?
  - Does the ratio of S-/C- type and H-type trichomes differ with depth?
- Does biomass availability link with flamingo presence at lakes?

The following null hypotheses are tested:
- All East African soda lakes are uniform in phytoplankton and zooplankton composition
- There is no difference between planktonic and epipelic biomass or productivity
- There is no spatial or temporal difference in biomass availability
- *A. fusiformis* is uniformly distributed throughout the water column
- There is no relationship between biomass availability and flamingo presence at lakes

3.2 Methods

The methods used are described in Chapter 2, alongside full descriptions of each study site. Visits were made when it was logistically possible and timings of all visits made are outlined in Table 3.1.

Table 3.1: Timings of all visits made to lakes Bogoria, Oloidien, Elementaiata, Nakuru, Natron and Sonachi for sampling and quantifying biomass. *indicates chlorophyll *a* and carotenoids measured; †indicates *A. fusiformis* spatial variation studied

Lake	Visits
Lake Bogoria	August 2009†, August 2010, August 2011, April 2012, August 2012*†, April 2013*, August 2013*†
Lake Oloidien	September 2009, August 2010, April 2011, August 2011, April 2012*, August 2012*†
Lake Natron	December 2009, April 2011
Lake Nakuru	September 2009, August 2012*
Lake Elementaita	September 2009, August 2011
Lake Sonachi	September 2009

3.3 Results

3.3.1 Physico-chemical parameters

The six lakes studied varied in physical and chemical parameters. Five of the six lakes were visited more than once and since 2009, all of these experienced a rise in lake level. Lake Bogoria had a maximum depth of ca. 10 m in 2009, which rose to over 16 m in 2013; Lake Elementaita was 20 centimetres deep in 2009 and over 2 m in 2012; Lake Oloidien had a maximum depth of 4 m in 2009, rising to 7 m in 2012. Lake Nakuru and Lake Natron experienced less dramatic increases in depth, although due to the local topography, the surface area of both lakes increased significantly. Table 3.2 summarises the main physical-chemical parameters of the six lakes.

Table 3.2: Geographical and physico-chemical parameters of lakes Bogoria, Oloidien, Nakuru, Natron, Elementaita and Sonachi; maximum and minimum values recorded throughout this study are displayed where applicable

	Lake Bogoria	Lake Oloidien	Lake Nakuru	Lake Natron	Lake Elementaita	Lake Sonachi
Max. depth	10.3 - 16 m	4 - 7 m	4.5 – 6.5 m	1 - 2 m	0.2 - 2 m	4 - 18 m
Conductivity ($\mu S\ cm^{-1}$)	25,000-77,000	3,890-5,270	11,000-160,000	6,000-160,000	11,900-45,000	>9,000
pH	9-12	~10.3	~ 10.5	9-11	~ 9.8	~ 10.3

3.3.2 Chemical stratification at Lake Bogoria

The main chemical parameters showed some variation between 2009 and 2013 at Lake Bogoria (Figure 3.1). All three basins were very similar in 2009; however, in 2013 there was considerable variation between the three basins and a return to a very clear stratification of conductivity. The North and Central basins of Lake Bogoria experienced the greatest influx of freshwater and the surface conductivity was over 40

mS cm^{-1} lower than was recorded in 2009. The South basin also had reduced conductivity; however the surface conductivity was almost 10 mS cm^{-1} higher than in the North and Central basins.

In 2009, the surface temperature was around 30°C, however the temperature reduced to 26°C after half a meter and then stayed relatively constant. In the Central basin in 2013, the temperatures recorded from the surface to 3 m depth matched closely those of 2009, however beyond 3 meters depth, a slight increase in temperature was recorded, peaking at 5 m depth and then staying relatively constant. In 2013, the surface temperature in the North basin was 26°C, rising to over 28°C in the subsequent two metres and falling back down to 26°C at 2 m depth. Below this depth, the temperature profile closely matched that of the Central basin. The South basin displayed the least variation in temperature, staying relatively constant, although a small temperature increase was again recorded around 5 m in depth. The slight increase in temperature in all three basins at 5 m depth corresponds with the level of conductivity stratification in all three basins.

In 2009, oxygen concentration was highest at the surface and the oxycline occurred between 3 and 4 m, however in 2013 a different pattern was observed in the oxygen stratification; in the North basin, surface oxygen was 12 mg L^{-1}, increasing to over 30 mg L^{-1} at half a meter in depth, before declining at a relatively constant rate, with the oxycline occurring between 3 and 4 m. In the Central basin, the surface oxygen was double that of the North at 24 mg L^{-1}, increasing to over 32 mg L^{-1} at 25 cm below the surface and the oxycline occurred between 4 and 5 m. In the South basin, an increase in oxygen was again observed between the surface and 25 cm depth, the following pattern of decline in oxygen fell between the constant rate of decline recorded in the North, and the pattern of increasing decline with increasing depth recorded in the Central basin; the oxyline occurred between 4 and 5 m.
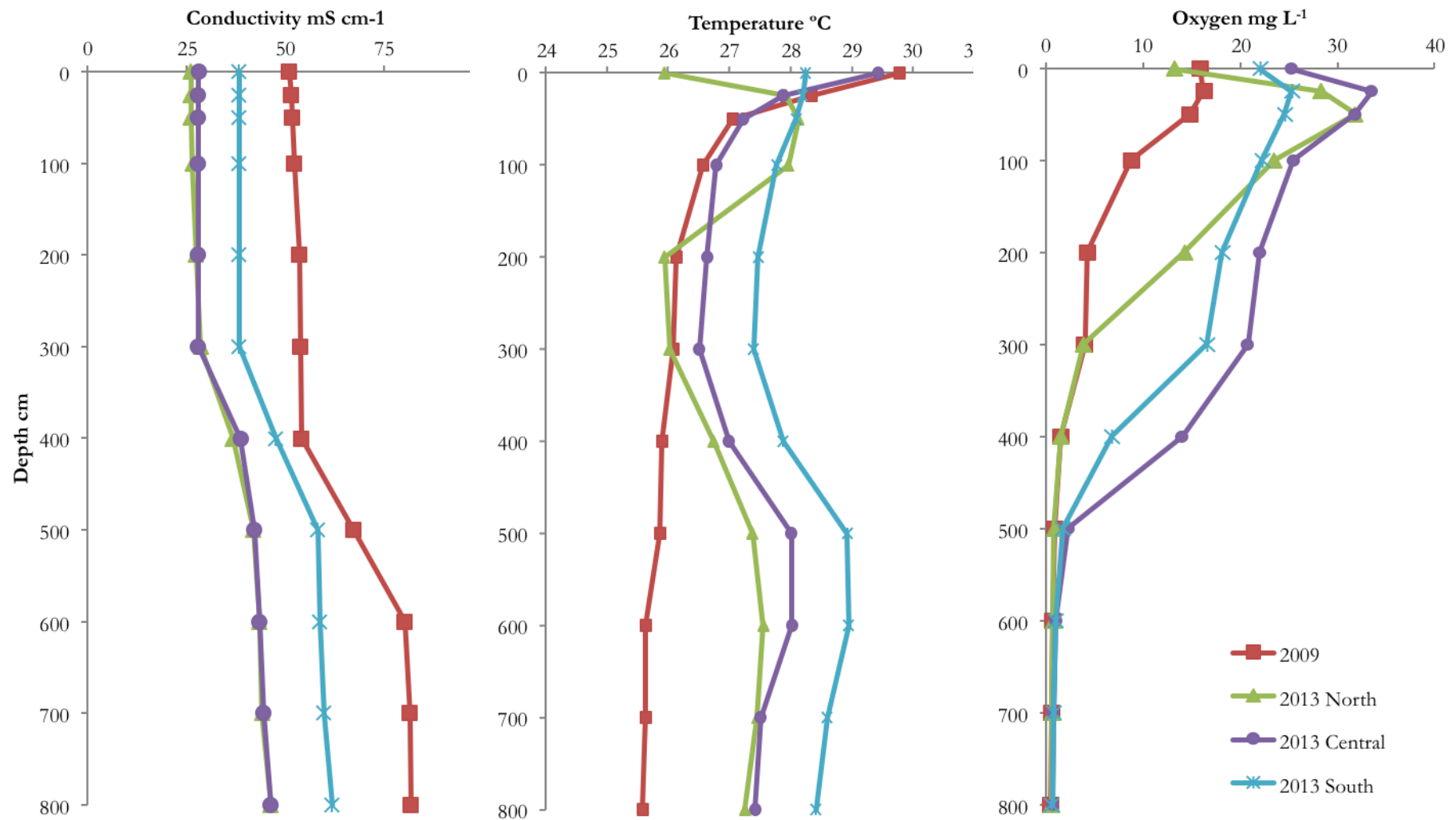
Figure 3.1: Vertical stratification of physico-chemical parameters at Lake Bogoria in 2009 and 2013; each basin is represented by their own profile in 2013

3.3.3 Taxonomic composition

Four taxonomic groups of phytoplankton were recorded – Cyanobacteria, Bacilliarophyceae, Protozoa and Rotifera. Table 3.3 summarises the compositions of each lake and Plates 3.1, 3.2 and 3.3 display images of some of the species identified.

Lake Bogoria was dominated by *Arthrospira fusiformis*, had abundant diatoms around the lake edges and copious protozoans and rotifers, often more concentrated in the shallow water. Lake Oloidien was dominated by *A. fusiformis var minor* but other cyanobacteria were also present including *Oscillatoria* sp. and *Spirulina subsulsa,* a more diverse range of diatoms was identified than at Lake Bogoria and similar rotifers and protozoans. Lake Elementaita had no dominant cyanobacteria, although single celled *Synechococcus* sp. and *Croococcus* sp. were abundant; Lake Elementaita also had the highest species richness of diatoms of any of the study lakes. *A. fusiformis* dominated Lake Sonachi, which was the least species rich in terms of phytoplankton taxa, rotifers were present, but no *Hexarthra Jenkinae* were identified. Lake Nakuru was dominated by *Anabaenopsis abijatae* and *Anabaenopsis magna* with many other cyanobacteria present, including *Tetraspora gelinosa*, which (to my knowledge) has never been recorded in an East African soda lake before. Lake Nakuru had abundant zooplankton and a rich diatom flora. Lake Natron had no dominant cyanobacteria and although diatoms were abundant, the taxonomic richness was lower than at other lakes. Other than *Frontonia* sp. no zooplankton were identified at Lake Natron.

The least similar are Natron and Nakuru (Sorenson's Quotient = 0.44) whilst the most similar are Elementaita and Nakuru (SQ = 0.81). Overall, Natron was least similar to any other lake, which appears to be due to the lack of micro-zooplankton found in the samples.

Table 3.3: Summary of microbial species composition at lakes Bogoria, Oloidien, Elementaita, Sonachi, Nakuru and Natron (3 = dominant, 2 = abundant, 1 = present, presence indicated by a + in diatom samples)

Taxon	Bogoria	Oloidien	Elementaita	Sonachi	Nakuru	Natron
Cyanobacteria						
Arthrospira fusiformis	3	1	1	3	1	-
A. fusiformis var. minor	-	3	-	-	-	-
Arthrospira sp.	1	1	-	-	1	-
Anabaenopsis magna	-	-	1	-	3	-
Anabaenopsis abijatae	-	-	1	-	2	-
Anabaena arnoldii	-	1	-	-	3	1
Spirulina subsulsa	-	1	-	1	-	1
Oscillatoria sp.	1	1	1	1	-	1
Lyngbya pseudospirulina	-	1	1	-	1	1
Synechococcus sp.	1	1	2	1	1	1
Croococcus sp.	-	-	2	-	1	-
Selenastrum sp.	-	-	1	-	-	-
Tetraspora geltinosa	-	-	-	-	1	-
Bacillariophyceae						
Amphora veneta	-	-	+	-	-	-
Amphora sp.	+	+	-	-	-	+
Anomoeoneis sphaerophora	+	+	+	+	+	-
Anomoeoneis sp.	+	+	+	+	+	-
Coscinodiscus sp.	+	-	+	+	+	-
Cyclotella sp.	-	+	+	-	+	+
Cymbella sp.	-	+	+	-	-	+
Epithemia sp.	-	-	+	-	+	-
Fragilaria sp.	-	+	+	-	+	+
Gomphonema sp.	-	+	-	-	-	-
Melosira sp.	+	+	+	-	-	+
Navicula elkab	+	+	+	+	+	+
Navicula sp.	+	+	-	+	+	+
Nitzschia frustulum	+	+	+	+	+	+
Nitzschia sp.	+	+	+	+	+	+
Synedra ulna	-	+	+	-	-	-
Tabellaria flocculosa	-	-	+	-	+	-
Protozoa						
Amoeba sp.	-	2	-	-	-	-
Campanella sp.	-	2	-	-	-	-
Condylostoma magnum	2	1	1	1	2	-
Euplotes sp.	2	-	-	-	1	-
Frontonia sp.	3	3	1	3	3	1
Litonotus sp.	1	1	1	1	1	-
Rotifera						
Brachionus dimidiatus	2	2	2	1	2	-
Brachionus plicatilis	2	2	2	2	2	-
Hexarthra jenkinae	2	2	1	-	2	-
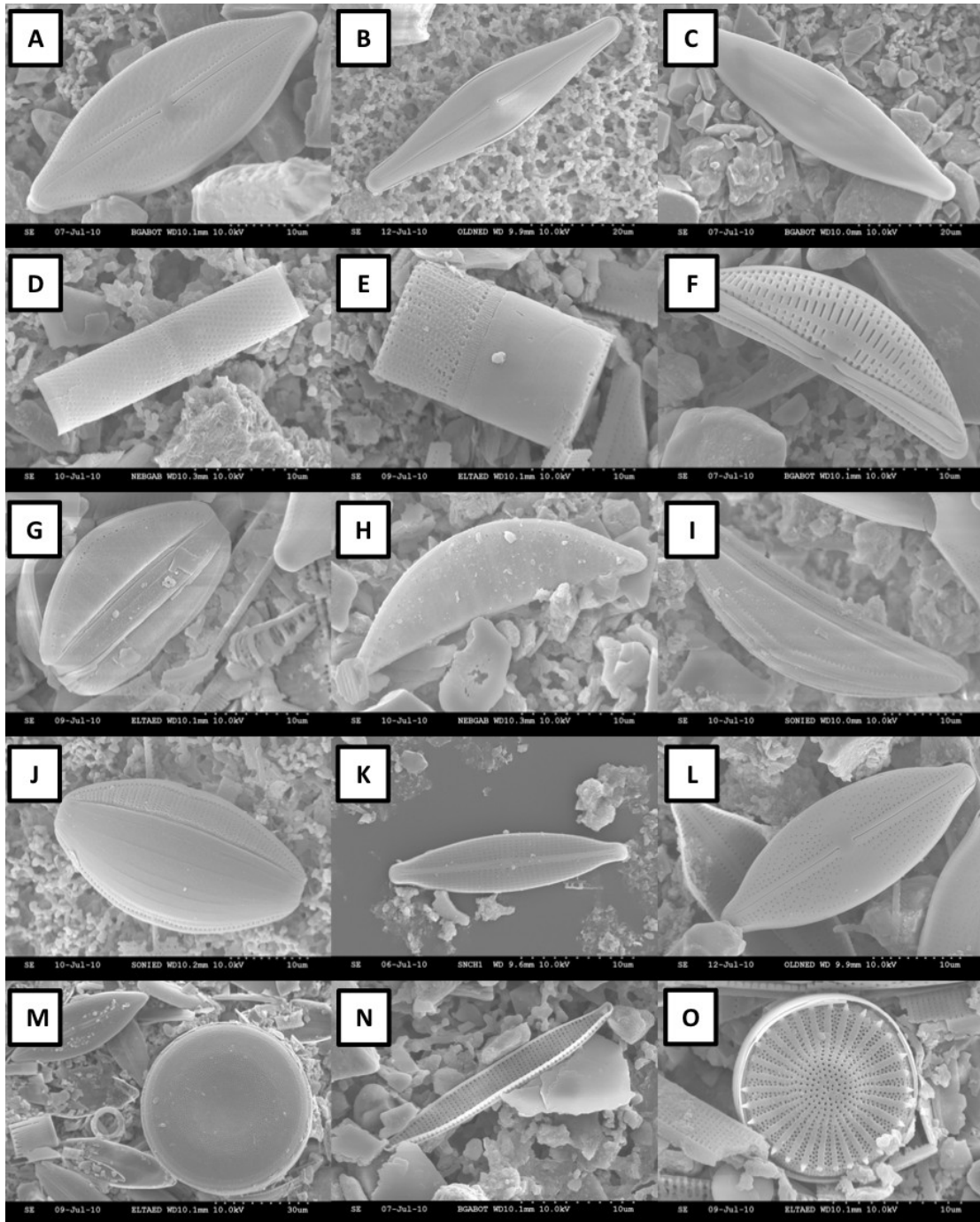
Plate 3.1. Electron micrographs of some of the diatoms found in the alkaline-saline lakes of the Kenyan Rift Valley. **A**: *Anomoeoneis sphaerophora* **B&C**: *Anomoeoneis* sp. **D&E**: *Melosira* sp. **F**: *Amphora veneta* **G-J**: *Amphora* sp. **K**: *Navicula elkab* **L**: *Navicula* sp. **M**: *Coscinodiscus* sp. **N**: *Nitzschia frustulum* **O**: *Cyclotella* sp. (Electron microscopy by Stephan Hyman with Victoria Robinson)
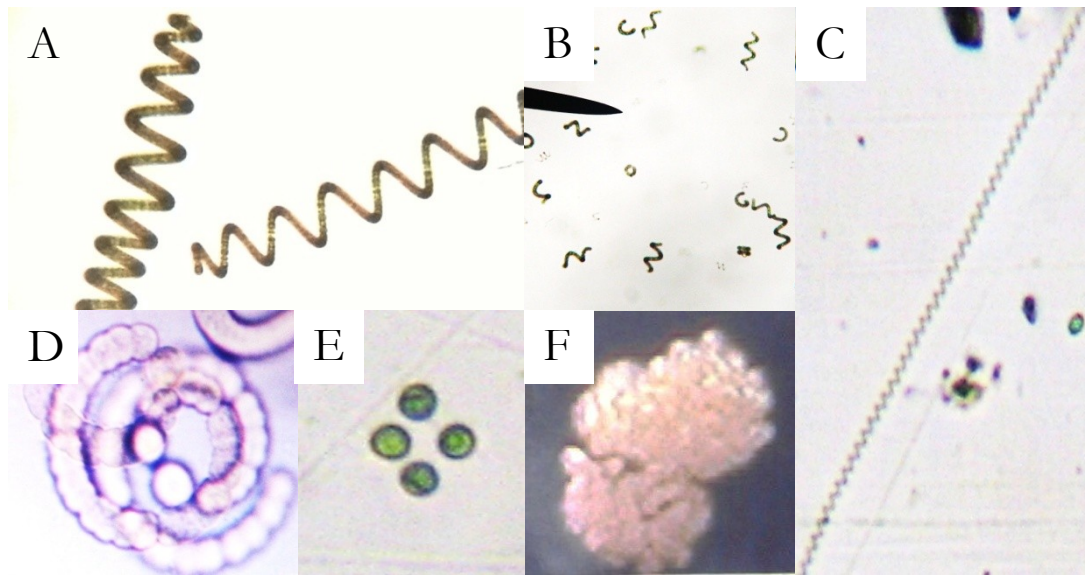
Plate 3.2: Photographs of cyanobacteria taken down a microscope; A: *Arthrospira fusiformis*; B: *Arthrospira fusiformis var. minor*; C: *Spirulina subsulsa*; D: *Anabaena arnoldii*; E: *Tetraspora gelatinosa* F: *Anabaenopsis abijartae* (All photography by Victoria Robinson)
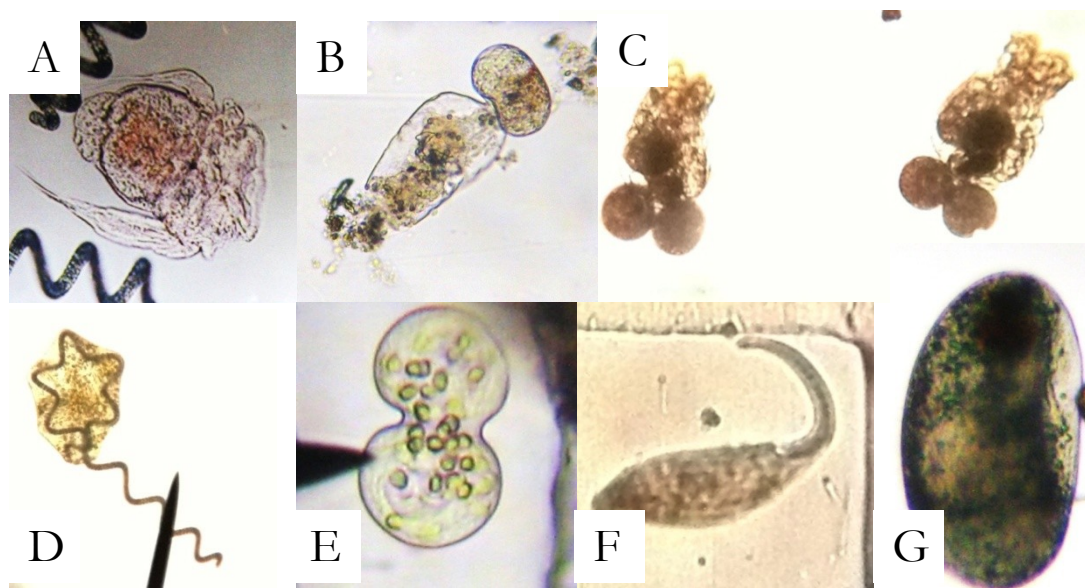
Plate 3.3: Photographs taken down a microscope of rotifer species (A-C) and protozoans (D-G) A: *Hexarthra jenkiniae;* B: *Brachionus plicatus*; C: *Brachionus dimidiatus*; D: *Frontonia* sp. ingesting *A. fusiformis*; E: *Campanella* sp.; F: *Litonotus* sp.; G: *Frontonia* sp. (All photography by Victoria Robinson)

The contribution of cyanobacteria, bacillariophyceae (diatoms), protozoans and rotifera to the overall biomass of each lake is displayed in Figure 3.2.
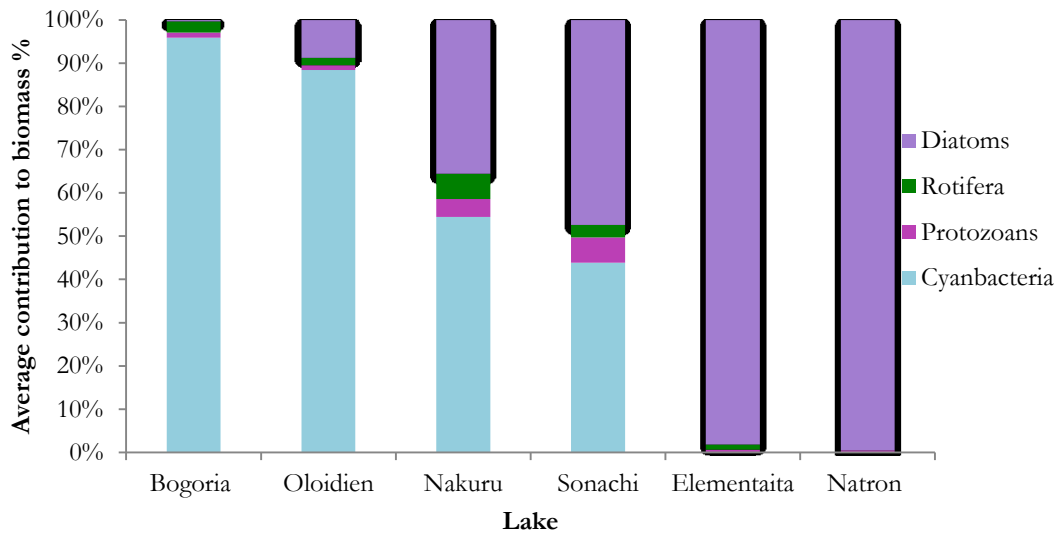
Figure 3.2: The average percentage contribution of identified cyanobacteria, rotifera, protozoans and bacillariophyceae (diatoms) to the biomass composition of six East African Rift Valley soda lakes: Bogoria, Oloidien, Nakuru, Sonachi, Elementaiata and Natron

Arthrospira fusiformis contributed over 95% of the biomass At Lake Bogoria on average over the study period. Cyanobacteria accounted for 90% of the biomass at Lake Oloidien and over 50 % and 40% at lakes Nakuru and Sonachi respectively. Over 10% of biomass was zooplankton (protozans and rotifers) At both Nakuru and Sonachi, and the remainder came from diatoms (both planktonic and epipelic). Diatoms contributed the majority of the identified biomass at lakes Natron and Elementaita (over 95% in both lakes). A one-way between-groups multivariate analysis of variance (MANOVA) testing four dependent variables (diatoms, rotifera, protozoans and cyanobacteria) with the independent variable "lake" found a statistically significant difference between lakes on the combined dependent variable, $F_{(20, 5532)} = 47.42$, p < 0.001; Pillai's Trace = 0.59; partial eta squared = 0.15. When the results for dependent variables were considered separately, all four had statistically significant differences; cyanobacteria (using a Bonferroni adjusted alpha level of 0.07), $F_{(5, 1383)} = 22.14$, p = 0.002, partial eta squared = 0.07; protozoa (using a Bonferroni adjusted alpha level of 0.11), $F_{(5, 1383)} = 34.87$, p < 0.001, partial eta squared = 0.11; rotifera (using a Bonferroni adjusted alpha level of 0.33), $F_{(5, 1383)} = 135.23$, p < 0.001, partial eta squared = 0.33; diatoms (using a Bonferonni adjusted alpha level of 0.13), $F_{(5, 1383)} = 43.71$, p <0.001, partial eta squared = 0.14. The estimated marginal means

and standard error are displayed in Table 3.4 and the results of the Bonferroni post hoc tests are displayed in Table 3.5.

Table 3.4: Means and standard error of the biomass contribution of cyanobacteria, protozoans, rotifer and diatoms at lakes Bogoria, Oloidien, Nakuru, Sonachi, Elementaita and Natron (mg L^{-1})

		Bogoria	Oloidien	Nakuru	Sonachi	Elementaita	Natron
Cyanobacteria	M	152.77	160.33	72.39	53.65	0.14	$1.02*E^{-12}$
	SE	6.58	9.76	22.84	35.44	27.76	17.32
Protozoans	M	1.68	0.48	5.06	7.12	0.50	1.08
	SE	0.13	0.19	0.44	0.68	0.53	0.33
Rotifera	M	0.87	0.50	6.99	3.61	1.03	0
	SE	0.07	0.11	0.25	0.39	0.30	0
Diatoms	M	0.63	10.82	58.03	57.94	57.37	76.79
	SE	2.23	3.30	7.73	11.99	9.40	5.86

Table 3.5: Results of the Bonferroni post hoc tests; significant differences indicated by asterisks

	Cyanobacteria	Protozoans	Rotifera	Diatoms
Bogoria vs. Oloidien	-7.55	1.21***	0.38	-10.19
Bogoria vs. Nakuru	80.39*	-3.38***	-6.12***	-57.40***
Bogoria vs. Sonachi	99.12	-5.48**	-2.74**	-57.31***
Bogoria vs. Elementaita	152.64***	1.18	-0.16	-56.74***
Bogoria vs. Natron	152.77***	0.61	0.87***	-76.16***
Oloidien vs. Nakuru	87.94**	-4.58***	-6.49***	-47.21***
Oloidien vs. Sonachi	106.68	-6.68***	-3.12***	-47.12**
Oloidien vs. Elementaita	160.19***	-0.03	-0.54	-46.55***
Oloidien vs. Natron	160.34***	-0.60	0.50	-65.98***
Nakuru vs. Sonachi	18.73	-2.10	3.38**	0.09
Nakuru vs. Elementaita	72.25	4.56***	5.96***	0.66
Nakuru vs. Natron	72.39	3.98***	6.99***	-18.76
Sonachi vs. Elementaita	53.52	6.65***	2.58***	0.57
Sonachi vs. Natron	53.65	6.08***	3.61***	-18.85
Elementaita vs. Natron	0.13	-0.57	1.03	-19.43
***p < 0.0001 **p < 0.01 *p < 0.05				

3.3.4 Standing crop of lesser flamingo food resources

3.3.4.1 Planktonic biomass

Between 2009 and 2013, Lake Oloidien had a significantly higher density of planktonic biomass (183 mg L^{-1}) than lakes Sonachi (122 mg L^{-1}), Bogoria (90.4 mg L^{-1}) and Nakuru (76.3 mg L^{-1}), X^2 (3, n = 879) = 49.4, p < 0.001 (Kruskal-Wallis). Post hoc tests revealed significant differences between Oloidien and all other lakes at p < 0.0001, no other significant results were identified.

The highest density planktonic biomass was recorded at Lake Oloidien in September 2009 (801 mg L^{-1}), followed by Oloidien in August 2010 (255.32 mg L^{-1}) and Lake Bogoria in April 2012 (165.34 mg L^{-1}). The lowest was recorded at Lake Nakuru in August 2012 (4.81 mg L^{-1}) and the second and third lowest were both recorded at Lake Oloidien in April and August 2012 (47.74 and 51.08 mg L^{-1} respectively). Lake Oloidien, in September 2009, had significantly higher planktonic biomass than was recorded at any of the lakes during any sampling visit, X^2 (15, n = 879) = 431, p < 0.001 (Kruskal-Wallis). Table 3.6 and Figure 3.3 display the planktonic biomass of all sampling visits and Games-Howell post hoc test results are shown in Table 3.7, with significant results identified by asterisks.

Table 3.6: Mean standing crop of the planktonic community (at lakes Bogoria, Oloidien, Nakuru and Sonachi); with standard deviation and number of samples

Site	Month/Year	Standing crop mg L^{-1}	Standard deviation	N
Bogoria	August 09	142.05	75.75	45
	August 10	76.89	31.72	30
	August 11	99.33	61.83	20
	April 12	165.34	109.16	45
	August 12	86.98	61.79	132
	April 13	69.63	188.03	90
	August 13	59.83	56.46	150
Nakuru	August 09	102.06	38.98	25
	August 12	4.81	1.83	9
Oloidien	September 09	801.58	219.26	30
	August 10	255.32	73.39	40
	April 11	77.35	36.45	60
	August 11	146.53	53.81	86
	April 12	47.74	10.96	30
	August 12	51.08	13.70	60
Sonachi	September 09	122.34	150.18	27
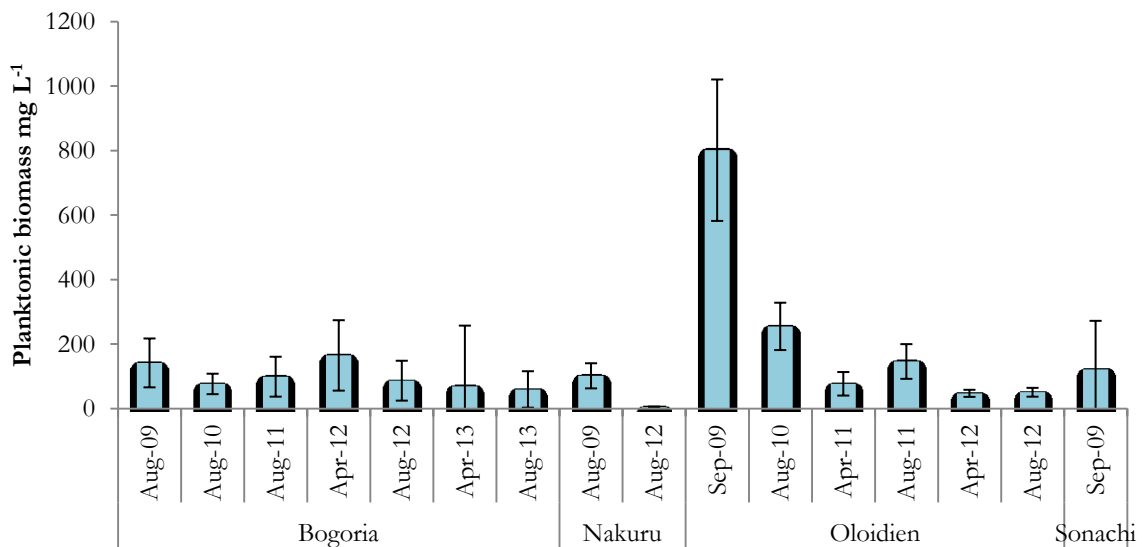
Figure 3.3: Mean standing crop of the planktonic community at lakes Bogoria, Nakuru, Oloidien and Sonachi on visits between 2009 and 2013; ± 1 standard deviation

Table 3.7: Games-Howell post hoc tests results for differences in mean standing crop (mg L^{-1})

	Bogoria Aug 09	Bogoria Aug 10	Bogoria Aug 11	Bogoria Apr 12	Bogoria Aug 12	Bogoria Apr 13	Bogoria Aug 13	Nakuru Aug 09	Nakuru Aug 12	Oloidien Sep 09	Oloidien Aug 10	Oloidien Apr 11	Oloidien Aug 11	Oloidien Apr 12	Oloidien Aug 12	Sonachi Sep 09
Bogoria Aug 09		65.2***	42.7	-23.4	55.1**	72.4	82.2***	40.0	137.2***	-659.5***	-113.3***	64.7***	-4.5	94.3***	91.0***	19.7
Bogoria Aug 10			-22.4	-88.5***	-10.1	7.3	17.1	-25.2	72.1***	-724.7***	-178.4***	-0.5	-69.6***	29.1**	25.8*	-45.5
Bogoria Aug 11				-66.1	12.4	29.7	39.5	-2.7	94.5***	-702.2***	-156.0***	22.0	-47.2	51.6	48.3	-23.0
Bogoria Apr 12					78.4**	95.8	105.6***	63.3	160.6***	-636.2***	-89.9**	88.0***	18.9	117.7***	114.3***	43.0
Bogoria Aug 12						17.4	27.1*	-15.1	82.2***	-714.6***	-168.3***	9.6	-59.5***	39.2***	35.9***	-35.4
Bogoria Apr 13							9.8	-32.4	64.8	-732.0***	-185.7***	-7.7	-76.9	21.8	18.5	-52.7
Bogoria Aug 13								-42.2**	55.0***	-741.8***	-195.5***	-17.5	-86.7***	12.1	8.8	-62.5
Nakuru Aug 09									97.2***	-699.5***	-153.3***	24.7	-44.5**	54.3***	51.0***	-20.3
Nakuru Aug 12										-796.8***	-250.5***	-72.5***	-141.7***	-42.9***	-46.3***	-117*
Oloidien Sep 09											546.3***	724.2***	655.1***	753.8***	750.5***	679.2***
Oloidien Aug 10												178.0***	108.8***	207.6***	204.2***	133*
Oloidien Apr 11													-69.2***	29.6***	26.3***	-45.0
Oloidien Aug 11														98.8***	95.4***	24.2
Oloidien Apr 12															-3.3	-74.6
Oloidien Aug 12																-71.3
Sonachi Sep 09																

***p < 0.0001 **p < 0.01 *p < 0.05

3.3.4.2 Epipelic biomass

Lake Nakuru recorded significantly higher average epipelic biomass (215.0 mg m^{-2}) than both lakes Natron (93.2 mg m^{-2}) and Elementaita (111.6 mg m^{-2}), X^2 (2, n=146) = 47.68, p < 0.001 (Kruskal-Wallis). No significant difference was found between Natron and Elementaita (Games-Howell).

The highest epipelic biomass was recorded at Lake Nakuru in 2009 (239.0 mg m^{-2}), almost 100 mg m^{-2} more than the next highest amount recorded at Elementaita in 2009 (140 mg m^{-2}). The lowest epipelic biomass was recorded at Elementaita in 2011 (46.6 mg m^{-2}). Lake Nakuru in 2009 recorded significantly higher epipelic biomass than was recorded at any lake during any other visit, X^2 (5, n=146) = 96.38, p < 0.001 (Kruskal-Wallis). Table 3.8 and Figure 3.4 display the epipelic biomass of all sampling visits and Games-Howell post hoc test results are shown in Table 3.9, with significant results identified by asterisks.

Table 3.8: Mean standing crop of the epipelic community (at lakes Elementaita, Nakuru and Natron); with standard deviation and number of samples

Site	Month/Year	Standing crop mg m^{-2}	Standard deviation	N
Elementaita	September 2009	142.0	111.2	15
	August 2011	46.6	15.3	7
Nakuru	August 2009	239.0	121.2	25
	August 2012	115.1	20.8	6
Natron	December 2009	67.4	36.9	53
	April 2011	121.3	18.1	40
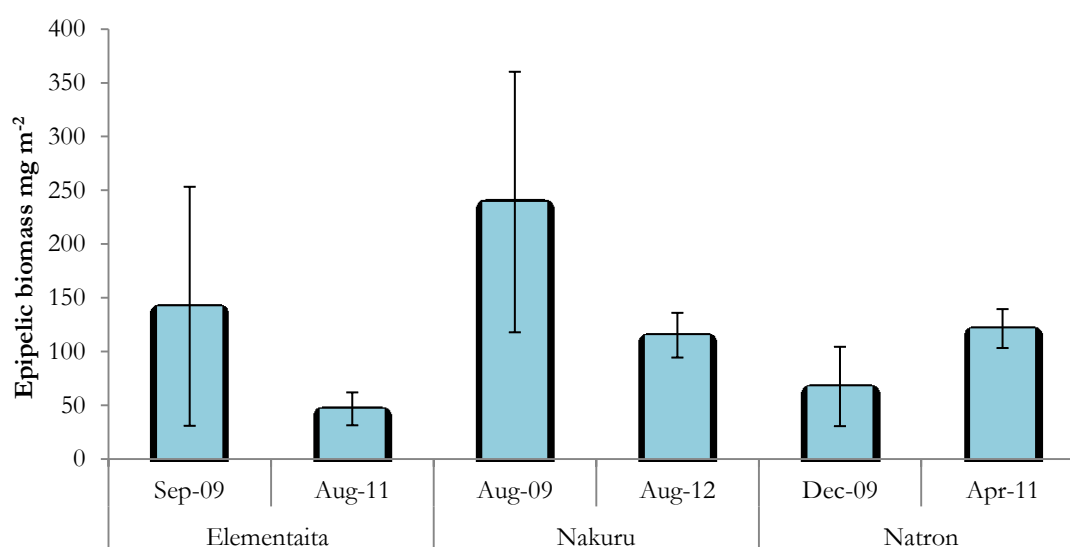
Figure 3.4: Mean standing crop of the epipelic community at lakes Elementaita, Nakuru and Natron on visits between 2009 and 2011; error bars ± 1 standard deviation

Table 3.9: Games-Howell post hoc tests results for differences in mean standing crop (mg m^{-2})

	Elementaita Sept 2009	Elementaita Aug 2011	Nakuru Aug 2009	Nakuru Aug 2010	Natron Dec 2009	Natron Apr 2011
Elementaita Sept 2009		95.4*	-97.0	26.9	74.6	14.7
Elementaita Aug 2011			-192.4***	-68.4**	-20.8	-80.6***
Nakuru Aug 2009				124.0**	171.6***	111.7**
Nakuru Aug 2010					47.6**	-12.2
Natron Dec 2009						-59.8***
Natron Apr 2011						
***p < 0.0001; **p < 0.01; *p < 0.05						

3.3.4.3 Suspended epipelic biomass

The average suspended epipelic biomass at Elementaita (4.25 mg L^{-1}) was higher than at Lake Natron (0.67 mg L^{-1}), however, this result was not statistically significant. In August 2011, the suspended epipelic biomass at Lake Elementaita (7.44 mg L^{-1}) was significantly higher than either Elementaita in September 2009 (1.05 mg L^{-1}) or at Lake Natron in December 2009 (0.67 mg L^{-1}), X^2 (2, n=42) = 8.974, p < 0.05 (Kruskal-Wallis). No significant differences were found between Elementaita and Natron for the 2009 visits. Table 3.10 and Figure 3.5 display the suspended epipelic biomass of all sampling visits and Games-Howell post hoc test results revealed no significant differences between Elementaita and Natron in 2009.

