

**ASSESSMENT OF ALTERNATIVE FOOD RESOURCES OF THE LESSER
FLAMINGO (*Phoeniconaias minor*) IN SOME RIFT VALLEY SALINE LAKES IN
KENYA AND TANZANIA**

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Photo: Lesser flamingos (*Phoeniconaias minor*) engaged in different activities at Lake Bogoria. A large group in the courtship dance at the back while a few are feeding in the front (Photograph by Margaret Kyalo)

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DECLARATION

This thesis is my original work and has not been presented for a degree in any other University or Institution.

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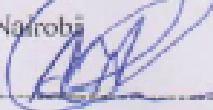
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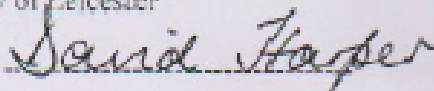
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DEDICATION

To my parents Dr. Richard (Late) and Sarah Luti, and to my special grandmother
Susu Afia who have colored my life with inexpressible meaning.

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TABLE OF CONTENTS

DECLARATION	i
DEDICATION	ii
ACKNOWLEDGEMENTS	iii
ABBREVIATIONS	xii
ABSTRACT	xiii
CHAPTER ONE	
INTRODUCTION	1
1.1. Background	1
1.2. Objectives	2
1.3. Research questions	2
1.4. Hypothesis	2
CHAPTER TWO	
LITERATURE REVIEW	3
2.1. Classification and geographical distribution of lesser flamingos	3
2.2. Geology, climate and hydrology in shaping the East African alkaline-saline lakes	3
2.3. Biological characteristics of alkaline-saline lakes	5
2.4. Main food resources of <i>Phoeniconaias minor</i>	5
2.5. Filter feeding adaptation of lesser flamingo	6
2.6. Lesser flamingo feeding behaviours	7
2.7. Other food resources of the lesser flamingo	8
2.8. Lesser flamingo population trends	9
2.9. Productivity of saline lakes	12
2.10. Justification of the study	13
CHAPTER THREE	
STUDY AREA, MATERIALS AND METHODS	15
3.1. Study area	15
3.1.1. Description of study sites	16

3.2.	Materials and Methods.....	23
3.2.1.	Determination of the composition of lesser flamingo food	23
3.2.1.1.	Sample collection.....	23
3.2.1.2.	Species identification.....	24
3.2.2.	Assessment of available food	24
3.2.2.1.	Photosynthetic pigment analysis.....	24
3.2.2.2.	Calculation of the standing crop of available food.....	25
3.2.3.	Assessment of primary productivity.....	26
3.2.3.1.	Exposure experiment method	26
3.2.3.2.	Exposure experiment for measurement of planktonic and epipellic primary productivity	28
3.2.3.3.	Exposure experiment for measurement of planktonic primary productivity.....	29
3.2.4.	Statistical analysis.....	29

CHAPTER FOUR

RESULTS	30	
4.1.	General observations and explanation of terms.....	30
4.2.	Taxonomic composition	30
4.3.	Standing crop of the various categories of <i>P. minor</i> food resources	36
4.3.1.	Standing crop of the planktonic and suspended epipellic food resource.....	36
4.3.2.	Standing crop of the sedimented <i>Arthrospira fusiformis</i> and the epipellic food resource.	38
4.3.3.	Standing crop of the lake shore mud food resource.....	40
4.4.	Effect of water depth on the standing crop of the various food resources.....	41
4.5.	<i>P. minor</i> population estimates and standing crop of the different food resources	43
4.6.	Primary productivity of the various communities	44
4.6.1.	Primary productivity of the planktonic and suspended epipellic community.....	44
4.6.2.	Primary productivity of the sedimented <i>Arthrospira fusiformis</i> and epipellic community	46

CHAPTER FIVE

DISCUSSION, CONCLUSION AND RECOMMENDATIONS	48
5.1. Energy budget by <i>P. minor</i>	48
5.2. Primary producer community categories	49
5.3. Production rate of lesser flamingo food.....	50
5.4. Foraging options	51
5.5. Conclusion	52
5.6. Recommendations.....	53
5.6.1. Further research actions.....	53
5.6.2. Conservation and management actions.....	53
REFERENCES	54
APPENDIX	61

LIST OF TABLES

Table 4.1: Species composition of the microbial community at the study lakes during the study period. ((3) dominant, (2) abundant, (1) present , (-) absent (p) present).....	32
Table 4.2: Mean (\pm se) standing crop of the planktonic community	36
Table 4.3: Mean (\pm se) standing crop of the suspended epipellic community	37
Table 4.4: Mean (\pm se) standing crop of the sedimented <i>Arthrospira fusiformis</i>	38
Table 4.5: Mean (\pm se) standing crop of the epipellic community	39
Table 4.6: Mean (\pm se) standing crop of the lake shore mud algae.	40
Table 4.7 : Comparison of primary productivity values measured during this study with others from previously published work from different locations.	43
Table 4.8 : Mean (\pm se) primary productivity and respiration of the plankton community.	45
Table 4.9 : Mean (\pm se) primary productivity and respiration of the suspended epipellic community.	45
Table 4.10 : Mean (\pm se) primary productivity and respiration of the sedimented <i>Arthrospira fusiformis</i>	46
Table 4.11: Mean (\pm se) primary productivity and respiration of the epipellic community.	47
Table 5.1: Comparison of primary productivity values measured during this study with others from previously published work from different locations.	51

LIST OF FIGURES

Figure 2.1: Lesser flamingo population trends for the East African population	11
Figure 2.2: Population trend at Lake Natron, the only viable breeding site in East Africa	11
Figure 2.3: Lesser flamingo population trend at Lake Bogoria, a major feeding site..	11
Figure 2.4: Population trend of lesser flamingo at Lake Nakuru, a major feeding site	11
Figure 3.1: The location of study lakes in the Eastern Rift Valley.....	15
Figure 3.2: The location and image of Lake Bogoria in the Eastern Rift Valley.	17
Figure 3.3: The location and image of Lake Nakuru in the Eastern Rift Valley.	18
Figure 3.4: The location and image of Lake Elementeita in the Eastern Rift Valley.	19
Figure 3.5: The location and image of Lake Oloidien and Lake Naivasha from which it was separated.	20
Figure 3.6: The location and image of Lake Sonachi in the Eastern Rift Valley	21
Figure 3.7: The location and image of Lake Natron in the Eastern Rift Valley.	22
Figure 4.1: Mean (\pm se) standing crop of planktonic food resource in the study lakes.	36
Figure 4.2: Mean (\pm se) standing crop of suspended epipellic food resource in the study lakes.....	37
Figure 4.3: Mean (\pm se) standing crop of sedimented <i>A. fusiformis</i> at Lake Bogoria.	38
Figure 4.4: Mean (\pm se) standing crop of epipellic food resource in the study lakes.	39
Figure 4.5: Mean (\pm se) standing crop of lake shore mud algae in the study lakes.	40
Figure 4.6: Mean (\pm se) planktonic standing crop at varying water depths of all the study lakes	41
Figure 4.7: Mean (\pm se) epipellic standing crop at varying water depth of the study lakes	41
Figure 4.8: The comparison between the mean planktonic and sedimented <i>A.</i> <i>fusiformis</i> standing crop at Lake Bogoria at different water depths.....	42
Figure 4.9: Comparison between the mean suspended epipellic and epipellic biomass of Lake Natron and Lake Elementeita at different water depths.....	42
Figure 4.10: Mean (\pm se) net and gross primary productivity and respiration of the planktonic community of the lakes studied.	45

Figure 4.11: Mean (\pm se) net and gross primary productivity and respiration of the suspended epipellic community of the lakes studied.	46
Figure 4.12: Mean (\pm se) net and gross primary productivity and respiration of the sedimented <i>A. fusiformis</i> at Lake Bogoria.	47
Figure 4.13: Mean (\pm se) net and gross primary productivity and respiration of the epipellic community of the studied lakes.	47

LIST OF PLATES

Plate 2.1: The head of <i>P. minor</i> showing (a) the upper mandible (UM) and the lower mandible (LM), (b) the transverse section of the bill and (c) the lamellated area of the bill. From Jenkin (1957)	6
Plate 2.2: Lesser flamingo feeding behaviours (a) filter feeding while swimming in deep water and (b & c) filter feeding while standing on shallow water (modified from Ridley <i>et al.</i> , 1955).	7
Plate 3.1: Gilson's corer showing the position of (a) the planktonic community and (b) the epipelagic community in the water column, and (c) sediment.	23
Plate 3.2: (a) Oxygen and temperature meter and (a ₁) probe, (b) metabolism chamber top, (c) metabolism chamber base plate, (d) motor and (d ₁) stirrer, (e) metabolism chamber dark cover.	26
Plate 3.3: (a) Set up of productivity exposure experiment, (a ₁) dark metabolism chamber, (a ₂) light metabolism chamber and (a ₃) oxygen meter. (b) exposure experiment set up <i>in situ</i>	27
Plate 4.1: Cyanobacteria taxa identified. A. <i>Arthrospira fusiformis</i> (i) extended and (ii) compressed. B. <i>Arthrospira spp.</i> C. <i>Spirulina subsalsa</i> . D. <i>Anabaena spp.</i> E. <i>Anabaenopsis abijatae</i> . F. <i>Lyngbya pseudospirulina</i> . G. <i>Oscillatoria spp.</i> (i) <i>O. limosa</i> (moving), (ii) <i>O. limnetica</i> (stationary).	33
Plate 4.2: Some of the Bacillariophyta species identified. A-D. <i>Navicula sp.</i> E. & F. <i>Melosira spp.</i> G. <i>Cyclotella spp.</i> H. <i>Amphora spp.</i> I. <i>Sellaphora spp.</i> J. <i>Cymbella spp.</i> K. <i>Pleurosigma spp.</i>	34
Plate 4.3: Protozoan species (A-H) and rotifer species (I & J). A. <i>Frontonia spp.</i> B. <i>Euplotes spp.</i> C. an Euglenophyte species present at lake Nakuru only. D. <i>Condylostoma spp.</i> E. <i>Campanella spp.</i> was seen only at Lake Oloidien. F. Unidentified species 1. G. Unidentified species 2 (Tumbler). H. <i>Amoeba sp.</i> only seen in Lake Oloidien. I. <i>Brachionus plicatilis</i> J. <i>Hexarthra jenkinsae</i>	35

LIST OF APPENDICES

Appendix 1.a: Mann-Whitney U Test results for planktonic standing crop.	61
Appendix 1.b: Mann-Whitney U Test results for the standing crop of the suspended epipellic community.	62
Appendix 1.c: Mann-Whitney U Test results for standing crop of the sedimented <i>Arthrospira fusiformis</i>	62
Appendix 1.d: Mann-Whitney U Test results for standing crop of the epipellic community.	63
Appendix 1.e: Mann-Whitney U Test results for standing crop of the wet mud community.	64
Appendix 2.a: Mann-Whitney U Test results for primary productivity of planktonic community.	65
Appendix 2.b: Mann-Whitney U Test results for primary productivity of the suspended epipellic community.	66
Appendix 2.c: Mann-Whitney U Test results for primary productivity of the sedimented <i>Arthrospira fusiformis</i>	67
Appendix 2.d: Mann-Whitney U Test results for primary productivity of the epipellic community.	68
Appendix 3.a: Energy calculations for standing crop and net primary productivity of the planktonic food resource.	69
Appendix 3.b: Energy calculations for standing crop and net primary productivity of the suspended epipellic food resource.	69
Appendix 3.c: Energy calculations for standing crop and net primary productivity of the sedimented <i>Arthrospira fusiformis</i> food resource.	69
Appendix 3.d: Energy calculations for standing crop and net primary productivity of the epipellic food resource.	70
Appendix 3.e: Energy calculations for standing crop and net primary productivity of the wet mud food resource.	70

ABBREVIATIONS

Chl <i>a</i>	Chlorophyll <i>a</i>
C	Carbon
O	Oxygen
DW	Dry weight
mg	Milligram
cm	Centimeter
M	Meter
hr	Hour (Time)
L	Litre
μS	Micro-Siemens
SC	Standing crop
SC _{max}	Maximum standing crop
SC _{min}	Minimum standing crop
NPP	Net primary productivity
GPP	Gross primary productivity
Resp.	Respiration
Sd	Standard deviation
r.p.m.	Revolutions per minute
kcal	Kilo calories

ABSTRACT

The saline lakes of Kenya and Tanzania are of high economic value and of great conservation and scientific value. They host >75% of the world's lesser flamingo population, which are a major income earner for these countries. The lesser flamingos (*Phoeniconaias minor*) are of scientific concern as they are near threatened. The analysis of the food resources that sustain the lesser flamingo populations and the ecology of alkaline saline ecosystems are useful in developing conservation strategies for these lakes and the flamingos. The study was carried out at saline lakes of the eastern rift valley within Kenya and Tanzania. The lakes were Bogoria, Nakuru, Elementeita, Oloidien, Sonachi and Natron. The study explored the diversity of the lesser flamingo food resources and their significance to the lake's ecology.