Table 3.10: Mean standing crop of the suspended epipelic community (at lakes Elementaita and Natron); with standard deviation and number of samples

Site	Month/Year	Standing crop mg L^{-1}	Standard deviation	N
Elementaita	September 2009	1.05	2.05	15
	August 2011	7.44	14.71	7
Natron	December 2009	0.67	0.21	20
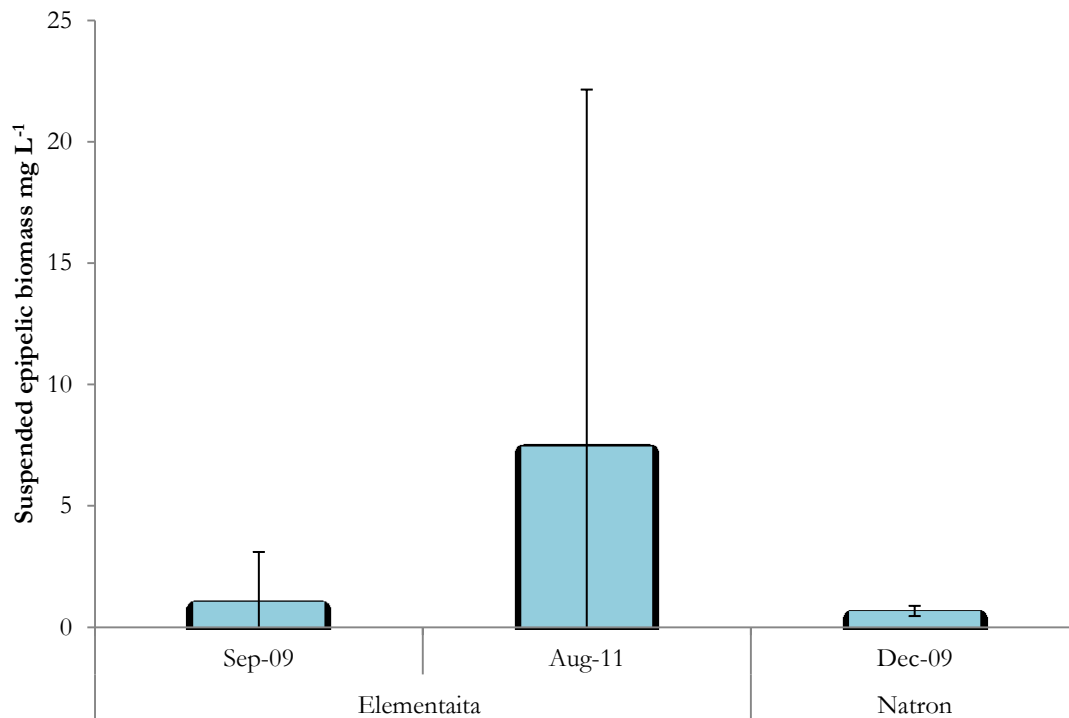
Figure 3.5: Mean standing crop of the suspended epipelic community lakes Elementaita and Natron on visits in 2009 and 2011; ± 1 standard deviation

3.3.4.4 Sedimented *A. fusiformis* biomass

Sedimented *A. fusiformis* was only observed in Lake Bogoria between 2009 and 2012 and a temporal decline in the abundance was recorded (Table 3.11 and Figure 3.9), from consistently high concentrations above the lakebed to only occasional pockets of concentrated *A. fusiformis*. The biomass of sedimented *A. fusiformis* recorded in August 2009 (526.8 mg L^{-1}) was significantly higher than in subsequent years, X^2 (4, n = 272) = 167.37, p < 0.001. Games-Howell post hoc tests revealed statistically significant differences between August 2012 and August 2009, August 2010 and April 2012. No other significant differences were found.

Table 3.11: Mean standing crop of the sedimented *A. fusiformis* (mg L^{-1}) at lake Bogoria; with standard deviation and number of samples

Site	Month/Year	Standing crop mg L^{-1}	Standard deviation	N
Bogoria	August 2009	526.8	441.8	45
	August 2010	339.4	87.9	30
	August 2011	294.0	198.0	20
	April 2012	338.4	203.9	45
	August 2012	156.7	217.5	132
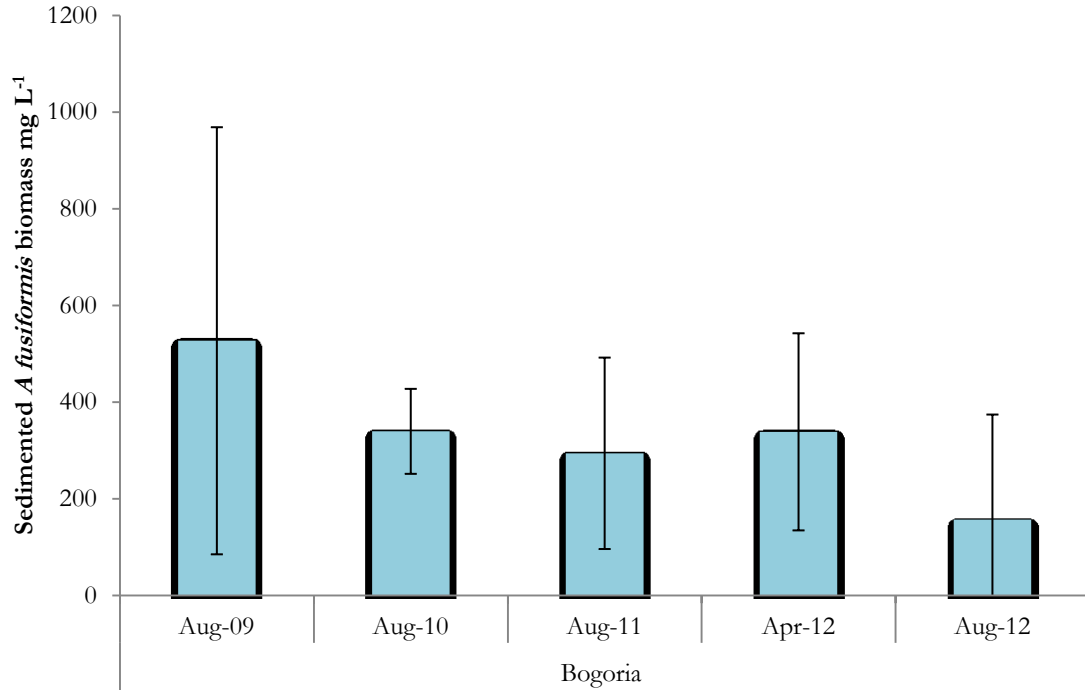
Figure 3.6: Mean standing crop of sedimented *A. fusiformis* at Lake Bogoria between 2009 and 2012; error bars ± 1 standard deviation

3.3.5 Spatial and temporal variation in lake phytoplankton and zooplankton communities

3.3.5.1 Lake Bogoria spatial variation

Spatial variation in overall average biomass was recorded at Lake Bogoria in 2009, 2010, 2012 and 2013. In 2009, the South basin had significantly lower average biomass (121.16 mg L^{-1}) than the North and Central basins (396.15 and 485.9 mg L^{-1} respectively), X^2 (2, 90) = 33.92, p < 0.001 (Kruskal-Wallis). The South basin recorded significantly higher biomass (385.59 mg L^{-1}) than both the Central and North basin (58.03 and 53.16 mg L^{-1} respectively) in 2012, X^2 (2, 144) = 79.73, p < 0.001 (Kruskal-Wallis). In 2013 much lower biomass was recorded overall, however, the biomass in the South basin (124.96 mg L^{-1}) was, again, significantly higher than in either the Central or North basins (43.29 and 16.17 mg L^{-1} respectively), X^2 (2, 105) = 71.78, p < 0.001. In 2010, the highest biomass was recorded in the Central basin (318.01 mg L^{-1}), followed by the North basin (279.08 mg L^{-1}) and the lowest biomass in the South (233.63 mg L^{-1}); however, this variation was not statistically significant. Figure 3.7 displays the average biomass recorded in each basin of Lake Bogoria in 2009, 2010, 2012 and 2013.
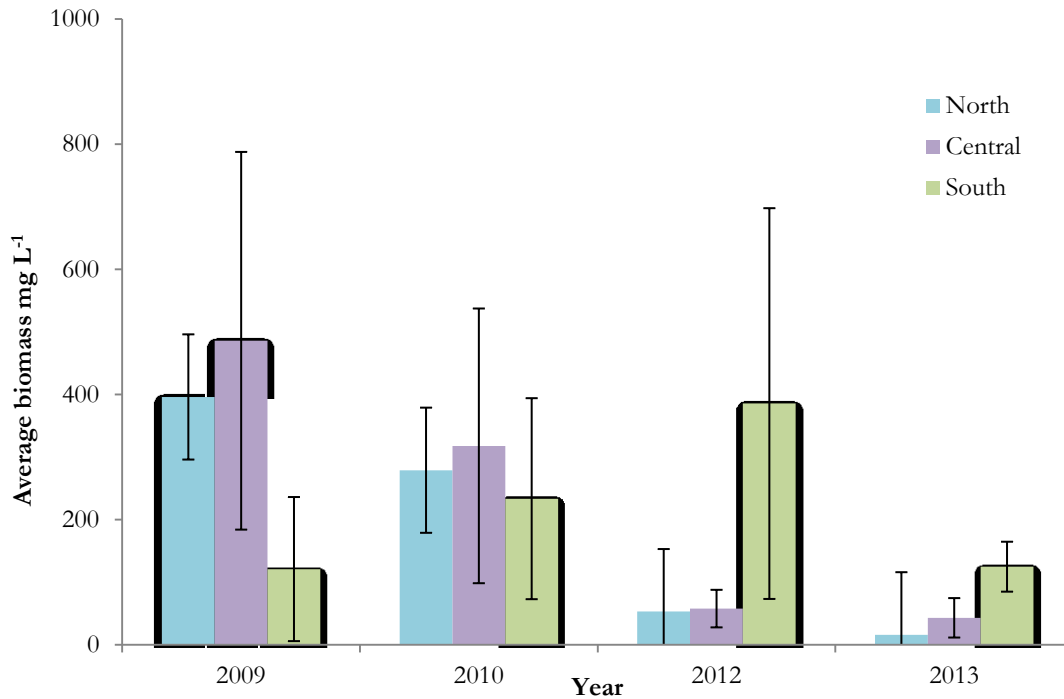
Figure 3.7: The average biomass (mg L^{-1}) of the three basins of Lake Bogoria in 2009, 2010, 2012 and 2013; error bars ± 1 standard deviation

There was considerable variation in the surface biomass in 2009, beginning at around 200 mg L^{-1} in the North, a peak of over 1200 mg L^{-1} was recorded in the middle of the Central basin before dropping back down (Figure 3.8). A second smaller peak was recorded between the Central and South basins. There was little variation recorded in the biomass travelling from North basin to the South basin, at 5 cm, 15 cm, 25 cm or 50 cm below the surface of the lake. Biomass remained relatively constant At 5 cm depth, until the South basin when there was a small peak up to 418 mg L^{-1}, from fluctuating between 150-200 mg L^{-1}. At 15 cm depth, a small, yet significant, decline was recorded from North to South (*rho* = -0.78, p < 0.01; Spearman's Rank Correlation Coefficient). At both 25 and 50 cm depths, the fluctuations were minimal.

The lake level at Lake Bogoria rose between 2012 and 2013, with large influxes of water coming from the Waseges and Loburu rivers in the North and Central basin respectively. The effects of freshwater inflow showed in the biomass distribution in both 2012 and 2013 as the North basin had very little *A. fusiformis* whilst the South still had relatively high concentrations of the cyanobacteria.

In 2012, there was little *A. fusiformis* in any of the sampled locations within the North and Central basins (Figure 3.9). The biomass was lowest in the North basin, remaining low in the Central basin, although a small peak occurred between the two basins. In the South basin the biomass increased dramatically. The three planktonic samples (open, 10 m top and 20 m top) all recorded significant increases from the North to the South (*rho* = 0.83, p = 0.011; *rho* = 0.77, p = 0.026; *rho* = 0.86, p = 0.006 respectively; Spearman's Rank Correlation Coefficient). These three samples all had much lower increases in the South basin than were recorded for the edge samples or sedimented *A. fusiformis* (10 m bottom and 20 m bottom), which had three times as much biomass in the South. These increases in biomass in all three surface / lakebed interface samples in the South were significantly larger than the rest of the lake but no linear correlation was identified.

Relatively large fluctuations were recorded in 2013, along the length of the lake at all depths; with fluxes of over 100 mg L^{-1} from one site to the next. An increase in biomass from the North to South was recorded at all depths (Figure 3.10) from the surface to 50 cm (*rho* = 0.86; *rho* = 0.90; *rho* = 0.90; *rho* = 0.94 and *rho* = 0.78 respectively, all p < 0.001; Spearman's Rank Correlation Coefficient).
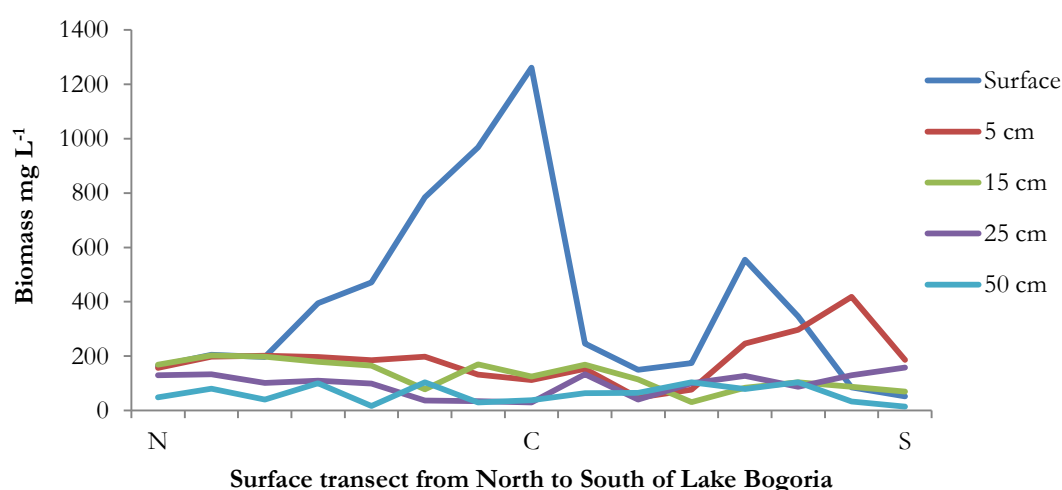
Figure 3.8: The average biomass of Lake Bogoria, in 2009, at varying depths, along a surface transect from North to South
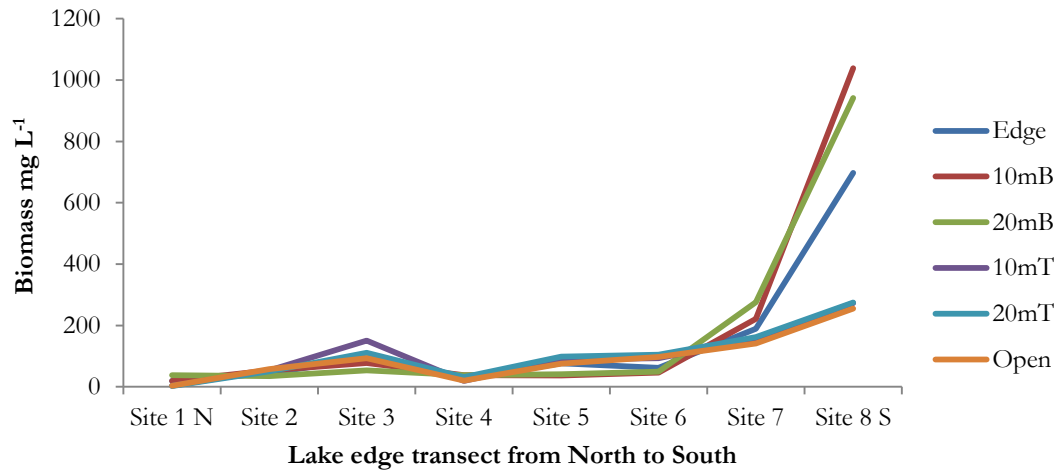
Figure 3.9: The average biomass of Lake Bogoria, in 2012, along a shoreline transect from North to South, surface samples taken from the edge, 10 m out, 20 m out and 50 m out (surface); sedimented *A. fusiformis* samples taken 10 and 20 m out
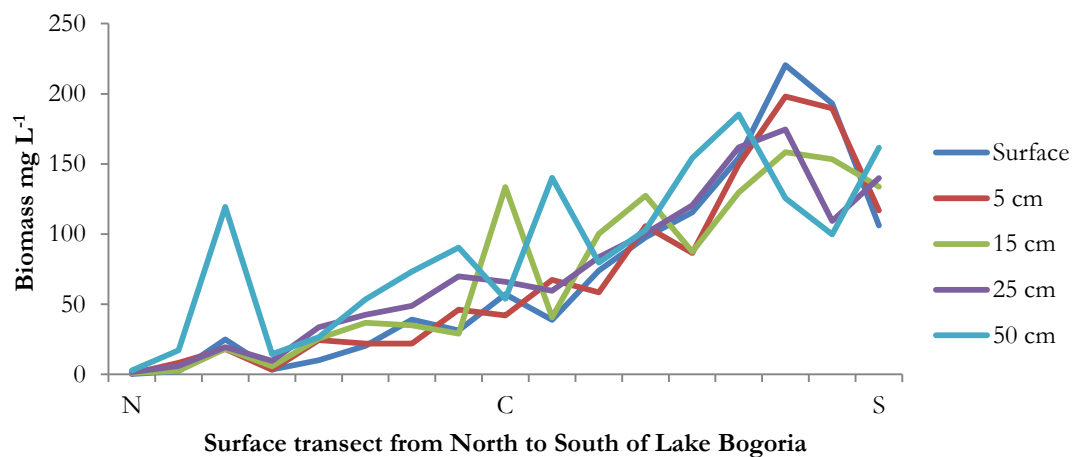
Figure 3.10: The average biomass of Lake Bogoria in 2013, at varying depths, along a surface transect from North to South

3.3.5.2 Lake Oloidien spatial variation

Lake Oloidien has a much smaller surface area than Bogoria and is not divided into separate basins. The Public Jetty recorded significantly lower biomass (105.06 mg L^{-1}) than Oloidien Bay (171.2 mg L^{-1}), Oserian (167.48 mg L^{-1}) and Oserian Corner (159.33 mg L^{-1}), X^2 (3, n = 36) = 10.47, p = 0.015 (Kruskal-Wallis). Oloidien Bay, Oserian and Oserian Corner all recorded similar biomass (Figure 3.11).
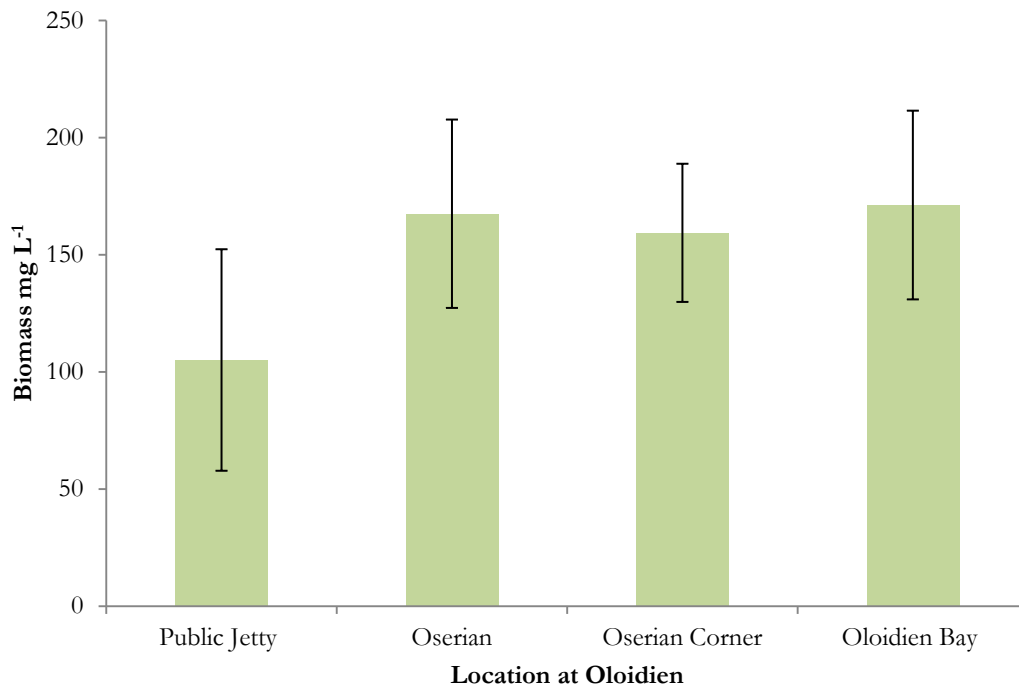
Figure 3.11: The average phytoplankton and micro-zooplankton biomass (mg L^{-1}) of the four areas of Lake Oloidien in August 2011; error bars ± 1 standard deviation

3.3.5.3 Lake Bogoria temporal variation

The highest average biomass was recorded in 2009 At Lake Bogoria, (334.40 mg L^{-1}), whilst the lowest was recorded in 2013 (54.35 mg L^{-1}). The temporal variation in biomass recorded was significant, X^2 (6, n = 784) = 303.03, p < 0.001 (Kruskal-Wallis) and overall there was a significant decline in biomass from August 2009 to August 2013 (Figure 3.12), (*rho* = -4.02, p <0.01; Spearman's Rank Correlation Coefficient). This decline coincides with the increase in lake level, through freshwater inflow, from a maximum depth of 10 m in 2009 to over 16 m in 2013. A small decline in biomass occurred from 2009 to 2011, followed by a slight increase in April 2012 happening prior to significant decline in August 2012 through to August 2013. Games-Howell post hoc tests identified are displayed in Table 3.12.
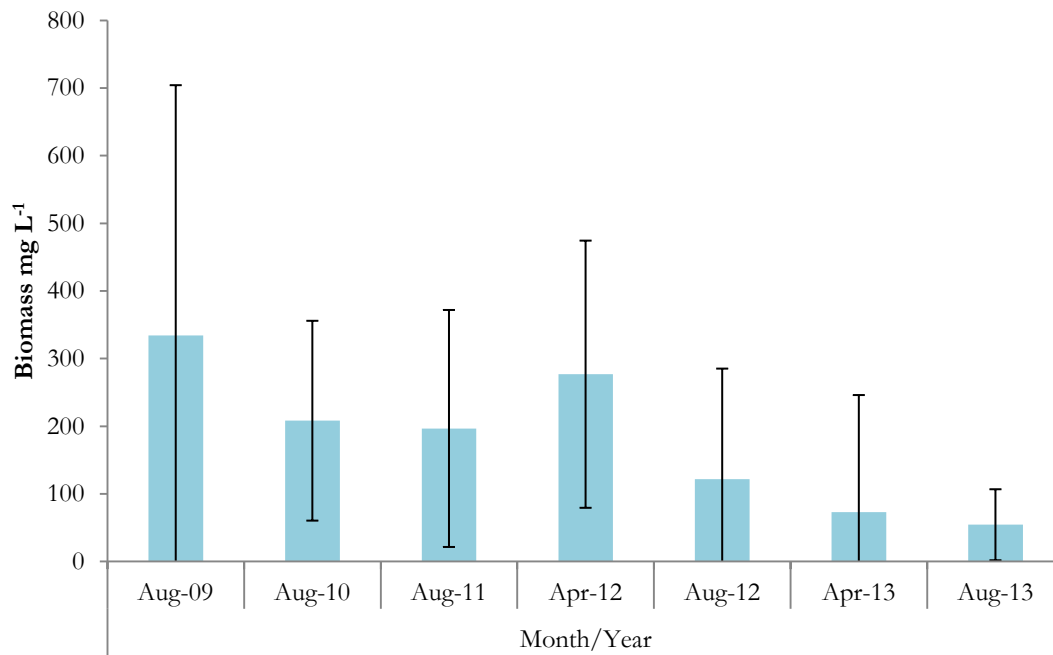
Figure 3.12: The average phytoplankton and micro-zooplankton biomass (mg L^{-1}) of Lake Bogoria from 2009 to 2013; error bars ± 1 standard deviation

Table 3.12: Games-Howell post hoc tests for difference in average biomass at Lake Bogoria from 2009 to 2013; significant results indicated by asterisks

	Aug 09	Aug 10	Aug 11	Apr 12	Aug 12	Apr 13	Aug 13
Aug 09		126.24	137.72	57.50	212.55**	261.37**	280.05**
Aug 10			11.49	-68.74	86.31*	135.13**	153.82**
Aug 11				-80.23	74.82	123.64*	142.33**
Apr 12					155.05**	203.87**	222.56**
Aug 12						48.82	67.51**
Apr 13							18.69
Aug 13							
**p < 0.001; *p < 0.01							

3.3.5.4 Lake Oloidien temporal variation

A significantly greater biomass was recorded at Lake Oloidien in September 2009 than on any other visit to the lake, X^2 (5, n = 356) = 260.31, p < 0.001 (Kruskal-Wallis). The highest average biomass recorded was in 2009 (801.58 mg L-1) and the lowest was recorded in April 2012 (47.74 mg L^{-1}). There was a significant biomass decline recorded from April 2012 to August 2013 (Figure 3.13)(*rho* = -0.653, p < 0.001; Spearman's Rank Correlation Coefficient) coinciding with lake level rise as, in 2012, Lake Oloidien reconnected with Lake Naivasha for a few weeks, further diluting the soda lake with fresh water. Games-Howell post hoc tests revealed statistically

significant difference between all months and years, with the exception of April 2012 (*Md* = 44.72, n = 30) and August 2012 (*Md* = 54.89, n = 60) that were not significantly different.
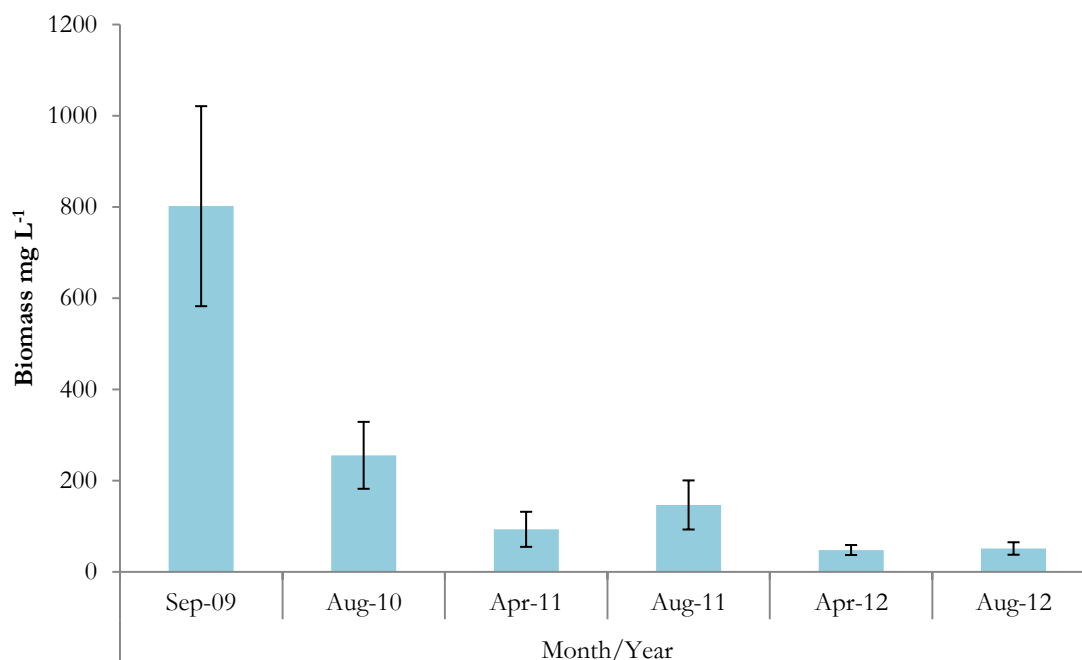
Figure 3.13: Average biomass of Lake Oloidien from 2009 to 2012; error bars ± 1 standard deviation

3.3.6 Biomass, chlorophyll and carotenoid concentration

Increasing biomass at lakes Bogoria, Oloidien and Nakuru was closely linked with increasing chlorophyll *a* (Chl *a*) and carotenoid concentration, which are in turn also linked (Figures 3.14 – 3.19). The Pearson product moment result and p-values are displayed in Table 3.13.

The highest biomass recorded in any single sample was at Lake Bogoria in 2012, 1137 mg L^{-1}, corresponding with Chl *a* of 12,730 ug L^{-1} and a carotenoid concentration of 7,840 ug L^{-1} (Figure 3.14). This suggests that 1 mg L^{-1} biomass generated a concentration of 11.2 ug L^{-1} Chl *a* and of 6.9 ug L^{-1} carotenoid.

The highest biomass recorded at Lake Nakuru in 2012 was much lower than at Bogoria, 137 mg L^{-1}, corresponding to Chl *a* concentration of almost 700 ug L^{-1} and carotenoid concentration of almost 500 ug L^{-1} (Figure 3.15). This suggests that 1 mg L^{-1}

of biomass at Lake Nakuru only generates a Chl *a* concentration of 5.1 ug L^{-1} and a carotenoid concentration of 3.6 ug L^{-1}, considerably lower than Bogoria.
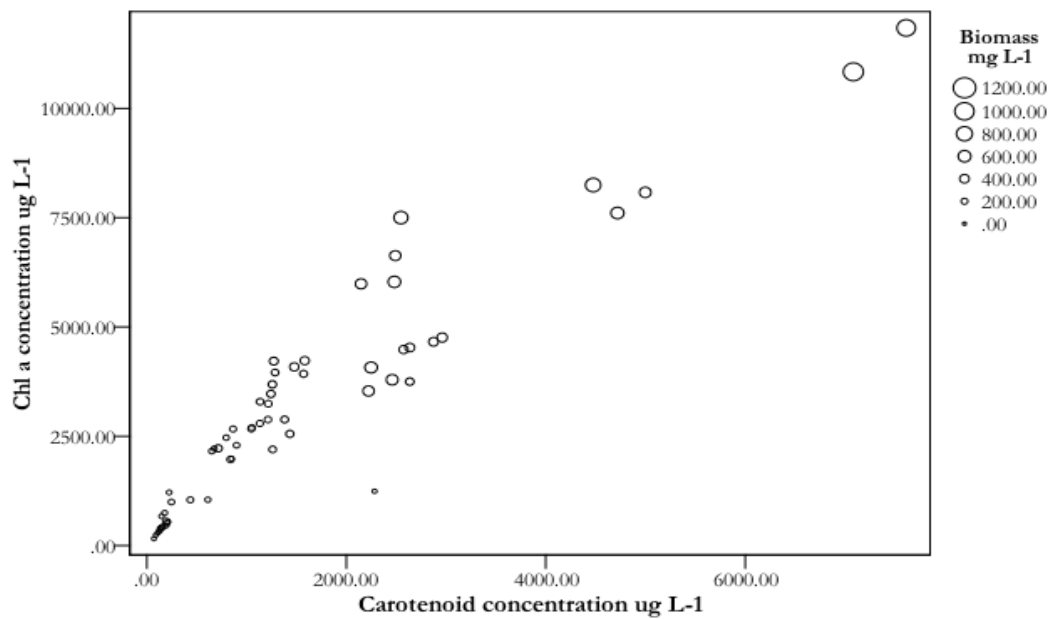
Figure 3.14: Bubble plot displaying the relationship between Chlorophyll *a* concentration, carotenoid concentration and biomass at Lake Bogoria in 2012
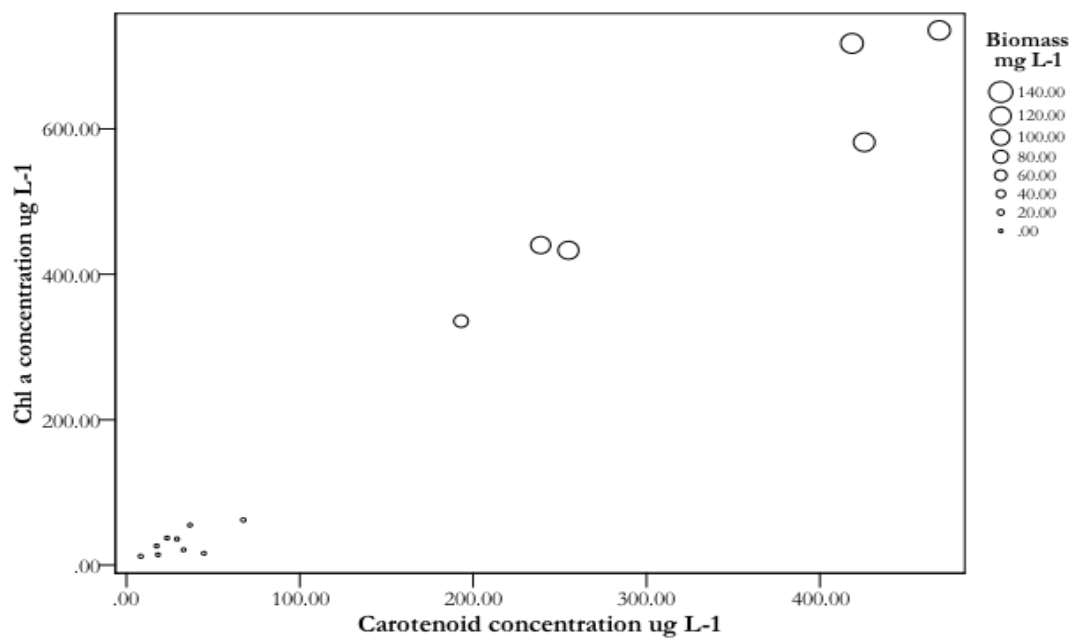
Figure 3.15: Bubble plot displaying the relationship between Chlorophyll *a* concentration, carotenoid concentration and biomass at Lake Nakuru in 2012

The highest biomass recorded in April 2012 at Lake Oloidien was 65 mg L^{-1}, corresponding with Chl *a* concentration of 780 ug L^{-1} and a carotenoid concentration of 424 ug L^{-1} (Figure 3.16), suggesting that 1 mg L^{-1} of biomass generated 12 ug L^{-1} and 6.5 ug L^{-1} of Chl *a* and carotenoids respectively. A similar relationship was identified in August 2012 (Figure 3.17), suggesting 1 mg L-1 of biomass generated 9.2 ug L^{-1} and 5.3 ug L^{-1} of Chl *a* and carotenoids respectively.
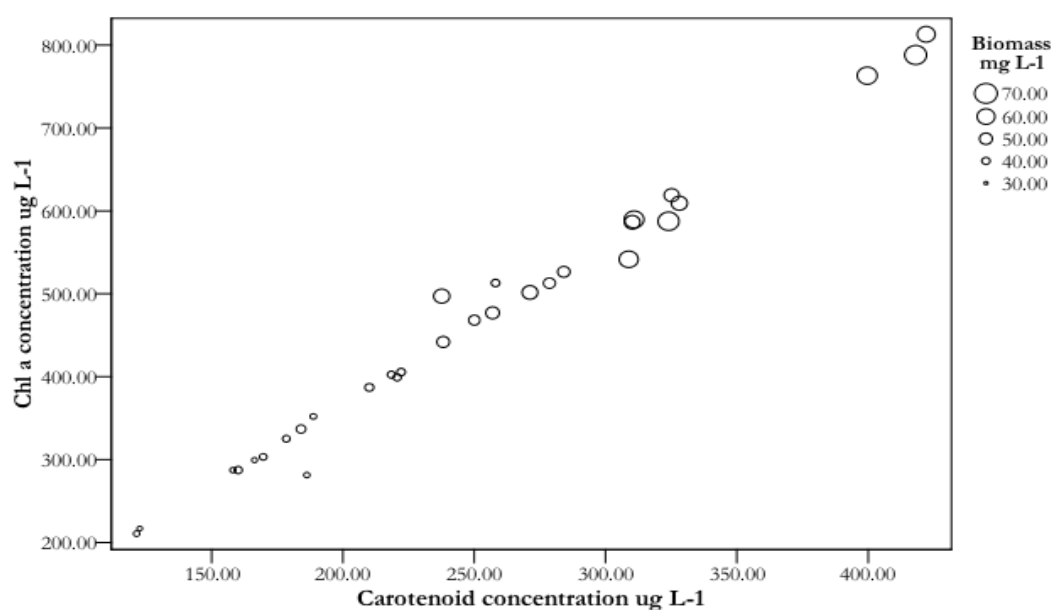
Figure 3.16: Bubble plot displaying the relationship between Chlorophyll *a* concentration, carotenoid concentration and biomass at Oloidien in April 2012
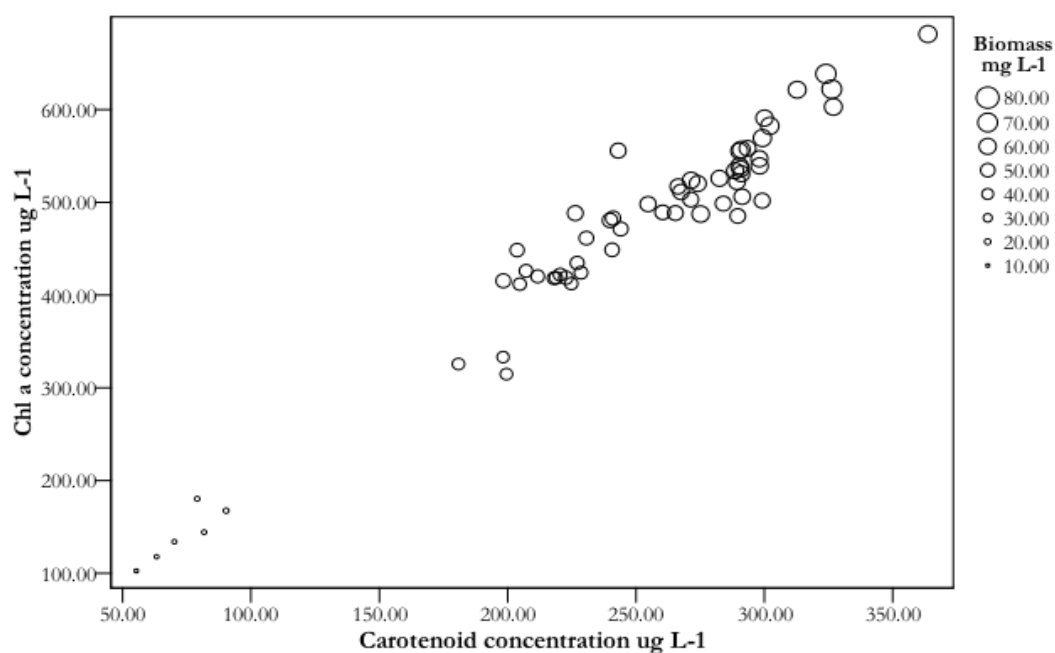
Figure 3.17: Bubble plot displaying the relationship between Chlorophyll *a* concentration, carotenoid concentration and biomass at Lake Oloidien in August 2012

The highest biomass recorded at Lake Bogoria in April 2013, was 1,186 mg L^{-1}, corresponding with a Chl *a* concentration of 20160 ug L^{-1} and a carotenoid concentration of 11,380 ug L^{-1} (Figure 3.18). This indicates that 1 mg L^{-1} biomass is responsible for 17 ug L^{-1} of Chl *a* and carotenoids of 9.6 ug L^{-1}, much higher than in August 2013 (Figure 3.19) when 1 mg L^{-1} corresponded with 6.9 ug L^{-1} and 2.9 ug L^{-1} of Chl *a* and carotenoids respectively.
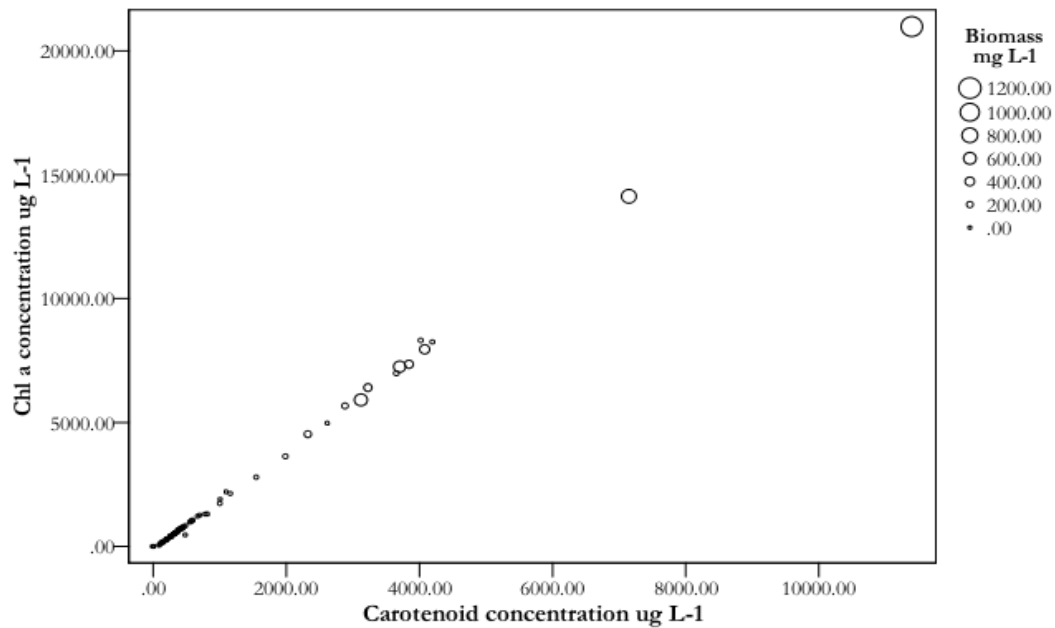
Figure 3.18: Bubble plot displaying the relationship between Chlorophyll *a* concentration, carotenoid concentration and biomass at Lake Bogoria in April 2013
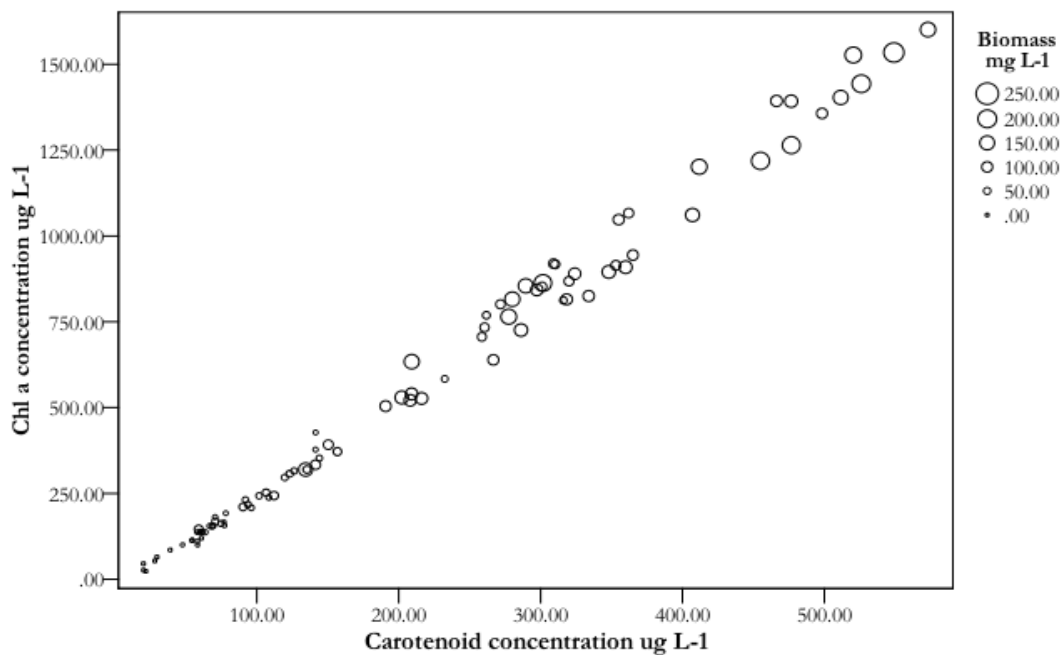
Figure 3.19: Bubble plot displaying the relationship between Chlorophyll *a* concentration, carotenoid concentration and biomass at Lake Bogoria in August 2013

Table 3.13: Pearson product moment test result and p values for the relationships between biomass, carotenoids and Chl *a* at differing lakes throughout 2012 and 2013

Lake	Month / Year	Biomass / Chl a	Biomass / Carotenoid	Chl a / Carotenoid	N
Bogoria	2012	r = 0.942, p < 0.001	r = 0.913, p < 0.001	r = 0.939, p < 0.001	60
Nakuru	2012	r = 0.975, p < 0.001	r = 0.957, p < 0.001	r = 0.989, p < 0.001	15
Oloidien	Apr 2012	r = 0.891, p < 0.001	r = 0.896, p < 0.001	r = 0.993, p < 0.001	31
	Aug 2012	r = 0.978, p < 0.001	r = 0.970, p < 0.001	r = 0.976, p < 0.001	60
Bogoria	Apr 2013	r = 0.904, p < 0.001	r = 0.910, p < 0.001	r = 0.999, p < 0.001	90
	Aug 2013	r = 0.839, p < 0.001	r = 0.846, p < 0.001	r = 0.996, p < 0.001	90

3.3.7 *Arthrospira fusiformis* positioning in the water column

The percentage of *A. fusiformis* colonies which were in the uncoiled state (S- or C- type trichomes) varied significantly at the surface, 25 cm below the surface (mid) and 50 cm below the surface (bottom), over the course of the day (Figure 3.20).

At the surface, the highest percentage of uncoiled colonies was present at the surface at 9am (78.1%) and the lowest at midday (41%). The highest percentage of uncoiled colonies in the mid and bottom samples were at 9 pm (79.6%) and 3 am (75.2%) respectively. The lowest percentage of uncoiled colonies in the mid and bottom samples were found at midnight (51.9%) and 9 pm (57.7%) respectively.

Significant variation in the percentage of uncoiled colonies was recorded over the course of the day at all three depths, X^2 (7, n = 80) = 62.96; 55.48; 37.44 p < 0.001 (Kruskal-Wallis for surface, mid and bottom respectively). All differences were found to be significant for the surface samples (Games-Howell post hoc), with the exception of: midnight and midday; 3 am and 6 pm; 6 am and 9 am; 6 am and 3 pm; 6 am and 9 pm and finally 9 am and 3 pm. All other differences were significant at p < 0.01. Post hoc tests for the 25 cm and 50 cm depths revealed less significant differences, outlined in Table 3.14.
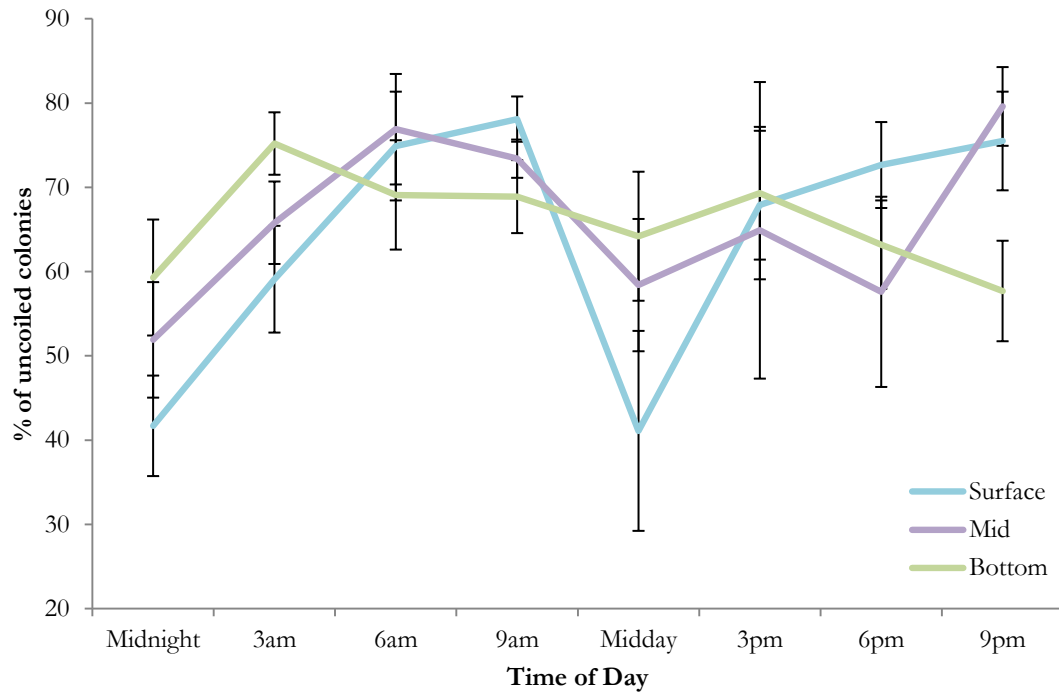
Figure 3.20: The percentage of uncoiled *A. fusiformis* colonies present at the surface, 25 cm depth and 50 cm depth over the 24 hours at Lake Bogoria

Table 3.14: Games-Howell post hoc tests for difference in percentage of uncoiled colonies of *Arthrospira fusiformis*; significant results indicated by asterisks

		Midnight	3 am	6 am	9 am	Midday	3 pm	6 pm	9 pm
Midnight	Mid		-13.9**	-25.0***	-21.5***	-6.5	-13.0	-5.7	-27.7***
	Bottom		-15.9***	-9.8	-9.6*	-4.9	-10.0	-3.9	1.6
3 am	Mid			-11.1**	-7.6*	7.4	0.9	8.2	-13.8***
	Bottom			6.1	6.3*	11.0*	5.9	12.0***	17.5***
6 am	Mid				3.5	18.5***	12.0	19.3**	-2.7
	Bottom				0.2	4.9	-0.2	5.9	11.4*
9 am	Mid					15.0**	8.5	15.8*	-6.2**
	Bottom					4.7	-0.4	5.7	11.2**
Midday	Mid						-6.5	0.8	-21.2***
	Bottom						-5.1	1.0	6.5
3 pm	Mid							7.3	-14.7
	Bottom							6.1	11.6*
6 pm	Mid								-22.0**
	Bottom								5.5
9 pm	Mid								
	Bottom								
***p < 0.001; **p < 0.01; *p < 0.05									

3.3.8 Lesser flamingo numbers and lake biomass

The largest population of lesser flamingos on a single lake, during this study, was 975,000 at Bogoria in August 2013, corresponding with the lowest biomass recorded,

53.45 mg L^{-1}. The lowest population was 358 at Elementaita in August 2011 when the average biomass recorded was 47.92 mg L^{-1} (Table 3.15). No statistically significant correlation was found between the number of lesser flamingos present on a lake and the average biomass for the lake at that time (r = 0.003, p > 0.05).

There is an indication that lower biomass was associated with lower lesser flamingo populations within the diatom-dominated lakes, Natron and Elementaita, as increasing biomass at both lakes correlated with an increasing population.

No pattern was observed between number of flamingos and biomass; at lakes Bogoria and Oloidien, both lakes supported their largest flock at times when biomass was very low and high biomass did not correspond with increasing numbers. However, the biomass at Lake Nakuru decreased notably between 2009 and 2011, which did correspond with a large reduction in the number of flamingos.

Table: 3.15: The average biomass of each lake at different times and the average population size of lesser flamingos on the lake at the same time

Lake	Month & Year	Average biomass mg L^{-1}	Lesser flamingo population	Estimate by
Bogoria	August 2009	334.40	480,150	This study
	August 2010	208.17	918,500	This study
	August 2011	196.68	220,000	This study
	April 2012	276.91	390,500	This study
	August 2012	121.86	228,200	This study
	April 2013	73.04	512,500	This study
	August 2013	54.35	975,000	This study
Oloidien	September 2009	801.58	12,950	This study
	August 2010	255.32	5,100	This study
	April 2011	189.33	6,800	This study
	August 2011	146.53	21,300	This study
	April 2012	47.74	400,000	This study
	August 2012	51.08	3,000	This study
Elementaita	August 2009	142.01	6,325	NMK July 2009
	August 2011	47.92	358	This study
Nakuru	August 2009	170.54	255,294	NMK July 2009
	August 2012	48.90	2,500	This study
Sonachi	September 2009	122.36	2,680	This study
Natron Marsh	December 2009	76.07	5,400	This study
Natron Lagoon	December 2009	90.70	6,050	This study
Natron North	April 2011	127.26	12,800	This study

3.4   Discussion

The lakes studied showed considerable variation in both taxonomic community composition and average biomass. Three primary producer categories had earlier been identified (Tuite, 1981) and these can be classified by the dominant photosynthesizes. Firstly, "*Arthrospira fusiformis* dominated phytoplankton"; secondly, single celled cyanobacteria such as *Synechococcus* sp., and thirdly benthic / epipelic diatoms. This study indicates that the second category would be better described as "other filamentous cyanobacteria" as the lakes can be dominated by *Anabaena* sp. or *A. fusiformis var minor*, whilst single-celled cyanobacteria are often present alongside diatoms. The results of this study suggest that Lake Bogoria and Lake Sonachi fall into the first classification categorised by high biomass of *A. fusiformis*, often appearing as a monoculture of the planktonic waters. Lake Sonachi also had a very high abundance of epipelic diatoms in 2009; potentially due to the preceding falling lake levels, which resulted in large exposed areas of mud, covered by a thin layer of water (1 – 2 cm) which allowed a film of diatoms to grow, creating a second food resource at the lake to accompany the planktonic *A. fusiformis*. Lake Oloidien and Lake Nakuru fell into the second classification where the planktonic community was dominated by other cyanobacteria that form an adequate food source for lesser flamingos. The third category was comprised of lakes Natron and Elementaita, whereby benthic diatoms dominate and the phytoplankton is scarce but made up of single celled species, such as *Synecochoccus*, when present.

These classifications for alkaline-saline lakes are a useful way of categorising lake communities but cannot define each lake individually, as there is evidence to suggest that shallow soda lakes transition between the states. Lake Nakuru has been widely studied since the 1970s when it was dominated by *A. fusiformis*. In 2009 other cyanobacteria such as *Anabaenopsis magna, Anabaenopsis abijatae, Anabaena arnoldii* and epipelic diatoms dominated and in 2012, the lake was primarily dominated by single-celled cyanobacteria with epipelic diatoms in the shallower parts and at the lakes edge. This transitioning between states is not unique to Nakuru, Lake Elementaita has also had periods where it was dominated by *A. fusiformis* or other multicellular cyanobacteria, however, it was diatom, *Synechococcus* sp. and *Croococcus* sp. dominated when I last visited in August 2012. This suggests that changes in lake level and the

chemical parameters of shallow soda lakes have a significant impact on the phytoplankton community.

Lake Bogoria is often reported to be more chemically stable than shallow alkaline-saline lakes as it is deep and therefore protected from large, short-term fluctuations in lake water chemistry. The main chemical parameters at Lake Bogoria differed dramatically in 2013 from the initial findings in 2009, after a prolonged period of freshwater inflow. All three basins of the lake displayed similar oxygen, temperature and conductivity depth profiles in 2009, but this was not the case in 2013, when significant differences were observed between the three basins. The abundant influx of freshwater had dramatic effects on the conductivity, in all three basins between the surface and 3 m depth, conductivity measurements were all below 40 mS cm^{-1}, the value often given as the lowest recorded at Lake Bogoria in published literature (Harper *et al.*, 2003). The decrease in conductance did not have dramatic effects on the pH but appears to have destabilised the lake environment, leading to changes in food abundance (Arengo & Baldassarre, 1999; Odour & Schagerl, 2007a; Hill *et al.*, 2013). *A. fusiformis* is able to tolerate a wide range of conductivities as it is found in hypersaline environments where the conductivity exceeds 160,000 uS cm^{-1} as well as those where the conductivity is 6,000 uS cm^{-1} (Fužana *et al*, 2010), however, abundance has been positively correlated with conductivity (Krienitz & Kotut, 2010; Hill *et al.*, 2013) and this is a plausible reason for the observed declines in biomass. The oxycline shifted down two meters and surface oxygen in 2013 was much lower than at 5 cm below the surface. The large inflows of freshwater contained sediment, potentially accounting for reduced surface oxygen and causing light attenuation, which again could account for biomass reduction, as *A. fusiformis* needs light to photosynthesise and would have been shielded.

Daily fluctuations in the vertical distribution of *A. fusiformis* have been reported (Melack, 1979), however, this is the first study to systematically assess the percentage of S-type and H-type trichomes (Jeeji Bai & Seshardi, 1980; Hindák, 1985) at different depths of the water column over 24 hours. Previous studies have shown that S-type trichomes predominate in low light conditions whilst H-types predominate in high light conditions (Jeeji Bai & Seshardi, 1980). This study found that the surface samples contained 40% S-type trichomes at both midnight and midday, rising to 75% between

these times with a small drop to 50% at 6pm. The was a negligible change in overall surface phytoplankton biomass over the 24 hours indicating that the changes must be due to migration through the water column. No substantial evidence was found of S-types predominating at deeper depths where light intensity was lower, rather that migration appears to be cyclical over a 12-hour cycle. S-types do seem to avoid the surface at midday when light intensity is strongest, with H-types dominating the surface samples at midday. However, as the same pattern is seen at midnight, suggesting other factors may also be involved in vertical migration.

Lake Oloidien has only been utilised by lesser flamingos as a feeding lake since 2006 (David Harper, pers comm.) and in 2009 both *A. fusiformis* and *A. fusiformis var minor* were present, however, since 2010 there has been almost monospecific dominance of *A. fusiformis var minor*. *Arthrospira fusiformis var minor* is substantially smaller than *A. fusiformis* yet still filterable and whilst previously uncommon, it had been recorded in Nakuru (Vareschi, 1978) and the final sewage pond in Nakuru Town (Krienitz & Kotut, 2010); this smaller ecotype is now abundant and exploited as an important food resource (ibid). Over 500,000 lesser flamingos were present at Lake Oloidien in March 2012, (Timothy Mwinami, pers comm.), the largest flock observed at the Lake since 2006. 100,000 had left by April, and the biomass recorded was very low. On April 9th 2012, I observed a mucilaginous, diatomatous scum present at the edge of Lake Oloidien, by the public jetty. Beneath this scum there was no *A. fusiformis var minor* and although by August 2012 the scum was gone, biomass remained low and the number of lesser flamingos on the lake was 3,000. I suggest that this phenomenon may have been caused by the increasing water levels (dulcification) having a detrimental effect on the lake chemistry and subsequent phytoplankton.

The presence of rotifers and protozoans at each of the lakes varied; very few were found at those dominated by diatoms, whilst increasing numbers were identified at Lake Nakuru (in excess of 23 mg L^{-1} for some samples). Rotifer blooms were also found in the South basin of Lake Bogoria (in excess of 20 mg L^{-1}), when cyanobacteria were abundant. The crop samples of 11 freshly deceased flamingos investigated contained both rotifers and protozoans and there was evidence of casings in the faeces. This indicates that such food cannot be excluded from lesser flamingos' diet and when

they are present in high abundances it appears that they form an important part of it, as suggested by Vareschi (1978).

Many published studies often report a single figure for the average biomass of the East African alkaline-saline lakes, frequently based on a series of single surface or subsurface samples that rarely represent the whole area and therefore assume uniformity. This assumption is not a valid one, surface samples alone do not give an accurate insight into the standing crop of either the planktonic or epipelic biomass. This study is the first to document the presence of sedimented *A. fusiformis* at the water / lakebed interface of Lake Bogoria and if only surface or surface and 50 cm depth samples are taken, this highly concentrated cyanobacteria is omitted from the 'average biomass'.

All the lakes that were visited more than once expressed a trend of reducing biomass from 2009 to 2013, with the exception of Lake Natron. This reduction in biomass corresponded with increasing lake levels / surface area across all lakes suggesting that the large influxes of fresh water had a negative impact on the phytoplankton communities. *A. fusiformis* was continuously present at Lake Bogoria, but the inflows of fresh water, carrying a lot of sediment, initially floated above the alkaline-saline waters. This restricted the ability of light to penetrate to the colonies of *A. fusiformis* below, resulting in a dramatic decline in the biomass. Similar reductions in biomass were identified at Lake Oloidien, and in 2012 the aforementioned diatomatous mucilaginous scum could have preceded a reduction in the biomass of *A. fusiformis var minor* from 146.53 mg L^{-1} (in 2011) to 47.74 mg L^{-1}.

Rising lake levels in the diatom dominated lakes, caused a reduction in biomass at Lake Elementaita but an increases at Lake Natron. The reduction at Lake Elementaita was due to depth increase reducing the light penetration into the water, resulting in a smaller area in which diatoms were able to grow. Lake Natron, depth was not altered dramatically but surface area increased from ca. 850 to 1,050 km^2, by the increased freshwater inputs, giving a much larger area in which diatoms were able to grow.

Chlorophyll *a* is often used as an indicator of biomass; however the relationship appears more complex than once thought. At Lake Bogoria, *A. fusiformis* was always present and the main contributor of Chl *a*, but 1 mg L^{-1} of *A. fusiformis* accounted for a

Chl *a* concentration of 11.2, 17 and 6.9 ug L^{-1} in August 2012, April 2013 and August 2013 respectively and a carotenoid concentration of 6.9, 9.6 and 2.9 ug L^{-1} respectively. The differences could be indicative of the health state of cyanobacteria, but this would need to be studied in greater detail to develop a better understanding.

This study found exceptionally high Chl *a* concentration, for some samples at Lake Bogoria; in excess of 25,000 ug L^{-1} for sedimented *A. fusiformis* and the surface algal scums recorded a Chl *a* concentration of ca. 57,000 ug L^{-1}. Recently an algorithm to calculate Chl *a* concentration from satellite images was developed (Tebbs, 2013); however, this focuses on surface phytoplankton and whilst useful for quantifying blooms, the Chl *a* value obtained may not be inclusive of all biomass sources as it would not register the sedimented *A. fusiformis*. The sedimented *A. fusiformis* may not have the same nutritional value as the surface phytoplankton (this would need to be explored further) but it is very densly concentrated. The omission from the satellite algorithm would therefore not accurately represent the food available to lesser flamingos, as they are able to utilise this newly discovered food source (further discussed in Chapter 4).

No correlation between algal biomass and the number of flamingos on a lake at any given time was found. The largest population of lesser flamingos was found on Lake Bogoria in August 2013, consisting of 975,000 birds when the average biomass was at its lowest, 54.35 mg L^{-1}. This finding mirrors that of Vareschi (1978) who also reported a lack of correlation between algal biomass and flamingo numbers; however, it contradicts the findings of Kihwele *et al.* (2014) that found a positive correlation between average *A. fusiformis* biomass and lesser flamingo population at Lake Manyara. It is possible therefore that in some cases there may be a localised positive correlation but there does not appear to be a large-scale correlation across all lakes within the range. The lakes all vary in size and therefore are not all able to support the same proportion of the East African population. In this study, the diatom dominated lakes in did show an increase in population with an increase in biomass, as did Lake Nakuru, however, neither Lake Oloidien nor Bogoria recorded any significant relationship between the biomass available to lesser flamingos and the number present on the lake, although grazing pressure could be a factor. In Lake Nakuru, Vareschi (1978) established that the entire flock of 1 million lesser flamingos would extract ~60 t d^{-1} of

cyanobacteria or 50-90% of the daily production of the lake. This was calculated when phytoplankton biomass was > 200 mg L-1, higher than at most lakes during this study. At lakes where lesser flamingos were present in large numbers but there was comparatively low biomass, strong grazing pressure could be the cause of reduced biomass. An in depth continuous study monitoring lake biomass and flamingo numbers would be needed to gain a greater understanding of any correlation as this would also allow for the inclusion of time delay as a possible factor. The strong grazing pressure could reduce biomass whilst the population was still high and consequently there may be a delay between the apparant low biomass and lesser flamingos leaving a lake.

Overall, this chapter has built on the work of Vareschi (1978) and Tuite (1981), aiming to explore the importance of epipelic / benthic food resources of lesser flamingos as well as explore the variation in alkaline-saline lakes of the East African Rift. This study suggests that diatoms constitute much more than an "emergency food source", forming an integral part of the diet of lesser flamingos. This is especially true at lakes where they dominate and have been present in excess of 125 mg L^{-1}, including Lake Natron, the only known breeding site for this population.

The lake level rise across all the lakes has been detrimental to the phytoplankton communities within the lakes. Very low biomass was recorded at Bogoria in 2013 and I observed on a brief visit to Lake Oloidien in December 2013, 250 exhausted, underweight lesser flamingos frantically feeding and barely registering human presence, allowing people to walk right up to them. Freshly deceased flamingos were appearing daily with some weighing as little as 680 g and completely emaciated. It is likely that the lesser flamingos that died at Lake Oloidien in 2013 were already malnourished upon arrival at the lake and due to the low biomass they were unable to restock their energy reserves and fly on.

This chapter highlights how varied alkaline-saline lake ecosystems are and how small climatic changes can have drastic effects on the biomass of a lake, therefore affecting the suitability of a lake to support lesser flamingos. The planktonic and epipelic standing crops vary between and within lakes. Lake Bogoria has a relatively large surface area and the average biomass varies considerably between the three basins.

Lake Oloidien is much smaller but also showed substantial spatial variation. Differences in biomass were not found solely within the surface samples, Lake Bogoria is unique in that it has extensive aggregations of sedimented *A. fusiformis* above the lakebed. These aggregations are not uniform in distribution or abundance, they vary dramatically and seem to be greatest in areas where large flocks of lesser flamingos are found within the lake, suggesting that they may be adapting to utilise this food source (discussed further in Chapter 4).

Chapter 4

Chapter 4 Covariance between feeding behaviour and food availability in lesser flamingos (*Phoeniconaias minor*)

Abstract

Birds are well known for adapting their behaviour in response to food availability. An understanding of the relationship between food availability and foraging behaviour can illustrate the dominant food source available to lesser flamingos (*Phoeniconaias minor*) at each lake, give an indication of resource abundance and also suggest how the resource is distributed. In this study, lesser flamingos were found to exhibit 10 individual feeding behaviours, all of which were recorded at Lake Bogoria; eight were recorded at both lakes Nakuru and Oloidien; four at Sonachi and three at both Natron and Elementaita. The dominant feeding behaviour changed throughout the day at lakes Nakuru and Bogoria but at the other four lakes the dominant feeding behaviour remained consistant. Two deep water feeding behaviours common in greater flamingos (*Phoenicopterus roseus*) were recorded in the lesser flamingo and were occurring with greater frequency than has been previously detailed. Feeding behaviours varied within and between lakes and at Lake Bogoria a positive correlation was identified between the biomass accessible through different feeding behaviours and the percentage of birds utilising those feeding behaviours (*rho* = 0.542; p < 0.001).

4.1   Introduction

Animals characteristically select food sources and engage foraging behaviours that maximise their intake of energy (Pyke, 1984; Stephens & Krebs, 1986). The acquisition of nutrition and energy often has a direct effect on breeding success and individual survival rate (Lemon, 1991); therefore foraging behaviours are often modified with varying food availability. Individuals are able to intensify their feeding effort in times of food scarcity to ensure sufficient energy is obtained (Hutto, 1990; Cope, 2003) and as a result understanding the relationship between foraging behaviours and food availability can give an indication of the ecosystem status (Hutto, 1990).

Maximising foraging effort can be measured by quantifying the time spent feeding as many species spend longer feeding when there is a reduction in food availability (Hill & Ellis, 1984; Percival & Evans, 1997) (discussed further in Chapter 5). In some species

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the foraging behaviours themselves are adjusted, irrespective of time spent feeding, when their food supply is variable. Dabbling ducks were found to increase their rate of surface feeding of they would swin faster in order to encounter more food (McKnight, 1998) whilst diving ducks alter their dive duration in response to availability of prey (Tome, 1988).

Few studies have discussed feeding behaviour directly in relation to lesser flamingos; however, feeding behaviour has been more widely studied in South and Central American species such as Caribbean flamingos (*Phoenicopterus ruber*), James' flamingos (*Phoenicoparrus jamesi*) and Andean flamingos (*Phoenicoparrus andinus*). James' flamingos use their bill to stir up the sediment at the bottom of the lake and feed on the diatoms that become suspended in the water (Mascitti, 1998). They have a fixed preference for larger diatoms and shallow water microhabitats, which allow the nares to be kept above the water's surface (ibid.). Small diatoms were the most profuse in this habitat, however, a proportionally higher abundance of large diatoms (21 – 60 μm) was found in the gizzards, suggesting either selective feeding or that the smaller diatoms are more likely to escape the bill during the filtering process (Zweers *et al.*, 1995).

Mixed and single-species flocks of Chilean (*Phoenicopterus chilensis*), Andean and James' flamingos were studied in Argentina to investigate foraging depth and feeding behaviour, attributing the differences to variances in their diets (Hurlbert, 1982; Mascitti & Castañera, 2006). Chilean flamingos tended to feed in deeper water, either at the benthic interface or from the lake surface when an abundance of microzooplankton was present (Mascitti & Castañera, 2006). The Andean flamingos were most flexible, they would always feed from the water-sediment interface, but would either feed in the shallows or the deep water dependent on whether there were more James' or Chilean flamingos in the flock (ibid.).

Wet mud feeding, stand filter feeding and swim feeding have been widely reported in lesser flamingos, although the full range of behaviours has not been intensively studied until now. Deep water feeding has been mentioned (Brown, 1975; Tuite, 2000) but never quantified, although it is common in the three shallow keeled flamingo species, with both types of deep water feeding being consistently demonstrated by the sympatric greater flamingo (Jenkin, 1957; Espino-Barros & Baldassarre, 1989).

This chapter aims to assess the feeding behavioural repertoire of lesser flamingos; explore when and where they engage in different behaviours and investigate the spatial variability of *A. fusiformis* and other food resources to study whether this has an effect on the foraging behaviour. Finally it will consider whether lesser flamingos are able to assess the quality and quantity of available food and therefore whether they selectively feed in order to maximise their feeding efficiency.

By answering the following questions:

- Do lesser flamingos have a more diverse repertoire of feeding behaviours than widely reported?
- Are different feeding behaviours occurring at different times of day?
  o Is there a difference in feeding behaviour between night and day?
- Do feeding behaviours vary between / within lakes?
- Do lesser flamingos adjust their feeding behaviours depending on the type of food available?
- Do lesser flamingos adjust their feeding behaviours in response to food abundance and distribution?

The following null hypotheses are tested:

- Lesser flamingos have only three feeding behaviours
- Feeding behaviours occur equally at all times of day
  o Feeding behaviours are the same during the night and day
- Feeding behaviours occur equally within lakes
- Lesser flamingo feeding behaviour is independent of the type of food available
- Lesser flamingo feeding behaviour is independent of food abundance and distribution

4.2   Methods and study sites

This study incorporates behavioural observations with cyanobacteria, diatom and zooplankton calculations from August 2009 to August 2013 primarily at lakes Bogoria and Oloidien with initial studies also carried out at lakes Elementaita, Sonachi, Nakuru
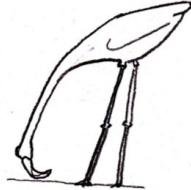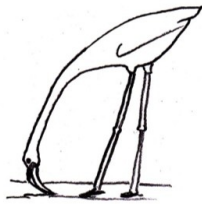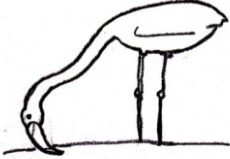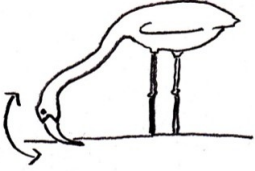
and Natron in the Gregory arm of the Rift Valley. Full descriptions of methods and study sites are contained in Chapter 2.
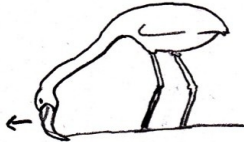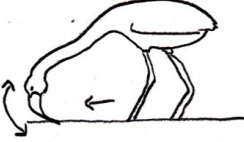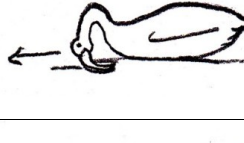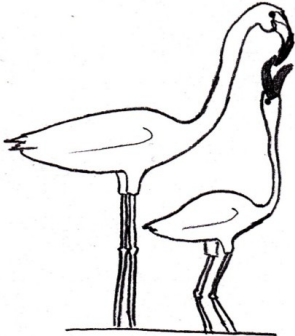
4.3 Results

4.3.1 Feeding behaviours

Ten individual feeding behaviours (Table 4.1) were recorded across the six lakes; all 10 were identified at Lake Bogoria, eight at both Lake Oloidien and Lake Nakuru, four at Lake Sonachi and three at lakes Natron and Elementaita. Crop feeding was seen at both Oloidien and Natron, however it is omitted from this chapter, as it is not an individual feeding behaviour.

Table 4.1: Detailed descriptions of lesser flamingo feeding behaviours

Type of Feeding	Description	Sketch
Wet Mud Feeding (WMF)	Bill held parallel to the wet mud, skimming the surface	
Shallow Water Mud Feeding (SWMF)	Bill held parallel to the wet mud, submerged in a few centimetres of water, skimming the surface	
Stand Filter Feed 1 (STF1)	Bill held parallel to and just below the water's surface, sieving algae from the top few centimetres of the water column	
Stand Filter Feed 2 (STF2)	As STF1 but whilst swinging the head from side to side	

Walk Filter Feed 1 (WF1)	As STF1 but whilst walking forwards	
Walk Filter Feed 2 (WF2)	As STF2 but whilst walking forwards	
Swim Filter Feed 1 (SW1)	Swimming on open lake, scything head from side to side to filter food from top five cm	
Swim Filter Feed 2 (SW2)	Swimming on open lake in a straight line, often following scum or bubble lines	
Deep Water Feed	Whole head and neck submerged, feeding on epipelic mud community or sedimented algae at the bottom of the water column	
Deep Water Kick Feed	Whole head, neck and half of body submerged, legs visibly kicking to enable feeding on epipelic mud community or sedimented algae at the bottom of the water column.	
Crop Feed	Adult flamingos regurgitating crop milk into the mouths of juveniles	

4.3.1.1 Lake Bogoria

At Lake Bogoria, the two dominant feeding behaviours were STF1 and SW1, which were both utilised by 13.25% of the lesser flamingos on the lake over 24 hours,

followed by DWF utilised by 6.47%. DWKF was exhibited least often, being utilised by 0.53% over 24-hour period, on average (Figure 4.1). There was significant disparity between the number of lesser flamingos engaged in each of the feeding behaviours (Kruskal-Wallis), X^2 (9, n = 6,850) = 1,286.62, p < 0.001; only two behaviours (STF1 and SW1) were engaged in for over 10% of the day and four were utilised for less than 2%, or under half an hour (DWKF, SWMF, WMF and WF2). Games-Howell tests, the results are displayed in Table 4.2.

Figure 4.1: The average proportion of birds exhibiting each feeding behaviour at Lake Bogoria at any given time; error bars ± 1 standard deviation

Table 4.2: Games-Howell post hoc test results for the difference in number of flamingos engaged in different feeding behaviours at Lake Bogoria; statistically significant results identified by asterisks

	WMF	DWF	STF1	STF2	SW1	SW2	DWKF	SWMF	WF1	WF2
WMF		-4.4**	-11.6**	-2.8**	-11.6**	-2.8**	1.1**	0.5	-0.8*	0.1
DWF			-7.2**	1.6*	-7.2**	1.6*	5.5**	4.9**	3.6**	4.5**
STF1				8.9**	0	8.9**	12.7**	12.1**	10.8**	11.7**
STF2					-8.9**	0	3.8**	3.2**	1.9**	2.9**
SW1						8.9**	12.7**	12.1**	10.8**	11.7**
SW2							3.8**	3.2**	1.9**	2.9**
DWKF								-0.6*	-1.9**	-1.0**
SWMF									-1.3**	-0.4
WF1										0.9*
WF2										
**p < 0.001; *p < 0.01										

A principal component analysis (PCA) with a Varimax (Orthoganal) rotation of all 10 feeding behaviours was conducted on all observations. An examination of the Kaiser-

Meyer-Olkin measure of sampling adequacy suggested that the data were factorable (KMO = 0.644).

The majority of the variability (53.5%) is explained by 4 components (Table 4.3). The most common behaviours in Factor 1 are SW1 and STF1, but the two behaviours are negatively correlated which suggests that either swim feeding whilst swinging their heads from side to side or stationary stand filter feeding dominates at any given time, they are unlikely to occur simultaneously in high abundance. The strong correlation between STF1 and STF2 suggests an ability to swap between the two behaviours. This is also seen in the correlation between SW1 and SW2 suggesting that lesser flamingos are able to interchange between swim feeding behaviours. Therefore, Factor 1 identifies two groups of behaviours which can both dominate but are unlikely to occur at the same time with SW1 and STF1 being the dominate behaviours of the two groups, although always feeding in the top few centimetres of the water column.

Factor 2 identifies a positive correlation between SWMF and WMF, which indicates that lesser flamingos can swap between feeding on the exposed wet mud or the wet mud in the shallows. The two behaviours are likely to occur simultaneously where there is an abundance of diatoms or sedimented *A. fusiformis* on the wet mud.

Factor 3 identifies a strong positive correlation between DWKF and DWF whereby feeding is occurring on food resources at the bottom of the water column but in deep water. These behaviours appear to be interchangeable and are likely to occur concurrently as lesser flamingos are utilising concentrations of sedimented *A. fusiformis* above the lakebed. There is also a weak correlation with WF2 as when there is abundant sedimented *A. fusiformis,* there is often lower concentrations at the surface so lesser flamingos walk whilst swinging their heads from side to side in a scything motion to increase the surface area they cover and therefore their foraging rate at lower density.

Factor 4 detects a positive correlation between WF1 and WF2, indicating an ability to swap between the behaviours when necessary. Both WF1 and WF2 involve feeding on the top few centimetres of the water column whilst moving, suggesting they may be need to cover a large surface area.