Four categories of the food resources that are utilized by lesser flamingos are presented here. These include planktonic, sedimented, epipellic food resources and algae growing on wet mud. The planktonic food resource which occurred within the water column was mainly composed of *Arthrospira spp.* Sedimented *A. fusiformis* was observed at Lake Bogoria where it formed a film on the sediment in the shallow water. The epipellic food resource was mainly composed of benthic diatoms which grow on the water-sediment interface in shallow water where light penetrated to the sediment. The wet mud resource was also composed of diatoms growing on mud along the lake edges. The study confirmed that lesser flamingos are indeed the main primary consumers on the saline lakes. At a daily energy intake of 314 kcal for body maintenance, the species can consume > 92% of the cyanobacteria at Lake Bogoria, Lake Oloidien and Lake Sonachi. It was found that epipellic and wet mud diatoms significantly contribute to the lesser flamingo diet. These food resources supported >98% of the lesser flamingo's food requirement at Lake Natron's southern lagoon. This was also true for Lake Elementeita in August 2009 when the lake level was very low and the maximum wadeable depth was not more than 3 cm.

Lesser flamingos cannot be sustained by cyanobacterial and algal food alone. Their diet is naturally enriched with 'animal' protein provided by protozoa and rotifer species. At least eight protozoan species were found with the commonest being *Frontonia spp.* which was found in all the lakes and dominant in some of the lakes. Some protozoan species were restricted to certain lakes, such as *Amoeba spp.* and *Campanella spp.* which only occurred in

Lake Oloiden. Two rotifer species, *Brachionus spp.* and *Hexarthra spp.*, were present in all lakes except in Lake Natron, where none was recorded.

The lakes exhibited very high primary productivity for both planktonic and epipellic measurements. The highest net primary productivities were recorded at Lake Bogoria with 204.6 mg C m⁻² hr⁻¹ for planktonic cyanobacterial and 103.01 mg C m⁻² hr⁻¹ for sedimented *Arthrospira*. This is the first study to describe the primary productivity of the epipellic community of saline lakes and its contribution to the ecology of the rift valley lakes studied. At the shallow lakes, Lake Elementeita and Lake Natron, it contributed 100% to the primary production. The highest epipellic net primary productivity was recorded at Lake Elementeita with 73 mg C m⁻² hr⁻¹, while negative values of up to -33 mg C m⁻² hr⁻¹ were recorded for the suspended epipellic community at Lake Natron. The epipellic and wet mud resources contribute greatly to the lesser flamingo diet than earlier thought and more so to the maintenance of the food chains on the saline lakes. The epipellic community is the main primary producer in the shallow lakes such as Natron.

CHAPTER ONE

INTRODUCTION

1.1. Background

The Eastern Rift Valley, which bisects Kenya from North to South, contains a series of shallow alkaline saline lakes. These lakes are in closed basins without outlets, and have high concentrations of sodium carbonate and bicarbonate (Melack and Kilham, 1974) as high evaporation leaves the salts behind. For this reason, Brown (1973) described the Kenyan saline lakes as “harsh wastes” since they are extremely saline with lakes Bogoria and Nakuru having conductivities of 40,000 – 80,000 $\mu\text{S cm}^{-1}$ (Harper *et al.*, 2003) and 14,000 – 26,000 $\mu\text{S cm}^{-1}$ (Vareschi, 1978) respectively.

Brown (1973) acknowledged that flamingos are one of the world’s greatest ornithological spectacles. The shores of these saline lakes are occasionally lined with enormous congregations of lesser flamingos (*Phoeniconaias minor* Geoffroy). Indeed, the saline lakes of the Kenyan Rift Valley are recognized worldwide as theatres for the magnificent pink aggregations of lesser flamingos, which are a major tourist attraction and foreign income earner for Kenya. These lakes are of significance to flamingos because they can support very high densities of their primary food organism that can sustain for example, up to a 1.5 million *P. minor* in Lake Nakuru (Vareschi, 1978).

The birds are known to feed predominantly on colonies of the microscopic planktonic cyanobacterium *Arthrospira fusiformis* (synonym *Spirulina platensis*). They feed by filtering *A. fusiformis* from few centimetres of the surface water. In addition, *P. minor* have been recorded to glean for food on mud along the shores of saline lakes, where the food consists mainly of diatoms (Tuite, 1981). The food resources vary from time to time in quantity and flamingos have evolved a nomadic behaviour to cope with this variability. The lesser flamingo population at a lake has been associated with varying food quantity.

Recently, *P. minor* have been observed displaying unusual feeding behaviour that has never been documented in detail before - they immerse their heads, sometimes also including the neck, into the water to feed at the water-mud interface in the littoral zone. These different feeding behaviours suggest that the birds were utilizing the epipelagic microbial community, which grows on the water-mud interface where light could penetrate to the sediment surface. This could potentially be an

important food resource for lesser flamingos. This study is built on this premise and aimed to investigate and quantify the alternative food resources of lesser flamingos in various saline lakes in Kenya and Lake Natron in Tanzania.

1.2.Objectives

The broad objective was;

To investigate the alternative food resources of lesser flamingos and quantify their contribution to the algal primary productivity of the Rift Valley saline lakes.

The specific objectives were;

1. To determine the composition of the planktonic, epipellic and the lake shore mud food resources.
2. To establish the relative importance of these communities as possible food resource for the *P. minor* by measuring respective *in situ* biomass of the planktonic, epipellic and the lake shore mud microbial communities.
3. To measure the productivity of the planktonic and epipellic microbial communities.

1.3.Research questions

1. Is the blue-green algae *Arthrospira fusiformis* from the Rift Valley saline lakes the only food resource for lesser flamingo population in eastern Africa?
2. What other food resources support the lesser flamingo population?
3. What is the diversity of these food resources?
4. What is the production rate of the food resources?
5. How do the various food resources contribute to the primary productivity of these lakes?

1.4.Hypotheses

1. The food resources utilized by the lesser flamingos are variable and the eastern Africa population of lesser flamingos could not be maintained on planktonic *A. fusiformis* alone.
2. Epipellic and lake shore mud microbial communities contribute significantly to the algal primary productivity of the saline lakes of East Africa and consequently to the food resources of lesser flamingos.

CHAPTER TWO

LITERATURE REVIEW

2.1. Classification and geographical distribution of lesser flamingos

Flamingos belong to the family Phoenicopteridae which is made up of birds with remarkably long thin legs and extremely long flexible necks. They are descendants of an ancient lineage of microphagous, colonial wading birds that inhabited hypersaline lakes of tropical and subtropical regions (Bildstein *et al.*, 1993) but their relationship to other birds is unclear (Jenkins, 1957). Today, there are six living flamingo species in the world. Two species occur in East Africa, that is, the greater flamingo (*Phoenicopterus ruber roseus*) and the lesser flamingo (*Phoeniconaias minor* Geoffroy Saint-Hilaire, 1798). Lesser flamingo stand out distinctively with their pink plumage and dark-red bills (Stevenson and Fanshawe, 2002)

P. minor is the most numerous of all flamingo species (Childress *et al.*, 2008) with four recognized populations that are probably separate. The global population is estimated to be between 2,220,000 to 3,240,000 with the largest population which is more than 75% of the total population in the East African eco-region of approximately 1.5 to 2.5 million individuals. Other small populations of *P. minor* occur in West India/Pakistan with 650,000 individuals, 55,000-65,000 in southern Africa and 15,000- 25,000 in West Africa. Lesser flamingos inhabit alkaline saline lakes and pans in Africa and Asia. In Eastern Africa they are found within the Eastern Rift valley from Ethiopia through Kenya down to the saline lakes of Tanzania.

2.2. Geology, climate and hydrology in shaping the East African alkaline-saline lakes

The East African Rift Valley was formed in the Cenozoic approximately 40 million years ago (Ma) as a result of volcanism and tectonic activity. In the Pliopleistocene, 2.5 Ma the African climate became drier due to the onset of the glacial cycles in the Northern Hemisphere (deMenocal 1995). From this time the East African region started experiencing periods of alternating humidity and aridity between 2.7-0.9 Ma (Trauth, 2005).

Diatomite evidence depicts the presence of very large lakes within the central Rift with deep lakes of more than 250m depth between 1.9-0.9 Ma, receiving 2000

mm yr⁻¹ of rainfall. The lakes have been hypothesized to have contributed to the evolution of early hominids by forming barriers both when full of water and when dry (Trauth *et al.*, 2010). A large lake still existed 9,200 years ago within the central Rift but by 3,000 years it had become smaller (Richardson and Richardson, 1972). The present small lakes within the central Rift are all remnants of this large lake.

Recent historical sediment studies have shown the presence of lake level fluctuations accompanied by conductivity changes at Lake Sonachi (Verschuren *et al.*, 1999) and Lake Oloidien (Verschuren *et al.*, 2004) during the 19th century. The two lakes experienced dry spells in the mid 19th century with conductivity of 7,000 – 13,000 $\mu\text{S cm}^{-1}$ at Sonachi and 12,700 – 13,600 $\mu\text{S cm}^{-1}$ at Oloidien in 1883. In 1940-1960 the lakes went through another dry spell. The low lake level and incidents of major environmental episodes also coincide with ecological succession events of chironomids, diatoms (Verschuren *et al.*, 1999; Verschuren *et al.*, 2004) and rotifers (Epp *et al.*, 2010). Similar changes can be inferred for the other lakes at the same time.

The lakes are characterized by high alkalinity with pH as high as 10 or more due to high levels of Na⁺ trachyte lava from the surrounding volcanic highlands which is washed into the rivers that drain into these lakes. Low Mg²⁺ and Ca²⁺ ions lead to the formation of an alkaline salt Na₂CO₃·NaHCO₃·2H₂O (Grant, 2004), known as trona or soda ash and locally referred to as ‘magadi’. The lakes within the rift valley are endhorreic without outlets and over time trona has accumulated as it is left behind after evaporation. It has been industrially mined to make glass, toothpaste and has been traditionally used in its raw form as a food tenderizer and additive (Nielsen and Dahi, 1995).

The lakes are renowned for their high salinity with high but stable conductivity of around 70,000 $\mu\text{S cm}^{-1}$ at deeper lakes such as Lake Bogoria (Harper *et al.*, 2003; Schagerl and Oduor, 2008) and high variability at shallow lakes such as Lake Nakuru 11,000 – 160,000 $\mu\text{S cm}^{-1}$ due to lake level fluctuations (Verschuren *et al.*, 2004). As a result of the high alkalinity and salinity the lakes are referred to as alkaline saline lakes.

2.3. Biological characteristics of alkaline-saline lakes

The phytoplankton is often dominated by the cyanobacteria *Arthrospira fusiformis*, *Anabaenopsis* sp. and the single celled *Synechococcus* sp. Common diatom species include *Anomoeoneis* sp. *Navicula* sp. and *Nitzschia* sp. (Oduor and Schagerl, 2007). Phytoplanktonic primary productivity is very high, with the main primary consumer of the cyanobacteria being the lesser flamingo.

Rotifer species of *Brachionus dimidiatus*, *B. plicatilis* and *Hexartha jenkiniae* characterized the zooplankton. A copepod *Lovenula africana* is sometimes a dominant primary consumer at Lake Nakuru. An alkaline-water cichlid fish *Alcolapia alkalicus graham* (formerly *Sarotherodon alkalicus graham*) (Vareschi and Jacobs, 1984) is present in lakes Natron, Magadi, Nakuru and Elementeita, where it has a population refuge in the hot springs. The fish sustains the large numbers of pelicans of more than 22,000 individuals as recorded in 1969 by Bartholomew and Pennyquick (1973).

2.4. Main food resources of *Phoeniconaias minor*

Phoeniconaias minor are able to congregate in large numbers on these Kenyan saline lakes particularly because of the availability of their primary food resource, the microscopic cyanobacteria, mainly *Arthrospira fusiformis*. The major lakes in Kenya utilized by lesser flamingos include Lake Bogoria, Lake Nakuru and Lake Elementeita and most recently Lake Oloidien, which was separated from Lake Naivasha, a freshwater lake, in the 1980s due to declining water level (Harper and Mavuti, in McClanahan and Young, 1996) and has been slowly salinizing progressing towards an alkaline-saline lake.

In these lakes, *A. fusiformis* can sustain a continuous steady algal bloom but from time to time, unpredictably, there is a crash (Tuite, 1981). For this reason *P. minor* are nomads of saline lakes because of their random movements from lake to lake in search of suitable ecological conditions and food. According to Tuite (1979), the saline lakes often have high densities of flamingos, which coincide with high densities of *A. fusiformis*. Diatoms are also a food resource for *P. minor* and seem to have more stable densities in shallow lakes where light can reach the sediment (Tuite, 1981) with a mean of $\sim 45 \text{ mg Chl } a \text{ m}^{-2}$ in shallow lakes. Not much research has been conducted on assessing how much diatoms contribute to the food of lesser

flamingo or to the ecology of the saline lakes. The most notable studies relating to the food of lesser flamingo are those carried out in the 1970s at Lake Nakuru by Vareschi (1978 & 1982) and Vareschi and Jacobs, (1984, 1985); however they focused more on *A. fusiformis* because it occurred in higher densities in most lakes than the other cyanophytes and algal species.