Table 4.3: Obliquely rotated component loadings for the 10 feeding behaviours (loadings ≥ 0.3). The highest loading for each of the behaviours is highlighted, showing the strongest correlations

	Component			
	1	2	3	4
SW1	-.745			
STF1	.609			
STF2	.570			
SW2	-.504			.394
SWMF		.808		
WMF		.658		
DWKF			.732	
DWF			.706	
WF1				.756
WF2			.310	.574

4.3.1.2 Lake Oloidien

Lake Oloidien had one dominant feeding behaviour, STF1, which was utilised by 30.10% of the flock at any given time amounting to about seven hours for each bird. All of the remaining feeding behaviours were engaged in by less than 10% at any given time (Figure 4.2) and WF2 was the least common (1.34% or 20 minutes per bird). The number of lesser flamingos engaged in STF1 was significantly higher than the other seven feeding behaviours, X^2 (7, n = 3,168) = 1,143.72, p < 0.001 (Kruskal-Wallis). Games-Howell test results are displayed in Table 4.4.
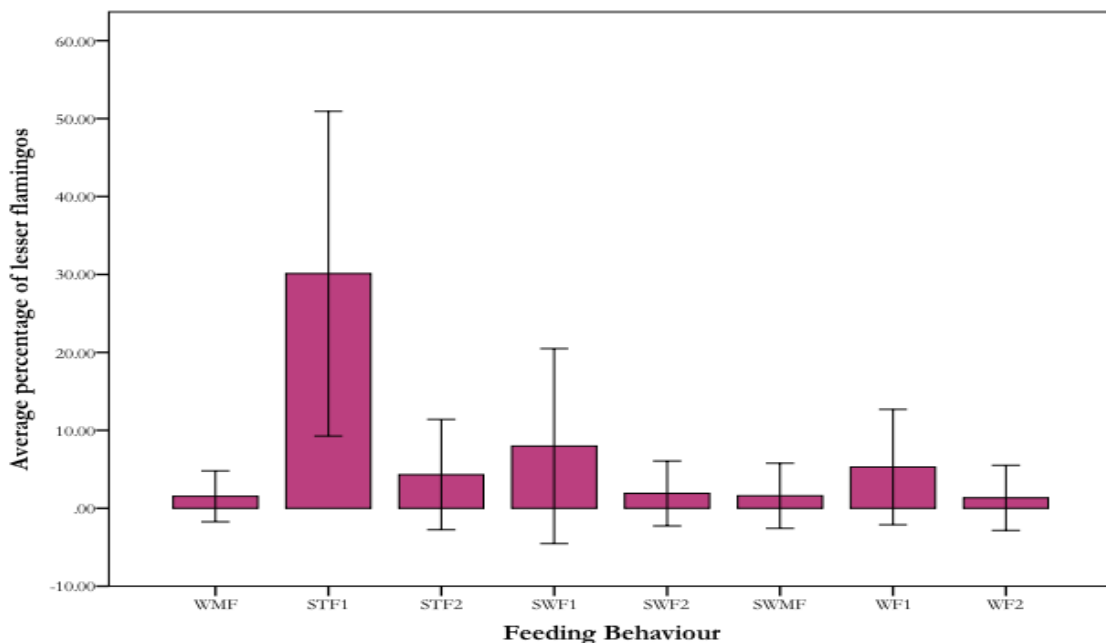
Figure 4.2: The average proportion of birds exhibiting each feeding behaviour at Lake Oloidien at any given time; error bars ± 1 standard deviation

Table 4.4: Games-Howell post hoc test results for the difference in number of flamingos engaged in different feeding behaviours at Lake Oloidien; statistically significant results identified by asterisks

	WMF	STF1	STF2	SW1	SW2	SWMF	WF1	WF2
WMF		-28.56**	-2.78**	-6.44**	-0.36	-0.07	-3.74**	0.21
STF1			25.78**	22.12**	28.20**	28.49**	24.81**	28.76**
STF2				-3.66**	2.42**	2.71**	-0.96	2.99**
SW1					6.08**	6.37**	2.70*	6.65**
SW2						0.29	-3.38**	0.57
SWMF							-3.67**	0.27
WF1								3.95**
WF2								
**p < 0.001; *p < 0.01								

A principal component analysis (PCA) with a Varimax (Orthoganal) rotation of all eight feeding behaviours was conducted on all observations. An examination of the Kaiser-Meyer-Olkin measure of sampling adequacy suggested that the data were factorable (KMO = 0.607).

The majority of the variability (51.7%) is explained by 3 components (Table 4.5). The most common behaviours in Factor 1 are SWMF and STF1, but the two behaviours are negatively correlated which suggests that either shallow water mud feeding or stand filter feeding, whilst keeping the head relatively still, occur at any given time, they are unlikely to happen simultaneously in high abundance. The strong correlation between SWMF, STF2 and WF2 suggests an ability to swap between the three behaviours when required. The interchange between STF2 and WF2 indicates that lesser flamingos can switch between stationary and moving whilst swinging their heads from side to side in a sweeping motion and as this could indicate low food abundance at the surface they can switch to feeding on the surface of the mud if providing a richer food source.

Factor 2 indicates a strong negative correlation between SW1 and WF1 suggesting that either can dominate but they are not likely to occur in large numbers at the same time. There is a positive correlation between STF2 and WF2, again indicating and ability to switch between stationary and moving as seen in Factor 1. WF2 is negatively correlated with SW1 suggesting that they are unlikely to occur simultaneously.

Factor 3 identifies a strong positive correlation between SW2 and WMF suggesting that when SW2 dominates, WMF is likely to be occurring concurrently. SW2 was occurring when flamingos were swimming in and out from the lake shoreline and could indicate reduced quantity of surface food, therefore other birds could be utilising

a secondary resource simultaneously. Both SW2 and WMF are weakly negatively correlated with SW1 indicating that they are unlikely to occur at the same time in high abundance.

Table 4.5: Obliquely rotated component loadings for the eight feeding behaviours (loadings ≥ 0.3). The highest loading for each of the behaviours is highlighted, indicating the strongest correlations

	Component		
	1	2	3
SWMF	.712		
STF1	-.674		
STF2	.620	.483	
WF2	.520		
SW1		-.659	-.386
WF1		.670	
SW2			.794
WMF			.507

4.3.1.3 Lake Nakuru

Five feeding behaviours were being utilised by more than 10% of the lesser flamingo population at Lake Nakuru (amounting to over 2 and a half hours for each behaviour), significantly more than the remaining three which were utilised by less than 5% at any given time (Figure 4.3), X^2 (7, n = 656) = 202.47, p < 0.001 (Kruskal-Wallis). SW1 was the most common feeding behaviour (14.94%), followed by WMF (13.80%) and STF2 was the least common feeding behaviour (2.26%). Games-Howell test results are displayed in Table 4.6.
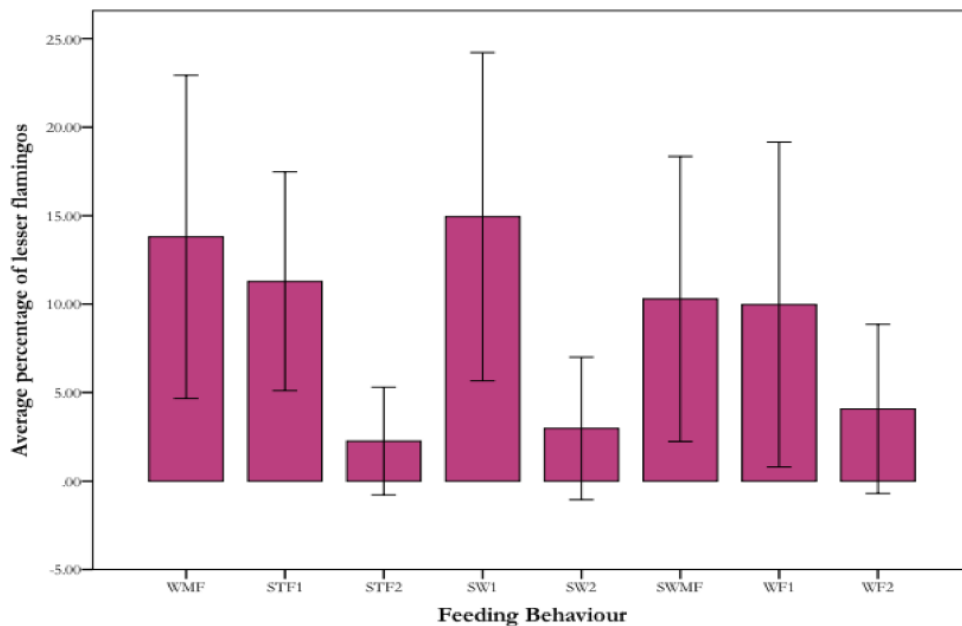
Figure 4.3: The average proportion of birds exhibiting each feeding behaviour at Lake Nakuru at any given time; error bars ± 1 standard deviation

Table 4.6: Games-Howell post hoc test results for the difference in number of flamingos engaged in different feeding behaviours at Lake Nakuru; statistically significant results identified by asterisks

	WMF	STF1	STF2	SW1	SW2	SWMF	WF1	WF2
WMF		2.52	11.54**	-1.14	10.83**	3.51	3.83	9.73**
STF1			9.03**	-3.65	8.31**	0.99	1.31	7.22**
STF2				-12.68**	-0.72	-8.03**	-7.71**	-1.81
SW1					11.96**	4.65*	4.97*	10.87**
SW2						-7.32**	-7.00**	-1.09
SWMF							0.32	6.22**
WF1								5.90**
WF2								
**p < 0.001; *p < 0.01								

A principal component analysis (PCA) with a Varimax (Orthoganal) rotation of all eight feeding behaviours was conducted on all observations. An examination of the Kaiser-Meyer-Olkin measure of sampling adequacy suggested that the data were factorable (KMO = 0.606).

The majority of the variability (64.75%) is explained by 3 components (Table 4.7). The most common behaviours in Factor 1 are WF1 and SW1, which are strongly negatively, correlated indicating that one or other is likely to dominate, rarely occurring in high abundance at the same time. There is a positive correlation between SW1, WMF, ST2 and to a lesser extent, STF1 suggesting they all occur simultaneously, with the latter being least abundant.

Factor 2 indicates a strong correlation between SWMF and SW2 implying that when there is a high abundance of lesser flamingos swim feeding on the open lake in straight lines, with little head movement, there is likely to be shallow water mud feeding occurring concurrently.

The most common feeding behaviour in factor 3 is STF1, suggesting that it dominates at times. It is weakly correlated with STF2 and WF2 indicating that STF1 will be accompanied by both behaviours. There is a weak negative correlation with SW1 and WMF, which implies that when STF1 dominates, it is unlikely that there will be high abundance of either behaviour.

Table 4.7: Obliquely rotated component loadings for the eight feeding behaviours (loadings ≥ 0.3). The highest loading for each of the behaviours is highlighted, indicating the strongest correlations

	Component		
	1	2	3
WF1	-.739		
SW1	.646	.491	-.337
WMF	.620		-.332
STF2	.572	-.382	.480
WF2	-.543		.485
SWMF		.789	
SW2		.653	
STF1	.454		.667

4.3.1.4 Lake Sonachi

Four feeding behaviours were observed at Lake Sonachi in 2009, significantly more birds were utilising SW1 than any of the other three behaviours, X^2 (3, n = 164) = 74.73, p < 0.001(Kruskal-Wallis; Figure 4.4). SW1 was utilised by 39.20% of lesser flamingos at any given time and the next most popular behaviour was SWMF (18.38%) less than half those engaged in SW1. SW2 was the least common at 5.64%. Games-Howell post hoc tests revealed statistically significant differences between all pairs of behaviours at p < 0.001, with the exception of STF1 and SW2, which was not significant.
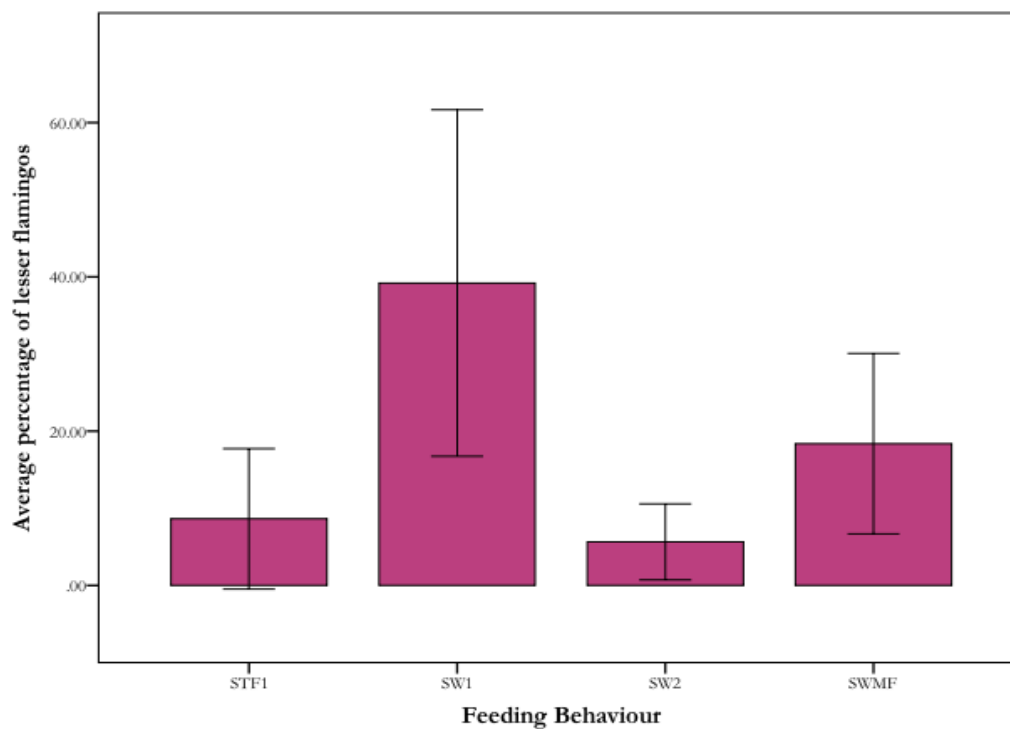
Figure 4.4: The average proportion of birds exhibiting each feeding behaviour at Lake Sonachi at any given time; error bars ± 1 standard deviation

A principal component analysis (PCA) with a Varimax (Orthoganal) rotation of the four feeding behaviours was conducted on all observations. An examination of the Kaiser-Meyer-Olkin measure of sampling adequacy suggested that the data were factorable (KMO = 0.762).

A single component explains the majority of the variability (60.54%), indicating a positive correlation between SWMF and STF1, both of which are neagatively correlated with SW1 and SW2. This suggests that both swim feeding behaviours occur simultaneously and when swim feeding dominates, minimal other feeding will be occurring. When SWMF dominates, it is likely to be accompanied by STF1 whilst minimal swim feeding will be occurring.

4.3.1.5 Lake Natron

Significantly more lesser flamingos were utilising SWMF than either DWF or WMF at Lake Natron, X^2 (2, n = 291) = 194.96, p < 0.001 (Kruskal-Wallis; Figure 4.5). The most common feeding behaviour was SWMF (62.78%) and the least common was WMF (5.19%). Significant differences were identified between SWMF and both WMF and DWF at p < 0.001. No significant difference was found between DWF and WMF (Games-Howell post hoc).
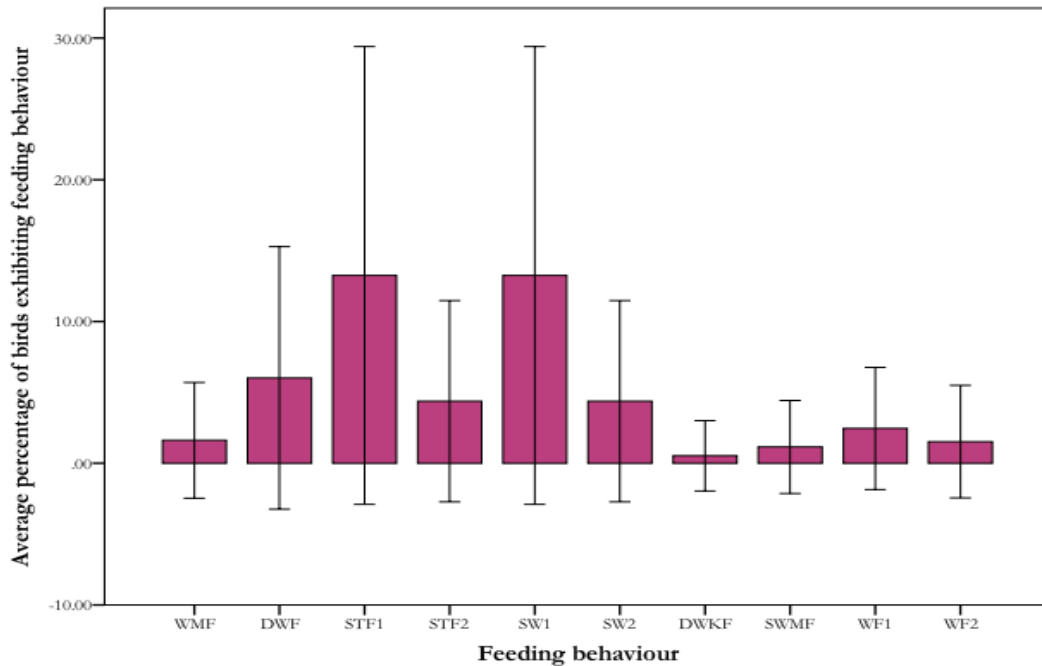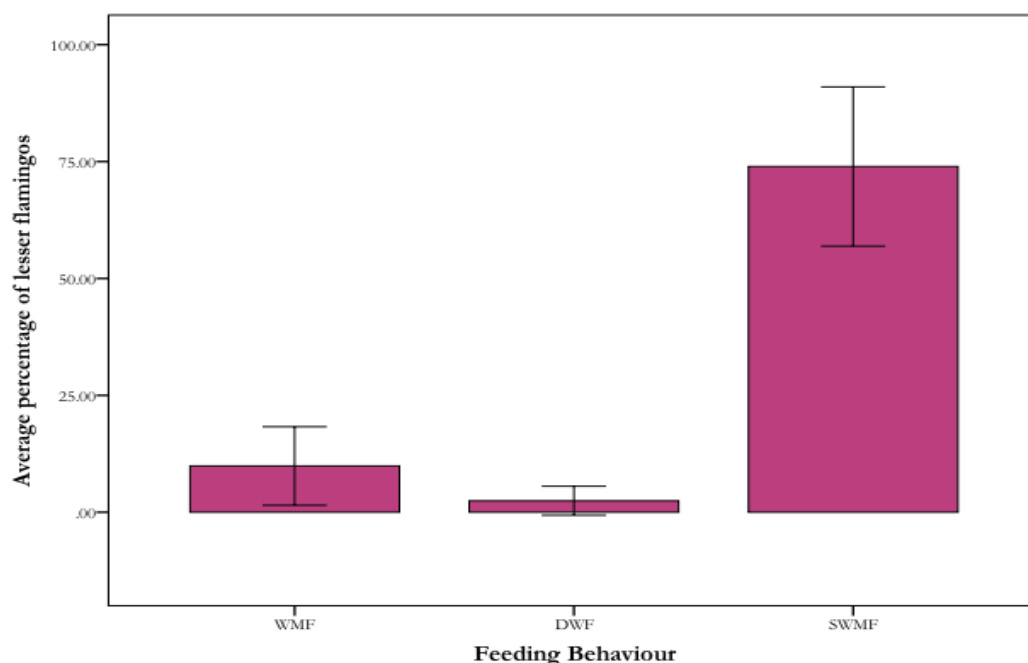

Figure 4.5: The average proportion of birds exhibiting each feeding behaviour at Lake Natron at any given time; error bars ± 1 standard deviation

The data were inputted into a PCA, however an examination of the Kaiser-Meyer-Olkin measure of sampling adequacy suggested that the data were not factorable (KMO = 0.363).

4.3.1.6 Lake Elementaita

Lake Elementaita mirrored the pattern of Lake Natron as significantly more lesser flamingos were engaged in SWMF than either DWF or WMF at Lake Natron, X^2 (2, n = 126) = 94.37, p< 0.001 (Kruskal-Wallis; Figure 4.6). The most common feeding behaviour was SWMF (75.28%) and the least common was WMF (3.49%). Games-Howell post hoc tests revealed significant differences between each pair of variables at p < 0.001.
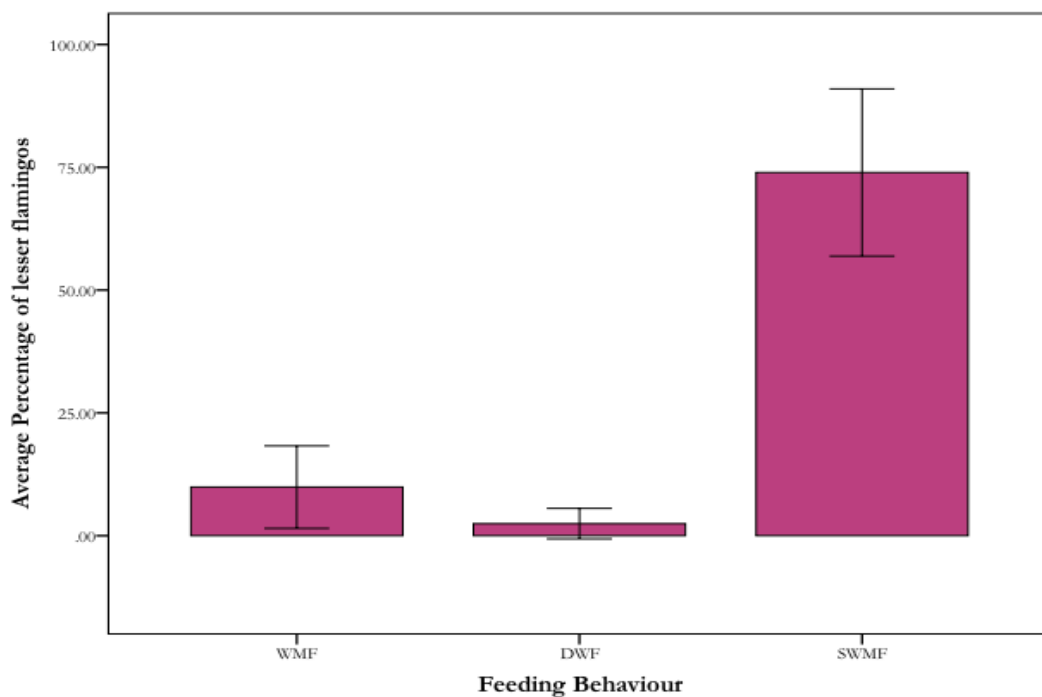
Figure 4.6: The average proportion of birds exhibiting each feeding behaviour at Lake Elementaita at any given time; error bars ± 1 standard deviation

A principal component analysis (PCA) with a Varimax (Orthoganal) rotation of the three feeding behaviours was conducted on all observations. An examination of the Kaiser-Meyer-Olkin measure of sampling adequacy suggested that the data were factorable (KMO = 0.630).

The majority of the variability (75.12%) is explained by a single component identifying WMF and SWMF as negatively correlated, which suggests they are unlikely to both, occur in high abundance simultaneously. DWF is positively correlated with WMF indicating that they are likely to occur at the same time.

4.3.2   Spatial variations in feeding behaviours at Lake Bogoria

In the North basin, STF1 was the dominant feeding behaviour, followed by DWF, SW1 and SW2 and the two least common feeding behaviours were WMF and SWF. This was a different pattern to that observed in the Central basin where SW1 was the most utilised, followed by DWF and the popularity of the remaining behaviours was relatively similar with the exception of DWKF, the least common, utilised by 3.29% of birds on average. The South basin only recorded six feeding behaviours with more than one percent of lesser flamingos engaged in at them any given time. SW1 was most prevalent, utilised by over double the number of lesser flamingos engaged in the second most common behaviour, which was STF1. The proportion of lesser flamingos utilising DWKF, SWMF, WF1 and WF2 was negligible in the South basin.

The average proportion of lesser flamingos engaged in each of the feeding behaviours varied significantly between the three basins of Lake Bogoria in 2009 (Figure 4.7). The Kruskal-Wallis test statistic result, p value and Games-Howell exceptions for each feeding behaviour are displayed in Table 4.8.

Table 4.8: The Kruskal-Wallis test statistic result, p value and Games-Howell exceptions for each feeding behaviour; df = 2 and n = 153

Feeding Behaviour	Kruskal-Wallis test statistic	p value	Games-Howell exceptions (no statistically significant differences)
WMF	7.19	< 0.05	North and South
DWF	8.83	< 0.05	North and Central
STF1	8.87	< 0.05	Central and South
SW1	14.653	< 0.01	Central and South
DWKF	16.209	< 0.001	North and Central
SWMF	25.803	< 0.001	North and Central
WF1	48.231	< 0.001	North and Central
WF2	30.88	< 0.001	North and Central
No significant differences found for STF2 or SW2			
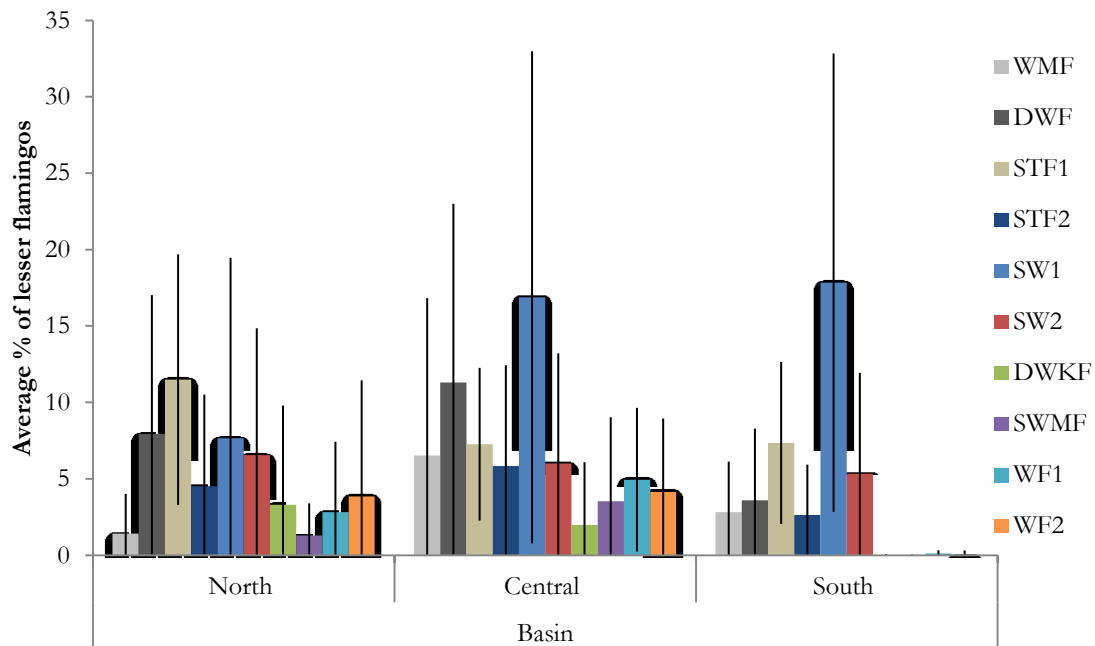
Figure 4.7: Spatial variation in lesser flamingo feeding behaviours at Lake Bogoria in 2009; error bars ± 1 standard deviation

4.3.3   Temporal variations in feeding behaviours

4.3.3.1 Year to year

4.3.3.1.1   Lake Bogoria

In 2009, SW1 was the most common feeding behaviour, followed by STF1, DWF and SW2 and the least common were SWMF and DWKF. In 2010, SW1 remained the most common feeding behaviour, followed by STF1 and SW1; DWF declined but was still the fourth most utilised behaviour. WMF, DWKF and SWMF were rarely used in 2010, with less than 1% of the lesser flamingos on the lake engaged in them at any given time. In 2011, SW1 remained the most common feeding behaviour, increasing in popularity with 28.6% of the flock utilising this behaviour whilst all other behaviours had less than 4%. The pattern completely changed in April 2012 and STF2 was the most popular behaviour, closely followed by STF1 and DWF. SW1 had declined to just 5.3% of the population and all other behaviours were utilised by less than 3% of the birds; DWKF and SWMF were completely absent. SW1 regained popularity in August 2012, sharing dominance with STF1, 12.9% of the lesser flamingos occupying both behaviours, DWKF and SWMF were used again but only by a very small proportion on the population. In 2013, STF2 was dominant again, followed by STF1 and SW2, all

other behaviours were recorded, but utilised by very small proportions of the lesser flamingos present on the lake.

The average proportion of lesser flamingos engaged in each of the feeding behaviours varied significantly between 2009 and 2013 (Figure 4.8a; Table 4.9). The Kruskal-Wallis test statistic result, p value and Games-Howell exceptions for each feeding behaviour are displayed in Table 4.10.

Table 4.9: The average proportion of lesser flamingos engaged in each feeding behaviour, at any give time, during separate study periods

	2009	2010	2011	Apr 2012	Aug 2012	2013
WMF	3.4	0.2	2.5	0.8	2.1	1.1
DWF	7.6	4.1	1.3	11.1	8.3	0.1
STF1	8.7	11.5	3.9	13.1	12.9	10.8
STF2	4.3	2.9	0.4	13.7	4.9	13.7
SW1	14.1	17.1	28.6	5.3	12.9	2.1
SW2	6.0	7.1	3.1	2.6	5.4	9.1
DWKF	1.8	0.1	0	0	0.8	0.04
SWMF	1.6	0.3	0.3	0	1.2	3.8
WF1	2.6	1.8	2.4	1.5	6.3	0.6
WF2	2.7	1.3	0	0.5	3.4	1.2

Table 4.10: The Kruskal-Wallis test statistic result, p value and Games-Howell exceptions for each feeding behaviour; df = 5 and n = 685

Feeding Behaviour	Kruskal-Wallis test statistic	p value	Games-Howell exceptions (no statistically significant differences, p > 0.05)
WMF	86.09	< 0.001	2009 & 2011; 2009 & Aug 2012; 2011 & Aug 2012; 2010 & Apr 2012; 2010 & 2013; Apr 2012 & 2013
DWF	109.71	< 0.001	2009 & Apr 2012; 2009 & Aug 2012; 2011 2013; Apr 2012 & Aug 2012
STF1	71.88	< 0.001	Apr 2012 & Aug 2012; 2009 & 2010; 2009 & 2013; 2010 & April 2012; 2010 & Aug 2012; 2010 & 2013; Apr 2012 & 2013; Aug 2012 & 2013
STF2	139.01	< 0.001	2009 & 2012; 2009 & Aug 2012; 2010 & 2013; Apr 2012 & 2013
SW1	127.39	< 0.001	2009 & 2010; 2009 & Aug 2012; 2010 & Aug 2012; Apr 2012 & 2013
SW2	41.74	< 0.001	2009 & 2010; 2009 & Aug 202; 2010 & Aug 2012; 2011 & Apr 2012
DWKF	54.03	< 0.001	2010 & 2013
SWMF	108.32	< 0.001	2009 & Aug 2012; 2010 & 2011
WF1	119.68	< 0.001	2009 & 2010; 2009 & 2011; 2010 & 2011; 2010 & Apr 2012
WF2	97.06	< 0.001	2010 & 2013; 2009 & Aug 2012

4.3.3.1.2   Lake Oloidien

There was much less variation in the feeding behaviours being utilised at Lake Oloidien than was observed at Lake Bogoria and STF1 was the most dominant feeding behaviour throughout every observation period (ranging from 19.1% of the population at its lowest in 2010 to 45.9% in August 2011). In 2009, SW1 was the second most common feeding behaviour and no walk feeding was observed (either WF1 or WF2); all other feeding behaviours were utilised by less than 4% of the lesser flamingos on the lake. In 2010, STF2 and SW1 were the next most utilised after STF1 (both 6.8%); WF1 and WF2 were observed at Lake Oloidien for the first time in 2010, although only utilised by a small proportion of the population. WF1 was the third most utilised behaviour in Apr 2011, after STF1 and SW1; no shallow water mud feeding was recorded at this time. In August 2011, over 45% of all lesser flamingos were engaged in STF1 and this behaviour accounted for over 90% of feeding during this observation period, all other behaviours were recorded but in negligible amounts. WF1 and SW1 regained popularity in Apr 2012 with over 10% of the flock utilising either one at any given time. STF1 was significantly most dominant again in August 2012, being utilised by nearly five times as many birds as the second most common behaviour, which was SW1.

The average proportion of lesser flamingos engaged in each of the feeding behaviours varied significantly between 2009 and 2012 (Figure 4.8b). The average proportion of lesser flamingos engaged in each feeding behaviour during the study periods is displayed in Table 4.11. The Kruskal-Wallis test statistic result, p value and Games-Howell exceptions for each feeding behaviour are displayed in Table 4.12.

Table 4.11: The average proportion of lesser flamingos engaged in each feeding behaviour, at any give time, during separate study periods

	2009	2010	Apr 11	Aug 11	Apr 2012	Aug 2012
WMF	0.7	2.0	1.1	1.4	1.9	2.0
STF1	30.5	19.1	36.7	45.9	20.1	25.7
STF2	3.8	6.8	4.3	2.0	3.6	5.0
SW1	18.9	6.8	9.7	0.4	10.1	5.6
SW2	1.9	3.3	1.2	0.3	3.4	1.9
SWMF	2.8	4.1	0	0.4	1.7	2.0
WF1	0	3.9	6.7	3.1	10.5	5.2
WF2	0	1.1	0.3	0.1	6.3	1.1

Table 4.12: The Kruskal-Wallis test statistic result, p value and Games-Howell exceptions for each feeding behaviour; df = 5 and n = 396

Feeding Behaviour	Kruskal-Wallis test statistic	p value	Games-Howell exceptions (no statistically significant differences, p > 0.05)
STF1	59.83	< 0.001	2009 & Apr 2011; 2009 & Aug 2012; 2010 & Apr 2012; 2010 & Aug 2012; Apr 2011 & Aug 2011; Apr 2012 and Aug 2012
STF2	25.51	< 0.005	2010 & April 2012
SW1	66.39	< 0.001	2010 & Apr 2011; 2010 & Apr 2012; 2010 & Aug 2012; April 2011 & April 2012; Apr 2011 & Aug 2012; Apr 2012 & Aug 2012
SW2	26.71	< 0.005	2009 & Aug 2012; 2010 & Apr 2012; Apr 2011 & 2009; Apr 2011 & Aug 2012
SWMF	46.44	< 0.001	2009 & Aug 2012; Apr 2012 & Aug 2012
WF1	71.10	< 0.001	2010 & Aug 2011; Apr 2011 & Aug 2012
WF2	73.22	< 0.001	Apr 2011 & Aug 2011; 2010 & Aug 2012
Differences for WMF were not statistically significant			

4.3.3.1.3   Lake Natron

At Lake Natron, DWF was only observed in 2009, however, the observation location in 2011 was at the opposite end of the lake and the lake was no more than 5 cm deep for at least 200 m. WMF occurred in both years although the proportion of birds utilising this behaviour was negligible in comparison to SWMF, which was the most dominant behaviour in both years. The percentage of lesser flamingos utilising SWMF was significantly higher in 2009 than in 2011 (Figure 4.8c), U = 1672.5, z = 1.862, p < 0.001. No other significant differences were found.
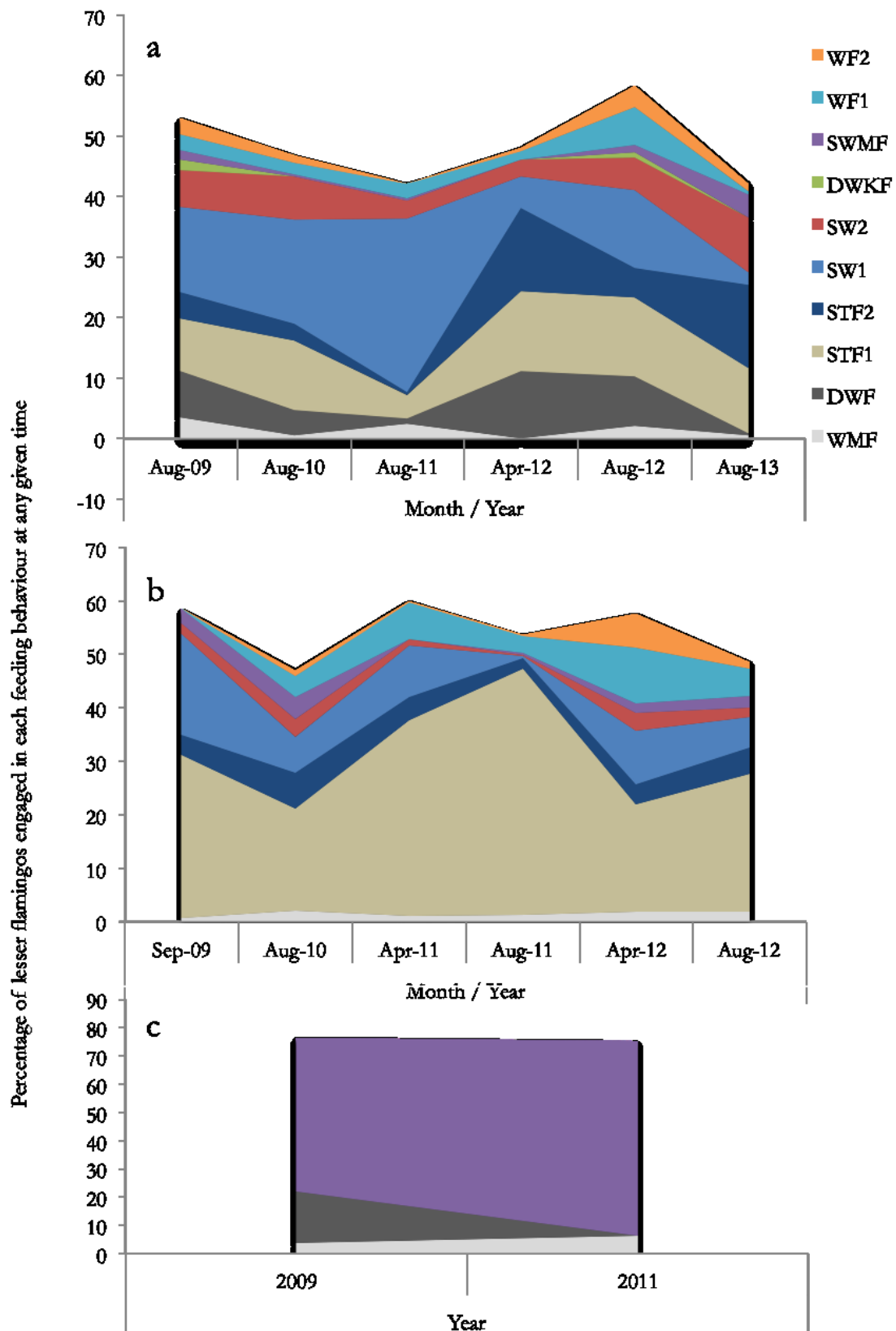
Figure: 4.8: Temporal variation in lesser flamingo feeding behaviours at a) Lake Bogoria between 2009 and 2013; b) Lake Oloidien between 2009 and 2012 and c) Lake Natron between 2009 and 2011

4.3.3.2 Night versus day

4.3.3.2.1   Lake Bogoria

SW1 was the dominant feeding behaviour during the day whilst STF1 was dominant during the night. The proportion of lesser flamingos utilising STF1, STF2 and WF1 increased at night, all other behaviours decreased and DWKF stopped altogether. Five of the 10 feeding behaviours varied significantly between night and day (Figure 4.9; Mann-Whitney U tests), the U, z and p values are displayed in Table 4.13. There was no significant difference identified for STF2, SW1, WF1 or WF2.

Table 4.13: The Mann Whitney U test results for the difference in feeding behaviours between night (1915-0545) and day (0600-1900) at Lake Bogoria; mean and n displayed

Behaviour	*Mean* day	*Mean* night	U	z	p	n
WMF	1.95	0.17	26,779.0	-5.915	<0.001	685
DWF	6.97	1.92	22,257.5	-7.242	<0.001	685
STF1	9.39	14.01	44,165.5	4.113	<0.001	685
SW2	4.95	1.91	30,056.0	-3.159	<0.01	685
SWMF	1.31	0.46	32,666	-2.266	<0.05	685
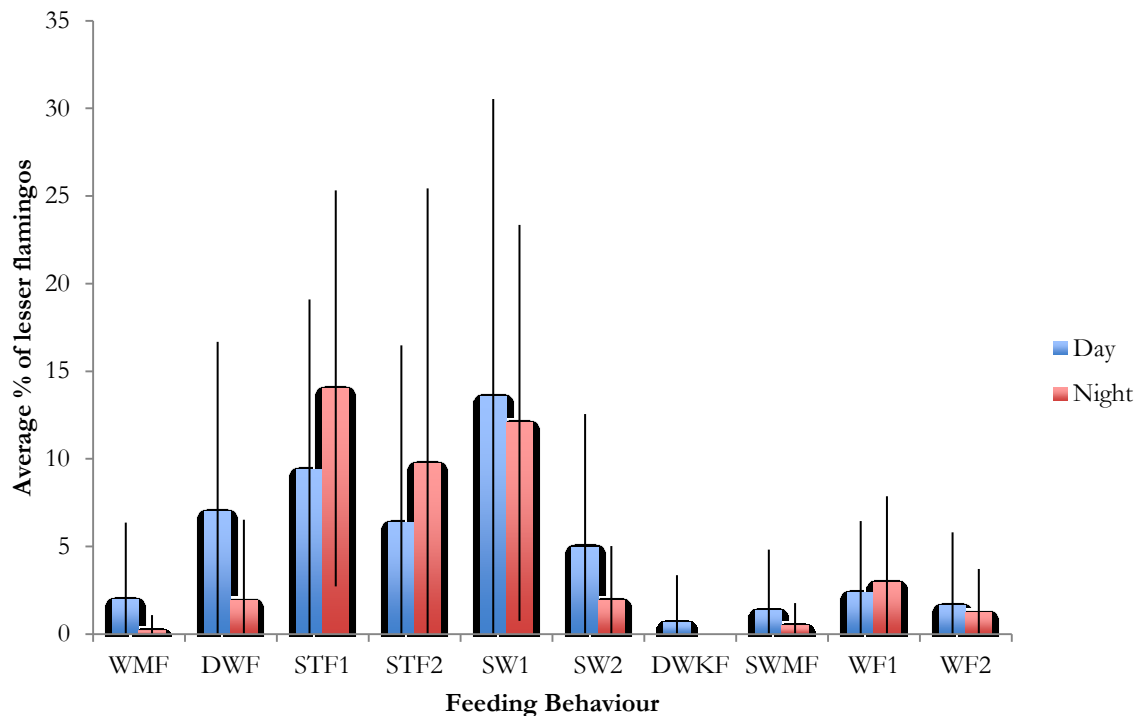
Figure: 4.9: The variation in lesser flamingo feeding behaviours at Lake Bogoria between night and day; error bars ± 1 standard deviation

4.3.3.2.2 Lake Oloidien

STF1 was the dominant feeding behaviour during both the day and the night. There were small increases in the proportion of lesser flamingos utilising STF1, STF2, WF1 and WF2 from the day to the night. Five of the eight feeding behaviours varied significantly between night and day (Figure 4.10; Mann-Whitney U tests), the *U*, z and p values are displayed in Table 4.14. There was no significant difference identified for STF1, STF2 or SWF1, which constituted the majority of the feeding.