2.5. Filter feeding adaptation of lesser flamingos

Flamingos are filter feeders; they are adapted to this mode of feeding by being equipped with specialized and unique filtering equipment (shown on Plate 2.1). They have lamellae with platelets that form a filter that acts as a sieve within the bills. The six species of flamingos have different sizes of filters that enable them to sieve organisms of different sizes. *P. minor* has the finest filter that enables it to sieve organisms in the size range 20-100 μ (Jenkin, 1957).

The tongue functions as a pump pressing water through the bill while the platelets strain out the cyanobacteria and algae. These are the main food for *P. minor* in the alkaline-saline lakes of Kenya. Such an adaptation allows *P. minor* not only to acquire food in such harsh conditions but also to avoid consuming the lethal waters of alkaline saline lakes that may cause physiological damage.

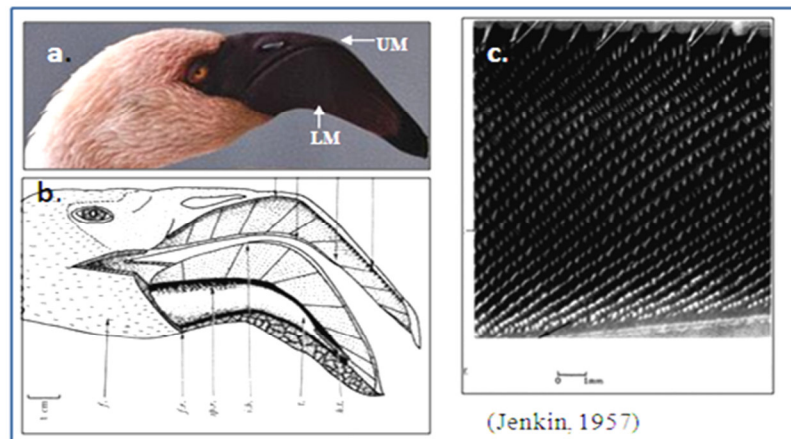


Plate 2.1: The head of *P. minor* showing - (a) the upper mandible (UM) and the lower mandible (LM), (b) the transverse section of the bill and (c) the lamellated area of the bill. From Jenkin (1957)

According to the study by Pennycuick and Bartholomew (1973), flamingos have a constant pumping rate, but the concentration of cyanobacteria and algae in the water is what determines how much time *P. minor* would devote to feeding. To make a positive energy surplus, a minimum *A. fusiformis* concentration of 120 g dry weight (DW) m⁻³day⁻¹ is required by a non-breeding lesser flamingo and a breeding one would require 250 g DW m⁻³day⁻¹ to produce an egg. This could be achieved if the flamingo spends 80% of its time feeding. Feeding rates decrease with decreasing algal densities and feeding stops at algal concentrations of 100 g DW m⁻³ and below (Pennycuick and Bartholomew, 1973; Varesechi, 1978).

2.6. Lesser flamingo feeding behaviours

Different patterns of feeding behaviours displayed by *Phoeniconaias minor* have been documented. For instance, Ridley *et al* (1955) explained that they feed by sweeping the surface of the water with their beaks while swinging their heads from side to side to collect floating phytoplankton from the upper two inches (Brown, 1973) of water. They can feed in this way while swimming or standing in shallow water (Plate 2.2). Jenkin (1957) mentioned an additional feeding behaviour of *P. minor*, the stamping of their webbed feet to stir up food from the bottom in shallow waters. In another study, Varesechi (1978) observed lesser flamingos feeding on mud flats during times of very low *Arthrospira fusiformis* density. He suggested that they may have been feeding on diatoms, a food resource found growing mostly on the sediment in shallow water or on the lake shore mud (Hecky and Kilham, 1973).

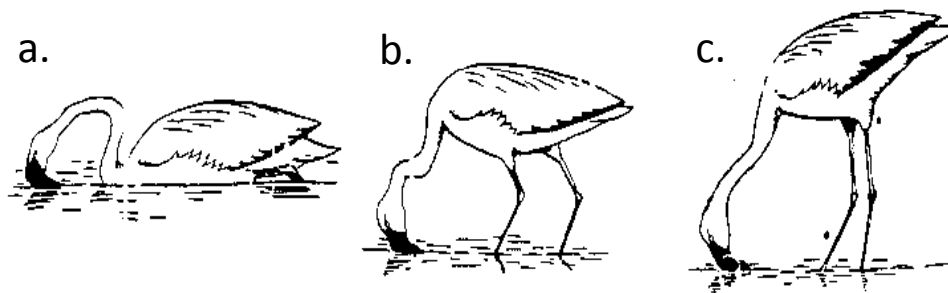


Plate 2.2: Lesser flamingo feeding behaviours (a) filter feeding while swimming in deep water and (b& c.) filter feeding while standing on shallow water (modified from Ridley *et al.*, 1955)

2.7. Other food resources for the lesser flamingos

Whilst *P. minor* are very specialized in the unique way they feed, they are generalist feeders in that they can ingest anything of the size range of 20-100 μ (Jenkins, 1957). Although Vareschi (1978) recognized *A. fusiformis* as the main food resource for *P. minor*, he expounded on other possible food resources for *P. minor*. He demonstrated that, during seasons of high rotifer densities- of 19 mg DW L⁻¹ at Lake Nakuru - the rotifers significantly supplemented the *P. minor* diet by up to 20%.

Other minor food resources include cyanobacterial species of the genera *Anabaenopsis* and *Anabaena*, and diatoms. *Anabaenopsis* and *Anabaena* flourish at Lake Nakuru and Lake Elementeita when there is low *Arthrospira fusiformis* biomass (Vareschi, 1978). Single-celled cyanobacteria of the genus *Synechocystis*, *Synechococcus* and *Monoraphidium* dominate the phytoplankton of saline lakes such as Lake Nakuru from time to time. They are too small (2-6 μ in diameter) to be retained by the lamellae. Between 1974- 1975 single celled cyanobacteria dominated Lake Nakuru, which coincided with low *P. minor* population.

In research carried out in 1974 at Lake Nakuru, Vareschi (1978) also observed that at times of low densities of *A. fusiformis*, *P. minor* tended to feed on the mud flats at the lake edges where there was a film rich in diatoms that seemed to be a sustainable food source for them. He noted a remarkable increase in flamingo numbers at a time when the cyanobacterial density was low and suggested that this film of diatoms on the mud flats could significantly substitute for *A. fusiformis* as food for lesser flamingos. It is reasonable to imagine that benthic diatoms could sufficiently meet the nutritional needs of *P. minor* and may be of equal or even higher importance as flamingo food than *A. fusiformis* when they occur in high densities.

Apart from *A. fusiformis*, rotifers and diatoms, other organisms in these lakes that fall in the size range filterable by *P. minor* include desmids, protozoans and other cyanobacteria species. For this reason, a very wide variety of additional food resources for the *P. minor* do exist. The proposed study seeks to explore these alternatives.

2.8. Lesser flamingo population trends

A National Waterbird census is carried out in Kenya every January and July over the last two decades. Flamingo census is done at lakes Nakuru, Bogoria, Elementeita, Sonachi and most recently Lake Oloidien. Due to its recent salinisation and colonization by *A. fusiformis* (Ballot *et al.*, 2009) lesser flamingos recently started to be utilized it as a feeding site.

Different methods are used in estimating flamingo populations, the most affordable being ground census where the lake is divided into sections and teams cover the shore by foot counting birds encountered (Owino *et al.*, 2001). The teams are led by an experienced ornithologist and the members estimate the numbers of flamingos within a specified crowd of flamingos. The numbers that are within close range among the group members are averaged while those that are far out of the group's range are excluded. This is the method used for the national water birds census to estimate flamingo numbers. The method's main limitation is its inability to accurately estimate numbers in large groups of flamingo but it has been proved reliable (Morales-Roldan *et al.*, 2011).

Aerial photography surveys have also been used to estimate flamingo population (Tuite, 1979), where photographs are taken from airplane flying over a lake. Other than the cost implications it seems to be the most reliable. New methods are being developed such as use of photographs taken using mobile phones (Iliffe *et al.*, 2011) to estimate flamingo populations.

The earliest available reports from observations in the 1950s by Brown (1973) reported very high estimates of 4 million lesser flamingos within Kenya and Northern Tanzania (Fig. 2.1.). In October 1958 he observed more than 500,000 breeding pairs that may have resulted in at least 460,000 young chicks by February of 1959 at Lake Natron. Thereafter, between 1968 and 1969 Bartholomew and Pennycuik (1973) reported a total population of 1,043,000 from an areal survey in 24 lakes in Kenya and Tanzania. The National Waterbirds Census conducted each January since 1991 has recorded numbers that ranged from 337,000-1,470,000 from 1991-1999 within the Kenyan saline lakes (Owino *et al.*, 2001). In 1994, Woodworth *et al.* (1997) conducted an aerial photographic survey of flamingo population at 9 lakes in Tanzania and recorded a total of 907,000 birds. An estimated 2,800,000 birds were reported in 13 lakes with 1% of the population being greater flamingos (Bartholomew

and Pennycuick, 1973). Between 1974 and 1976 estimates by Tuite (1979) at 22 lakes in Kenya and Northern Tanzania gave a lower estimate of 350,000 – 550,000 birds with some lakes having no flamingos. In 2002, 634,440 birds were recorded in 13 lakes in Tanzania (Raini and Ngowe, 2009).

A survey of nests at Natron for three years from 1965-1967 gave a total of ~ 100,000 nests whereas no breeding was reported in 1968 while in 1969 a minimum of 100,000 nests were recorded (Fig. 2.2). Most recently in January 2011, Baker (2011) recorded 35,000 hatchlings at Natron. At Lake Bogoria, lesser flamingo numbers varied from 40,000 in December 2000; 297,000 in January 2001; 510,000 in August 2001 to 30,000 birds in 2003 (Fig. 2.3.). In the 1970's high population of approximately one million flamingos was recorded at Lake Nakuru (Fig. 2.4.) by Vareschi (1978). Periods of high mortality have also been witnessed such as at Lake Bogoria in August 2001 where 114 birds died daily (Harper *et al.*, 2003).

There is certainly a big disparity between earlier estimates by Brown (1973) and more recent reports that suggests a serious decline in numbers. In fact there are reports of declining population in different locations; Etosha Pan in Southern Africa (Simmons, 1995), Sambhar Salt Lake in India (Kulshreshtha *et al.*, 2011) and Lake Natron in Tanzania (Clamsen *et al.*, 2011). These declines can be explained by the fact that flamingos often disperse outside the main feeding lakes, which are mostly surveyed. Counts seem to only concentrate on the easily accessible lakes and those seen to occasionally harbour large flamingo populations.

Nonetheless, these reports of declining population (Simmons, 1996; Clamsen *et al.*, 2011) raise concern. In 1988 the IUCN Red List had classified *P. minor* as a species of 'Low Risk/Least Concern'. Although it is the most numerous flamingo species its status was raised in 2000 to 'Low Risk/Near Threatened' and again in 2004 to the current 'Near Threatened' (IUCN, 2010) status. This is due to increasing concern owing to reports that imply decreasing population and threats posed to the only breeding site, Lake Natron, for the East Africa population by the development of a soda mining facility.

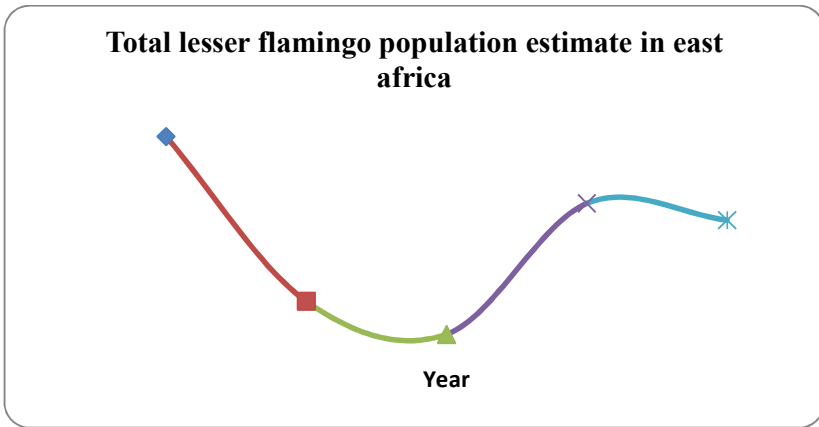


Fig. 2.1: Lesser flamingo population trends for the East African population.

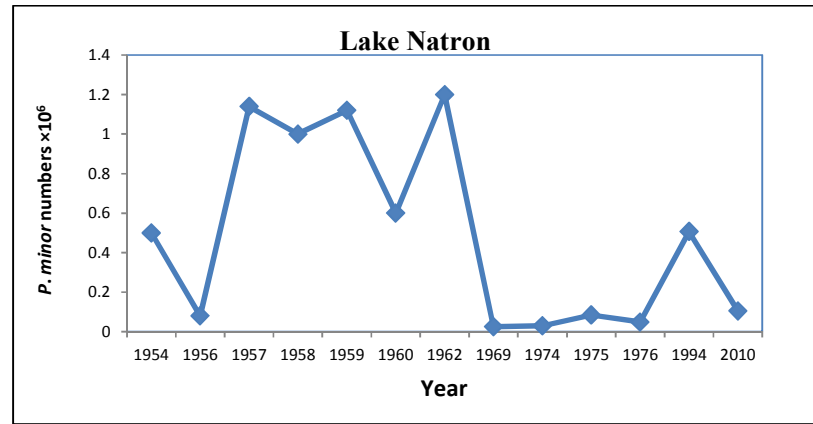


Fig. 2.2: Population trend at Lake Natron, the only viable breeding site in East Africa.

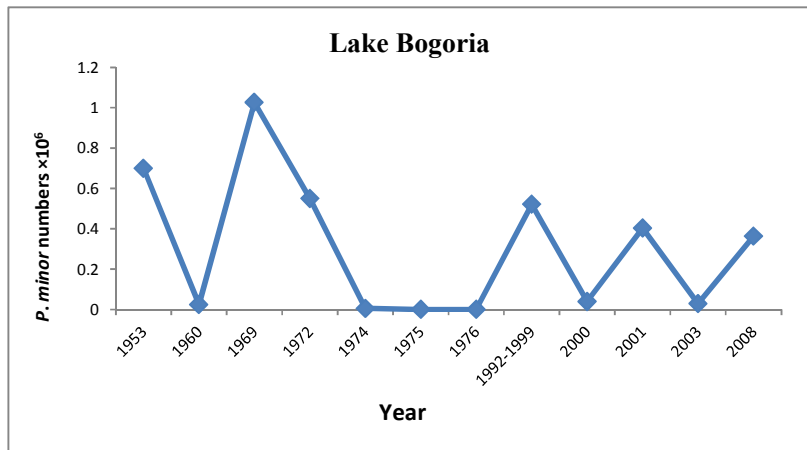


Fig. 2.3: Lesser flamingo population trend at Lake Bogoria, a major feeding site.

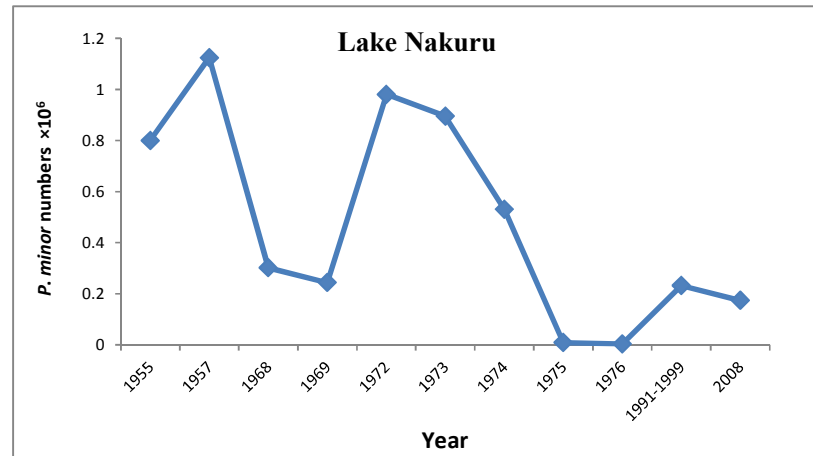


Fig. 2.4: Population trend of lesser flamingo at Lake Nakuru, a major feeding site.

References: Brown, 1973; Bartholomew and Pennycuik, 1973; Tuite, 1979; Vareschi, 1978; Woodworth *et al.*, 1997; Owino *et al.*, 2001; Harper *et al.*, 2003; IUCN, 2010; Clamsen *et al.*, 2011.

2.9. Productivity of saline lakes

Apart from their rich bird life, tropical saline lakes are fascinating because of the magnitude of the rate of primary production of the algal blooms that support the huge flocks of *P. minor*. An understanding of the productivity of algae is essential because primary producers are the principal source of energy for saline lake ecosystems (Vareschi and Jacobs, 1985). Hammer (1981) gave a global review of the variability of primary production rates of saline lakes in three continents, Africa, Australia and North America. The highest reported phytoplankton primary productivity was $10,000 \text{ mg C m}^{-3} \text{ h}^{-1}$ at Lake Aranguadi in Ethiopia. Indeed, such a high primary productivity clearly shows that saline lake ecosystems are important ecosystems.

Most of what is known about the primary production of the saline lakes in Africa has come from studies by Talling *et al.*, (1973), Melack and Kilham, (1974) and Vareschi, (1982). They mainly studied the primary productivity of the phytoplankton, mainly dominated by *A. fusiformis* of lakes in East Africa and reported high primary productivity. These researchers measured phytoplanktonic primary production but did not lay much emphasis on the importance of the epipellic algae in these lakes and its contribution to the lakes' overall primary production.

According to Hammer (1981) the importance of the epipellic microbial community to the flora of tropical saline lakes has been previously underestimated because of sampling difficulties. Nevertheless, studies carried out in temperate regions have demonstrated the importance of benthic algae production to total lake production. For instance, Stanley (1976) established that epipellic production is very important in aquatic ecosystems. He carried out this study between 1971 and 1973 and worked on tundra ponds and lakes with depths ranging from 20 cm to 2 m. Stanley recorded epipellic primary productivity that was nine times higher than phytoplanktonic production. In tundra ponds 20 cm deep, he recorded epipellic production that ranged from 4 to $10 \text{ g C m}^{-2} \text{ yr}^{-1}$ compared to $1 \text{ g C m}^{-2} \text{ yr}^{-1}$ for the lakes 2m deep. Shallower ponds had a higher epipellic production than deeper lakes due to high light intensity at the sediment level. In another study, Björk-Ramberg and Ånell (1985) conducted experiments at Lake Stugsjön, a shallow Swedish subarctic lake. They found that epipellic algae constituted 70-83% of the total production in that lake.

Hammer (1981), referred to a study done by Wetzel (1964) at Borax Lake in North America on the primary production of blue-green algae that dominated the benthic littoral zone of the lake. The annual primary production was 267g C m⁻², which was 69% of the total primary production of Lake Borax. This indeed, suggests that the epipelagic microbial community of saline lakes may be very important to the total primary production of saline lakes. Nevertheless, no studies in the tropical regions have investigated the importance of the epipelagic microbial communities and its response to the dynamics of change of lakes in the tropical region yet it seems to be very significant to the general ecology of saline lakes.

2.10. Justification of the study

The lesser flamingo is of great conservation and scientific value and also of great economic value as the species is a major tourist attraction and foreign income earner for Kenya and Tanzania. At present, it is classified as ‘near threatened’ on the IUCN (International Union for Conservation of Nature) Red List (2010) due to its specialized habitat requirements. There is increasing concern due to large-scale die-offs of *P. minor* which have occurred with greater frequencies since 1993 (Ndetei and Muhandiki, 2005) than previously within the Kenyan saline lakes.

Recent studies in the East African flamingo eco-region indicated that cyanobacterial toxins may be the cause of *P. minor* deaths in Kenya (Krienitz *et al.*, 2003, Ballot *et al.*, 2004, Ballot *et al.*, 2005) and in Tanzania (Lugomela *et al.*, 2006). Ballot *et al.*, 2004 and Ballot *et al.*, 2005 attributed these deaths to the ingestion of hepatotoxins and neurotoxins produced mainly by *Arthrospira fusiformis*. Flamingo deaths have also been reported to also occur during times of algal crash, such as at Lake Bogoria. *P. minor* were weakened by lack of food at a time of *A. fusiformis* crash and those that could not move to other lakes eventually died of starvation (Owino *et al.*, 2001). There is also potential DDT contamination (Bettinetti *et al.*, 2011).

Saline lakes are faced with mounting pressures from deforestation of their catchments, water over-abstraction from the rivers that feed the lakes, siltation and alteration of habitats (Mwinami *et al.*, 2010). All these factors may have resulted in habitat modification hence contributing to decrease in the flamingo population. The rate of population decline is, however, difficult to quantify due to the birds nomadic

nature (Childress *et al.*, (2008). They move from lake to lake unpredictably in search of suitable ecological conditions and abundant food resources.

As the lesser flamingo is of great conservation and scientific value, it therefore makes the protection of their habitat an issue of major concern. A better understanding of the food and feeding requirements of *P. minor* is necessary so as to comprehend how saline lakes can provide alternative food resources to sustain food requirements of lesser flamingos throughout the year. This will enable further investigations into other possible causes of deaths of the species. In the face of a changing climate it is important to know how these changes would affect the food resources that the species depends on.

CHAPTER THREE

STUDY AREA, MATERIALS AND METHODS

3.1. Study area

The primary focus of the study was lakes Bogoria, Nakuru and Elementeita that lay within the Central Rift Valley in Kenya. However other study sites were considered in the study in order to obtain some regional estimates for comparison. These were lakes Oloidien and Sonachi (Crater Lake) within the Naivasha basin in Kenya and Lake Natron within the South Rift Valley in Tanzania (Fig. 3.1).

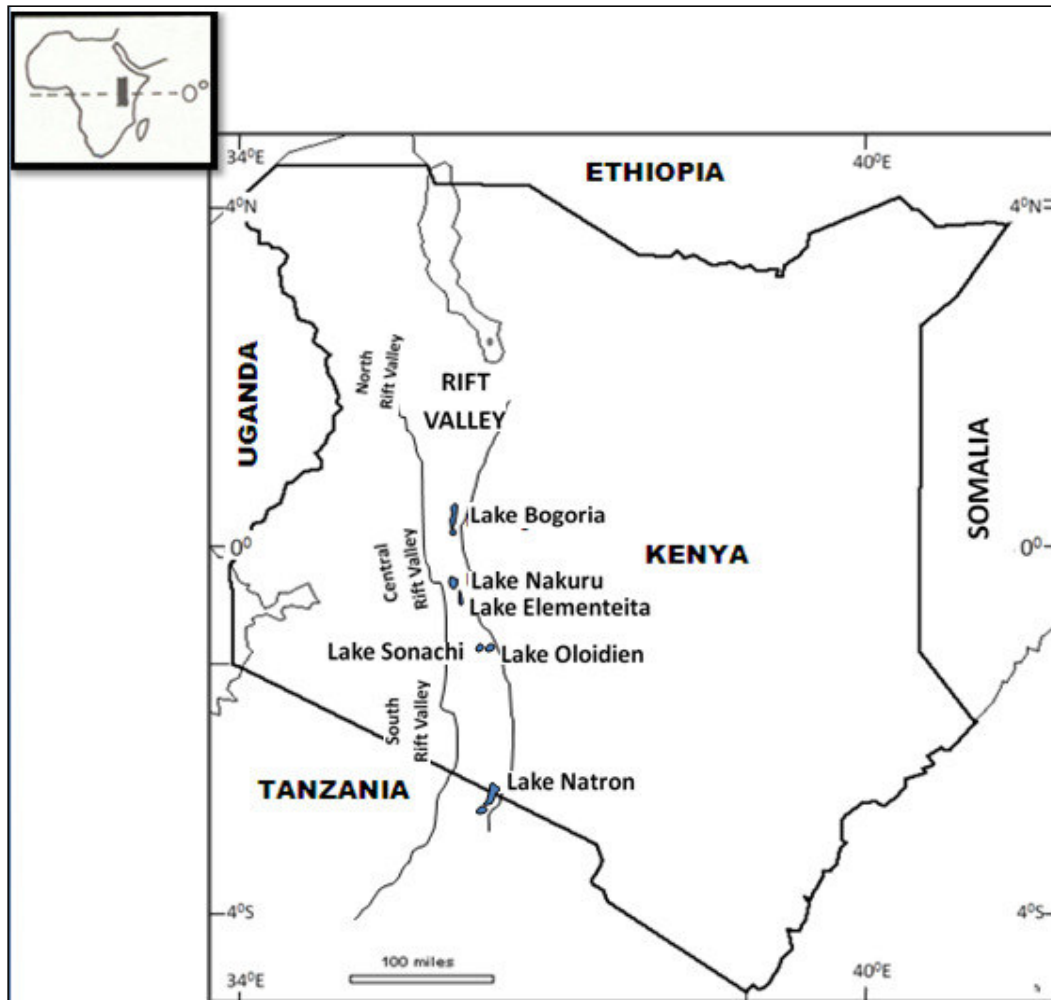


Fig. 3.1: The location of study lakes in the Eastern Rift Valley.

3.1.1. Description of study sites

The lakes of the East African Rift valley system have undergone periods of erratic extreme changes in water level and environmental conditions during the last hundreds of years (Verschuren, 2001) and on geological time scales (Trauth *et al.*, 2005). In spite of these lakes being in close proximity to each other they are stunningly different in hydrology, ecology and range in depth from less than 0.15 m at Lake Natron to a maximum depth of 10.2 m at Lake Bogoria. The phytoplankton and zooplankton communities of saline lakes are poor in species diversity and unpredictable in occurrence compared to freshwater and marine ecosystems.

Lake Bogoria

This lake, formally known as Lake Hannington, is situated at 00° 15'N, 36° 05'E. It lies at an elevation of 990 m above sea level with a mean rainfall of about 500 mm yr⁻¹. This lake is 3 km wide at its widest point with an area of approximately 34 km². The lake has three basins, the North, Central and South basins with the central basin being the deepest at 10.2 m (Fig. 3.2.). It is reasonably deep with an average depth of 5.4m (Hickley *et al.*, 2003). The lake's conductivity ranges between 40-77,000µS cm⁻¹ and pH of 10.3 (Vareschi, 1978; Harper *et al.*, 2003). The water budget is mostly maintained by the Waseges–Sandai River system in the North and the Emsos River in the South and the numerous springs from the nearby escarpments. Lake Bogoria differs from the other central rift lakes in that, despite water level fluctuations, the lake remains chemically stable (Harper *et al.*, 2003).