Table 4.14: The Mann Whitney *U* test results for the difference in feeding behaviours between night and day at Lake Oloidien; mean and n displayed

Behaviour	*Mean* day	*Mean* night	*U*	z	p	n
WMF	2.00	0.02	8955.0	-6.452	p < 0.001	396
SW2	2.43	0.13	10279.0	-5.005	p < 0.001	396
SWMF	1.79	0.99	12325.0	-2.203	p < 0.05	396
WF1	4.54	7.81	18973.5	5.718	p < 0.001	396
WF2	1.30	1.46	15595.5	2.860	p < 0.005	396
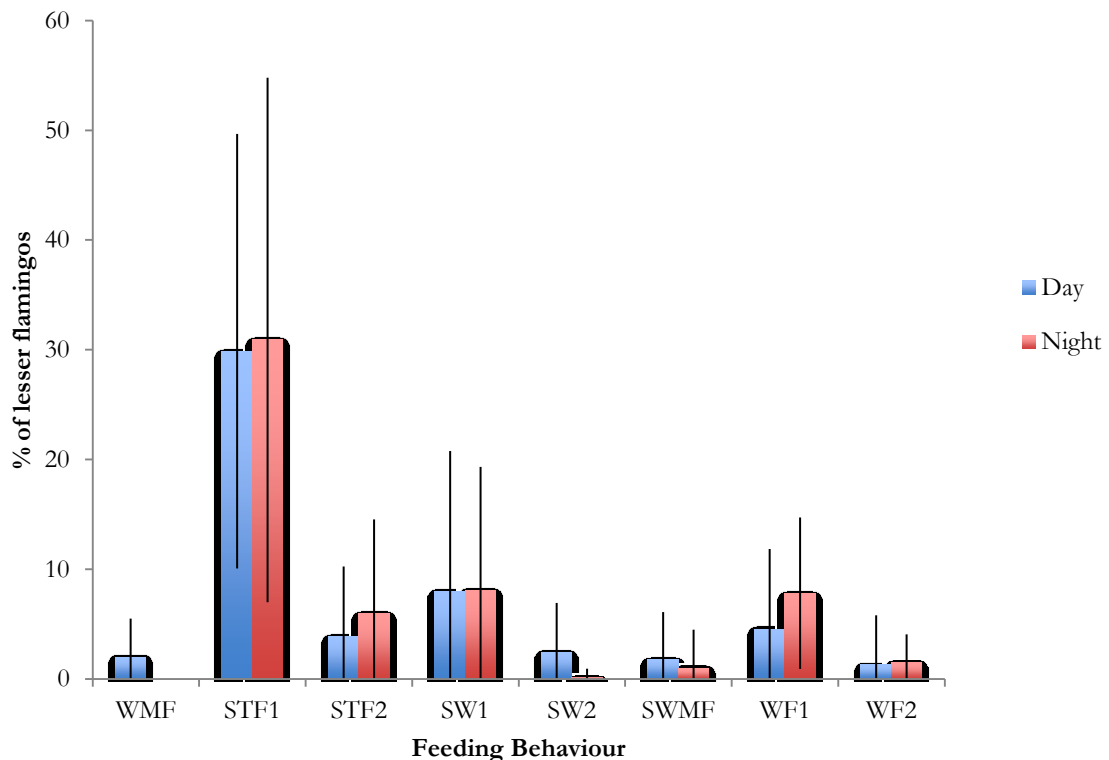
Figure: 4.10: The variation in lesser flamingo feeding behaviours at Lake Oloidien between night and day; error bars ± 1 standard deviation

4.3.3.3 24 hours

4.3.3.3.1   Lake Bogoria

SW1 was the dominant feeding behaviour during the dawn, morning, afternoon and post-midnight observation periods (being utilised by over 14% of lesser flamingos in each period). During the dawn observation period, STF1, SW2 and STF2 were all utilised by over 5% of the population, DWKF was absent and the remaining behaviours were utilised by less than 5% of the population. In the morning, in addition to SW1, only STF1 and STF were utilised by more than 5% of the flock. STF1 and STF2 remained common in the afternoon and DWF was also used by more than 5% of lesser flamingos. STF1 was the only other feeding behaviour being utilised by more than 4% of the population in the post-midnight observation period and was almost as common as SW1 at this time. In the evening observation period, DWF dominated, closely followed by STF1, STF2 and SW2, all other behaviours were being utilised by less than 4% of the population. STF2 and STF1 dominated the pre-midnight observation period with all other behaviours having less than 6% engagement.

The average proportion of lesser flamingos engaged in each of the feeding behaviours varied significantly between the times of day (Figure 4.11). The average proportion of lesser flamingos engaged in each feeding behaviour during the observation periods is displayed in Table 4.15. The Kruskal-Wallis test statistic result, p value and Games-Howell exceptions for each feeding behaviour are displayed in Table 4.16.

Table 4.15: The average proportion of lesser flamingos engaged in each feeding behaviour, during each time period, at Lake Bogoria

	Dawn	Morning	Afternoon	Evening	Pre-midnight	Post-midnight
WMF	2.4	2.8	2.2	1.2	0.2	0.1
DWF	3.9	4.9	8.6	10.6	3.6	1.5
STF1	10.2	10.0	8.5	7.9	12.0	15.0
STF2	5.7	5.3	6.6	9.0	13.1	3.5
SW1	18.4	14.5	15.1	8.2	5.9	15.6
SW2	9.5	4.1	3.5	3.6	3.1	2.0
DWKF	0	0.8	1.5	0.4	0	0
SWMF	1.1	1.0	1.8	1.5	0.3	0.4
WF1	3.1	2.5	1.8	2.2	2.1	3.2
WF2	1.5	1.2	2.7	0.6	1.9	1.2

Table 4.16: The Kruskal-Wallis test statistic result, p value and Games-Howell exceptions for each feeding behaviour tested across all periods of the day at Lake Bogoria; df = 5 and n = 685; D = Dawn, M = Morning, A = Afternoon, E = Evening, Pre = Pre-midnight & Post = Post-midnight

Feeding Behaviour	Kruskal-Wallis test statistic	p value	Games-Howell exceptions (no statistically significant differences, p > 0.05)
WMF	72.775	< 0.001	D & M; D & A; M & A; Pre & Post
DWF	73.040	< 0.001	D & M; D & Pre; M & Pre; A & E; Pre & Post
STF1	23.251	< 0.001	D & M; A & E; D & Pre; M & Pre
STF2	20.79	< 0.01	D & M; D & A; M & A; M & Post
SW1	36.578	< 0.001	D & A; D & Post; M & A; M & Post; A & Post
SW2	46.957	< 0.001	M & A; M & E; A & E; A & Pre; E & Pre
DWKF	42.962	< 0.001	M & E
SWMF	15.607	< 0.01	D & M; D & E; M & E; A & E; Pre & Post
WF2	25.317	< 0.001	D & M; D & Pre; Dawn & Post; M & Pre; M & Post; A & Post
No significant differences were identified for WF1			
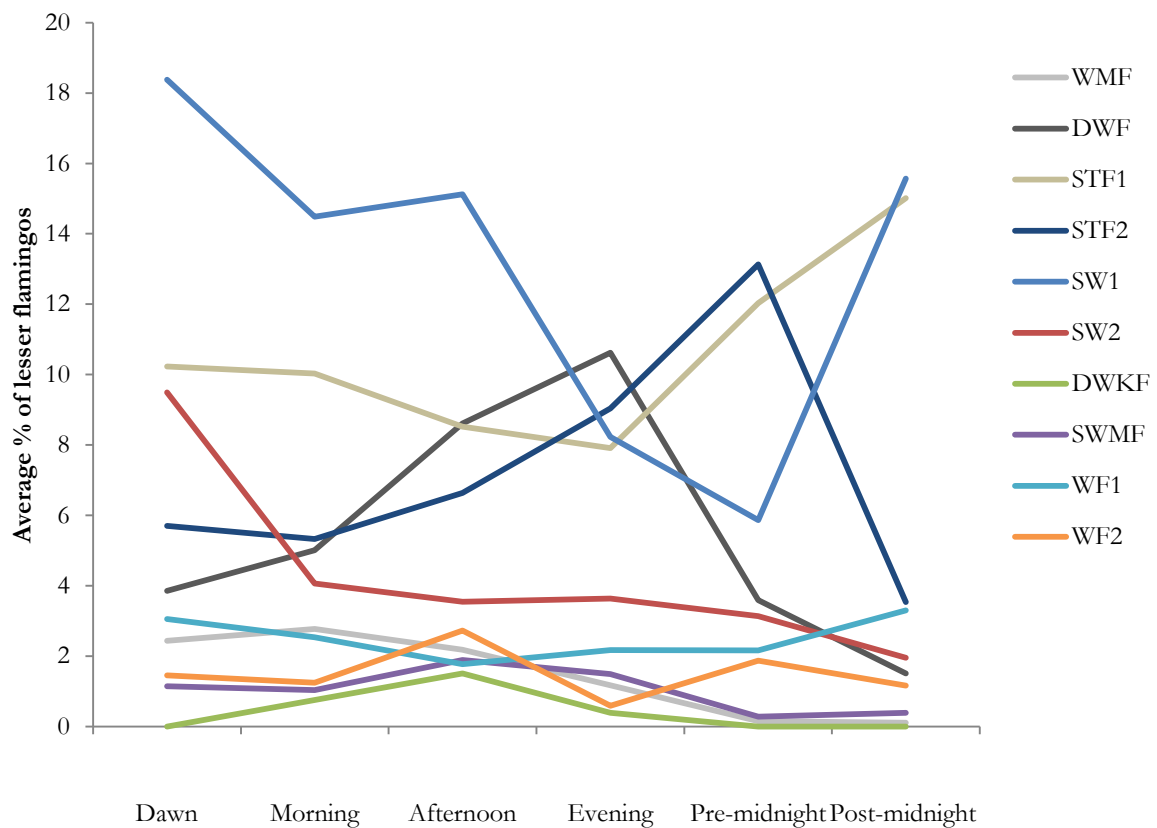
Figure: 4.11: The variation in lesser flamingo feeding behaviours at Lake Bogoria between different times of day

4.3.3.3.2   Lake Oloidien

STF1 was the dominant feeding behaviour across all periods of the day. The proportion of lesser flamingos engaged in SW1 was relatively high at dawn, in the

afternoon and pre-midnight as it was the second most common during these observation periods, however it dropped in the morning, evening and post-midnight. WMF was absent during both the pre- and post-midnight periods and most utilised at dawn and SWMF was most common in the morning. STF2 remained relatively constant, with two peaks in the afternoon and post-midnight and SW2 reduced significantly during pre- and post-midnight. WF1 was most common during the morning and post-midnight periods and WF2 was rare throughout all time periods with never more than 2% of lesser flamingos utilising this behaviour at any point.

The average proportion of lesser flamingos engaged in each of the feeding behaviours varied significantly between the times of day (Figure 4.12). The average proportion of lesser flamingos engaged in each of the feeding behaviours throughout the 24 hour period is displayed in Table 4.17. The Kruskal-Wallis test statistic result, p value and Games-Howell exceptions for each feeding behaviour are displayed in Table 4.18.

Table 4.17: The average proportion of lesser flamingos engaged in each feeding behaviour, during each time period, at Lake Oloidien

	Dawn	Morning	Afternoon	Evening	Pre-midnight	Post-midnight
WMF	3.3	1.6	0.9	2.5	0	0
STF1	17.8	31.4	34.3	33.5	42.5	21.2
STF2	2.5	3.3	2.4	7.2	3.1	8.3
SW1	8.9	4.0	11.2	7.1	16.3	1.1
SW2	3.4	3.0	1.4	2.2	0.1	0.2
SWMF	1.2	2.7	1.4	1.9	0.5	1.4
WF1	6.2	8.9	3.2	0.7	5.5	9.8
WF2	0.3	1.3	2.0	1.4	0.9	1.9

Table 4.18: The Kruskal-Wallis test statistic result, p value and Games-Howell exceptions for each feeding behaviour tested across all periods of the day at Lake Oloidien; df = 5 and n = 685; D = Dawn, M = Morning, A = Afternoon, E = Evening, Pre = Pre-midnight & Post = Post-midnight

Feeding Behaviour	Kruskal-Wallis test statistic	p value	Games-Howell exceptions (no statistically significant differences, $p > 0.05$)
STF1	63.26	< 0.001	D & Post; M & A; E & Post; A & E; A & Pre; E & Pre
STF2	39.56	< 0.001	D & M; D & A; D & Pre; M & A; M & Pre; A & Pre;
SW1	63.08	< 0.001	D & E
SW2	32.92	< 0.001	D & M; M & E; A & E; Pre & Post
WF1	101.36	< 0.001	D & Pre; D & M; M & Post; A & Pre
No statistically significant difference were identified for WMF, SWMF or WF2			
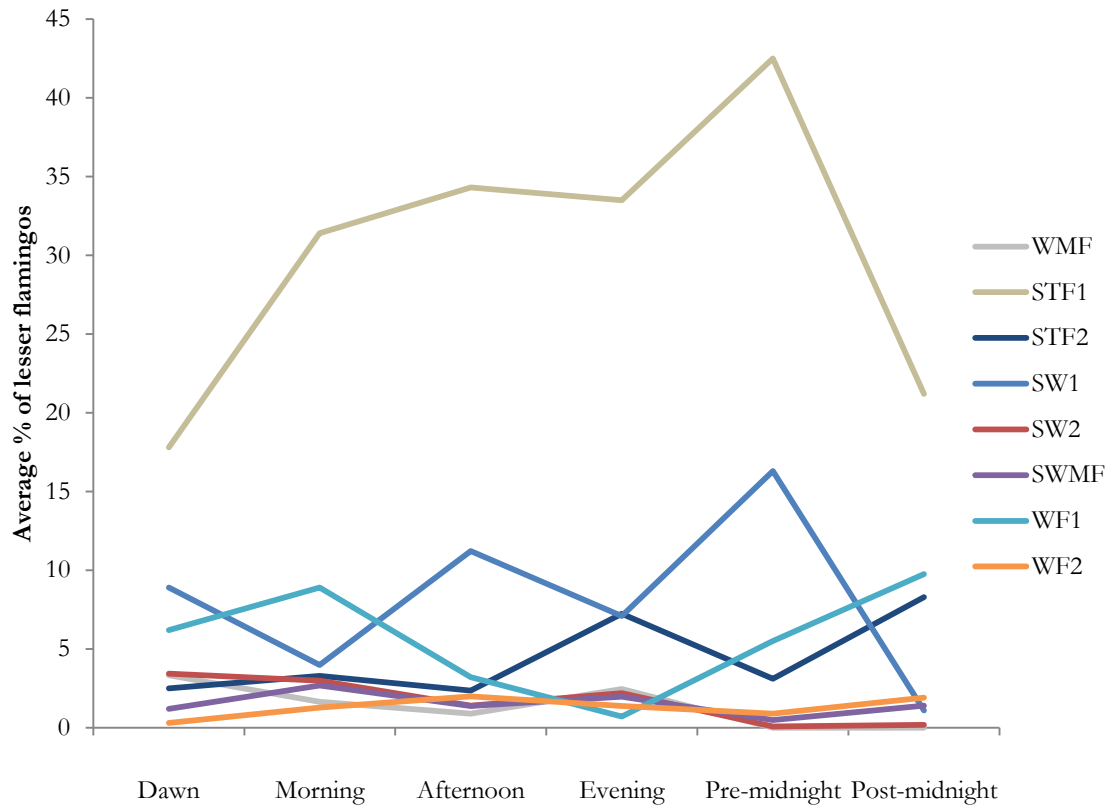
Figure: 4.12: The variation in lesser flamingo feeding behaviours at Lake Oloidien between different times of day

4.3.3.3.3 Lake Nakuru

A significantly higher proportion of lesser flamingos were engaged in WMF in the evening than the morning or afternoon, X^2 (2, n = 82) = 6.53, p < 0.05. WMF was least common in the morning, however, the number of lesser flamingos utilising it increased steadily throughout the three time periods until the evening, when it was the dominant feeding behaviour. STF1 was the second most common feeding behaviour in the morning and afternoon, dropping slightly in the evening, although this difference was not significant. STF2 was rarely used although there was a slight increase from the morning to the afternoon, before falling again in the evening (Figure 4.13).

SW1 was the most common feeding behaviour in the morning and second most utilised in the evening. There was a significantly lower proportion of lesser flamingos engaged in SW1 in the afternoon than the morning and evening, X^2 (2, n = 82) = 15.12, p < 0.01 (Games-Howell post hoc, p < 0.05 and p < 0.001 respectively). A small, non- significant, reduction in the population utilising SW2 was observed from the morning to the evening. SWMF was most common in the evening where it was the

fourth most utilised behaviour, it was also fourth most common in the afternoon, however, there were less birds utilising it at this time.

The proportion of lesser flamingos engaged in WF1 was significantly higher in the evening than the morning or afternoon, X^2 (2, n = 82) = 7.25, p < 0.05. WF2 was most common in the afternoon, with half as many birds engaging in WF2 in the morning and evening as in the afternoon.
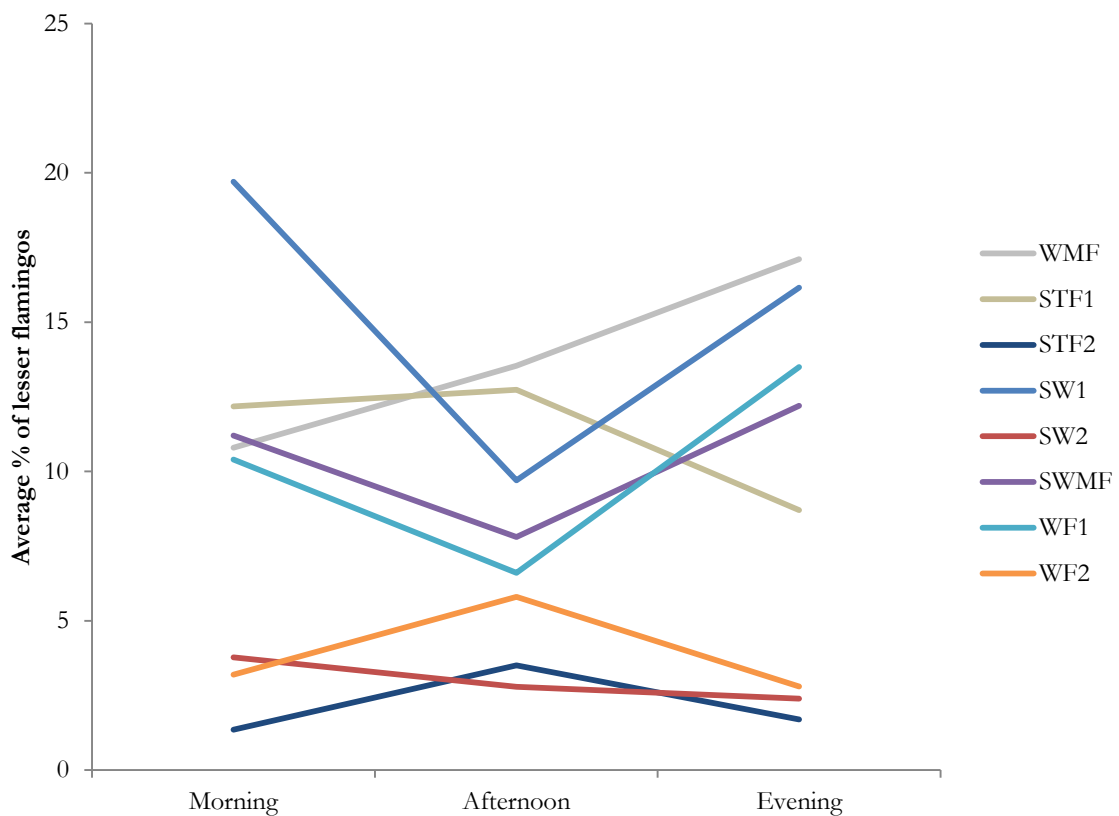
Figure: 4.13: The variation in lesser flamingo feeding behaviours at Lake Nakuru between different times of day

4.3.3.3.4   Lake Sonachi

Significantly more SW1 was occurring in the afternoon than in the morning and evening, X^2 (2, n = 41) = 25.07, p < 0.001 (Kruskal-Wallis and Games-Howell). There was little fluctuation in the proportion of lesser flamingos utilising STF1, SW2 or SWMF (No significant differences identified). Figure 4.14 displays the average percentage of lesser flamingos engaged in each of the feeding behaviours throughout the course of the day at Lake Sonachi.
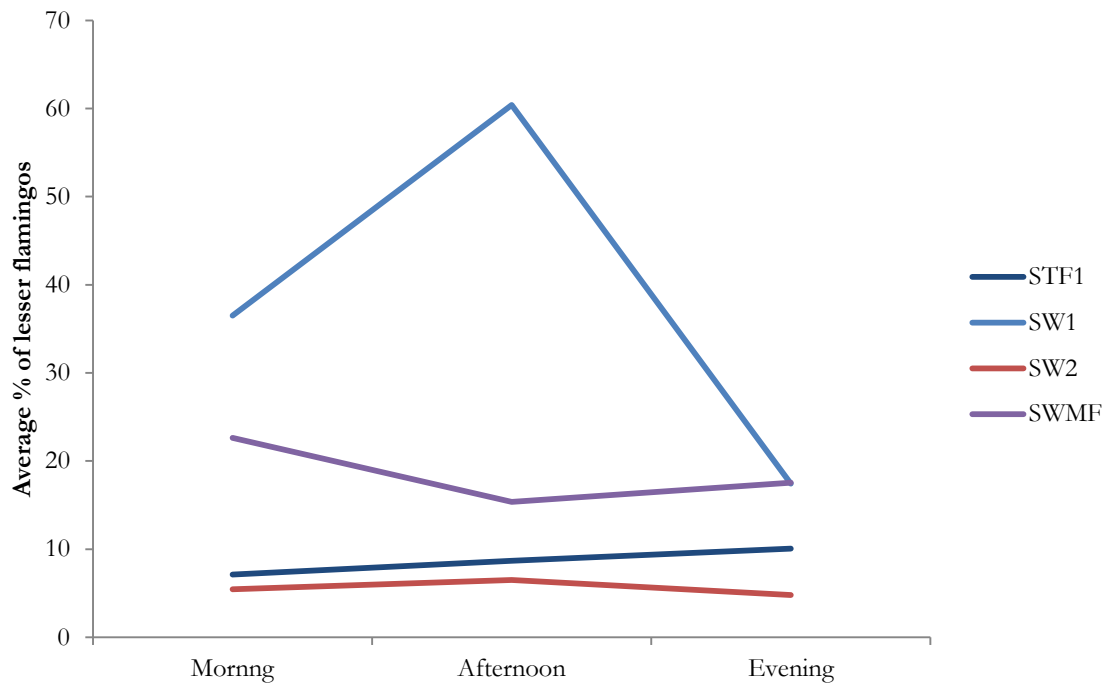
Figure: 4.14: The variation in lesser flamingo feeding behaviours at Lake Sonachi between different times of day

4.3.3.3.5   Lake Natron

The proportion of lesser flamingos engaged in WMF was significantly higher at dawn than any other time period, X^2 (3, n = 97) = 24.68, p < 0.001 (Kruskal-Wallis and Games-Howell). 15.15% of the population was utilising this behaviour at dawn, compared to 3.56%, 5.27% and 2.17% for the morning, afternoon and evening respectively. DWF was most common in the afternoon (16.55%) and was absent in the dawn observation block. There was significantly more DWF occurring in the afternoon than both the morning and evening, X^2 (3, n = 97) = 13.94, p < 0.005 (Kruskal-Wallis and Games-Howell)

SWMF was the most common feeding behaviour in all observation blocks, engaging between 50% and 70% of the population at all times, no statistically significant differences were identified. Figure 4.15 displays the average percentage of lesser flamingos engaged in each of the feeding behaviours throughout the course of the day at Lake Natron.
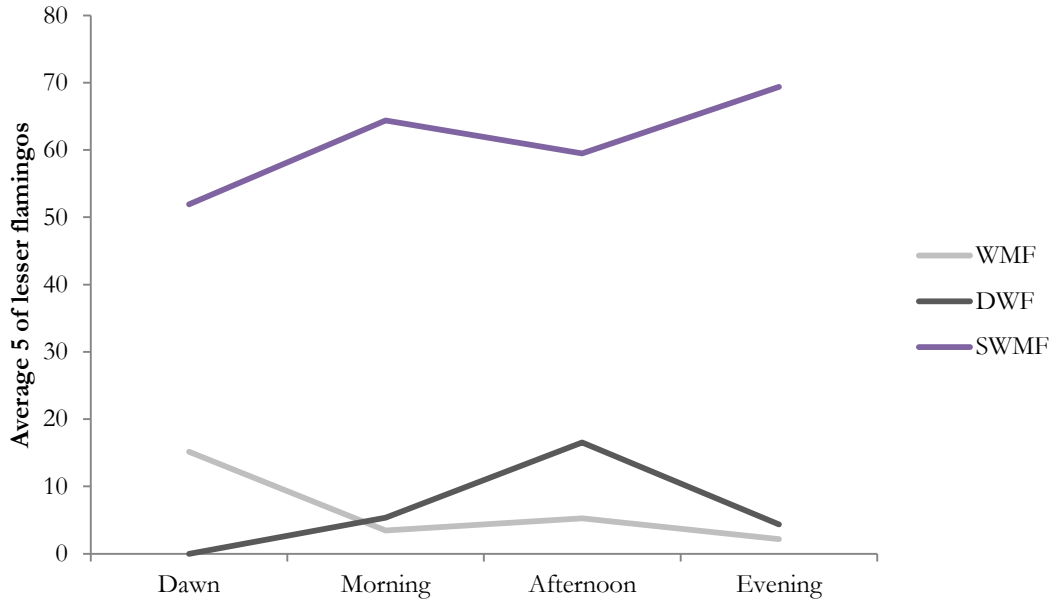
Figure: 4.15: The variation in lesser flamingo feeding behaviours at Lake Natron between different times of day

4.3.3.3.6   Lake Elementaita

SWMF was the dominant feeding behaviour throughout all time periods with a significantly higher proportion of lesser flamingos engaged in SWMF in the afternoon and evening than in the morning, X^2 (2, n = 42) = 16.56, p < 0.001 (Kruskal-Wallis and Games-Howell).

Significantly more DWF occurred in the morning than in both the afternoon and evening, X^2 (2, n = 42) = 12.61, p < 0.005 (Kruskal-Wallis and Games-Howell). Significantly less WMF occurred in than afternoon than in either the morning or evening, X2 (2, n = 42) = 10.45, p < 0.01 (Kruskal-Wallis and Games-Howell). Figure 4.16 displays the average percentage of lesser flamingos engaged in each of the feeding behaviours throughout the course of the day at Lake Elementaita.
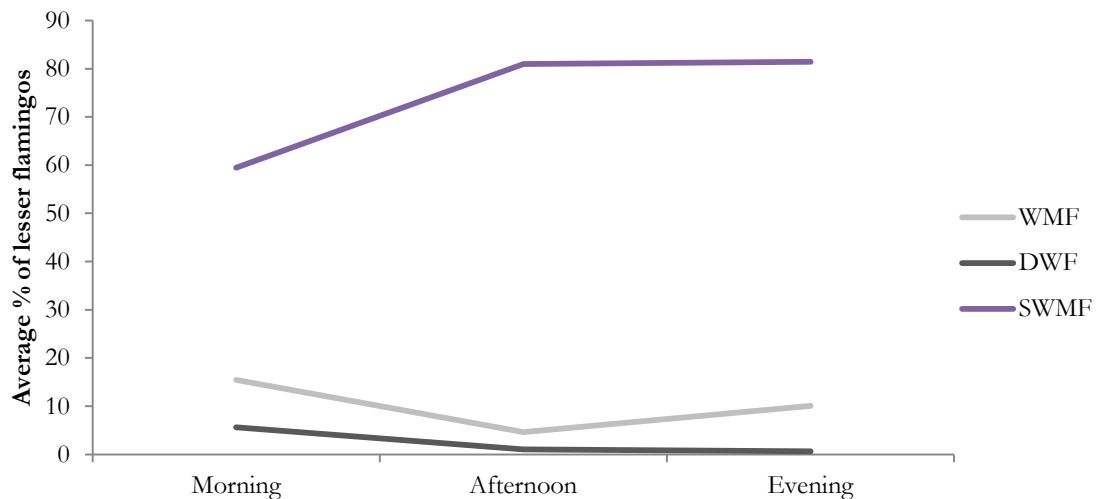
Figure: 4.16: The variation in lesser flamingo feeding behaviours at Lake Elementaita between different times of day

4.3.4 Effects of food type and distribution on feeding behaviour

4.3.4.1 Food type

There was a considerable difference in number of feeding behaviours exhibited by lesser flamingos at lakes, which were dominated by *A. fusiformis*, other cyanobacteria and diatoms. Both Natron and Elementaita were dominated by benthic or epipelic diatoms and only three feeding behaviours were displayed, WMF, SWMF and DWF. All three of these behaviours involve skimming food resources off the surface of the wet mud at the edge or further within the lake; there was no evidence of filtering planktonic food. Both Oloidien and Nakuru were dominated by a combination of cyanobacteria and diatoms and eight feeding behaviours were seen; neither DWF nor DWKF were seen at either of the two lakes. Therefore, Bogoria and Sonachi were both dominated by *A. fusiformis* and whereas 10 feeding behaviours were recorded at Bogoria, only four were recorded at Sonachi. Lesser flamingos at Sonachi only utilised STF1, SW1, SW2 and SWMF, indicating that there must be other factors that influence feeding behaviour, not just the type of food available.

4.3.4.2 Food distribution

Food resources are not distributed uniformly throughout the lakes (Chapter 3) and different feeding behaviours give access to varying food abundance. Figure 4.17 displays the average biomass (standing crop) of food accessed through the different feeding behaviours in the Central basin of Lake Bogoria in August 2012 and August 2013. Observations were conducted at the same site (taking into account lake level rise) both years to allow for a direct comparison between the feeding behaviours and food whilst keeping everything else as constant as possible. DWF gave access to the highest abundance of food overall (144.65 mg L^{-1}) and SWMF gave access to the least (43.42 mg L^{-1}). A statistically significant difference was found between the average standing crop accessible by different feeding behaviours (Kruskal-Wallis), X^2 (5, n = 144) = 21.46, p < 0.01. Significant differences identified by Games-Howell post hoc tests are displayed in Table 4.19.

Between August 2012 and August 2013, significant differences were revealed for the abundance of food accessible by each of the feeding behaviours at p < 0.001. The average food availability dropped from 121.86 mg L^{-1} in August 2012 to 54.35 mg L^{-1} in August 2013 and whilst no correlation was found between accessible biomass and average percentage of lesser flamingos (Figure 4.18; p > 0.05), the percentage of DWF was higher when more food was accessible through this behaviour. Between 2012 and 2013, the percentage of lesser flamingos engaged in SW2 and STF2 increased dramatically with large swings of the head from side to side indicating that during a reduction in food availability there is an increase in feeding effort.

Between the three basins significant differences were revealed for the abundance of food accessible by all feeding behaviours (Figure 4.19) at p < 0.001, with the exception of accessible biomass via STF/WF and SW between North and Central basins (Games-Howell). A weak positive correlation was identified between the average accessible biomass and the percentage of feeding accounted for by the equivalent feeding behaviours (*Rho* = 0.542, p < 0.01; Spearman's Rank Correlation Cofficient).
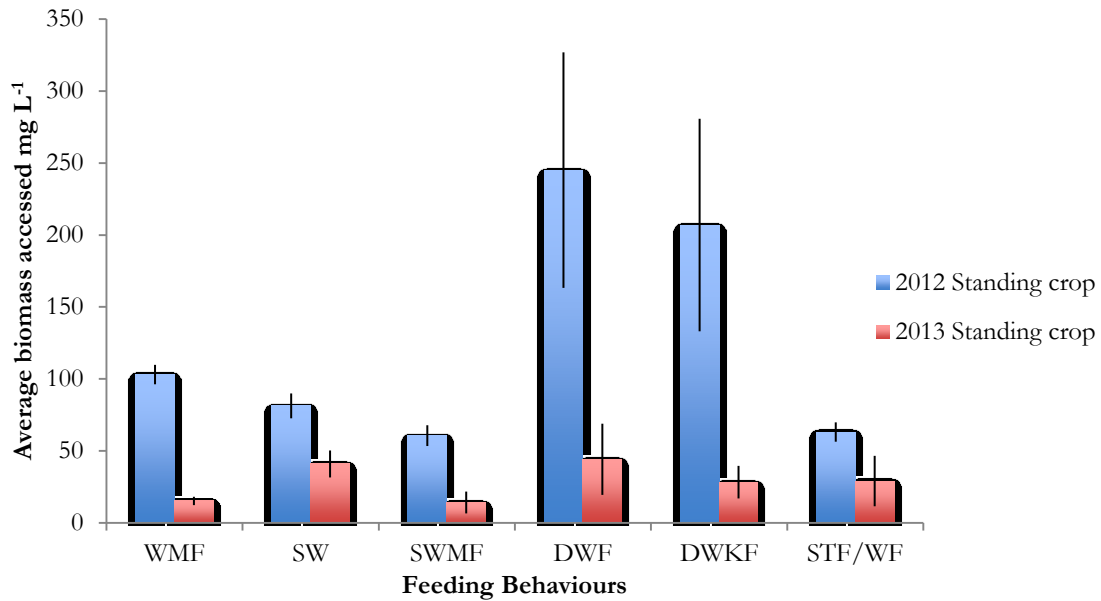
Figure 4.17: Average standing crop accessible through different feeding behaviours at Lake Bogoria in 2012 and 2013; error bars ±1 standard deviation

Table 4.19: Games-Howell post hoc results for differences in abundance of food obtained through different feeding behaviours

	WMF	SWF	SWMF	DWF	DWKF	STF/WF
WMF		-1.97	21.75	-85.47*	-58.46	13.05
SWF			23.73*	-83.50*	-56.48	15.02
SWMF				-107.22***	-80.21**	-8.70
DWF					27.01	98.52**
DWKF						71.51*
STF/WF						
***p < 0.001; **p < 0.01; *p < 0.05						
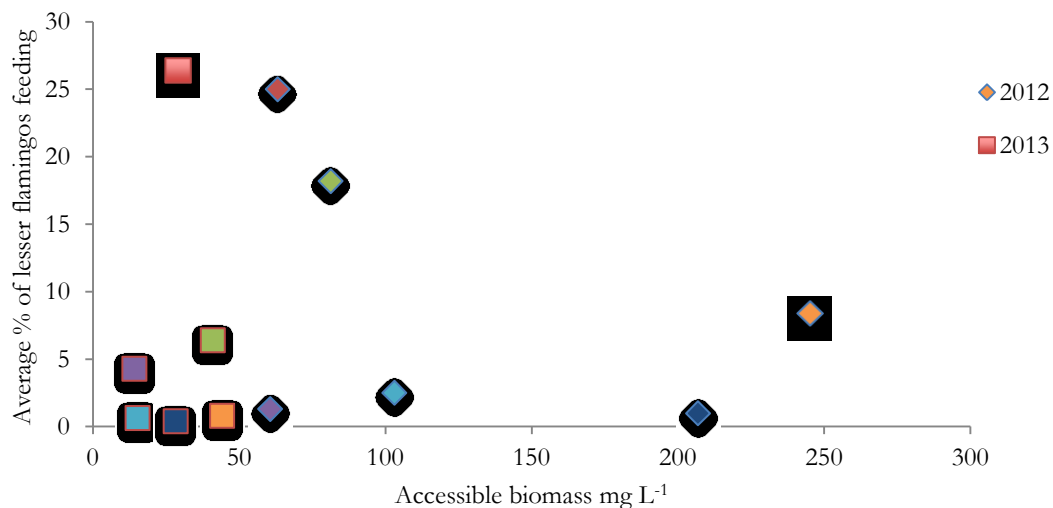
Figure 4.18: The average accessible biomass accessed through different feeding behaviours and the average percentage of lesser flamingos engaged in the equivalent behaviours in 2012 (diamonds) and 2013 (squares) at Lake Bogoria: Red = STF; Green = SW; Purple = SWMF; Light blue = WMF; Dark blue = DWKF; Orange = DWF

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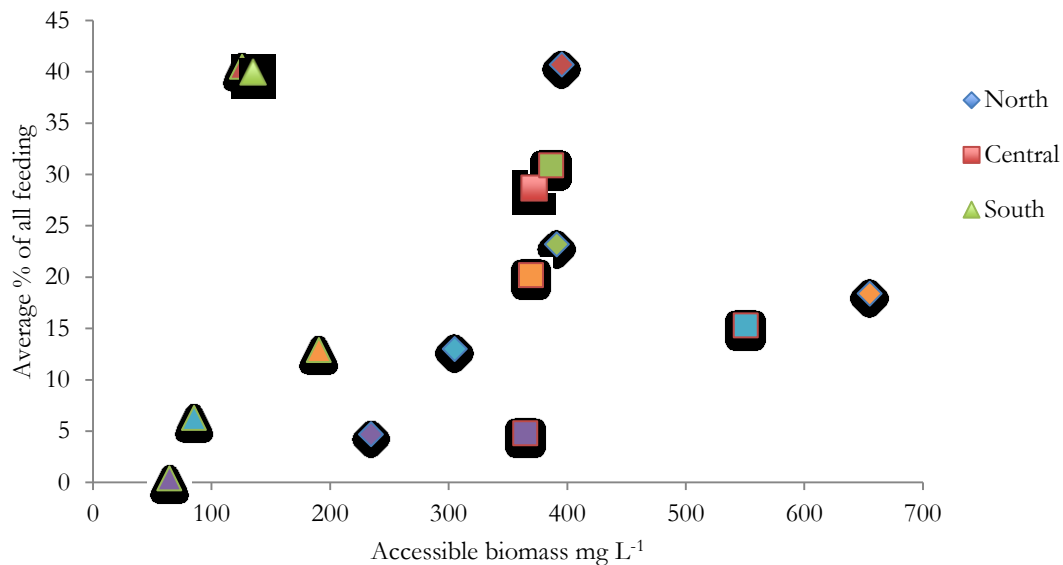
Figure 4.19: The average biomass accessible through different feeding behaviours and the average percentage of total feeding attributed to each behaviour group within the North (diamonds); Central (squares) and South (triangles) basins at Lake Bogoria in 2009: Red = STF; Green = SW; Purple = SWMF; Light blue = WMF; Orange = DWF

4.5   Discussion

Lesser flamingos have a more diverse repertoire of feeding behaviours than is widely reported in published literature, enabling them to access food from niches throughout the aquatic habitat: from the lake's edge, the open water and the lake-sediment interface. Wet mud feeding, stand filter feeding, swim filter feeding have been regularly reported and deep water feeding has been mentioned, however, this is the first in depth study of how lesser flamingos feed and when different feeding behaviours dominate.