The phytoplankton biomass, estimated between 5.8-51.4 mg L⁻¹, is dominated by the cyanobacteria *Arthrospira fusiformis* contributing over 80% (Schagerl and Oduor, 2008). Other phytoplankton species observed occasionally were *Synechocystis spp.*, and *Navicula halophila* and *Keratococcus spp.* The lake is one of the main feeding sites for *P. minor*, which may occur in upto 1 million individuals. The other important primary consumer is the zoobenthic chironomid larve *Paratendipes spp.* with a density of 4×10⁴organisms m⁻² (Harper *et al.*, 2003).

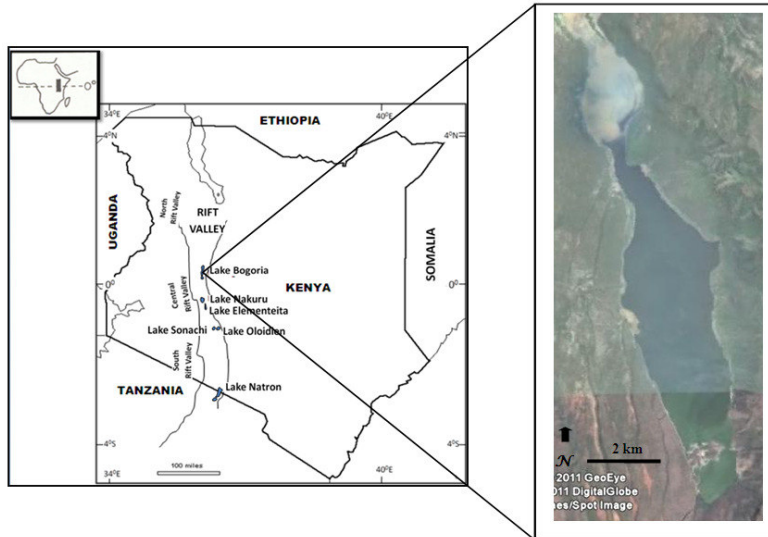


Fig. 3.2: The location and image of Lake Bogoria in the Eastern Rift Valley (Image from Google Earth 2011).

Lake Nakuru

The lake is located at $0^{\circ} 24'S$, $36^{\circ}05'E$ and lies at an altitude of 1,759m above sea level with a mean rainfall is about 800 mm yr^{-1} . The lake's surface area varies from 5 km^2 to 45 km^2 with a mean depth of 2.3 m (Ndetei and Muhandiki, 2005). The conductivity is highly variable and ranges between $11\text{--}160,000 \mu\text{S cm}^{-1}$ (Verschuren, 2004) with a pH of approximately 10.5 (Vareschi, 1978) (Fig. 3.3.). The water budget is maintained by recharge from four seasonal inflowing rivers namely, Rivers Njoro, Nderit, Makalia and Naishi, in addition to Baharini Springs and other springs along the eastern shoreline which are perennial. Treated wastewater from Nakuru Town also drains into the lake.

In 2003-2005 the net primary productivity was $10.7 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ while the algal biomass ranged between $40.3\text{--}77.9 \text{ mg L}^{-1}$ with *A. fusiformis* contributing 60% of the phytoplanktonic biomass (Oduor and Schagerl 2007). Other species of importance as flamingo food at the lake include cyanobacteria *Anabaenopsis arnoldii*, *Anabaenopsis abijatae* and *Anabaena spp.* and diatom species *Navicula halophila*, *Navicula elkab*, *Nitzschia frustulum*, *Nitzschia sigma* and *Anomoeoneis sphaerophora*. Other phytoplankton at the lake are *Synechococcus spp.* and the chlorophytes *Monoraphidium minutum* and *Chlorococcum spp.*

Lesser flamingo populations at the lake have been monitored for long and though erratic the lake can host 1 million flamingos which are the main primary consumer of the dominating cyanoabacteria species. Other primary consumers are alkaline-water cichlid fish *Sarotherodon alkalicus graham*, a calanoid copepod *Lovenula Africana*, rotifers *Brachionus dimidiatus*, *B. plicatilis*, *Hexarthra jenkiniae* and larval chironomids *Leptochironomus deribae*, *Tanytarsus horni* and water bugs *Anisopsvaria*, *Micronecta scuteilaris*, *M. jenkiniae* and *Sigara hieroglyphica kilimandjaronis* (Vareschi, 1978).

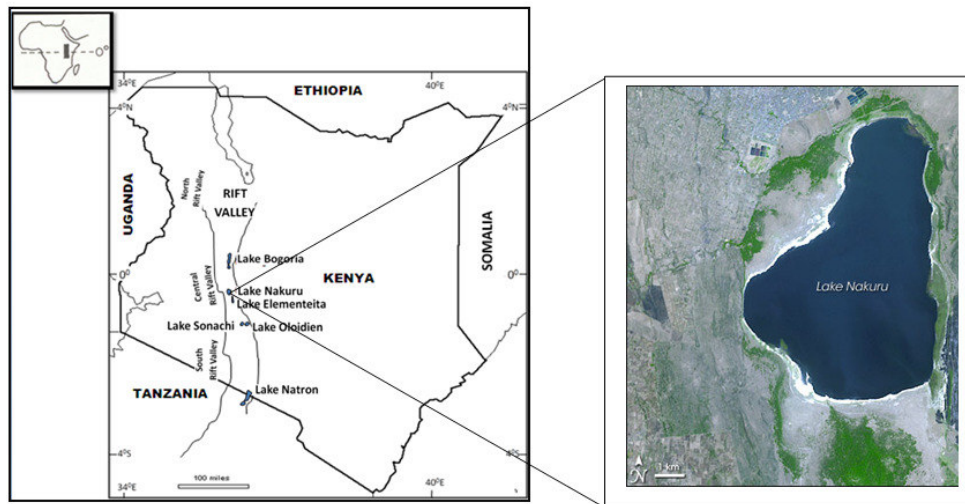


Fig. 3.3: The location and image of Lake Nakuru in the Eastern Rift Valley (NASA Earth Observatory, 2008).

Lake Elementeita

It is located $0^{\circ}27' S$, $36^{\circ}23' E$. Most of the lake falls within an elevation of 1800m above sea level. The area of the lake is approximately 19 to 21 km². The lake is quite shallow with a mean depth of about 1.2 m and a drainage basin of about 500 km² (Fig. 3.4.). The lake's conductivity is between 11.9– 25,000 $\mu S\ cm^{-1}$ with a pH of 9.8 (Vareschi, 1978). Water supplies come primarily from three inflowing rivers, Chamuka, Mbaruk and Kariandusi Rivers and warm springs on the southern lakeshore.

Elementeita has a similar assortment of phytoplankton as Nakuru. *A. fusiformis* contributes < 50% of the phytoplanktonic biomass *Anabaenopsis arnoldii*, *A. abijatae*, *Synechococcus spp.*, and *Anabaena spp.* are also present. Common

diatom species include *Navicula halophila*, *N. elkab*, *Nitzschia frustulum*, *N. sigma* and *Anomoeoneis sphaerophora* and the chlorophyte species *Monoraphidium minutum*, *Chlorococcum spp.* but also *Keratococcus spp.* (Oduor and Schagerl, 2007). The lake is one of the major feeding sites of lesser flamingos as the lake can support a bloom of cyanobacteria during high lake levels while during low lake levels it supports benthic diatoms which are presumed to also nourish the birds.

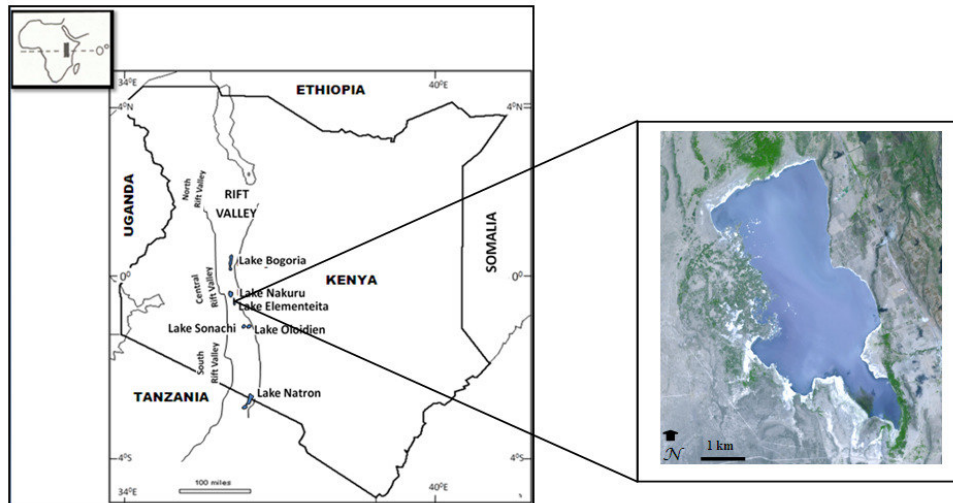


Fig. 3.4: The location and image of Lake Elementeita in the Eastern Rift Valley (NASA Earth Observatory, 2008).

Lake Oloidien

This lake is located $0^{\circ}50'S$ $36^{\circ}17'E$ at an altitude of 1887 m a.s.l. It is small with an area of 5.5 km^2 and shallow with a mean depth of 5.6 m (Harper and Mavuti, in McClanahan and Young, 1996), while the main inflow is from precipitation. Formerly, Lake Oloidien was a bay of Lake Naivasha but by 1984 it had become completely separated from Lake Naivasha due to decreasing lake levels (Fig. 3.5). It gradually became eutrophic (Lyngs, 1996) and has recently progressed towards a hypereutrophic alkaline-saline state. Information obtained from the sediment study of the lake by Verschuren *et al.* (2004) shows that the lake's conductivity has been changing through out its recent history depending on lake levels. From $12,700 - 13,600 \mu\text{S cm}^{-1}$ in the mid 19th century, $320-431 \mu\text{S cm}^{-1}$ in 1929–1931 when

Oloidien was connected to Lake Naivasha, $6500 \mu\text{S cm}^{-1}$ between 1946– 1957 during a period of low lake level, and $\sim 1200 \mu\text{S cm}^{-1}$ in 1991 after the separation.

The lake's ecology has also changed becoming more of an alkaline-saline lake. Between 2001 and 2005 there was a shift in the dominating phytoplankton from dominance of coccoid Chlorophyceae to cyanobacteria *Arthrospira fusiformis* and *Anabaenopsis elenkinii* (Ballot *et al.*, 2009). The chironomid community has been shifting with changing lake conductivity from fresh water species *Tanytarsus horni* and *Dicrotendipes septemmaculatus* to salt tolerant species *Microchironomus deribae*, *Kiefferulus disparilis* (Verschuren *et al.*, 2004). Due to colonization of the lake by *A. fusiformis* the lake has recently become a major feeding lake for lesser flamingos with reports of numbers up to 70,000 in 2006 (Harper *et al.*, 2006) and 25,000 in 2007 (Adhola *et al.*, 2009).

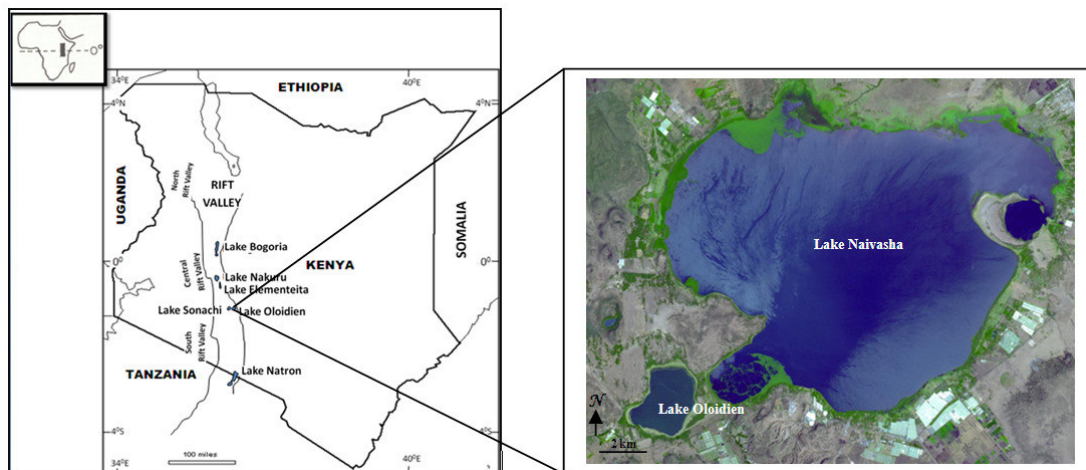


Fig. 3.5: The location and image of Lake Oloidien and Lake Naivasha from which it was separated (Image from Google Earth 2011).