Deep water and deep water kick feeding are both common feeding behaviours in greater, Chilean and Caribbean flamingos, which are known to feed on invertebrates living in the substrate at the bottom of lakes (Jenkin, 1957; Espino-Barros & Baldassare, 1989; Zweers *et al*, 1995; Mascitti & Castañera, 2006). Tuite (1979; 2000) was the first to document this behaviour in lesser flamingos, commenting that when reliant on a diet of diatoms they occasionally upended in shallow water to reach the mud at the bottom. Records of DWF are limited, which could indicate that lesser flamingos are not as well adapted to underwater feeding, both morphologically and physiologically, as their shallow-keeled relatives and therefore only engage in the

behaviour as a last resort; alternatively it could be a newly adaptive feeding behaviour being increasingly utilised.

This study is the first to show that these deep water behaviours are much more common than previously thought and that they are not unique to feeding on diatoms, being implemented at Lake Bogoria in areas where *A. fusiformis* aggregates in high concentration at the bottom of the water column. This indicates an adaptation in feeding, employing different behaviours or strategies to exploit a newly identified, concentrated, food resource identified during this study. A positive correlation was identified between forebrain size and feeding innovation frequency (Lefebvre *et al.*, 1997) indicating a physiological reasoning in adaptive behaviours. The presence of greater flamingos feeding through deep water feeding could have influenced the frequency of lesser flamingos utilising this behaviour through social learning (ibid.).

Lesser flamingos utilised different feeding behaviours at each of the lakes. Ten feeding behaviours were recorded at Lake Bogoria, eight at both Nakuru and Oloidien, four at Sonachi and three at both Natron and Elementaita. At Lake Bogoria, the two dominant behaviours overall were SW1 and STF1 and the principal component analysis indicated a negative correlation where they appear to switch between dominance. This suggests that there are periods of time when lesser flamingos feed on the open water and times when feeding along the shoreline is preferable. Similar patterns of shoreline and open water feeding are seen at Oloidien, Sonachi and Nakuru.

At lakes Elementaita and Natron, SWMF dominates and DWF is the least common. The distribution of diatoms is more uniform than that of cyanobacteria as they are able to grow where the light penetrates. The preference for SWMF suggests that a thin layer of water may make it easier to feed on diatoms as they can be suspended in the water and filtered rather than being filtered directly off the surface of the mud. DWF is the least utilised behaviour, which could indicate that lesser flamingos prefer to feed without submerging their entire heads if there is not a significant increase in reward. The density of diatoms did not increase with depth and therefore, as optimal foraging theory predicts, lesser flamingos could be selecting the most profitable patches in order to maximise their rate of energy intake (Pyke *et al.*, 1977)

The feeding behaviours utilised at Lake Bogoria varied between the three basins, as did the average biomass accessible through the different feeding behaviours, showing a marked spatial behavioural segregation. STF/WF were the most common type of feeding behaviour, however DWF had the highest biomass reward in both the North and Central basins. In the Central basin, the standing crop available when DWF was over double that accessible through other feeding behaviours, yet it accounted for just over 20% of total feeding. In the North and South basins, higher food abundance was also associated with DWF yet only 18.4% and 12.9% of feeding was DWF respectively. This suggests that DWF behaviours may not be a preferential feeding behaviour for long periods as the head is fully submerged, but it appears to be a way for lesser flamingos to get a large amount of food in a short time and therefore other behaviours can be utilised for the remainder of their daily requirement. Their response to risk in foraging could depend on comparison of their energetic requirement with their energetic intake, as identified in yellow-eyed juncos (Caraco *et al.,* 1980)

There is a distinction between the feeding behaviours that involve filtering the top few centimetres of the water column and those that involve filtering the surface of wet mud. The swim, stand and walk filter feeding behaviours never yield the highest standing crop at Lake Bogoria, yet in all three basins and between different years, they are the most utilised behaviours suggesting a preference to filter feed from the lake water, especially when there is a generally high abundance of *A. fusiformis*.

The feeding behaviours engaged in by lesser flamingos varied over the course of the day, between night and day and year on year. Food abundance and / or distribution may not be the only contributing factors as to when, why and for how long lesser flamingos utilise the different feeding behaviours; I suggest that there is a combination of factors, including predation, flock size and density, access to other resources (such as drinking water) and lake substrate, which determine the behavioural repertoire at any given time.

Predation, access to fresh water, lake substrate, food abundance and distribution all influence feeding (Pyke, 1984). Marabou storks (*Leptoptilos cruminiferus*), fish eagles (*Haliaeetus vocifer*), olive baboons (*Papio anubis*), spotted hyenas (*Crocuta crocuta*) and wild dogs (*Lycaon pictus*) were all seen predating on lesser flamingos along the shoreline,

therefore lower predation risks are associated with feeding on the open water and feeding in large flocks (Powell, 1974). Freshwater inlets occur along the shoreline of most of the soda lakes in the form of rivers and hot springs which lesser flamingos rely on for preening, bathing and drinking (Krienitz *et al.,* 2004). Food resources are not distributed uniformly throughout the lakes and the abundance of food varies both spatially and temporally (Chapter 3). No DWF occurs in areas where there is a rocky substrate, presumably so that the bill does not get damaged during feeding.

SW1 was the dominant feeding behaviour at Lake Bogoria from 2009-2011, followed by STF1. Between 2012 and 2013, STF2, WF2 and SW2 all increased at Lake Bogoria, corresponding with a large reduction in biomass abundance (Chapter 3). These feeding behaviours all involve large swings of the head from side to side in a scything motion, it has been suggested that this movement allows lesser flamingos to see where they are going and remain vigilant as their eye positioning leaves them effectively blind in their direction of movement (Martin *et al.*, 2005). Vareschi (1978) also reported that the head swings in SW1, increased in fervour with a reduction in food availability, indicating that lesser flamingos may be able to invoke systems to increase the food they are able to access when density is reduced, a common behavioural response in waterfowl (Hutto, 1990; McKnight, 1998). It is more energetically expensive to swing their heads but the beneficial increase in the rate of resource encounter must outweigh the energetic cost of the head swings. The idea that different feeding behaviours can alter the rate at which cyanobacteria (primarily *A. fusiformis*) is ingested would need to be studied in greater detail to gain a better understanding of this.

At Lake Oloidien, STF1 dominated in all years, with the proportion of the remaining seven feeding behaviours changing. Swim feeding (1 and 2 combined) was common in 2009 but by August of 2011 it was barely utilised at all, increasing slightly in 2012. This behaviour did not correspond with reduced biomass on the open lake and therefore suggests that something other than food abundance and distribution was driving this reduction in swim feeding. In 2011, boat safaris for tourists started at Lake Oloidien, allowing people to get better views of the lesser flamingos and hippos (*Hippopotamus amphibious*) that share the lake. The introduction of boat traffic on to the lake could have caused a change in behaviour, as 90% of lesser flamingos feeding were engaging

in STF1 in August 2011 suggesting that they may have stayed along the shoreline to avoid the disturbance from regular boats.

At Bogoria and Oloidien, STF1, STF2, SW1 and WF1 were the dominant night feeding behaviours, suggesting that there is significant feeding occurring both on the open water, as Brown (1979) suggested, but also along the shoreline where the predation risk at Lake Bogoria is lower at night. At Oloidien the predation risk increased at night due to the hyena presence (personal observation), increased vigilance was also observed when hippopotamuses vacated the lake to feed at night and therefore large groups at the edge of the lake were often disturbed, leading to greater dispersal along the shoreline.

This chapter has identified 10 distinct feeding behaviours of lesser flamingos, identified when and where the different behaviours occur and has shown that different food types generate different feeding strategies. The connection between food availability, distribution and feeding behaviour has also been identified and the factors affecting how long lesser flamingos feed for is investigated in Chapter 5.

Chapter 5

Chapter 5 The time the lesser flamingo (*Phoeniconaias minor*) spends feeding is directly related to food abundance

Abstract

Many species adjust the amount of time they spend feeding in response to variation in food abundance. This study investigated the time lesser flamingos (Phoeniconaias minor) spent feeding at six lakes in the East African Rift Valley (lakes Bogoria, Oloidien, Elementaita, Nakuru, Natron and Sonachi). Lesser flamingos spent least time feeding at Lake Bogoria (43%) where they were feeding on *Arthrospira fusiformis* and most at Elementaita (88%) where they were feeding on epipelic diatoms. A negative correlation was identified between the time spent feeding and the average biomass (*rho* = -.829, p < 0.05), when considering the six lakes, suggesting that feeding rates decreased with decreasing algae. However, a positive correlation was identified between average biomass and time spent feeding at Lake Bogoria indicating that feeding rates increased when there was high abundance of *A. fusiformis*. Juveniles were found to spend more time feeding than both adults and sub-adults (p = 0.002 and 0.006 respectively). No significant difference was found between the time spent feeding during daylight hours and the night. Cyclic feeding patterns were identified through autocorrelation with either one or two oscillations throughout the day at cyanobacteria dominated lakes; no discernable pattern was identified for lakes dominated by diatoms.

5. 1 Introduction

Optimal foraging theory assumes that all animals will attempt to maximise their rate of energy intake through selecting food that yields the greatest biomass per unit of feeding time (Schoener, 1971). In lesser flamingos, an increase in the availability of food should result in a Hollings type I functional response (Holling, 1959), a linear relationship between rate of intake and food density, uniquely found in filter feeders (Holling, 1965; Jeschke *et al.*, 2004). Therefore, with an increasing food density lesser flamingos should be able to spend less time feeding, leaving them with a greater amount of time available to devote to other activities, such as preening, drinking and courting.

Experimentally, however, type II and III Hollings functional responses have been observed in the greater flamingo with an increase in food density (Deville *et al.,* 2013). The authors hypothesised that this may be due to a clogging of the delicate filtering apparatus. Their results could also indicate a level of saturation whereby there may be a minimum amount of time that flamingos have to feed for in order to obtain their energy requirement even when food is in abundance.

The time that lesser flamingos spend feeding has only been addressed twice, with most literature focused on the availability of food and flamingo presence at feeding lakes. In 1973, Pennycuick and Bartholomew proposed an energy budget for the lesser flamingo by calculating the rate at which they are able to filter their food; subtracted the energy expenditure required for activities such as metabolism and the physical act of pumping the water through their bills. It was surmised that a net energy gain could be achieved if lesser flamingos spent 80% of their time feeding when the food concentration was in excess of 0.125 kg dry weight (DW) per m^3. They further suggested that the concentration would have to be at least double that during incubation (Pennycuick & Bartholomew, 1973). Their model was based on measurements made by Jenkin (1957), resulting in their estimation that lesser flamingos require about 90 g DW per day; it suggested that the time spent feeding could be reduced if concentration of food increased, predicting that for a non-breeding flamingo, a concentration of 0.25 kg DW per m^3 would only require 40% of the day allocated to feeding.

Further to this, in 1978, Vareschi studied the time spent feeding of both caged and free-living birds at Lake Nakuru. The caged birds were observed over 24 hours with their activity recorded every 15 minutes and the activity of the free-living birds was determined from photographs by day and estimations at night. The free-living birds monitored along the shoreline spent 48% of the 24-hour period feeding; including the 8% feeding on the open lake he concluded that they spent 52% or 12.5 hours feeding. In the same period, the caged birds spent 39.4% of their time feeding, showing that the free-living birds fed for 1.3 times as many hours (close to the factor of 1.5 identified for the wood stork (*Mycteria americana*) by Kahl in 1964).

The following year, Vareschi repeated the experiment with 19 individual observers, who photographed different areas of the shore throughout the day and an aerial census

was conducted periodically to assess the population on the open lake. At night, binocular observation from a floating platform was used to provide 24-hour data. The *A. fusiformis* concentration was half of the previous year and flamingos fed for 58% of their time or 13.9 hours (Vareschi, 1978). Later in the year the concentration dropped further and whilst most flamingos left, the few that remained increased their feeding effort to 70-80% of their time, with 70% of this occurring on mud flats (Vareschi, 1978).

Although not discussed in either of the papers on flamingo feeding, it has been suggested through conversation (Brooks Childress pers comm.) that flamingos spend a greater percentage of time feeding at night than day.

This chapter aims to assess whether lesser flamingos spend different proportions of their day feeding at different lakes; explore the effects of food source on how long lesser flamingos feed for; consider the difference in time spent feeding for different ages of bird; investigate whether different times of day are more popular for feeding and if feeding is more prevalent at night or during the day.

I addressed the following questions:
- Does the time spent feeding vary between lakes and locations?
- Does the total time spent feeding decrease as food abundance increases?
  - Do lesser flamingos stop feeding when concentrations drop below 100 mg L^{-1} as suggested by Vareschi (1978)?
- Does the dominant food source affect the time spent feeding?
- Does the age of the bird affect time spent feeding?
- Does time spent feeding vary over the course of the day?
  - Or between day and night?

Testing the resultant null hypotheses:
- There is no significance between location and time spent feeding
- There is no significant relationship between the abundance of food and the time spent feeding
- There is no significant relationship between the type of food available and time spent feeding

- There is no significant relationship between age of bird and time spent feeding
- There is no significant relationship between time of day and time spent feeding

5. 2   Methods

This study occurred at Lakes Bogoria, Oloidien, Elementaita, Sonachi, Nakuru and Natron from 2009 to 2013. For safety reasons in depth studies were only conducted at Lakes Oloidien and Bogoria when investigating the whole 24-hour feeding period as it was not possible to have a vehicle at the observations sites on other lakes. A vehicle was required in case of injury or any unexpected unknowns that may have occurred in the darkness. Full descriptions of methods and study sites are given in Chapter 2.

5. 3   Results

5.3.1   Time spent feeding at different lakes and locations

The average time that lesser flamingos spent feeding was not equal at all of the lakes (Figure 5.1). Birds spent significantly more time feeding at Lake Elementaita than any of the other lakes (Bogoria, n = 685; Oloidien; n = 396, Nakuru, n = 82; Sonachi, n = 41; Natron, n = 97; Elementaita, n = 42), X^2 (5, n = 1376) = 279.28, p < 0.0001 (Kruskal-Wallis). Lesser flamingos spent least time feeding at Lake Bogoria (43%), followed by Oloidien (54%), Nakuru (63%), Sonachi (69%), Natron (76%), spending most time feeding at Elementaita (88%). Games-Howell post hoc tests (Table 5.1) showed statistically significant differences between almost all of the lakes with three notable exceptions; Sonachi and Nakuru (2.26, p = 0.990), Nakuru and Natron (6.07, p = 0.109) and Natron and Sonachi (3.81, p = 0.870).
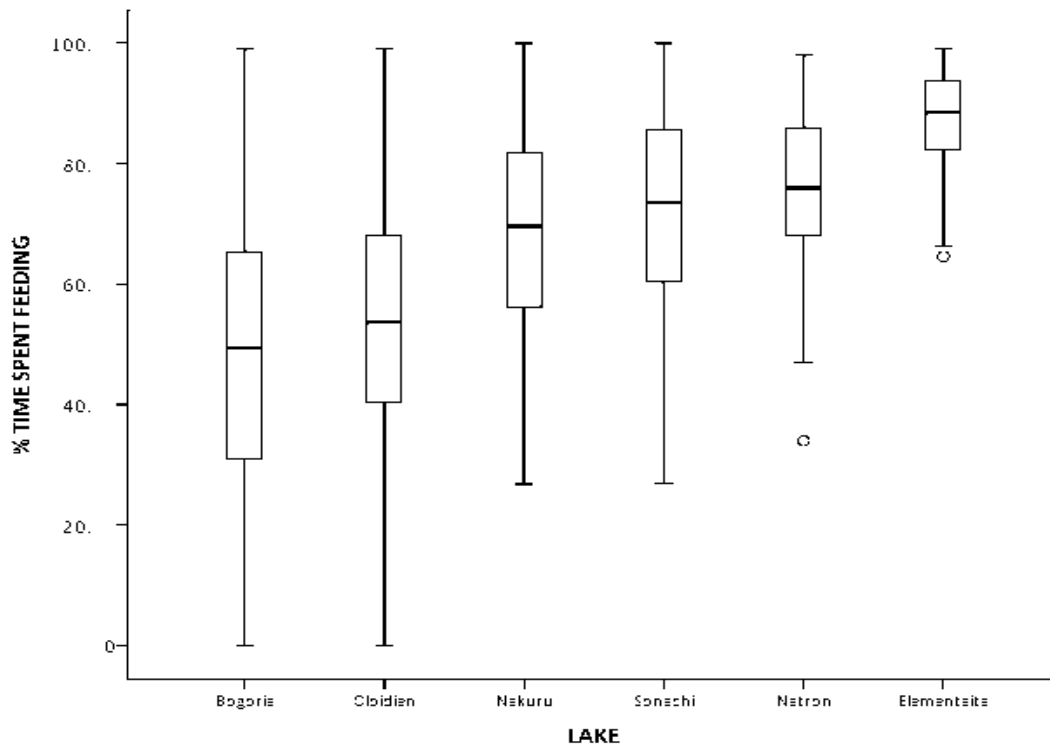
Figure 5.1: The average time spent feeding at lakes Bogoria, Oloidien, Nakuru, Sonachi, Natron and Elementaita; 95% confidence intervals depicted by the whiskers, box signifies the interquartile range and the median is represented by the black line within the box; circles indicate outliers

Table 5.1: Games-Howell results displaying the individual relationships between time spent feeding at lakes Bogoria, Oloidien, Nakuru, Sonachi, Natron and Elementaita; with statistically significant relationships identified by asterisks

	Bogoria	Oloidien	Nakuru	Sonachi	Natron	Elementaita
Bogoria		6.11**	21.62**	23.88**	27.68**	38.33**
Oloidien			15.51**	17.77**	21.58**	32.22**
Nakuru				2.26	6.07	16.71**
Sonachi					3.81	14.45*
Natron						10.65**
Elementaita						
**p < 0.0001; *p ≤ 0.001						

Investigating the 22 discrete observation periods, there was significant variance between many of the observation sites over the five year period, (Kruskal-Wallis) X^2 (21, n = 1376) = 414.87, p = 0.0001 (Figure 5.2). To further investigate these differences, the data is divided into subsets to look for spatial and temporal variation.
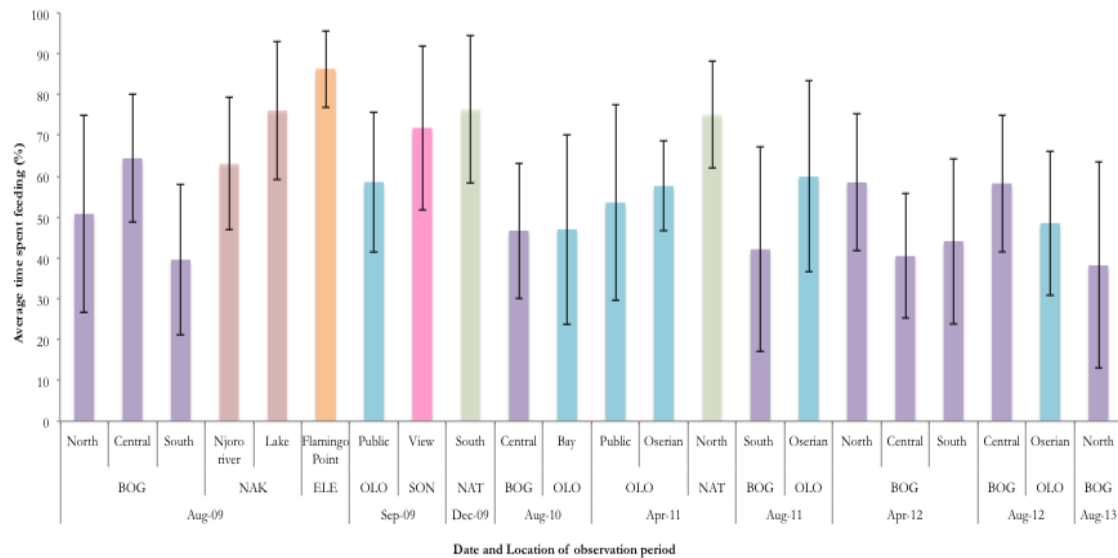
Figure 5.2: The average time spent feeding (%) throughout each observation period, error bars ± 1 standard deviation

In 2009, all 6 lakes were investigated (Figure 5.3), studying all three basins of Lake Bogoria and two separate sites at Lake Nakuru. Significantly less time was spent feeding at Lake Bogoria South than any of the other sites, X^2 (8, n = 400)) = 151.538, p < 0.0001 (Kruskal-Wallis). Lesser flamingos spent most time feeding at Lake Elementaita, closely followed by Nakuru main lake and Sonachi. Individually significant differences identified by Games–Howell post hoc tests are displayed in Table 5.2.

In 2010, the time spent feeding at the Central basin of Lake Bogoria was similar to the Time spent feeding at Lake Oloidien (47.3% and 48.1% respectively). No significant difference was found, however, in April 2011, there was significantly more time spent feeding at Lake Natron North (73.2%) than at either Oloidien Public or Oloidien Oserian (53.4% and 57.9% respectively), X^2 (2, n = 165)) = 40.41, p < 0.0001. No significant difference was revealed between the two Oloidien sites, only between Natron and both Oloidien Public and Oloidien Oserian (Games-Howell, p < 0.0001 in both cases).

In August 2011, significantly more time was spent feeding at Oloidien Oserian (62.7%) than Bogoria South (39.3%), U = 2916.5, z = 4.483, p < 0.0001, r = 0.32 (Mann-Whitney U test). Significantly more time was spent feeding at Bogoria North (56.1%) in April 2012 than in either Bogoria Central (39.8%) or Bogoria South (42.1%), X^2 (2,

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n = 147) = 29.68, p < 0.0001 (Kruskal-Wallis). No significant difference was revealed between Central and South, only between North and both other basins (Games-Howell, p < 0.0001 in both cases).

In August 2012, significantly more time was spent feeding at Lake Bogoria Central (56.9%) than at Lake Oloidien Oserian (51.3%), U = 3084.5, z = 3.958, p < 0.0001, r = 0.29 (Mann-Whitney U test).
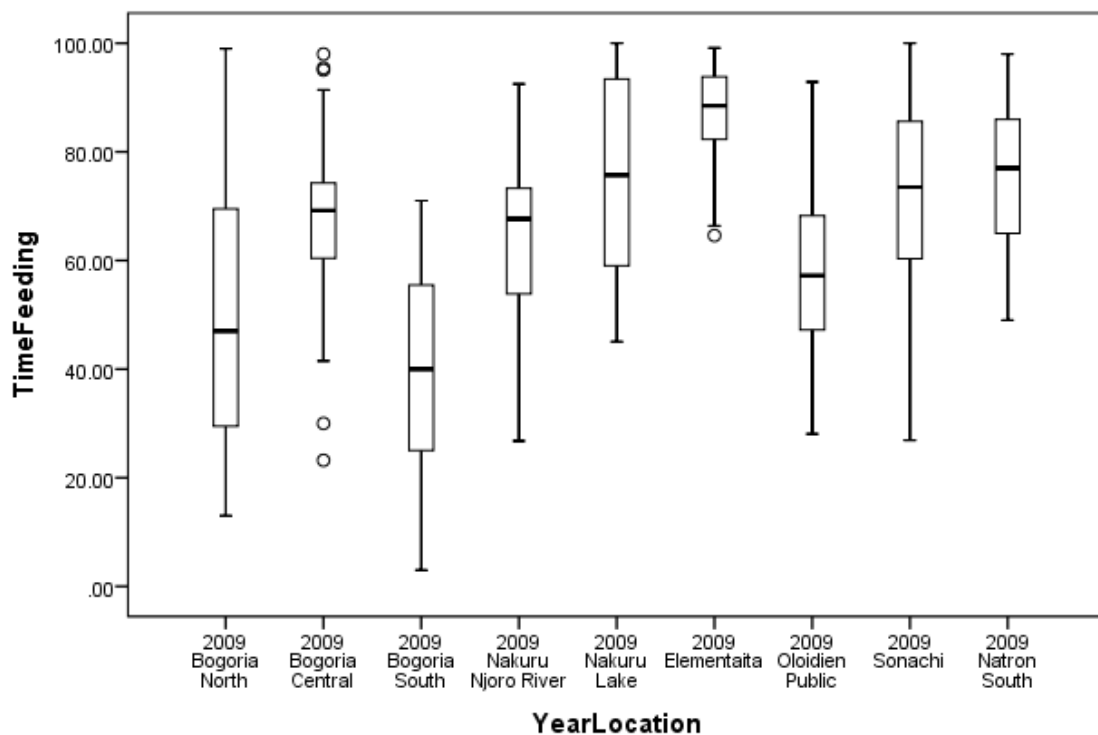
Figure 5.3: The average time spent feeding across all observation sites in 2009; 95% confidence intervals depicted by the whiskers, box signifies the interquartile range and the median is represented by the black line within the box; circles indicate outliers

Table 5.2: Games-Howell post hoc test results for the difference in time spent feeding between locations during 2009, with statistically significant relationships identified by asterisks

	Bogoria North	Bogoria Central	Bogoria South	Nakuru River	Nakuru Lake	Elemen-taita	Oloidien Public	Sonachi	Natron
Bogoria North		17.60**	11.24*	12.26	25.31***	35.50***	7.77	21.05**	25.59***
Bogoria Central			28.84***	5.34	7.71	17.90***	9.82	3.45	7.97
Bogoria South				23.50***	36.55***	46.74***	19.02***	32.29*	36.83***
Nakuru River					13.05	23.24***	4.49	8.78	13.32*
Nakuru Lake						10.19	17.54**	4.26	0.27
Elemen-taita							27.73***	14.45**	9.92*
Oloidien Public								13.27	17.81*
Sonachi									4.55
Natron									
***p < 0.0001; **0.0001 < p < 0.01; *0.01 < p <0.05									

Significantly more time was spent feeding in the Central basin of Lake Bogoria in 2009 (64.4%) than in all other basins, across all years (with the exception of the North basin in April 2012 (58.5%). Least time was spent feeding in the North basin of Lake Bogoria in 2009 (39.6%), closely followed by the Central basin in 2012 (40.5%). Statistically significant differences were found between the time spent feeding in different basins and over different years (Figure 5.4), X^2 (9, n = 685) = 115.87, p < 0.0001, individual Games-Howell test results highlight the significant differences (Table 5.3).

Significantly more time was spent feeding in the Central basin than in either the South or North basins across the entire five year period, X^2 (2, n = 685) = 26.398, p < 0.0001 (Kruskal-Wallis). Significant differences were not found between the North (44.2%) and South (41.3%), but were found between Central (51.1%) and both North and South (p < 0.05 and p < 0.0001, respectively).
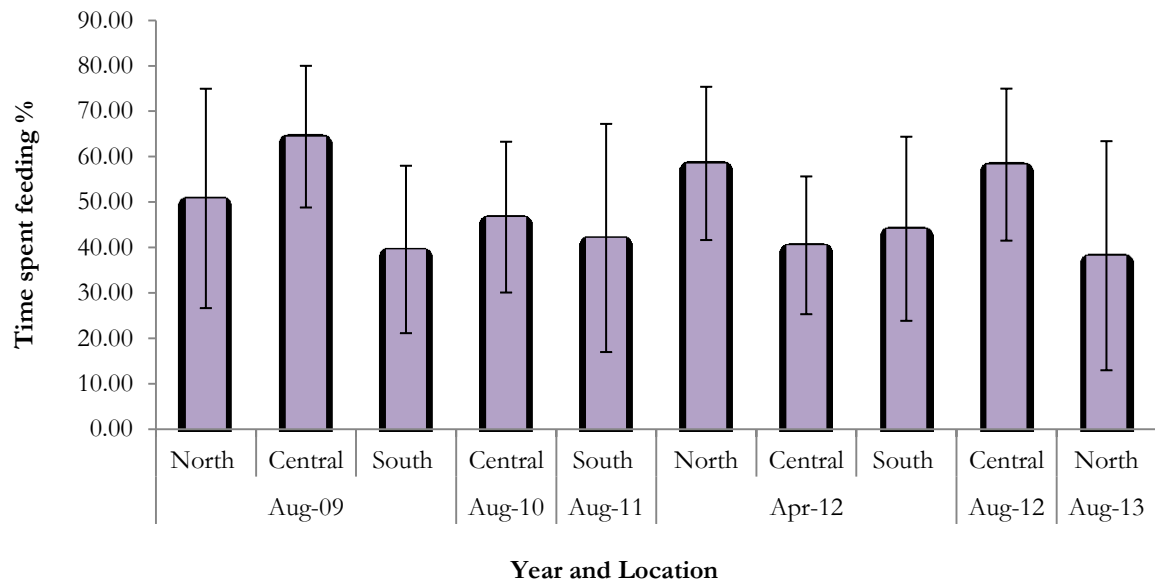
Figure 5.4: The average time spent feeding during each observation period at Lake Bogoria; error bars ±1 standard deviation

Table 5.3: Games-Howell post hoc test results for the difference in time spent feeding across each observation period at Lake Bogoria, with statistically significant relationships identified by asterisks

	2009 North	2009 Central	2009 South	2010 Central	2011 South	2012 North	2012 Central	2012 South	2012b Central	2013 North
2009 North		17.60**	11.24	4.04	8.71	7.71	10.56	6.69	7.44	12.62
2009 Central			28.84***	21.64***	26.31***	9.89	28.16***	24.29***	10.16*	30.22***
2009 South				7.2	2.53	18.95***	0.68	0.46	18.68***	1.38
2010 Central					4.67	11.74*	6.52	2.65	11.47***	8.58
2011 South						16.42***	1.85	2.02	16.15***	3.9
2012 North							18.26***	14.39*	0.27	20.32***
2012 Central								3.87	17.99***	2.06
2012 South									14.12*	5.93
2012b Central										20.05***
2013 North										
***p < 0.0001 **p ≤ 0.001 *0.001 < p ≥ 0.05										

5.3.2 Time spent feeding and food abundance

A statistically significant, strong negative correlation was identified between the average time spent feeding and the average biomass at each lake (*rho* = -.829, p < 0.05; Spearman's Rank Correlation Cofficient), indicating that increasing food abundance

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decreases average time spent feeding (Figure 5.5). No correlation was found between the biomass and time spent feeding for the individual lake visits as a result of the high variability of the average biomass available (Figure 5.6).
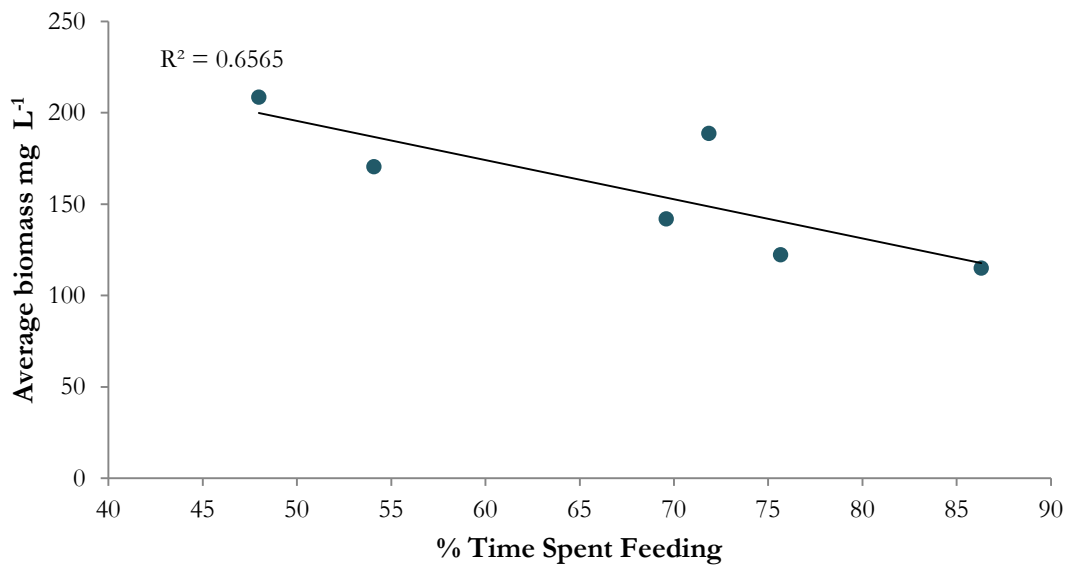
Figure 5.5: Negative correlation between time spent feeding and average biomass abundance at each of the six lakes
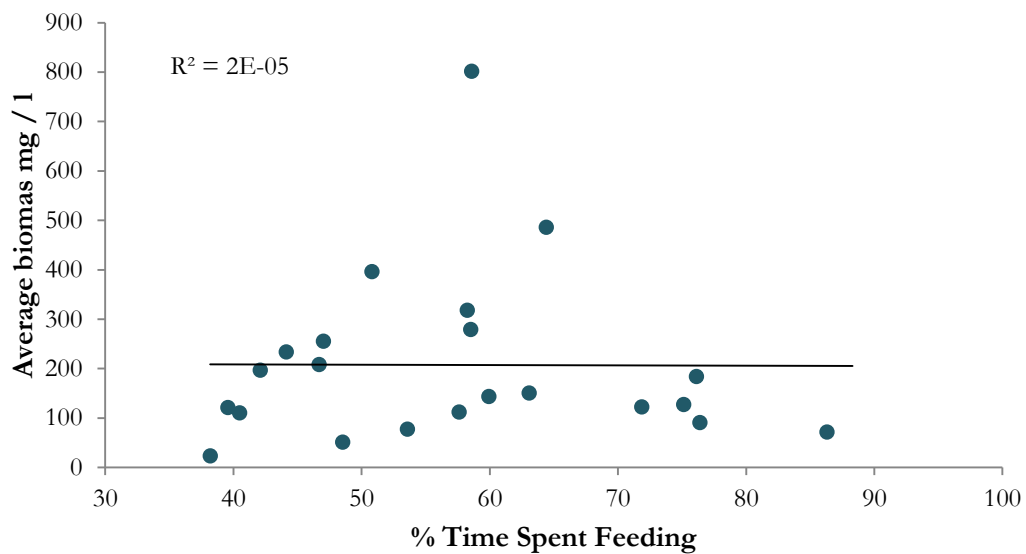
Figure 5.6: Average biomass availability of each observation block against the average time spent feeding

Focussing on Lake Bogoria, a strong positive correlation is seen between biomass and time spent feeding (Figure 5.7), (*rho* = 0.927, p < 0.01; Spearman's Rank Correlation Coefficient), indicating that as food abundance increases, time engaged in feeding activities also increases. This is the opposite relationship to the one generated when comparing across all the lakes.
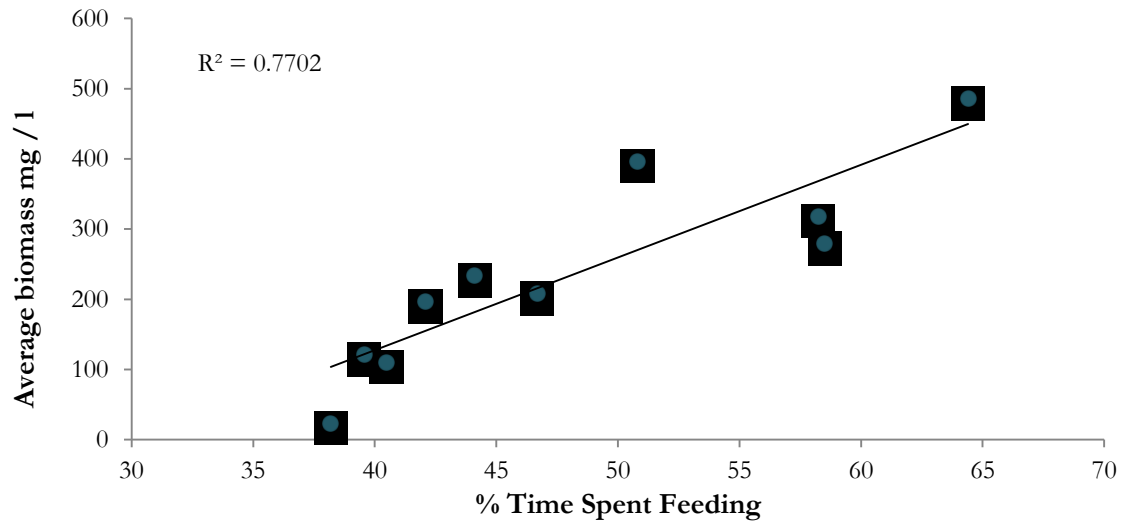
Figure 5.7: Positive correlation between time spent feeding and the biomass availability at Lake Bogoria

5.3.2.1 Time spent feeding when biomass is below 100 mg L^{-1}

There is a positive correlation between time spent feeding and biomass availability (Figure 5.10) when the biomass drops below 100 mg L^{-1} (*rho* = 0.700, p = 0.001; Spearman's Rank Correlation Coefficient) indicating that with a decreasing biomass, lesser flamingos spend less time feeding but it does not stop altogether. Feeding was occurring for almost 40% of the day, even when the biomass availability dropped to 23.27 mg L^{-1} in the North basin of Lake Bogoria in August 2013. Bogoria North in 2013 recorded both the lowest biomass and the least amount of time spent feeding by lesser flamingos. The relationship between time spent feeding and biomass below 100 mg L^{-1} is the opposite of that found when comparing across the six lakes.
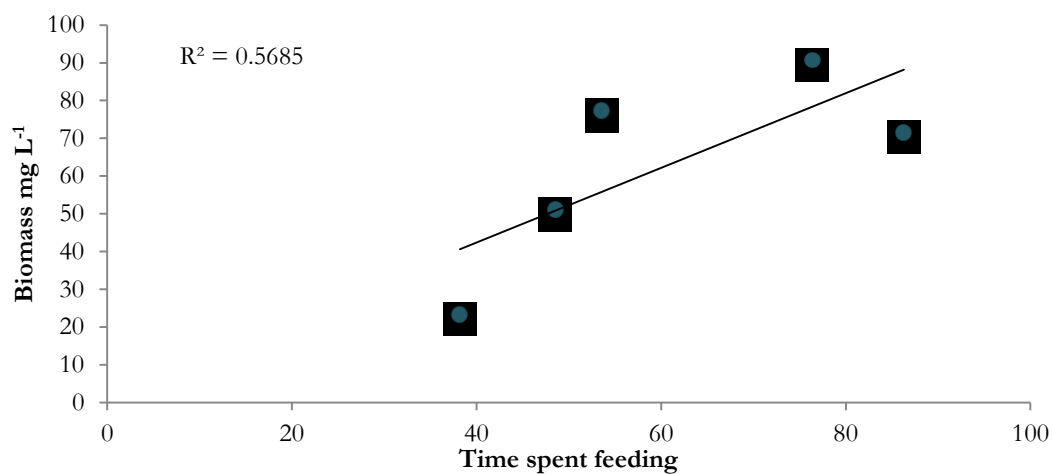
Figure 5.8: Positive correlation in time spent feeding by lesser flamingos when the biomass available is below 100 mg L^{-1}

5.3.3 Time spent feeding and food source

The biomass availability at lakes Natron and Elementaita is predominantly comprised of benthic or epipelic diatoms; whilst at Bogoria *A. fusiformis* dominates and at Lake Sonachi both diatoms and *A. fusiformis* were abundant. Lakes Oloidien and Nakuru are more complex in terms of their composition; in 2009 Oloidien's main biomass contributor was *A. fusiformis*, however since then it has been the smaller *A. fusiformis var minor*; lake Nakuru was principally diatoms at the Njoro river site but *Anabaenopsis abijatae* in the main lake. The lakes are described as diatom dominated, *A. fusiformis* dominated or other cyanobacteria dominated, as per Chapter 3 (Figure 5.9).

Significantly more time was spent feeding at diatom dominated lakes (83%) than either *A. fusiformis* (49%) or other cyanobacteria dominated lakes (56%), and significantly more time was spent feeding at other cyanobacteria dominated lakes than at *A. fusiformis* dominated lakes, X^2 (2, n = 1376) = 232.611, p < 0.0001 (Kruskal-Wallis). Games-Howell test results indicated significant differences between all pairs of variables at p < 0.0001.
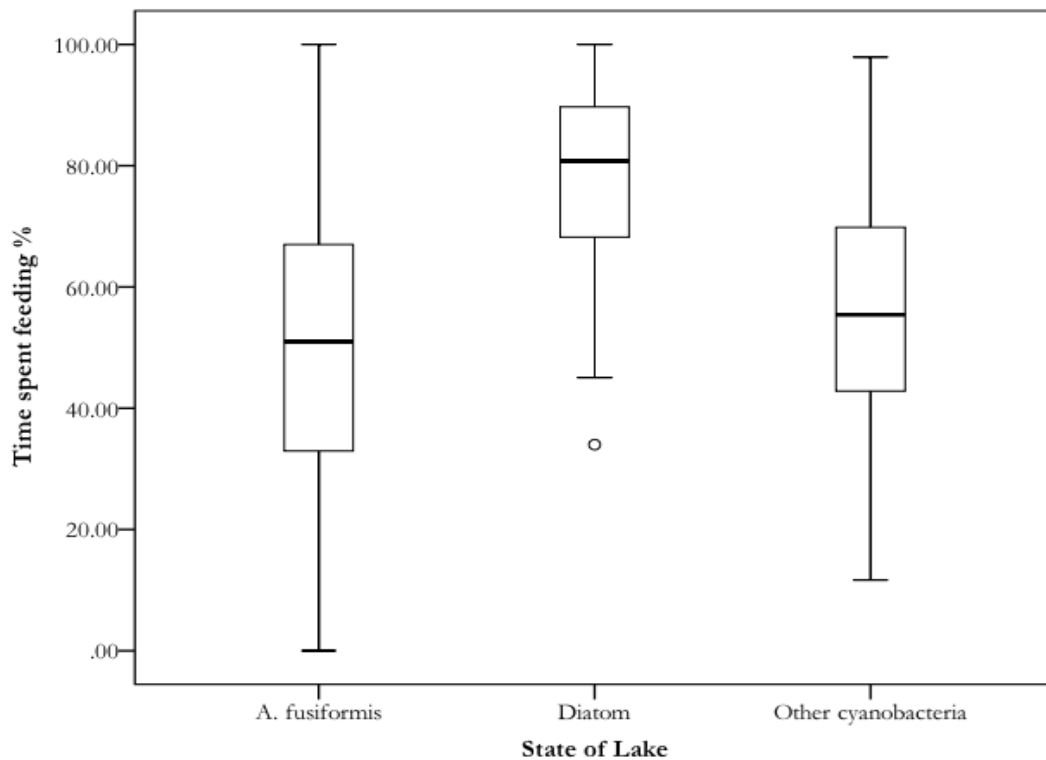
Figure 5.9: The difference in time spent feeding at dominated by different cyanobacteria; 95% confidence intervals are depicted by the whiskers, box signifies the interquartile range and the median is represented by the black line within the box; circles indicate outliers

5.3.4 Time spent feeding and age of bird

At Lakes Oloidien and Bogoria in April 2012, there were more juvenile lesser flamingos present than there had been throughout previous and subsequent observation blocks. At Oloidien, many of the juveniles were still being crop fed (Figure 5.10); 75 bouts were recorded in the dawn observation block and 62 in the evening, with the average duration being 14 minutes 26 seconds and 11 minutes 32 seconds respectively. There was no significant difference between the duration of crop feeding bouts at dawn ($Md = 862$, n = 15) and evening ($Md = 697$, n = 15) at the level of p < 0.5.

Figure 5.10: An adult lesser flamingo crop feeding a juvenile. Photo credit: Victoria Robinson

Due to the abundance of crop feeding at Oloidien it was not possible to accurately assess differences in the duration of feeding between different ages of birds. However, there was very little crop feeding observed at Lake Bogoria, which was supporting over 800,000 lesser flamingos and made finding a sub-population with adequate proportions of each age class possible in order to compare the time spent feeding across age class. Figure 5.11 displays the average percentage of each age class engaged in individual feeding (not crop feeding) over the course of the day. A statistically significant difference was found (Kruskal-Wallis) X^2 (2, n = 150) = 13.443, p = 0.001 and Games-Howell tests revealed significant results between juvenile ($Md = 67.5$, n = 50) and adult

(*Md* = 49, n = 50) at p = 0.002; juvenile and sub-adult (*Md* = 56.5, n = 50) at p = 0.006; no significant difference was found between adult and sub-adult.
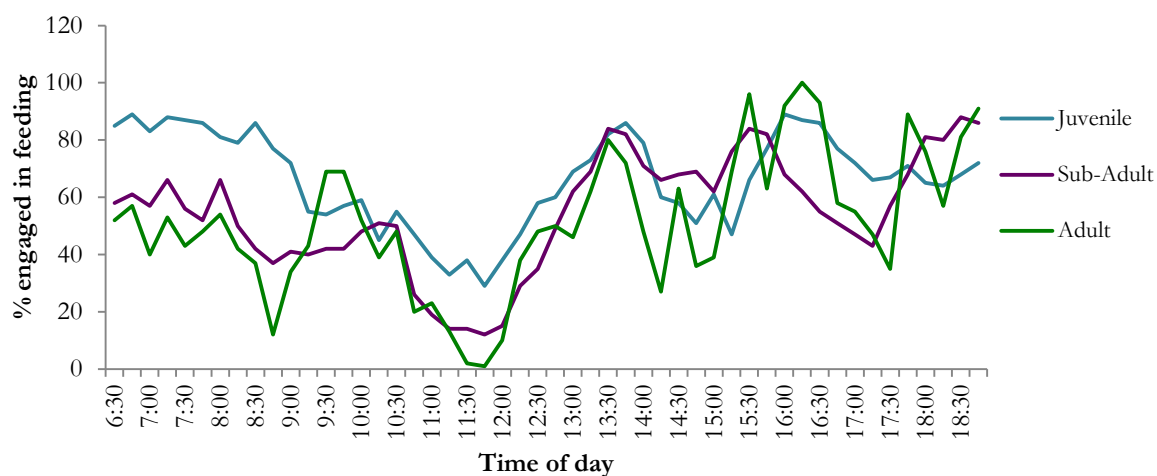
Figure 5.11: Average time spent feeding across the different age classes of lesser flamingo at Lake Bogoria in April 2011

5.3.5   Time spent feeding and time of day

Significantly less feeding occurred post-midnight (44%) than in any of the other time periods and there was a statistically significant difference between the average time spent feeding at different times of day (Figure 5.12), combining all observation periods and lakes (Kruskal-Wallis) X^2 (5, n = 1376) = 63.734, p < 0.0001. The afternoon recorded the most time spent feeding (63%), followed by the morning (60%), dawn (57%) and pre-midnight (51%). Table 5.4 displays the Games-Howell post hoc test results, with the individual significant differences identified.

Table 5.4: Games-Howell post hoc results for time spent feeding at different times of day; significant differences indicated by asterisks

	Dawn	Morning	Afternoon	Evening	Pre-midnight	Post-midnight
Dawn		4.97	8.23**	3.54	0.34	9.43**
Morning			3.26	1.44	5.31	14.40***
Afternoon				4.69	8.57*	17.66***
Evening					3.87	12.97***
Pre-midnight						9.09*
Post-midnight						
*** p < 0.0001; ** 0.0001< p ≤ 0.001; * 0.001 < p ≤ 0.05						

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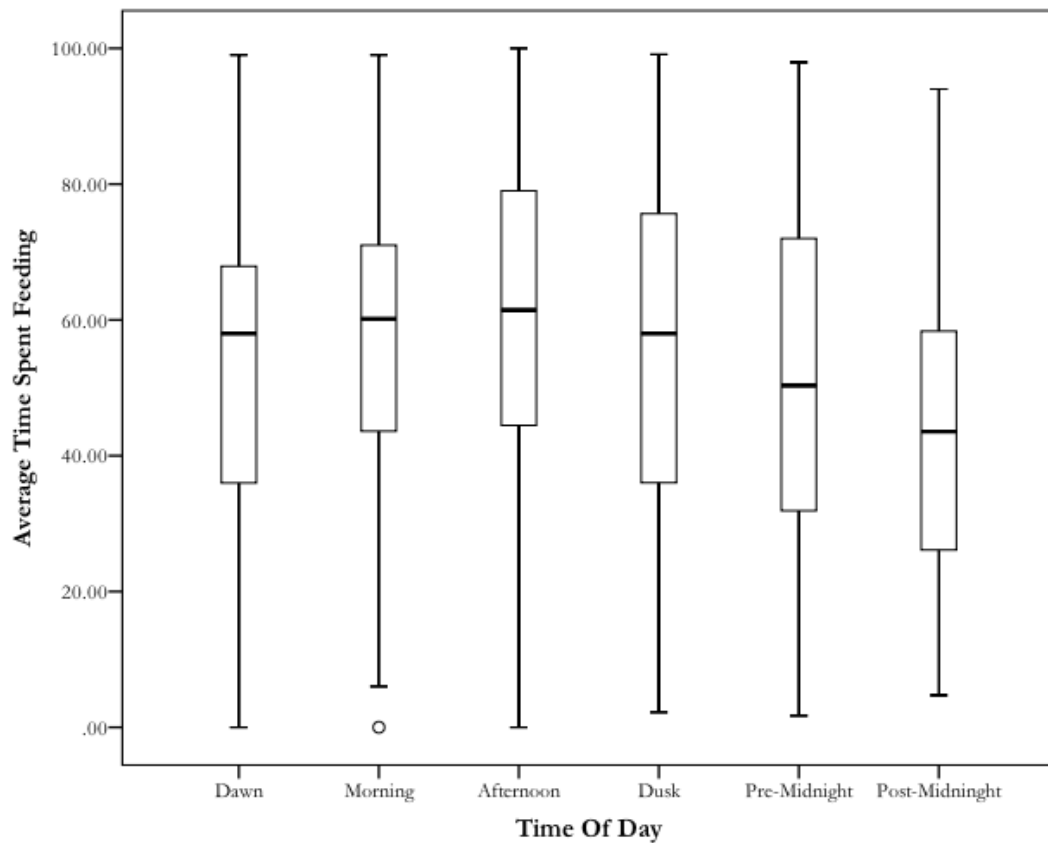
Figure 5.12: The difference in time spent feeding at different times of day at all sites; 95% confidence intervals depicted by whiskers, box signifies the interquartile range and the black line within the box represents the median; circles indicate outliers.

At Lake Bogoria, the majority of feeding occurred at dawn, closely followed by the afternoon and least feeding occurred during the pre- and post-midnight observation periods (Figure5.12). The pre-midnight period was most utilised for feeding at Lake Oloidien and least feeding occurred at dawn and post-midnight; the time spent feeding was relatively constant throughout the morning, afternoon and evening. At Lake Nakuru significantly less time was spent feeding during the afternoon than either the morning or evening. The evening was the most utilised time period at Lake Elementaita, although over 80% of time was spent feeding in all observation blocks. The majority of feeding at Lake Natron happened in the afternoon, as was observed at Lake Sonachi. There was a significant decline in time spent feeding at Lake Sonachi between the afternoon and evening.

The average time spent feeding at different times of day varied across the 6 lakes (Figure 5.13). Table 5.5 displays the average time spent feeding in each time period at

each lake and the Kruskal-Wallis test statistic result, p value and Games-Howell exceptions for each lake are displayed in Table 5.6

Table 5.5: The proportion, of each time of day block, spent feeding at each of the lakes

	Dawn	Morning	Afternoon	Evening	Pre-midnight	Post-midnight
Bogoria	55.76	47.26	52.51	44.79	42.22	42.54
Oloidien	43.57	56.03	56.71	55.78	71.74	43.81
Nakuru	-	72.66	62.55	74.66	-	-
Natron	67.08	73.69	81.23	76.00	-	-
Elementaita	-	80.47	86.67	92.17	-	-
Sonachi	-	71.71	91.00	49.87		

Table 5.6: The Kruskal-Wallis test statistic result, p value and Games-Howell exceptions for each feeding behaviour; Bogoria df = 5, n = 685; Oloidien df = 5, n = 396; Nakuru df = 5, n = 82; Natron df = 5, n = 98; Elementaita df = 5, n = 42; Sonachi df = 5, n = 41; D = Dawn, M = Morning, A = Afternoon, E = Evening, Pre – Pre-midnight, Post = Post-midnight

Feeding Behaviour	Kruskal-Wallis test statistic	p value	Games-Howell exceptions (no statistically significant differences, p > 0.05)
Bogoria	34.015	< 0.001	D & A; M & E; M & pre; M & Post; A & E; E & pre; E & Post; Pre & Post
Oloidien	51.782	< 0.001	D & Post; M & A; M & E; A & E
Nakuru	7.517	< 0.05	M & E
Natron	10.389	< 0.05	M & E; D & M
Elementaita	8.118	< 0.05	M & A
Sonachi	31.807	< 0.001	None
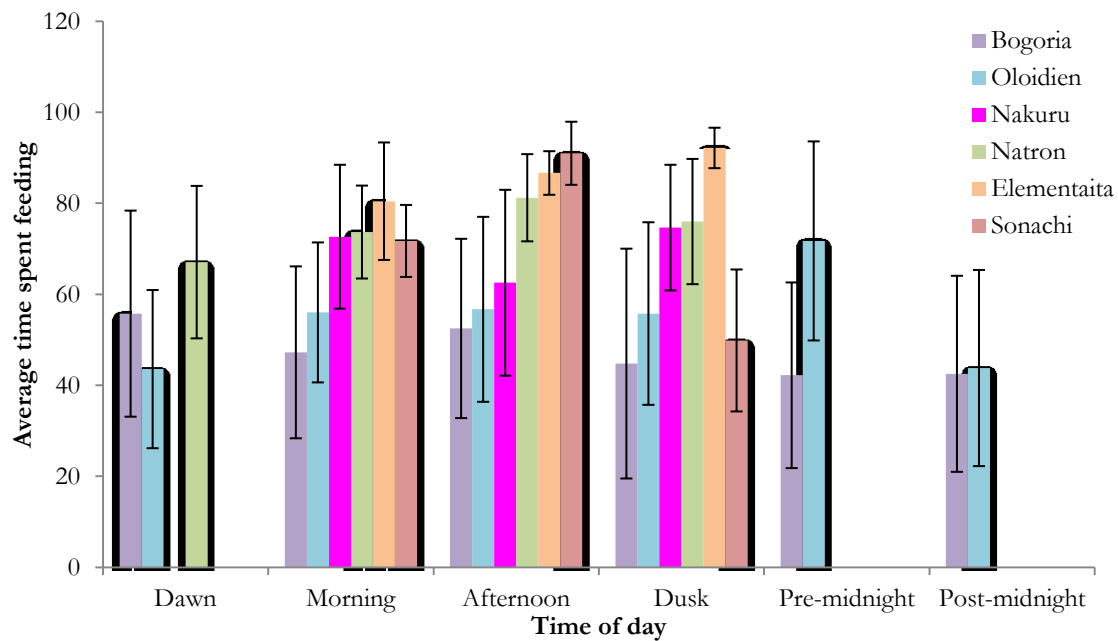
Figure 5.13: The average time spent feeding throughout differing periods of the day at all six study lakes

Time spent feeding is time series data, allowing autocorrelations to be conducted to assess for randomness and whether the time series data appears to be stationary or non-stationary.

Figures 5.14 displays the autocorrelation plots for the daylight hours observation periods and three distinct patterns can be seen in the plots. In all observation periods, with the exception of Lake Natron in both 2009 and 2011, the autocorrelations show that the time series data is non-stationary and as they all have positive significant autocorrelation at a lag of 1, each single observation of feeding level is linked to the observation that was immediately prior to it. As the observation periods were between 11 and 13 hours in duration, the autocorrelations were tested up to a lag of 12 (ca. n/4). A number of the observation periods showed statistically significant negative autocorrelations at a lag of 7 or higher indicating that there is a cyclic pattern in the duration of feeding, where the lags correlations are approaching zero but not negative, there is also an indication of a decreasing feeding trend over the initial few hours of the daylight. At Lake Natron, the correlations seem to mainly oscillate around zero, showing significance at very few lag values. This indicates that the time series is stationary; in this instance that there very little change in the percentage of birds feeding from one observation to the next.

There are three distinct patterns seen plotting the deviation from the mean; Bogoria South 2009, Oloidien Public 2011 and Natron North 2011 are good examples of each of these and Figure 5.15 displays the deviation from the mean (39.56, 53.57 and 75.125 respectively). These show a single cycle from high feeding levels to low and back to high throughout the daylight hours (Lake Bogoria South in 2009); a double oscillation from low to high to low to high and back to low (Lake Oloidien public in 2011); and no pattern, with smaller deviations from the mean showing similarity throughout the entire day (Natron North in 2011).
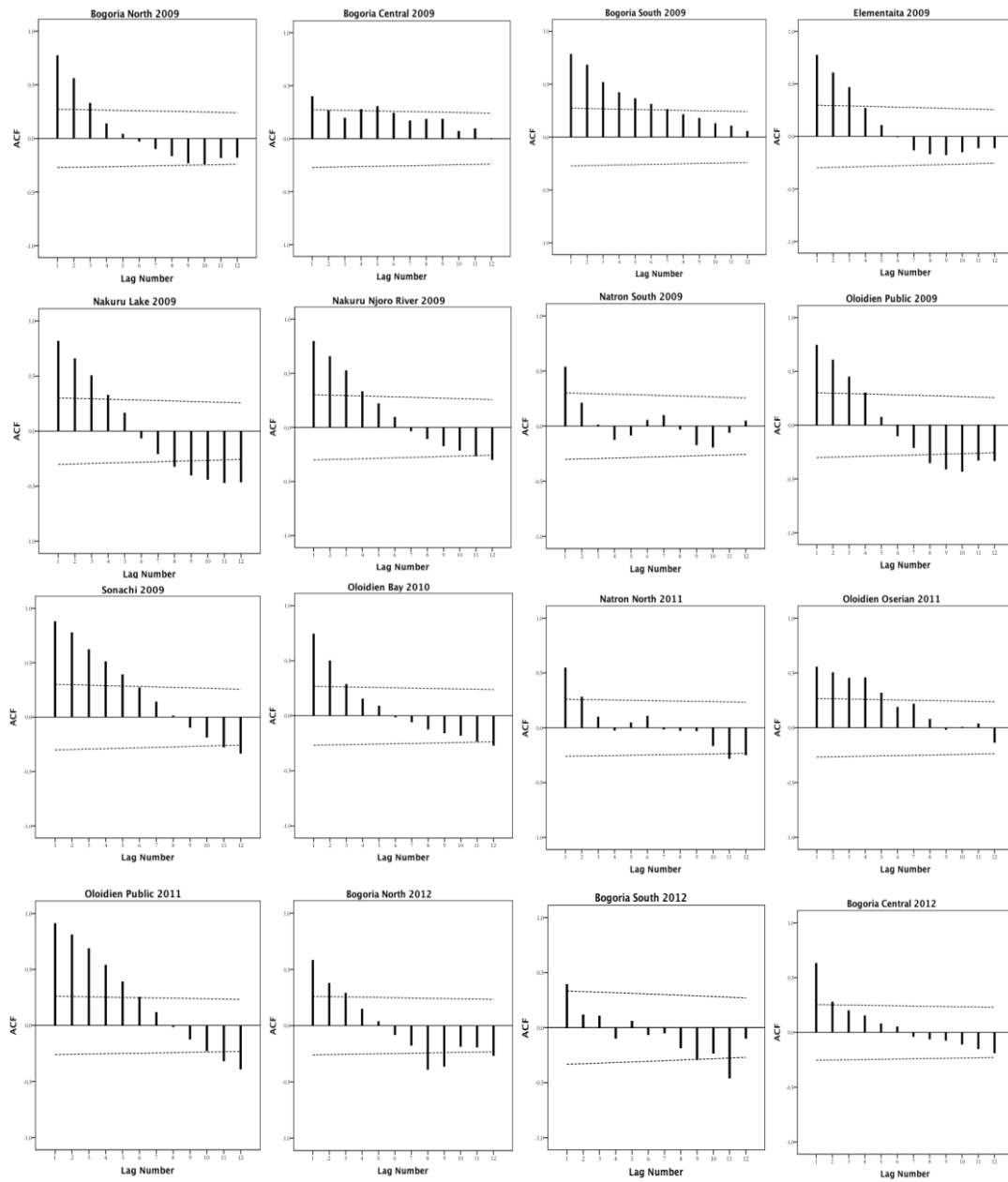
Figure 5.14: Autocorrelation plots for the time spent feeding throughout each of the observation periods; dashed lines indicate the positive and negative 95% confidence intervals

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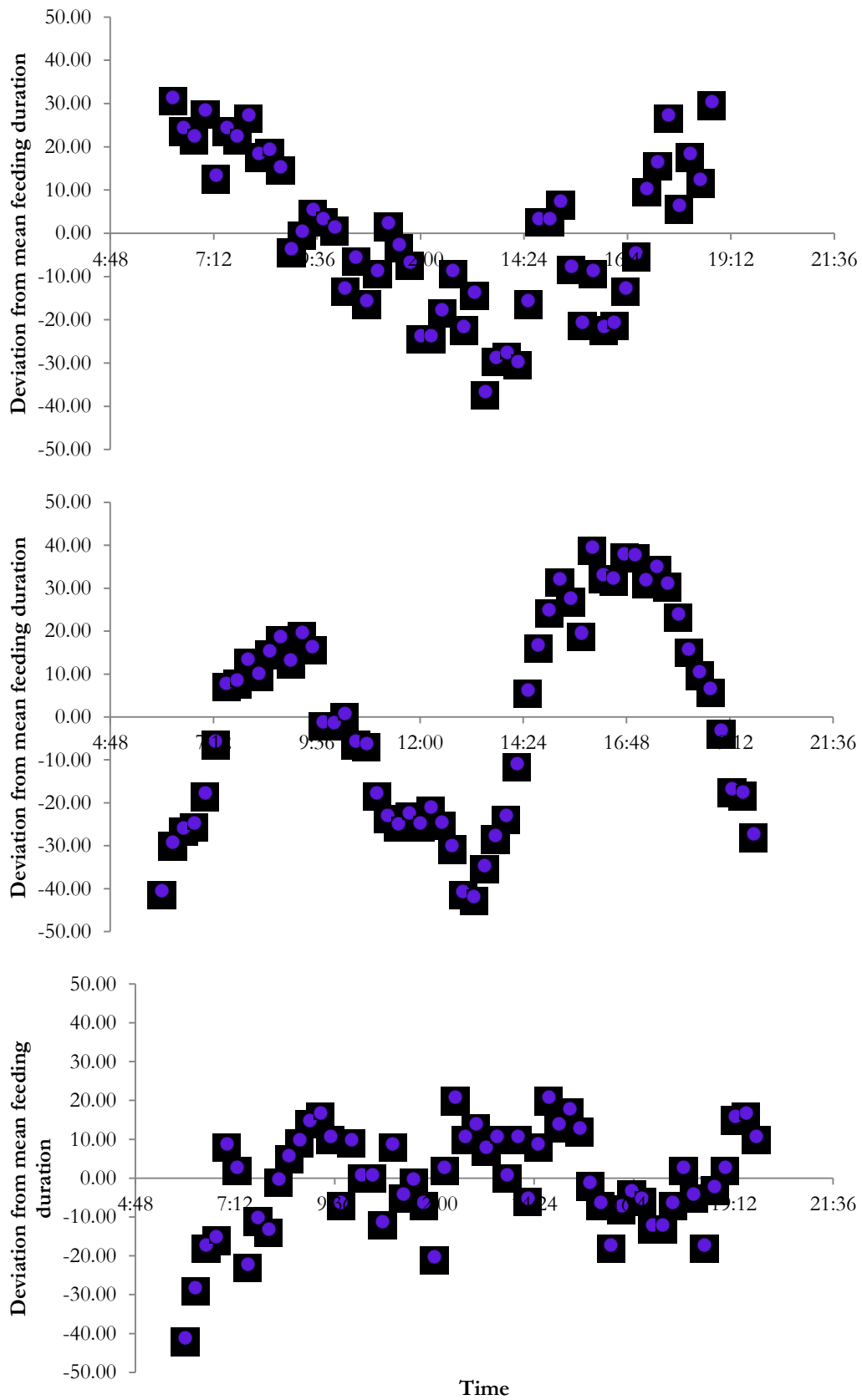
Figure 5.15: The deviation in percentage of flamingos engaged in feeding from the mean at Lake Bogoria South basin in 2009 (Top), Lake Oloidien public in 2011 (Centre) and Lake Natron North in 2011 (Bottom)

Figure 5.16 exhibits the autocorrelation for the 24-hour periods up to a lag of 24, as there were 96 observation points over the period (n/4). All show significant positive correlation in the initial lags indicating that the level of feeding is dependent on the prior level with low feeding following low feeding and high following high. There is an indication of an oscillating pattern in all observation periods with Bogoria South (2009) and Bogoria North (2013) showing the strongest autocorrelations.
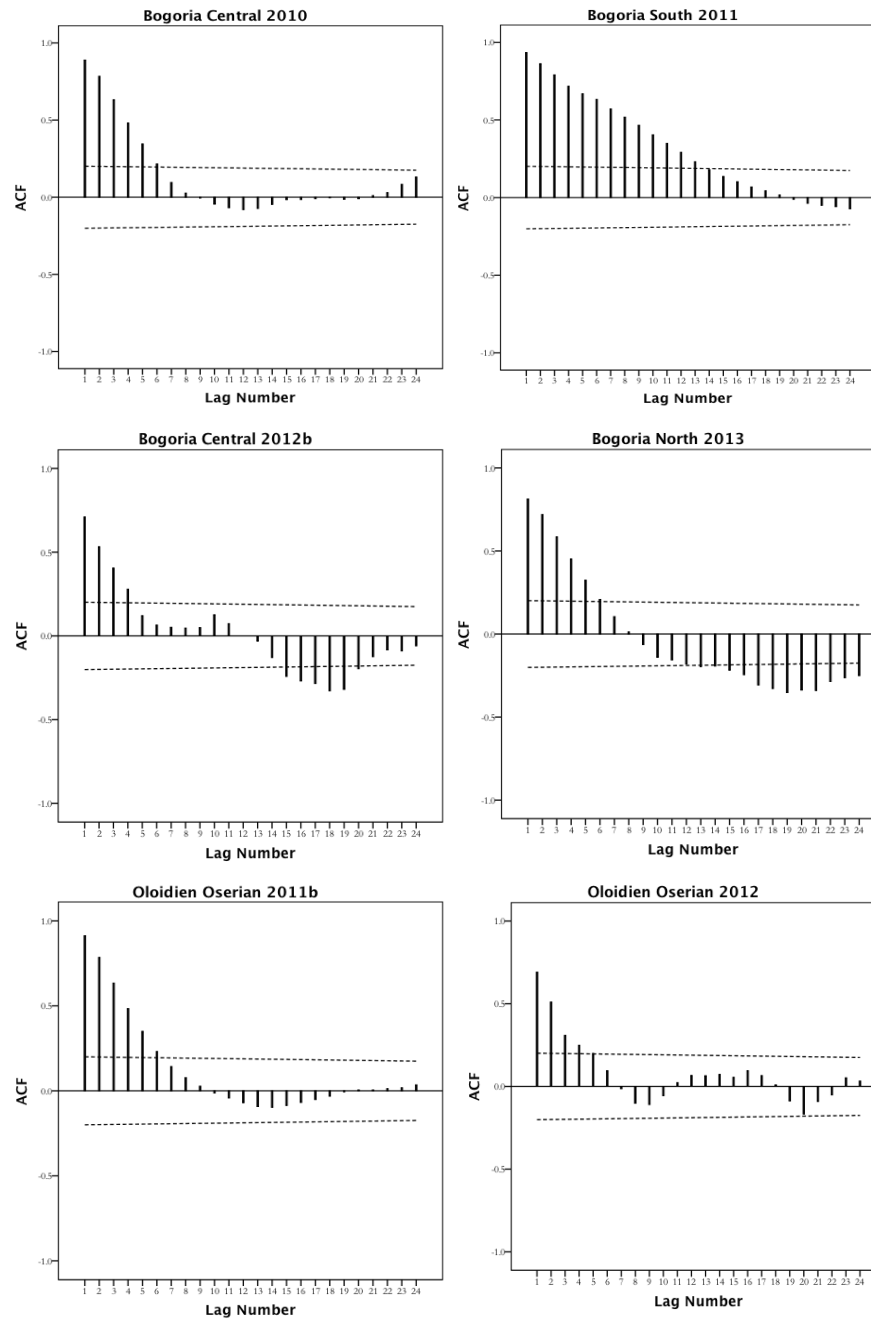
Figure 5.16: Autocorrelation functions of feeding time series for all 24-hour observation periods; dashed line indicates positive and negative 95% confidence intervals

5.3.5.1 Time spent feeding at night versus during the day

Six observation periods spanned the entire 24-hour and there was no significant difference between time spent feeding during the day (54%) and at night (46%), $U = 35977$, $z = -1.676$, $p = 0.07$, $r = 0.33$ (Mann-Whitney U test). At the South basin of Lake Bogoria in 2011, the population remained relatively constant (+/- 10%) however, significantly more time was spent feeding at night than during the day, $U = 1871$, $z = 5.312$, $p > 0.0001$, $r = 0.45$ (Mann-Whitney U test). None of the other individual observation periods showed any significant difference (Figure 5.17) and therefore indicates that calculating the time spent feeding throughout the daylight hours, gives a relatively accurate indication of overall feeding duration throughout 24 hours as there is minimal difference between them.
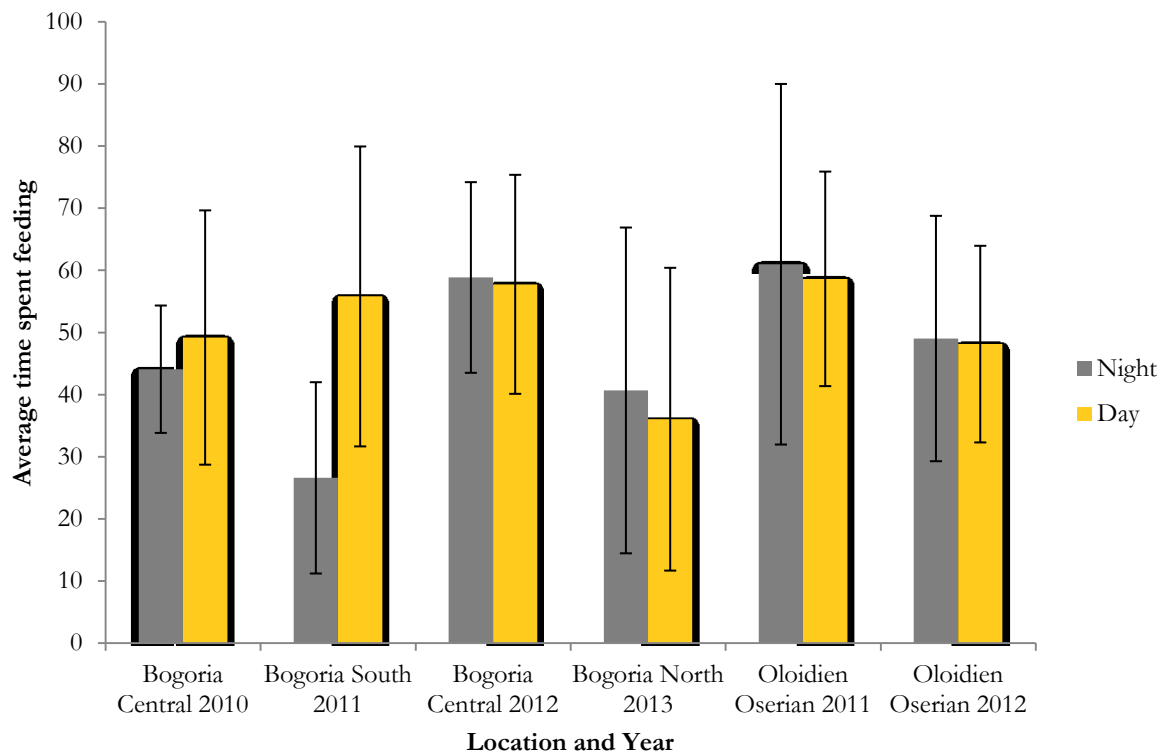
Figure 5.17: The average time spent feeding throughout the night and day in the six 24-hour observation periods

5.4   Discussion

The time that lesser flamingos spent feeding varied significantly both between and within lakes. Across the six lakes, an inverse correlation between time spent feeding

and biomass availability showed that a declining abundance led to a greater time investment in feeding and *vice versa*. Therefore at higher food abundances it appears that lesser flamingos are able to ingest the required amount of food in a shorter time, enabling them to devote more time to other activities (Smith & Sweatman, 1971), a relationship that has also been suggested to occur in the American flamingo (Arengo & Baldassarre, 1995). This is aligned with optimal foraging theory, as lesser flamingos appear to be maximising their feeding efficiency by acquiring their required energy intake in the shortest amount of time. It was expected that there would be a Holling's functional response type II or III as has been seen in greater flamingos (Deville *et al.*, 2013) but in practice the opposite relationship occurred.

A Hollings type I functional response was observed when looking at the time spent feeding and food availability at Lake Bogoria as expected in filter feeders (Holling, 1965; Jeschke *et al.*, 2004). Increasing food abundance correlates with an escalation in the time devoted to feeding, similar to the relationship found in Caribbean flamingos (Este & Casler, 2000) and could indicate that Lake Bogoria is an important feeding lake in the East African Rift Valley. Lake Bogoria often hosts large flocks of bright pink lesser flamingos, in breeding plumage, engaging in courtship dances and building practice nests along the shoreline. I did not see any courtship dancing at any of the other lakes and the increase in time spent feeding with high food abundance observed at Lake Bogoria could indicate that is critical biomass threshold, beyond which feeding increases to prepare for breeding. Pennycuick and Bartholomew, 1973, suggested that if breeding attempts occur in relation to their food supply then whenever food is available in high concentration, intense feeding would occur to build up fat reserves. This would allow for travel to other lakes to assess whether conditions are suitable for breeding and also restock energy reserves to compensate for egg production and incubation. I propose that Lake Bogoria is often the final feeding destination before a breeding event at Lake Natron and that lesser flamingos could potentially be using each of the lakes for different reasons. Lesser flamingos could be using some lakes to 'top up' on food whilst some others may be required to fully restock their reserves.

Pennycuick and Bartholomew (1973) also calculated a minimum required food concentration of 80-150 mg L^{-1} for non-breeding flamingos, whilst Vareschi (1978) calculated a lower limit of 140 mg L^{-1} and reported that captive birds stopped feeding

when the concentration dropped below 100 ± 5 mg L^{-1} because it was not energetically effective to feed. In this study, five of the observation periods, across four lakes had an average biomass below the critical 100 ± 5 mg L^{-1}. Feeding was still observed at all of these lakes, at lake Elementaita in 2009, an availability of 71.5 mg L^{-1} caused lesser flamingos to invest 86% of their time in feeding whilst the lowest concentration was recorded at Bogoria in 2013, 23.27 mg L^{-1}, when 38% of their time was invested in feeding. It was suggested that 80% was the maximum amount of time that could be devoted to feeding and still allow for adequate drinking, preening and resting (Pennycuick & Bartholomew, 1973), however, this study identified times when over 90% of time was spent feeding, indicating that there may be a trade-off between energy requirement and maintenance.

When food concentration is below 50 mg L^{-1} and feeding is occurring for 80% of the time, lesser flamingos would obtain ~18 g of their daily requirement, assuming a clearing rate of 31.8 L hr^{-1} and a feeding efficiency of 64 % (Vareschi, 1978). In the North basin of Lake Bogoria in 2013, lesser flamingos would have obtained ~ 9.12 g of their daily requirement (or 12.8%) if they were feeding for 80% of their time. They were, however, only feeding for 38% of the time, giving rise to just 4.53 g, an amount that would not be able to sustain them in the long term. Depending on their energy reserves when arriving at the lake, they may be able to survive at such low densities for a short while but would have to find a richer source of food to prevent starvation (Tuite, 1979). In 2013, the North basin was experiencing large inflows of freshwater, bringing with it sediment and an increase in light attenuation which could have caused truncation of the euphotic zone and consequently a drop in primary productivity (Sadro & Melack, 2012). Within the Central and South basins, there were also increased freshwater influx however, they were not as extreme and there were areas of the lake that did still support biomass availability over 100 mg L^{-1}. Thus, it is reasonable to assume that the lesser flamingos in the North basin may have been utilising the abundant freshwater available to bathe, preen and drink before flying south down the lake in search of a more abundance food patch as birds were frequently seen flying both North and South along the lake. I was able to visit the South basin briefly in 2013 and found that feeding was occurring with a greater frequency than was observed in the North. The lake road was inundated with water making it very difficult to access

the South and, therefore, it wasn't possible to quantify feeding at all locations of Lake Bogoria.

Alternatively, in keeping with optimal foraging theory, lesser flamingos may be preferentially selecting small-localised areas of high food density. The average biomass available was below 100 ± 5 mg L^{-1} at five lakes, however, there were often small areas that had much higher abundances, such as areas of sunken or sedimented *A. fusiformis,* high-density algal scums or benthic pockets rich in diatoms. At times of low food density in Lake Nakuru, Vareschi (1978) reported an increase in swim feeding alongside high-density surface colonies of *A. fusiformis,* also witnessed at Lake Bogoria (Tuite, 1981).

The amount of time that lesser flamingos spent feeding varied between 38% and 91% with the majority of observation periods recording between 45-65% of time spent feeding, in keeping with the 52% recorded at Lake Nakuru in the 1970s (Vareschi, 1978). Overall, the highest percentage of feeding occurred in the afternoon period and the lowest occurring in post-midnight and dawn. This finding is contradictory to those on the American (Bildstein *et al.*, 1991) and greater (Britton *et al.,* 1986) flamingos which found a reduction in feeding throughout the hottest period of the day. The lakes in this study, whilst all feeding sites for lesser flamingos, had contrasting compositions with the lakes dominated by diatoms experiencing a significantly larger proportion of time feeding than those dominated by *A. fusiformis* or other smaller cyanobacteria. Therefore, by combining all the lakes the results may be skewed as feeding needs to occur for much longer in some.

A reduction in time spent feeding was occasionally observed during the hottest part of the day ~11am-2pm, however, this crosses both the morning and afternoon periods and therefore may not be accurately represented in overall time spent feeding but can be observed in Figure 5.16. This coincides with the theory that feeding and processing is energetically more costly at high temperatures (Pennycuick & Bartholomew, 1973) and therefore often restricted to cooler periods of the day. Soon after 2pm, the wind often picked up, stirring up the water column and creating movement. This frequently corresponded with an increase in feeding, possibly due to a higher concentration of food at the surface of the water.

Juvenile lesser flamingos spent significantly more of their time feeding than either adults or sub-adults. There are a number of possible explanations for this; firstly, juveniles may not be as efficient at feeding as older birds and therefore may have to feed for longer to obtain their energy requirement; secondly, I occasionally observed crèches of juveniles with a few adults interspersed between them, therefore they may be able to feed without fear of predation as the adult birds could be keeping watch and alert them if there is danger; finally, as they are growing more quickly and have limited energy reserves, they may require more food for maintenance and growth than adults. Figure 5.12 indicates that the adult lesser flamingos have the most erratic feeding pattern, jumping from 39 % feeding to 96% feeding in the space of 30 minutes.