Lake Sonachi

It is a small crater lake located approximately $0^{\circ}47'S$ $36^{\circ}16'E$ at 1,884 m above sea level in the Rift Valley in Kenya. It is shallow with a depth of about 4.25 m recorded in 1993 (Fig. 3.6). Being a crater lake there are no rivers flowing into the lake, the main inlets are rainfall and ground water through subsurface flow from the large freshwater Lake Naivasha which is situated 3 km away (Verschuren *et al.*, 1999). Since the beginning of the nineteenth century, lake levels have fluctuated

frequently and reached maximum depths of 18 m during a high stand at the end of 19th century, and near desiccation in 2003.

Photosynthetic activity ranged between 150-870 mg O₂ m⁻² h⁻¹ in the 1970s (Melack, 1981) with the phytoplankton community dominated by cyanobacteria *Synechococcus bacillaris* which contributed 53% of algal biomass, *Lyngbya limnetica*, *Synechocystis aquatilis*, *Spirulina laxissima* and *Spirulina platensis* (which is now *Arthrospira fusiformis*). Green algae of species *Chlorella spp.* and *Oocystis parva* and diatom species *Nitzschia spp.*, *Navicula cryptocephala*, *Anomoeoneis sphaerophora*, *Craticula eklab*, have been recorded at the lake (Verschuren *et al.*, 1999).

The zooplankton community is composed of rotifer species of *Brachionus dimidiatus*, *B. Plicatilis* that dominated at different times in recent history of the lake (Epp *et al.*, 2010). The copepod *Paradiaptomus africanus* has been recorded at the lake and chironomid larvae of *Kiefferulus disparilis*, *Microtendipes sp.* and *Cladotanytarsus pseudomancus* with a density of 13,500 chironomids m⁻² (Verschuren *et al.*, 1999).

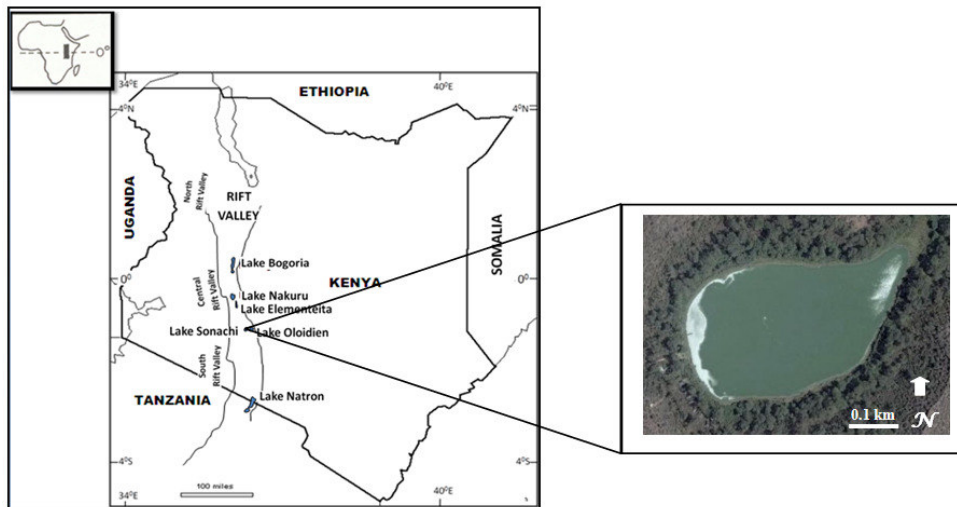


Fig. 3.6: The location and image of Lake Sonachi in the Eastern Rift Valley (Image from Google Earth, 2011).

Lake Natron

The lake is located 2⁰ 09' – 2⁰ 36' S and 35⁰ 54' - 36⁰ 06' E at an altitude of 610 m a.s.l. It is a large basin with an area of 1,039 km² and shallow with depth

ranging from a few centimeters to 2 m (Kasule *et al.*, 1993), the pH varies between 9 and 10. The lake is made up of several lagoons, the largest is the southern lagoon where the study was carried out (Fig. 3.7). Natron's water budget is mainly from the permanent Ewaso Ngiro River which rises from the Mau escarpment in Kenya. Seasonal rivers from the Loita hills, Loliendo Mountains, Ngorongoro highlands and Mt. Ngelai in Tanzania drain into the lake. Springs that occur all around the lake also contribute about a quarter of the water budget and maintain the lagoons during times of low rainfall. There is insufficient information regarding the biological characteristics of the lake. Only one alkaline water tilapia species *Oreochromis alcalica* is present and it sustains the pelicans and storks. The lake is significant to flamingos as it is the only viable breeding site for the East African *P. minor* population (Brown, 1973).

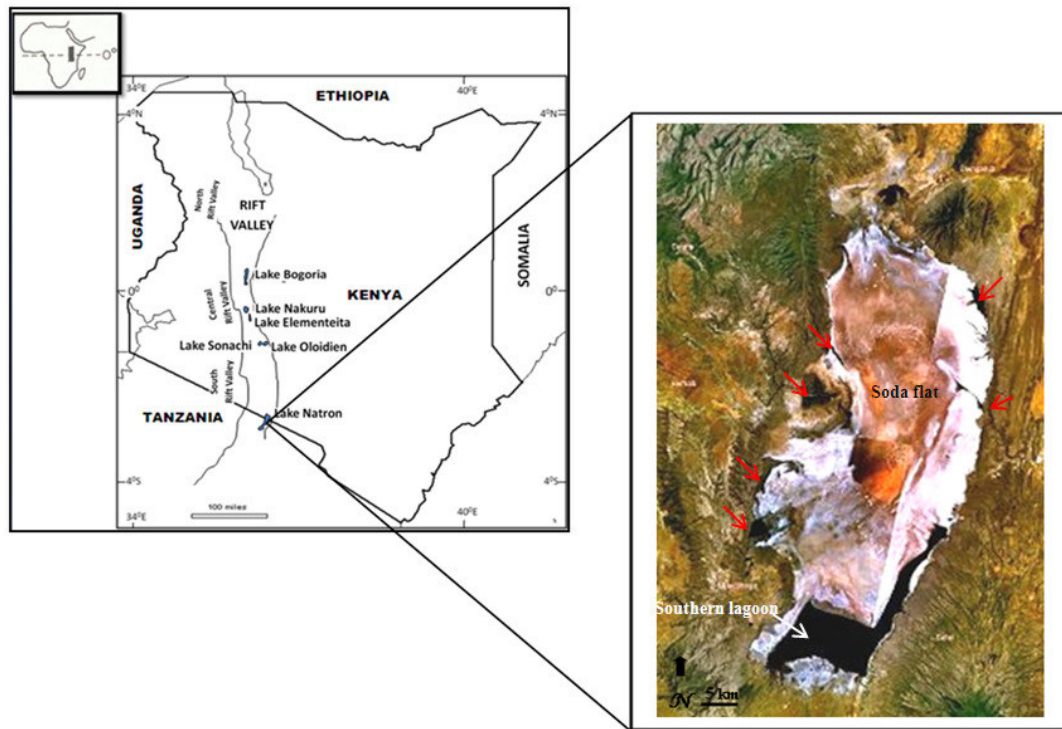


Fig. 3.7: The location and image of Lake Natron in the Eastern Rift Valley. The red arrows show some of the other smaller lagoons at the lake. (Image from NASA Earth Observatory, 2011).

3.2. Materials and Methods

3.2.1. Determination of composition of lesser flamingo food

3.2.1.1. Sample collection

A Gilson corer (Plate 3.1) was used to collect samples for assessment of planktonic standing crop, epipellic standing crop and the lake shore mud standing crop randomly on transects running from the lake shore to the maximum safely wadeable depth. The depth of the water in the corer was measured by ruler and the depth recorded. The water at the top and then at the bottom of the corer was carefully sucked using a 60 ml syringe sampler into sample bottles carefully avoiding mixing up the water and sediment. The remaining water in the corer was then swirled (without mixing up too much of the mud) to remove the attached epipellic community and poured into a separate sample bottle. The mud remaining at the bottom of the corer was unnecessary for this study and therefore was discarded.

Sampling for lake shore mud community was done at lakes where *P. minor* were observed feeding on shore mud. Samples were collected at water depths of 0-0.9cm on the lake edge, the whole sample was swirled to remove the epipellic community growing on the mud and if the sample collected had no water distilled water was added to help in removing the attached epipellic community. Different layers; plankton, epipellic and shore mud, were sampled for comparison of the food resource in these communities.

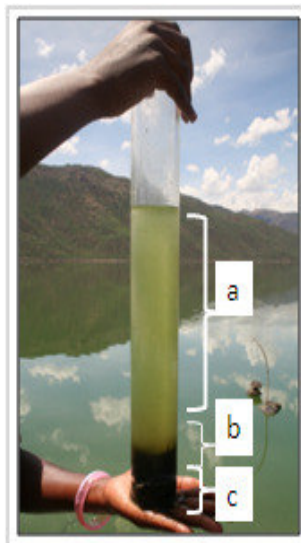


Plate 3.1: Gilson's corer showing the position of (a) the planktonic community, (b) the epipellic community in the water-mud interface and (c) sediment.

3.2.1.2. Species identification

The samples collected as described above were examined under the microscope for species present. A Sedgewick-Rafter cell counting chamber with a capacity of 1ml and evenly divided into 1000 squares was used to count the organisms present. Individuals of each species occurring in a minimum of 30 squares were counted. The number of organisms in 1 ml of the sample was calculated. For the cyanobacteria species *Arthrospira fusiformis* that is coiled, the number of coils was counted on ten colonies chosen at random.

Photographs of the species were taken using a Canon digital camera aligned with the eyepiece lens of the microscope to assist in identification. Diatom species were initially collectively counted as diatoms without counting per species later electron microscopy was used to identify species of diatoms. The species of microorganisms were identified at least to genus level using identification keys by Bellinger (1992), Barber and Haworth (1994) and Boney (1989) and with the help of experts and supervisors. The main output was a species check list.

3.2.2. Assessment of available food

3.2.2.1. Photosynthetic pigment analysis

Samples collected as described above (refer to section 3.2.1.1.) were measured for chlorophyll *a* (Chl *a*) content. The analysis of the photosynthetic pigment was used to determine the standing crop of cyanobacteria and algae as a measure of the food available for the lesser flamingo.

Subsamples of 50 or 100 ml of the water samples and 10 ml of lake shore mud samples were filtered through Whatman GF/C filter papers with a pore size of 0.47 µm to retain the algae. Each of the filter papers with the algae was ground in a mortar with a pestle in 5 ml of 90% acetone with MgCO₃ and a pinch of sand. When the contents were finely ground they were put in 15 ml centrifuge tube and filled to the 15 ml mark with 90% acetone. The samples were centrifuged in a hand-centrifuge at maximum speed, which was about 5000 r.p.m. The supernatant was decanted cautiously into a 1 cm path-length glass cuvette and the absorbance read against an acetone blank in a spectrophotometer at wavelengths of 750, 663 and 665 nm. Two drops of 1 M HCl were added to the sample in the cuvette to break down Chl *a* to

phaeophytin *a* and the absorbance was read again at the same wavelengths. Absorbance was converted to concentrations of Chl *a* using the formulae below (Sartory and Grobbelaar, 1984).

3.2.2.2. Calculation of the standing crop of available food

- a) Chl *a* absorbance was corrected using the equation that is below based on unpublished data by Nic Pacini.

$$\text{Corrected absorbance} = 5.3 \times \text{absorbance} - 0.026$$

- b) The chlorophyll *a* was calculated in $\mu\text{g cm}^{-2}$ using the following equation

$$\mu\text{g Chl } a \text{ cm}^{-2} = \left(\frac{26.7(E_{665_1} - E_{665_2}) \times V_e}{A_s \times l} \right)$$

Where;

26.7 = absorbance correction factor

E_{665_1} = corrected absorbance at 665 nm before adding HCl = (abs 665 – abs 750)

E_{665_2} = corrected absorbance at 665 nm after adding HCl = (abs 665 – abs 750)

V_e = represents volume of acetone used in the extraction (ml)

A_s = area of sample (cm^2)

l = path length of cuvette (cm)

c) $\mu\text{g Chl } a \text{ m}^{-2} = \mu\text{g Chl } a \text{ cm}^{-2} \times 10,000$

The maximum and minimum carbon value calculated using Falkowski (1985) conversion value for Chl *a* to carbon value.

- d) Maximum standing crop (SC max)

$$\text{mg C m}^{-2} = \frac{\text{Chl } a \mu\text{g cm}^{-2}}{1000 \times 0.003}$$

Where;

L = volume filtered (litre)

0.003 = conversion of Chl *a* to maximum Carbon value

1000 = conversion from μg to mg

e) Minimum standing crop (SC Min)

$$\text{mg C m}^{-2} = \frac{\text{Chl } a \text{ } \mu\text{g cm}^{-2}}{1000 \times 0.1}$$

Where;

L = volume filtered (litre)

0.003 = conversion of Chl *a* to maximum Carbon value

0.1 = conversion of Chl *a* to minimum Carbon value

1000 = conversion from μg to mg

3.2.3. Assessment of primary productivity

3.2.3.1. Exposure experiment method

Photosynthetic activity was determined by measuring the concentration of Oxygen (O_2) in the water using light and dark bottle technique. This technique measures the variations in the concentration of oxygen under different experimental conditions to infer net primary production (Vollenweider, 1974). The equipment that was used in measuring the rate of photosynthetic productivity is shown in Plate 3.2. It is composed of two transparent perspex metabolism chambers that fit tightly to a heavy bottom plate and one dark cover. Each chamber has an opening at the top that can fit an oxygen meter probe, and has a capacity of 4 litres and is equipped with a stirrer that (is run by a motor or hand) which ensures uniformity in the ambient conditions within the chamber.

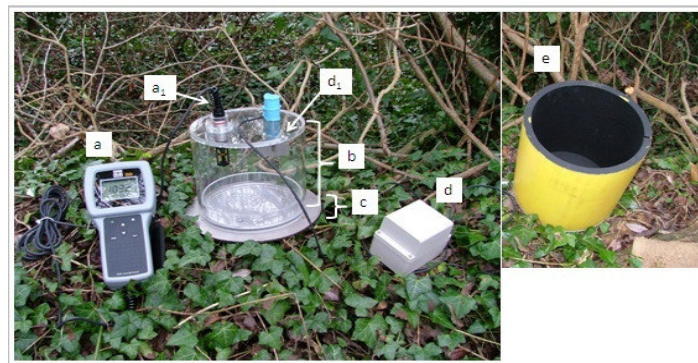


Plate 3.2: (a) Oxygen and temperature meter and (a₁) probe, (b) metabolism chamber top, (c) metabolism chamber base plate, (d) motor and (d₁) stirrer, (e) metabolism chamber dark cover.

Two metabolism chambers were used for each exposure; one of the chambers was covered with the dark cover to become the dark chamber, while the other one was left uncovered to become the light chamber (Plate 3.3).

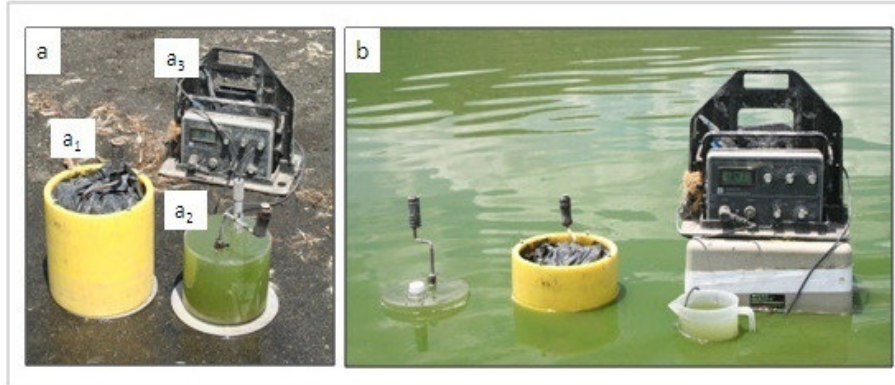


Plate 3.3: (a) Set up of productivity exposure experiment, (a₁) dark metabolism chamber, (a₂) light metabolism chamber and (a₃) oxygen meter. (b) Exposure experiment set up *in situ*.

Due to exposure to sunlight in the light chamber, photosynthesis was expected to take place, releasing oxygen as a by-product of photosynthesis and dissolved oxygen (DO) in the light chamber was expected to increase. Respiration by the whole community in the dark chamber was expected to result in a decrease in the dissolved oxygen in the dark chamber. The change in DO concentration in the chambers was measured using a YSI Professional Plus portable dissolved oxygen meter. The net primary production (NPP) was arrived at by deducting oxygen consumed by the respiration of the whole community (Resp., dark chamber) in the dark chamber from the gross primary productivity (GPP).

$$(F_l - F_d) - (I_n - F_d) = (F_l - I_n)$$

$(F_l - F_d)$ = the GPP per unit volume over the time interval involved

$(I_n - F_d)$ = the Resp. per unit volume over the time interval involved

$(F_l - I_n)$ = the NPP per unit volume over the time interval involved

Where;

I_n = the initial concentration of dissolved oxygen in the both the light and dark chambers

F_l = final concentration of dissolved oxygen in the light chamber

F_d = final concentration of dissolved oxygen in the dark chamber

The productivity which was measured as change in dissolved oxygen (Δ mg O_2 L^{-1} hr^{-1}) was converted to change in organic Carbon (Δ mg C L^{-1} hr^{-1}) using the relationship 1.0 mg of oxygen is equivalent to 0.30 mg of carbon to enable easy comparison with what is found in other ecosystems (Ref). The volumetric rate of primary productivity was converted into an area rate (mg C m^{-2} hr^{-1}) by dividing it by the height of the metabolism chamber.

Two primary production exposure experiments were carried out *in situ* on the shallow shores of the lake under investigation. The first exposure experiment measured both the planktonic and epipellic primary productivity while the second one measured only the planktonic primary productivity. This was to enable estimation of epipellic productivity by simple subtraction of the second measurement from the first one. The exposure experiments carried out were incubated between 10:00 and 14:00 hours because photosynthetic activity was expected to be highest at these hours.

3.2.3.2. Exposure experiment for measurement of planktonic and epipellic primary productivity

The base plates of both the light and dark metabolism chambers were filled with lake sediment and left in the shallow area of the lake at a depth of not more than 20 cm for approximately 24 hours. This allowed time for the sediment and the associated epipellic microorganism to settle. After 24 hours, the tops of the metabolism chambers were fitted carefully without disturbing the sediment and cautiously filled with lake water and one of them covered with the dark cover. This set up was meant for the measurement of the primary productivity of both the planktonic and epipellic microbial communities, ‘**total primary productivity**’. Once the equipment was set, the initial oxygen concentration in both chambers was measured using a dissolved oxygen meter (YSI model 58). The exposures were allowed a maximum time of one hour. This caution was taken because if they stayed longer than 1 hour, the oxygen concentration in the chambers could reach supersaturation level, which would be too high to be measured. Oxygen concentration within the chambers was measured repeatedly every 10 minutes. At the same time the concentration of oxygen in the open water was recorded. After 1 hour, the experiment was ended and the chambers emptied of all sediment and water.

3.2.3.3. Exposure experiment for measurement of planktonic primary productivity

The second exposure experiment was of lake water only this was to measure the productivity of the plankton microbial community. The exposures ran for 1 hour and oxygen concentration measures were repeated every 10 minutes. Samples of water and/or sediment were collected from each chamber at the end of each exposure.

Calculations for primary productivity and respiration of epipelagic community

$$a. \text{ Epipelagic primary productivity} = \text{Total primary productivity} - \text{planktonic primary productivity}$$

$$b. \text{ Epipelagic respiration} = \text{Total respiration} - \text{planktonic respiration}$$

Where:

Total primary productivity = primary productivity of both the planktonic and epipelagic community

Total respiration = respiration of both the planktonic and epipelagic community

3.2.4. Statistical analysis

The data were analyzed using the SPSS 10.0 programme. Most of the data were not normally distributed and therefore the non-parametric statistical tests were preferred. The Mann-Whitney U test was used together with Spearman's rank-order correlation, to test for significant relationships between the standing crop, water depth, and lesser flamingo population.

CHAPTER FOUR

RESULTS

4.1. General observations and explanation of terms.

1. The cyanobacteria within the water column is referred to as the **planktonic community**. During the study it was observed that at Lake Bogoria planktonic *Arthrospira fusiformis* often sank and formed a film of concentrated algal mass just above the bottom in shallow sheltered bays, upon which lesser flamingos fed on by diving down and submerging most of their bodies into the water.
2. At Bogoria there was no true epipelagic community but sunken *A. fusiformis*, which is referred to as **sedimented *A. fusiformis***.
3. In 2009, Lake Elementeita and Lake Natron's lagoon and marsh were very shallow with depth not exceeding 10cm. Light was able to penetrate to the bottom and benthic diatoms growing on the sediment surface formed a 'mat' which is referred to as the **epipelagic community**.
4. Lakes Elementeita and Natron did not have a truly planktonic community for the study period. The epipelagic community would become suspended in the water by the lesser flamingo trampling activities. The material suspended into the water column is referred to as the **suspended epipelagic community**. This was also observed in some few cases after a storm at Lake Natron.
5. Lesser flamingos were occasionally seen feeding on the mud at the lake shore. The biomass on the shore mud was measured and is referred to as the **lake shore mud community**.

4.2. Taxonomic composition

Four groups of taxa were encountered which were; Cyanobacteria, Bacillariophyceae, Protozoa and Rotifera. A taxon was considered dominant if it contributed 40% of the total count within its category or it was at least twice as numerous as the second most numerous species.

Table 4.1 summarizes the species that contribute to the flamingo food and Plate 4.1 shows some of these species. *Arthrospira spp.* was found in most lakes and achieved dominance at lakes Bogoria, Oloidien and Sonachi. Although *Anabaena spp.*, *Oscillatoria spp.*, *Lyngbya pseudospirulina* and *Spirulina spp.* were never dominant they were found in nearly all the lakes. *Anabaenopsis magna* and *Abijatae*

spp. occurred at Nakuru. *Arthrospira spp.* and *Anabaenopsis spp.* were characteristically missing from Lake Natron.

Presence of diatom species at a lake is denoted as 'p' in the table because diatom species were initially counted collectively as diatoms without counting per species and later identified from electron microscopy therefore abundances for each species is lacking. Several *Navicula spp.*, *Amphora spp.* and *Melosira spp.* were observed in all the lakes. Interestingly, *Sellaphora spp.* for which there is no previous record for saline lakes in Kenya was found only at Bogoria.

Among the protozoa *Frontonia spp.* was the most common and was present in all the lakes but in some it achieved dominance such as at lakes Bogoria and Sonachi. *Condylostoma spp.* was present in most but never achieved dominance. *Amoeba spp.* and *Campanella spp.* were recorded at Lake Oloidien only. *Dileptis spp.* and an unidentified species were found in Bogoria only. Lake Natron was very poor in protozoa with only *Frontonia spp.* Recorded while no rotifer species were seen. Plates 4.1, 4.2 and 4.3 show some of the species encountered during the study.

Table 4.1: Species composition of the microbial community at the study lakes during the study period ((3) dominant, (2) abundant, (1) present , (-) absent (p) present)

Taxon	Bogoria	Nakuru	Natron	Elementeita	Oloidien	Sonachi
Cyanobacteria						
<i>Arthrospira fusiformis</i>	3	2	-	1	3	3
<i>Arthrospira spp.</i>	-	1	-	-	3	-
<i>Anabaenopsis magna</i>	-	3	-	1	-	-
<i>Anabaenopsis abijatae</i>	-	3	-	1	-	-
<i>Anabaena spp.</i>	-	1	1	1	1	-
<i>Oscillatoria spp.</i>	1	2	1	1	1	1
<i>Lyngbya pseudospirulina</i>	-	1	1	1	1	-
<i>Spirulina subsalsa</i>	-	-	1	1	2	1
Bacillariophyceae	1	3	3	3	2	2
<i>Navicula spp.</i>	p	p	p	p	p	p
<i>Amphora spp.</i>	p	p	p	p	p	p
<i>Melosira spp.</i>	p	p	p	p	p	p
<i>Synedra/Flagillaria spp.</i>	p	p	p	p	-	-
<i>Cyclotella spp.</i>	-	p	p	p	-	-
<i>Cymbella spp.</i>	-	p	-	p	-	-
<i>Pleurosigma spp.</i>	p	-	-	-	-	-
<i>Sellaphora spp.</i>	p	-	-	-	-	-
Protozoa						
<i>Frontonia spp.</i>	3	2	1	1	2	3
<i>Condylostoma spp.</i>	2	2	-	1	1	1
<i>Euplotes spp.</i>	2	1	-	-	-	-
<i>Dileptis spp.</i>	1	-	-	-	-	-
<i>Campanella spp.</i>	-	-	-	-	2	-
<i>Amoeba spp.</i>	-	-	-	-	2	-
<i>Euglena spp.</i>	-	1	-	1	-	-
Unidentified species 1	2	-	-	-	-	-
Unidentified species 2	1	1	-	-	1	-
Rotifera						
<i>Brachionus spp.</i>	1	2	-	2	1	2
<i>Hexarthra jenkiniae</i>	1	2	-	1	-	-