It has been hypothesised that flamingos leave lakes when the food is not suitable (Pennycuick & Bartholomew, 1973), however, throughout this study; flamingos were persisting at lakes with seemingly very little food, whilst lakes with abundant food were housing relatively small populations. There may be more than one explanation as to why mass movements of lesser flamingos occur; they may engage in trade-offs between food availability, predation risk, food quality, crowding, disturbance or suitability for non–feeding activities (Mysterud & Ims, 1998) such as preening.

This chapter has shown that the time spent feeding varies within and between lakes and is correlated with food abundance both positively (at Lake Bogoria) and negatively (across all study lakes). The distribution of lesser flamingos between different lakes has been correlated with food availability, however, time spent feeding also varies within lakes, therefore distribution and food availability is explored in Chapter 6.

Chapter 6

Chapter 6 Local lesser flamingo (*Phoeniconaias minor*) distribution and density is determined by both abundance and distribution of food resources

Abstract

Animals often distribute themselves in accordance with food abundance. This study investigated how lesser flamingos distributed themselves across Lake Bogoria in relation to the food available. A significant positive correlation was identified between the average standing crop (biomass mg L^{-1}) and the local population of lesser flamingos on the lake (*rho* = 0.554, p < 0.01). The flock density varied between lakes suggesting that the food source impacts how densely flamingos flock together. Lesser flamingos where most clumped at Lake Bogoria (1095 g m^{-2}) where they were feeding on *Arthrospira fusiformis* and most dispersed at Lake Elementaita (25.5 g m^{-2}) where they were feeding on diatoms. The feeding behaviour being utilised also had a significant effect on flock density (p < 0.001) as when engaging in wet mud feeding flamingos were very dispersed but when engaged in STF1 they were densely clumped.

6.1 Introduction

The distribution and density of lesser flamingos has been studied only once, prior to this study, in relation to food availability, a study carried out in the 1970s (Tuite 1979; 2000). Tuite concentrated on the distribution between lakes in relation to the average abundance of food resources, rather than looking at how lesser flamingos distribute themselves within lakes. Two distinct distribution patterns were identified, firstly a 'clumped' pattern where the majority of the birds were aggregated at one or two of the lakes (usually Bogoria, Nakuru, Magadi and Natron). The second pattern was more dispersed with the population spread between many lakes, few of which held more than 100,000 (ibid.).

The standing crop of surface *A. fusiformis* (formerly *Spirulina*) was studied at both Lake Bogoria and Lake Nakuru, linking dense blooms (< 0.12 g L^{-1}) to the presence of over 1.2 million lesser flamingos in January 1974 (Tuite, 1979; 2000). As *A. fusiformis* density dropped throughout the year to 0.03-0.05 g L^{-1}, a significant decline in lesser flamingos

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followed (ibid.). A similar situation was recorded at Lake Bogoria where the density of *A. fusiformis* was < 0.02 g L^{-1} and the number of lesser flamingos fluctuated between 500 and 6,000 (ibid.) At this time, it was reported that many of the birds were feeding along scum lines where the density of *A. fusiformis* was 2–6 times higher than the average surface standing crop (ibid.), indicating an ability to selectively feed.

Tuite (2000) found that when *A. fusiformis* was not available throughout all East African soda lakes extreme fluctuations in the standing crop were observed. Significant declines in *A. fusiformis* often precluded a switch in the feeding of lesser flamingos to their secondary food source, benthic diatoms (ibid.). These two, different, components of their diet were the cause of the difference between the 'clumped' and 'dispersed' population patterns observed throughout the East African Rift Valley (ibid.).

Tuite (2000) suggested that the widespread availability and relatively small changes in diatom standing crop across space and time, created a constant reserve food source which was able to sustain the population but not in high abundance at a single lake. Feeding on diatoms required a different behaviour (as discussed in Chapter 4) with lesser flamingos upending to reach the mud at the bottom of the lakes, mentioned by Tuite (ibid) but not quantified.

The reliance on diatoms as a food source also generated a different flock pattern within lakes, not just between them (ibid.). Average biomass density of lesser flamingos was 755 g m^{-2} if *A. fusiformis* was abundant (assuming an average mass of 1,400 g), whilst a diet of diatoms produced a much-reduced density of 20.5 g m^{-2}.

This chapter builds on the work of Tuite (1979; 2000) but aims to investigate the local density of lesser flamingos within lakes and explore whether different feeding behaviours also generate different densities, through answering the following questions:

- Do lesser flamingos distribute themselves on a lake in accordance with the distribution of food?
- Do different food sources give rise to different flock densities?
  - Do diatoms generate a more dispersed feeding pattern, as seen in the 1970s?
- Do different feeding behaviours have an impact on flock density?

It will do this by addressing the following null hypotheses:

- Distribution of lesser flamingos is uniform throughout any given lake
- Flock density is independent of food source
- Flock density is independent of feeding behaviour

6.2   Methods

This study incorporates behavioural observations with flock density calculations and cyanobacteria, diatom and zooplankton calculations from August 2009 to August 2013 at lakes Bogoria, Oloidien and Elementaita. Full details of methods and study sites are contained within Chapter 2.

6.3   Results

6.3.1   Lesser flamingo distribution and standing crop

A significant positive correlation (Figure 6.1) was identified between the standing crop (mg L^{-1}) of *A. fusiformis* and the lesser flamingo flock size at eight sites along the shore of Lake Bogoria in August 2012 (*rho* = 0.554, p < 0.01; Spearman's Rank Correlation Coefficient).   The second largest local population was located in the South basin, where the standing crop was the highest (Mean 616.05 mg L^{-1}) and the smallest population was located in the north of the Central basin where standing crop was the lowest (29.48 mg L^{-1}). The largest population was located at the Loburu delta in the central basin, where the *A. fusiformis* abundance was 172.47 mg L^{-1}, much lower than in the South basin. The average standing crop and lesser flamingo population for each site are displayed in Table 6.1.

Table 6.1: The average standing crop and local lesser flamingo population size for eight sites, from North to South, at Lake Bogoria in August 2012

	Site							
	1	2	3	4	5	6	7	8
Average standing crop mg L^{-1}	14.87	48.69	95.50	29.48	172.47	81.06	199.73	616.05
Average lesser flamingo population	11150	6800	19800	4550	58800	5700	8600	56100
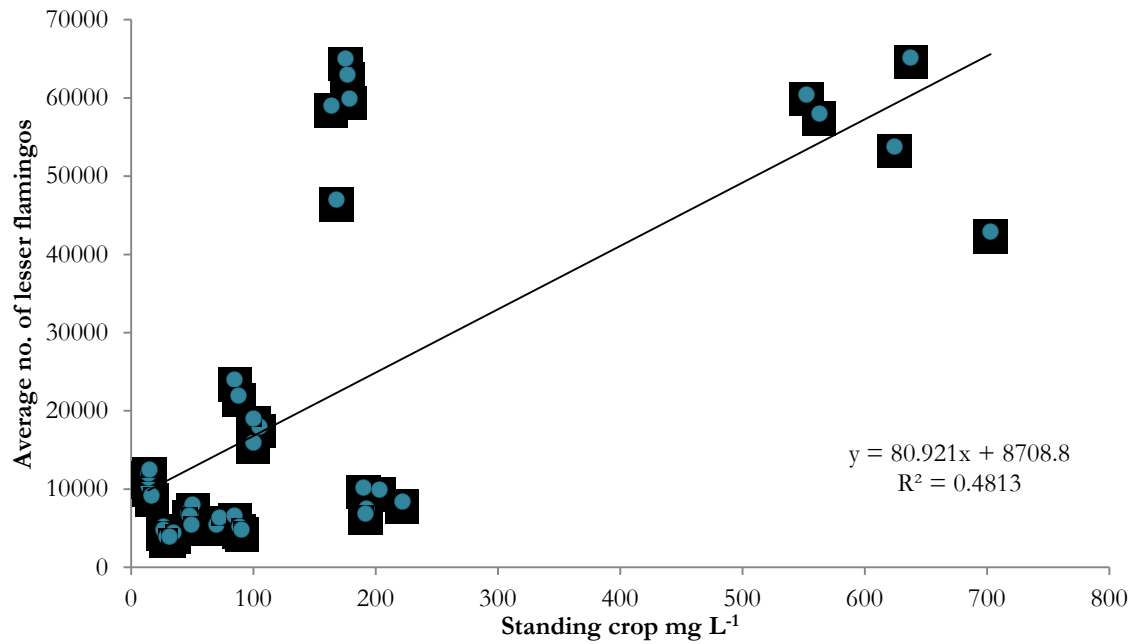
Figure 6.1: The correlation between average standing crop (mg L^{-1}) and local lesser flamingo population at Lake Bogoria in August 2012

6.3.2   Flock density and food source

The lesser flamingo was calculated to have an average body mass of 1,350 ± 60 g, from freshly deceased birds found in 2008 and 2009 and this was considered an accurate mass for a live adult bird in keeping with recent findings (Oaks, pers comm.). No cause was identified for this die off although cyanotoxins were ruled out (Straubinger-Gansberger *et al.*, 2014), and the presence of food in the crop and gut as well as general state of the birds did not indicate starvation (Oaks, pers comm.). The average flock density at Lake Bogoria was 1095 g m^{-2}, where lesser flamingos were feeding on *A. fusiformis*. The flock density at Lake Oloidien was 795 g m^{-2}, where lesser flamingos were feeding on the smaller *A. fusiformis var minor*. The lowest flock density was recorded at Lake Elementaita, where subsistence was on a diet of diatoms, 25.5 g m^{-2}. This result was statistically significant (Kruskal-Wallis; Figure 6.2). X^2 (2, n = 300) = 102.30, p < 0.001. Significant differences were found between all lakes, at p < 0.001, with the exception of Bogoria and Oloidien (Games-Howell post hoc).
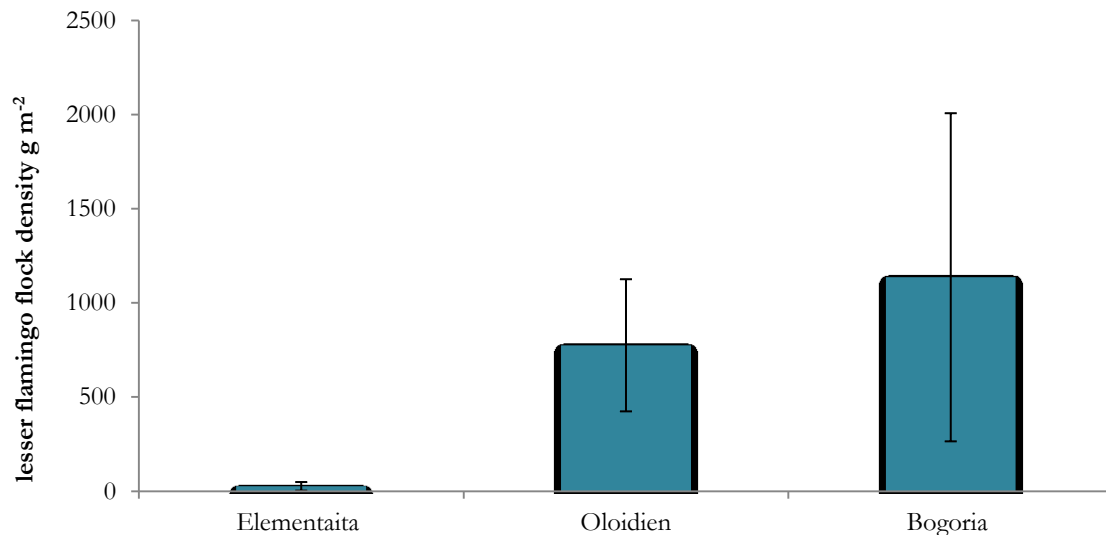
Figure 6.2: Average flock density at three alkaline-saline lakes (g m^{-2}); error bars ± 1 standard deviation

6.3.3 Flock density and feeding behaviours

At Lake Bogoria, the 10 feeding behaviours resulted in different flock densities (Figure 6.3); STF1 recorded the highest flock density (2295 g m^{-2}) and WMF recorded the lowest flock density (19.5 g m^{-2}). The two stand filter feeding and the two walk filter feeding recorded higher flock densities than the swim, deep water and wet mud feeding behaviours. The difference between the flock densities generated through the 10 feeding behaviours was statistically significant (One-way ANOVA), F (9, n = 500) = 72.31, p < 0.001. The effect size, calculated using eta squared, was 0.57.). Post-hoc comparisons using the Tukey HSD test indicated a number of significant differences between the behaviours; the results are displayed in Table 6.2. Figure 6.4 presents a sample of the aerial images used.
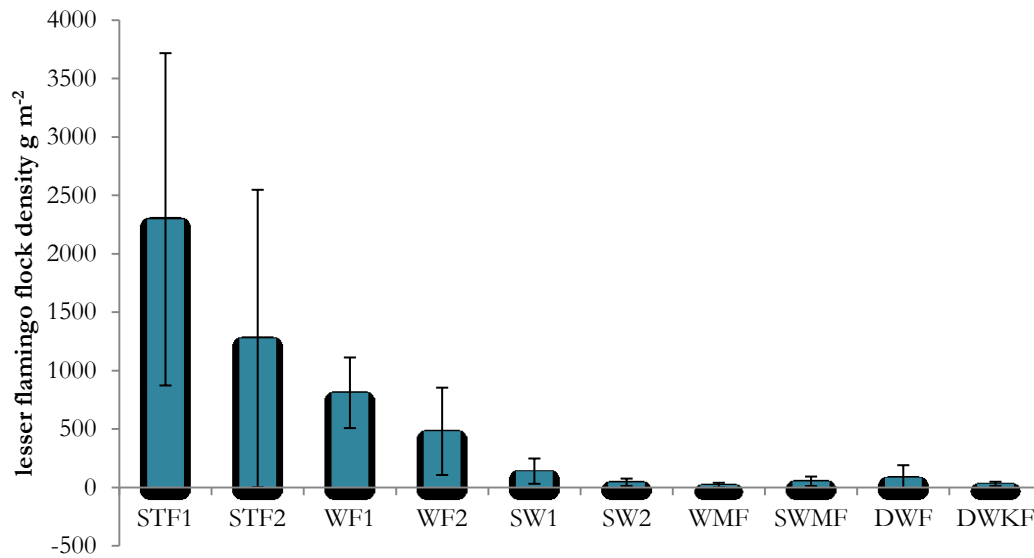
Figure 6.3: Average flock density associated with the 10 feeding behaviours at Lake Bogoria (g m^{-2}); error bars ±1 standard deviation

Table 6.2: Tukey HSD post hoc test results for differences between flock densities associated with different feeding behaviours; significant results marked by asterisks

	STF1	STF2	WF1	WF2	SW1	SW2	WMF	SWMF	DWF	DWKF
STF1		1020***	1485***	1815***	2156***	2251***	2276***	2243***	2212***	2265***
STF2			465**	795***	1136***	1231***	1256***	1223***	1192***	1245***
WF1				330	671***	766***	791***	758***	727***	780***
WF2					341	436*	461**	428*	397*	450*
SW1						95	120	87	56	109
SW2							24	-8	-39	13
WMF								-33	-63	-11
SWMF									-31	22
DWF										52
DWKF										
***p < 0.001 **p < 0.01 *p < 0.05										

The 10 feeding behaviours can be contained within four categories: stand-filtering, swim-filtering, shallow mud feeding and deep water feeding. The stand filtering behaviours have the highest flock density of the four categories, followed by swim, deep water and finally wet mud behaviours. Where two varieties of behaviour exist, the second variety involves scything the head from side to side rather than just holding the bill in the water and in all cases this reduced the flock density.

Figure 6.4: Aerial images for flock density at Lake Bogoria captured using an octocopter. Photo credit: Matt McCarthy

6.4   Discussion

Lakes dominated by large cyanobacterial blooms support larger populations of lesser flamingos than those dominated by diatoms (Vareschi, 1978). Ideal free distribution theory suggests that large numbers of individuals only congregate in areas of high prey density; otherwise competition would become too high, which is energetically costly to the individuals. Therefore large flocks of lesser flamingos will not tend to be present at lakes that cannot support them, as this would be detrimental to their survival.

The distribution of lesser flamingos between lakes was studied in the 1970s and was described as either clumped or dispersed, dependent on whether there are large cyanobacterial blooms at lakes such as Nakuru and Bogoria (Tuite, 2000). They may initially locate themselves in areas that they have prior experience of or where there is already a flock present (Stephens & Krebs, 1986). Lesser flamingos tend to aggregate in large numbers when dense blooms dominate the supporting lake (clumped) with much smaller flocks present at many of the other soda lakes within the Rift Valley (Tuite, 2000.). When no single lake has an obvious abundance of food, the East African population spreads itself throughout the feeding lakes (dispersed) (ibid.).

Lesser flamingos distribute themselves, within Lake Bogoria, along the shoreline in smaller groups. This study shows that this distribution is not random; there is a distinct correlation between flock size and the average standing crop of an area, as suggested by optimal foraging theory (Pyke *et al.*, 1977). Lesser flamingos gather in the largest numbers where there is the most food and the fewest are found in areas where food is scarcer as predicted by optimal foraging theory (Smith, 1970; Menge & Menge, 1974). There are exceptions to this, in areas where there is an abundance of fresh water; lesser flamingos will assemble in large numbers even if food is not as readily available as the fresh water is needed for other activities such as preening and bathing. The largest single flock counted at Lake Bogoria in 2012 was 58,800 birds in the Central basin, at an area where Loburu River and numerous hot springs enter the lake (many fresh enough for lesser flamingos to drink from and bathe in) but the standing crop was only 172.47 mg L^{-1}. This is significantly lower than in the South where a similar flock size was associated with a standing crop of 616.05 mg L^{-1} and higher than the North basin where the Waseges delta was supporting a flock of 11,140 birds on a standing crop of

14.87 mg L^{-1}. In both the South and Central basins, feeding was the dominant activity within the flocks, however, this was not the case in the North, where preening and bathing were dominating.

This suggests that lesser flamingos do distribute themselves across lakes in accordance with food distribution as areas where food abundance is highest support the largest flocks, as recorded in American flamingos (Arengo & Baldassare, 1995). However, as fresh water is required by lesser flamingos, they may be positively selecting sites where food is readily available but there is also an abundance of drinking / bathing water. There are a restricted number of sites with good access to fresh water at Lake Bogoria and flamingos were seen flying north to south and south to north continuously throughout the day which I suggest indicates that if food is abundant at one site they utilise that for their daily energy requirement and then fly to a fresh water source for drinking.

The same distribution patterns Tuite (1979; 2000) described between lakes can also be used to describe distribution within them. Lesser flamingos at lakes Bogoria and Oloidien can be described as clumped because they form small flocks over the lake surface and along the shoreline whilst at Lake Elementaita a dispersed pattern was seen. The average flock density at Elementaita was 25.5 g m^{-2} and lesser flamingos were spread across the lake, all apparently feeding from their own patch. The flock density at lakes Bogoria and Oloidien were considerably higher, 1095 and 795 g m^{-2} respectively, clumped, suggesting that they feed from smaller patches.

These flock densities are not dissimilar from those calculated by Tuite (1979; 2000) but they do include in a third lake state rather than just diatom or *A., fusiformis* dominated. Tuite recorded an average flock density of 755 g m^{-2}, which is much closer to my Oloidien value than the Bogoria one, and by investigating individual lakes it appears that tight flocks form to utilise different food sources. Lake Oloidien is dominated by *A. fusiformis var minor*, a smaller variant of *A. fusiformis* that is still filterable by lesser flamingos and the lower flock density indicated that they may need a slightly bigger patch when utilising this smaller food source.

The food source varied at each of the lakes, but so did biomass availability and it could be a combination of these two factors that results in the flock density observed. In American flamingos, the flock density decreased as food abundance decreased (Arengo & Baldasarre, 1995) however, the decrease was not as dramatic as recorded in lesser flamingos between the three lakes.

Each of the ten feeding behaviours generated a different flock density and it was relatively easy to map where feeding behaviours were occurring as lesser flamingos appear to show order and regulation in their behaviours, with loose bands or zones being attributed to each of the behaviours with limited cross over (personal observation during mapping of behaviours for density calculations). STF1 generated the highest flock density, as lesser flamingos were static, with little head movement when utilising this behaviour. The next highest flock densities were found in STF2, WF1 and WF2, behaviours that occurred in the shallows on the top few centimetres of the water column. Swim, wet mud and deep water feeding all generated much lower flock densities; in the case of swim feeding I suggest that this is because they have more space on the open lake and there is a reduced predation risk in open water, so they don't benefit from being tightly packed. In the case of deep water feeding I suggest that lesser flamingos spread out more as they have their heads completely submerged and are therefore visually restricted so are minimising competition and collision risk by increasing patch size. The wet mud feeding behaviours are generally utilising diatoms and therefore a similar distribution pattern to that of Elementaita is witnessed.

Overall, lesser flamingo distribution and density within East African Rift Valley lakes appears to be primarily determined by the abundance and distribution of food but with extent of fresh water access also having an impact.

Chapter 7

Chapter 7   General Discussion

In this chapter the main findings of the studies presented in the previous chapters of this thesis are drawn together. The specific findings of each study, in relation to existing theory and previous published literature have been discussed in detail in each of Chapters 3 to 6. The main findings are summarised leading to the readdressing of the energy budget proposed by Pennycuick and Bartholomew (1973). Following this recommendations for future work are discussed.

7.1   Food abundance and distribution

This study began by looking at the variance within soda lakes, highlighting large-scale fluctuations in phytoplankton biomass and composition. The alkaline-saline lakes of East Africa are known for their characteristic dense blooms of *Arthrospira fusiformis* and large numbers of lesser flamingos (*Phoeniconaias minor*), the primary consumer.

Maximum surface *A. fusiformis* biomass recorded ranged from over > 800 mg L^{-1} in 2009 to < 50 mg L^{-1} in 2013. The biomass available to lesser flamingos varied significantly across the six lakes studied. Spatial and temporal variation was observed and a new, highly concentrated, food source of sedimented *A. fusiformis* was identified at the lake-sediment interface.

Since this study commenced in 2009, the lake levels within the East African Rift Valley have been consistently rising; resulting in increased light attenuation due to increased suspended sediment in the water column and as a consequence there has been truncation of the euphotic zone, reduction in biomass and therefore primary productivity (Sadro & Melack, 2012). This phenomenon was observed at Lakes Bogoria, Nakuru, Elementaita and Oloidien. At Natron, the increasing inflow of freshwater has had a different effect as the surface area of the lake has increased but the lake is not much deeper, creating a larger area in which diatoms are able to grow and consequently was the only lake in this study to record an increase in available biomass since 2009.

Grazing pressure could also influence biomass as lesser flamingos have been recorded to extract over 90% of the daily primary production of *A. fusiformis* (Vareschi, 1978). Under normal conditions, the cyanobaterial biomass in a Bolivian saline lake increased dramatically following the exclusion of the Andean flamingo (Hurlbert & Chang, 1983) indicating the significant effect of flamingo grazing. During periods of high *A. fusiformis* abundance, lakes are able to support large flamingo populations as the grazing pressure stimulates further cyanobacterial growth. In 2013, the biomass at Lake Bogoria was very low and over 900 000 lesser flamingos were present at the lake. The low biomass may indicate that there is a critical threshold at which *A. fusiformis* is able to replace itself daily, below which it is unable to meet the grazing demands of such a large flock.

Distribution of food resources was not uniform in any of the lakes studied. The temporal and spatial variations observed could result from a number of factors including climatic conditions (rainfall and wind), conductivity, temperature, grazing pressure, light attenuation and nutrient availability; all of which contribute to a heterogeneous, inconsistent pattern of distribution of food resources (Odour & Schagerl, 2008; Blukacz *et al*, 2009; Green & Elmberg, 2014).

7.2   Feeding behaviour and food abundance / distribution

This study identified 10 distinct feeding behaviours utilised by lesser flamingos at different times of day and to access different food resources from a variety of niches throughout the aquatic habitat: from the lake's edge, the open water and the lake-sediment interface.

Deep water feeding has been mentioned in published literature (Tuite, 1979; 2000) but this was the first study to record both deep water feeding and deep water kick feeding occurring frequently at Lake Bogoria, where the newly identified food source of sedimented *A. fusiformis* was abundant. Tuite (1979; 2000) only described this upending feeding behaviour in relation to feeding on diatoms, which was observed at lakes Elementaita and Natron, but occurred more frequently at Lake Bogoria when there was high sedimented biomass.

Feeding behaviours and local lesser flamingo distribution were positively correlated with food abundance suggesting that lesser flamingos are able to selectively feed on 'patches' where food is more abundant in accordance with optimal foraging theory.

The time that lesser flamingos spent feeding varied between the six lakes and an inverse correlation was observed overall, signifying that reduced biomass resulted in a greater feeding effort (Hutto, 1990). Higher food abundance enables lesser flamingos to ingest their required daily intake in a shorter time, maximising their feeding efficiency and allowing them to allocate more time to other activities, as observed in the Carribean flamingo (*Phoenicopterus ruber roseues*) (Arengo & Baldassarre, 1995).

At Lake Bogoria, increasing food abundance resulted in an increased feeding effort as expected in filter feeders (Holling, 1965; Jeschke *et al.*, 2004). This suggests that Lake Bogoria is an incredibly important feeding site for lesser flamingos, as they appear to be restocking their energy reserves. Many courting lesser flamingos have been observed dancing at Lake Bogoria and therefore, the increase in feeding effort when abundance is high could be due to the higher energy requirements of breeding adults. Lake Bogoria could be the lake that lesser flamingos utilise to fully stock their energy reserves before flying to Lake Natron to breed.

7.3   Energy budget of the lesser flamingo (*Phoeniconaias minor*)

This study established the average weight of an adult lesser flamingo to be 1350 ± 60 g, slightly lower than 1730 ± 40 g as found by Vareschi (1978). In 1973, Pennycuick and Bartholomew proposed an energy budget for the lesser flamingo, which was then updated slightly by Tuite (1979). The work in the previous 4 chapters has enabled me to revise this energy budget so that it more accurately represents the current situation.

Pennycuick and Bartholomew (1973) made a number of assumptions and I suggest that some of these can be updated. The primary assumptions and calculations that I have altered are the energy content of the algae, the basal metabolic rate (BMR) and the factor by which the BMR should be multiplied in order to allow for general activity.

The energy content of the algae was arbitrarily given as 2 x 10^{7}J Kg-1 based on 5 kcal g$^-$^{1} of dry matter, however, the two energy budgets I have devised use a value of 1.2 x 10^7 J Kg^{-1} for *A. fusiformis* (based on an energy content of 2.9 kcal g^{-1} (Alvarenga *et al.*, 2011)) and 1.1 x 10^7 J Kg^{-1} for diatoms (based on energy content of 2.55 kcal g^{-1} (Correa-Reyes, 2008)).

The BMR was calculated from a modified version of the equation generated by Lasiewski & Dawson (1967), using 1.8 kg as the average mass of a lesser flamingo originally; Tuite (1979) later suggested that a lean mass mass of 830g should be used. I have used 1.35 Kg as the average mass as I conclude that the majority of the birds are not in a lean state when they are feeding (based on weights of freshly deceased birds at Bogoria in 2009). The basal metabolic rate for my energy budget is 7.3 W.

The final assumption I am changing results from my analysis of overall time spent feeding and time spent engaging in different activities. Pennycuick and Bartholomew used a factor of 2.5 to multiply the BMR by to allow for general activities. From my observations, I suggest that this factor should not be a constant value and should be variable dependent on time spent feeding as well as the feeding behaviours being utilised.

At diatom-dominated lakes, feeding occurs mainly by shallow water mud feeding that requires little movement and therefore doesn't have much affect (energy used in feeding via pumping water is already accounted for in the original equation). At *A. fusiformis* dominated lakes, feeding occurs in a variety of ways, some of which are more energetically expensive than others. Calculating the overall proportion of time engaged in each different feeding behaviour, I have assumed that an additional Watt of energy is required when feeding via behaviours that involve movement (swimming, walking, upending) as seen at Bogoria, Nakuru and Oloidien (BMR+1)

The time spent feeding at diatom-dominated lakes is also generally much higher than at lakes dominated by *A. fusiformis* and therefore I suggest that the constant by which the BMR is multiplied is on a variable scale dependent on time spent feeding. If lesser flamingos are spending 90 % of their time feeding then they only have 10 % of their time remaining to take part in other activities whereas birds only feeding for 30 % of

the day have 70% of their time to engage in other activities. The energy budgets I propose uses activity factors of one times the BMR when feeding for 100 % of the time, 1.5 times the BMR when feeding for 90 % of the time, increasing by 0.5 every 10 % less time feeding.

The equation from Pennycuick and Bartholomew (1973) that is used is:

$$E_s = t\ vr\ (0.8\ ec - 5p) - E_m$$

Where:

Es is the energy surplus

t = time spent feeding

v = stroke volume (5 x 10^{-7} m^3 estimated from Jenkin (1957))

r = pumping frequency (20 s^{-1})

0.8 = rate of acquiring usable energy from Kendleigh (1967)

e = energy content of algae (1.2 x 10^7 J Kg^{-1} for *A. fusiformis* (Alvarenga et al., 2011) and 1.1 x 10^7 J Kg^{-1} for diatoms (Correa-Reyes, 2008)

c = algal density in Kg m^{-3} (Kg m^{-2} for diatoms)

p = pumping pressure (2.5 x 10^4 N m^{-2} assumed by Pennycuick and Bartholomew (1973))

Em = BMR x activity factor for diatom-dominated; (BMR+1) x activity factor for *A. fusiformis* dominated lakes

These two energy budgets (Figure 7.1) do not appear dramatically different from the original; however, by updating the energy content of the food a more accurate representation of energy obtained it achieved. Pennycuick and Bartholomew (1973) produced a single energy budget but based on the activities engaged in, average time spent feeding and different calorific content of food resources, separate energy budgets have been produced for *A. fusiformis* and diatoms. The two energy budgets do not vary dramatically and if either A. fusiformis or diatoms were present at 0.15 Kg m^{-3} or m^{-2}, lesser flamingos would need to feed for 75% and 80% of their time respectively. This helps to support the fact that diatoms are a more important food source than previously considered.
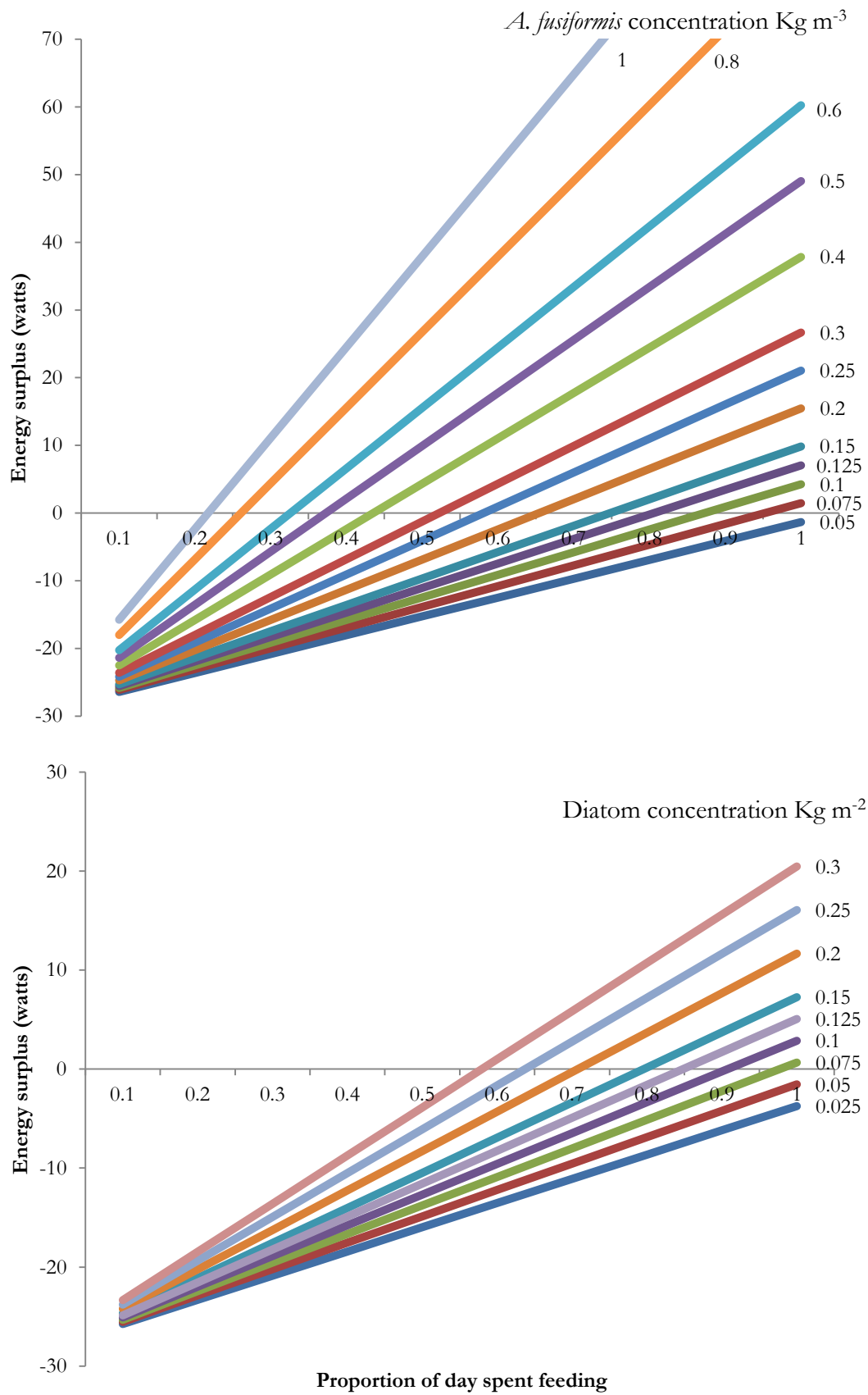
Figure 7.1: Revised energy budgets based on time spent feeding and food concentration of A. fusiformis dominated lakes (top) and diatom-dominated lakes (bottom). The food concentrations displayed represent the range of actual available biomass recorded within this study

7.4   Summary

The aim of this thesis was to build on the earlier works of Vareschi (1978) and Tuite (1981) by further investigating the importance of diatoms as a food source; the ability of lesser flamingos to adapt their feeding behaviours when feeding on differing food sources or different concentrations of food; the temporal and spatial differences in foraging behaviour; the relationship between food abundance and lesser flamingo distribution and the density of lesser flamingo flocks in relation to food source and feeding behaviour. This was achieved through behavioural observations and the collection of water samples at six East African alkaline-saline lakes.

Throughout this study, it has been shown that the East African alkaline-saline lakes vary considerably in terms of their phytoplankton and micro-zooplankton communities. The feeding lakes utilised by lesser flamongos are not all dominated by *A. fusiformis*, other cyanobacteria and bacillariophyceae can also dominate whilst providing adequate food resources for lesser flamingos. Epipelic resources (including diatoms and sedimented *A. fusiformis*) have been shown to make a considerable contribution to lake biomass and should always be considered when calculating the available biomass of East-African alkaline-saline lakes in future studies.

Diatom dominated lakes were supporting large lesser flamingo populations throughout the study period. The adjusted energy budget shows that flamingo can subsist on a diet of diatoms (where they are in abundance) and they are more than just an emergency food source (as proposed by Tuite, 1981). This finding could help to explain why flamingos are present at lakes that seemingly have little food when phytoplankton biomass is calculated.

This study identified 10 individual feeding behaviours and the types of feeding behaviour being utilised at each of the lakes can give an immediate indication of whether the lake is diatom or cyanobacteria dominated. The presence of deep water feeding behaviours at a lake dominated by cyanobacteria also indicates that there is a high concentration of epipelic food resources or sedimented *A. fusiformis* and adapting their behaviour accordingly. The positive correlation identified between the available biomass that could be accessed through the different feeding behaviours and the percentage of birds engaging in the behaviour at Lake Bogoria, indicates that they are

adapting their feeding behaviour in response to food availability. Further to this, when food availability was limited, an increase in head swinging behaviours was recorded, suggesting lesser flamingos are able to adjust their feeding behaviour in terms of rate, placement on the lake and style in response to food availability, as seen in other waterfowl (Hutto, 1990; Cope 2003).

A negative correlation was identified between the time spent feeding and the average biomass, when considering the six lakes, indicating that feeding duration increased with decreasing biomass, as expected for filter feeders (Jeschke *et al.*, 2004). However, when only considering Lake Bogoria, a positive correlation was identified between average biomass and time spent feeding which indicate that feeding duration increased with increasing biomass, suggesting that they may be stoking up on their energy reserves when food is abundant. This indicates that Lake Bogoria is an important feeding lake, which may also be exploited prior to breeding.

Lesser flamingos were found to distribute themselves within lake Bogoria in accordance with food abundance; areas of high biomass supported the largest flocks although freshwater supply was also found to be an important factor. The flock density varied, dependent on food source and therefore, is indicative of the state of the lake. The feeding behaviour being exhibited also had an affect on flock density with head swinging and wet mud behaviours requiring greater dispersion as a larger 'patch' was required.

This study achieved its aims and has provided a number of key outputs, which have contributed to improving the current understanding of lesser flamingo feeding behaviour and duration as well as the distribution of food resourses within soda lakes. This insight has provided valuable information for the future conservation of lesser flamingos as their foraging behaviours are indicative of food type and distribution and the duration of their feeding is suggestive of food abundance.

This study was limited in the times that visits to each of the lakes were made as it was not always logistically feasible to do so. The lakes are located in remote regions that require a vehicle, camp and sufficient food and water for the duration of the stay. I had to plan my sampling trips to coinside with 'Lakes of the East African Rift Valley' excursions for students and academics. Electricity in Kenya was intermittent and

occasionally I lost samples due to them spoiling in the freezer, which would have led to inaccurate results. Sampling visits were sometimes made difficult by restrictions on times that I was able to work within National Parks or roads flooding, preventing access to my observation sites. During this study, safety precautions had to be in place as I was often conducting behavioural observations in close proximity to wildlife (including, but not limited to: hippo, rhino, leopard, lion, hyena and buffalo). This meant that there were occasions on which I had to conduct my observations from the roof of the vehicle and collect minimal water samples to ensure my safety.

7.5   Future work

Further work should take four forms:

Firstly, I would like to build on what I have found in this study by investigating the feeding behaviours and time spent feeding of the different age classes, which would enable the production of an energy budget for different aged birds. Juveniles feed for longer than sub-adults and adults but initial observations suggest that their behavioural repertoire is less developed than their adult counterparts. Crèches of juveniles have also been observed but never studied in detail and their existence has never been quantified or verified through study.

Secondly, I would like to conduct a more intensive study of lesser flamingo food resources and feeding behaviours at Lake Bogoria, monitoring the food abundance, food distribution, lesser flamingo population and feeding behaviours every week for a year in order to build up an accurate time-series of feeding behaviours, time spent feeding and remaining activity budget in relation to the availability and distribution of food. I would also like to try and monitor flamingo movements with the lake to identify whether they fly along the lake from North to South in order to feed, or South to North for drinking as hypothesised in Chapter 5.

Thirdly, I would like to build on the satellite tracking work of Childress *et al.*, 2007 in order to identify whether Lake Bogoria is utilised as a final stop before a breeding event at Lake Natron as I have hypothesised.

Finally, I would like to complement the work of Torres *et al.*, (2014), who conducted a phylogenetic analysis using three mitochondrial (mtDNA) markers. The three deep-keeled species of flamingo are the lesser flamingo, Andean flamingo (*Phoenicoparrus andinus*) and James's flamingo (*Phoenicoparrus jamesi*), which are set apart from the *Phoenicopterus* genus that contains the remaining three shallow-keeled species. Torres *et al. (*2014) suggested that dividing the deep-keeled clade into two genera is arbitrary and unhelpful, stating that the lesser flamingo should be placed within the *Phoenicoparrus* genus based on the morphology of the mandible and phylogenetic relatedness. I would like to conduct a comparative behavioural study of the three deep-keeled species in order to identify whether behaviourally they are also similar. This would either provide evidence to support the suggestion of placing the lesser flamingo within the *Phoenicoparrus* genus or show that they are dissimilar and should remain with their own genus.

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