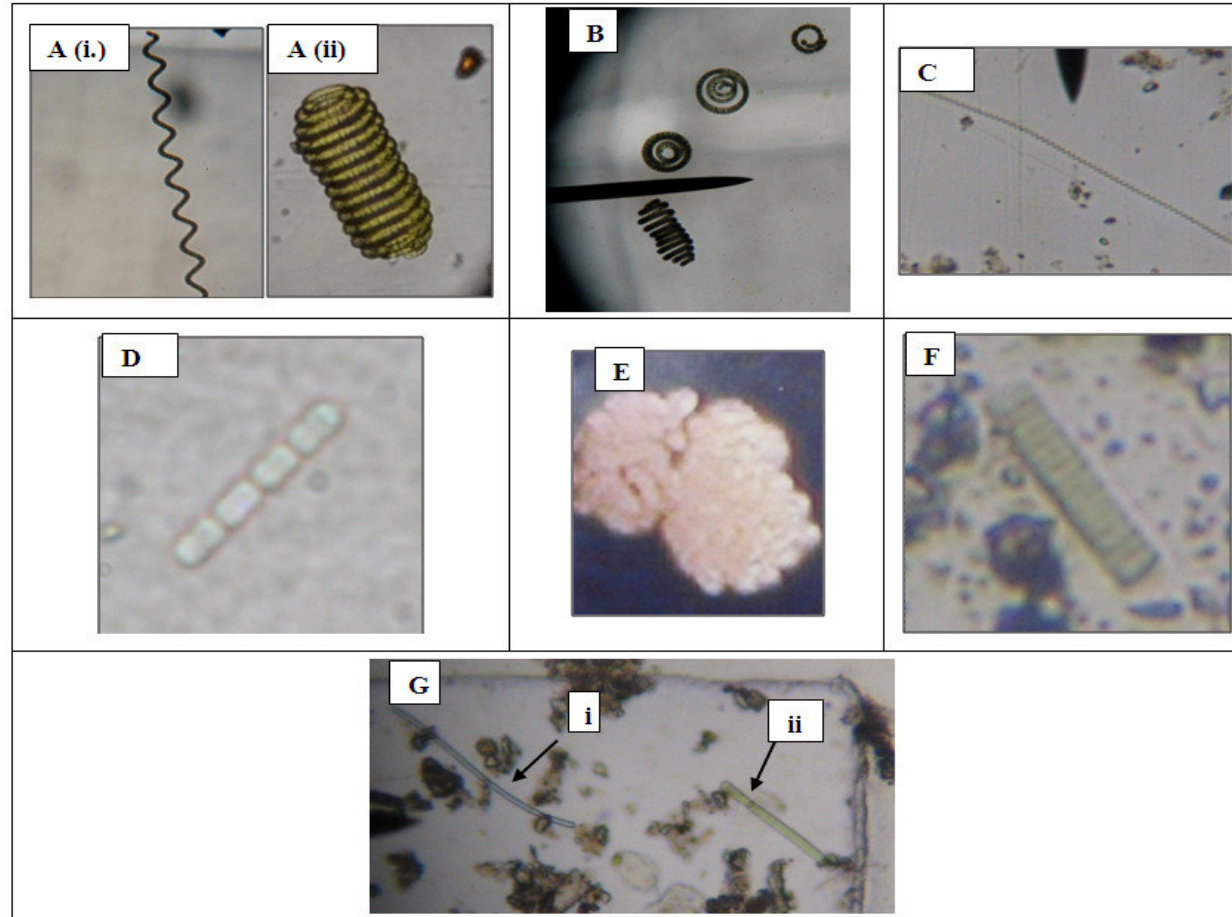


Plate 4.1: Cyanobacteria taxa identified (Bellinger, 1992 and Boney, 1989). **A.** *Arthrospira fusiformis* (i) extended and (ii) compressed. **B.** *Arthrospira* spp. **C.** *Spirulina subsalsa*. **D.** *Anabaena* spp. **E.** *Anabaenopsis abijatae*. **F.** *Lyngbya pseudospirulina*. **G.** *Oscillatoria* spp. **(i)** *O. limosa* (moving), **(ii)** *O. limnetica* (stationary).

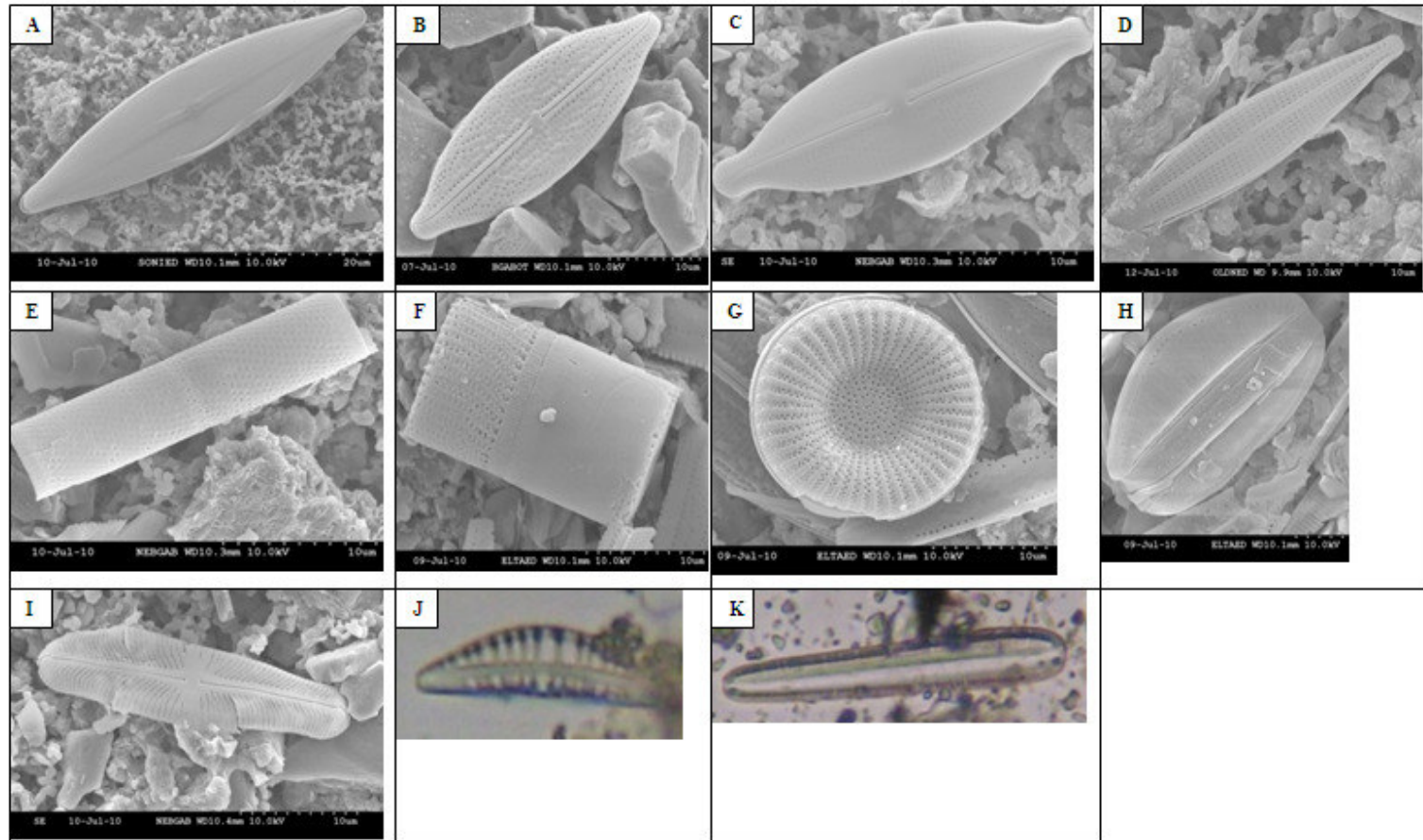


Plate 4.2: Some of the Bacillariophyta species identified (Bellinger, 1992 and Barber and Haworth, 1994) . **A-D.** *Navicula* spp. **E. & F.** *Melosira* spp. **G.** *Cyclotella* spp. **H.** *Amphora* spp. **I.** *Sellaphora* spp. **J.** *Cymbella* spp. **K.** *Pleurosigma* spp.

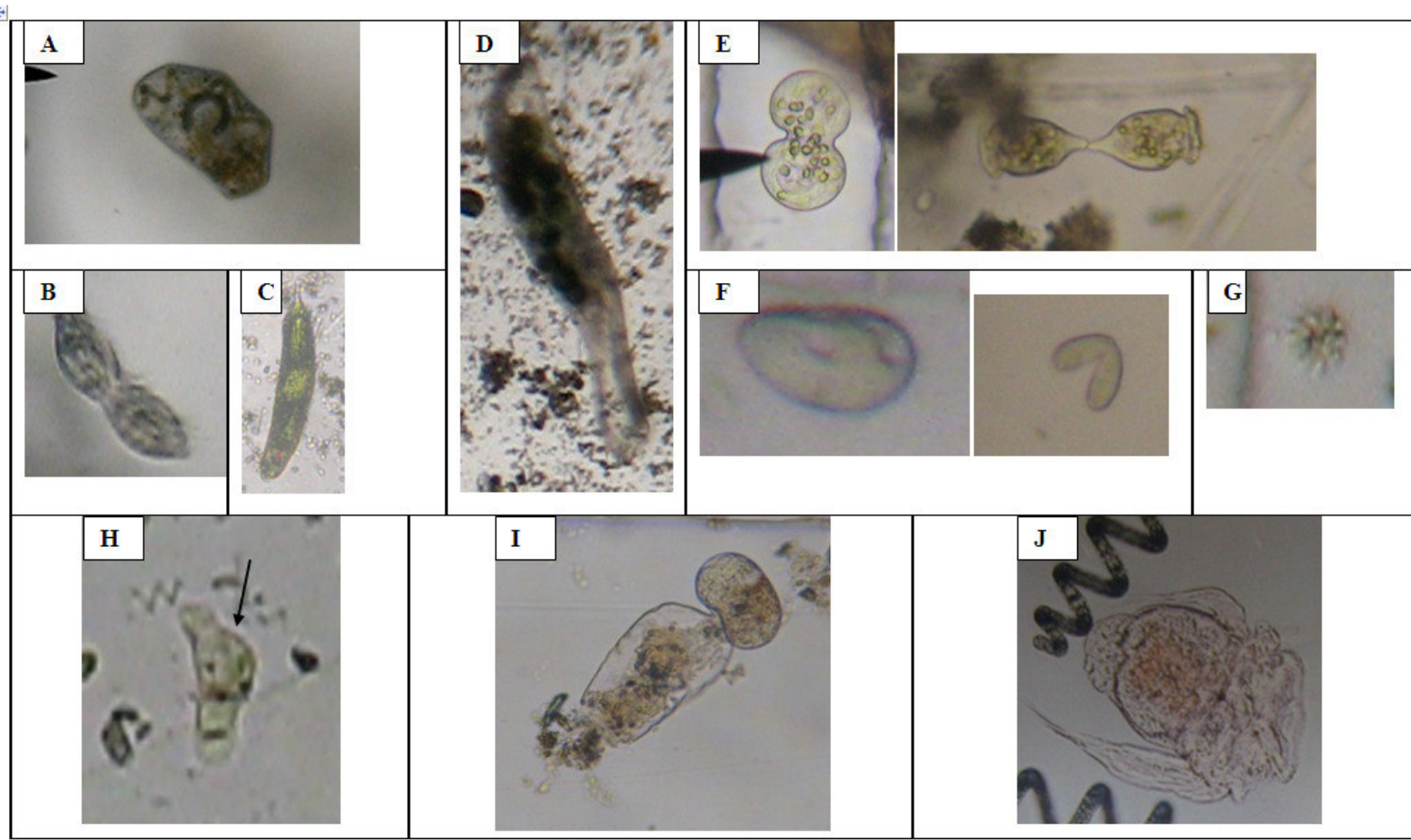


Plate 4.3: Protozoan species (A – H) and rotifer species (I & J) (Hall, 1953). **A.** *Frontonia* spp. **B.** *Euplotes* spp. **C.** An Euglenophyte species present at lake Nakuru only. **D.** *Condylostoma* spp. **E.** *Campanella* spp. was seen only at Lake Oloidien. **F.** Unidentified species 1. **G.** Actinosphaeridium. **H.** *Amoeba* spp. only seen in Lake Oloidien. **I.** *Brachionus plicatilis* **J.** *Hexarthra jenkiniae*.

4.3. Standing crop of the various categories of *P. minor* food resources

4.3.1. Standing crop of the planktonic and suspended epipellic food resource

The highest planktonic standing crop was recorded at Lake Bogoria in April 2009 with a mean of $37.74 \times 10^3 \text{ mg C m}^{-2}$. The lowest was recorded at Lake Sonachi with a mean of $0.56 \times 10^3 \text{ mg C m}^{-2}$ (Table 4.2, Fig. 4.1). The results from Lake Bogoria show a significant reduction ($p < 0.01$) in planktonic standing crop between April 2009 and August 2009 from 37.74×10^3 to $5.17 \times 10^3 \text{ mg C m}^{-2}$. The suspended epipellic biomass was generally low. The highest mean value of $4.29 \times 10^3 \text{ mg C m}^{-2}$ was significantly lower ($p < 0.01$) than the highest mean planktonic standing crop (Table 4.3, Fig. 4.2).

Table 4.2: Mean (\pm se) standing crop of the planktonic community.

Site	Month/year	Max $\text{mg C m}^{-2}(\times 10^3)$	Min $\text{mg C m}^{-2}(\times 10^3)$	se($\times 10^3$)	n
Bogoria	Apr-09	37.74	1.13	26.85	11
	Aug-09	3.24	0.10	5.17	40
	Aug-10	5.17	0.16	6.19	18
Nakuru Lake	Apr-09	11.97	0.36	2.51	3
	Aug-09	0.90	0.03	0.41	5
Nakuru Njoro river mouth	Aug-09	1.75	0.05	1.76	18
Sonachi	Sep-09	0.56	0.02	0.23	4
Oloidien	Sep-09	3.63	0.11	1.22	9

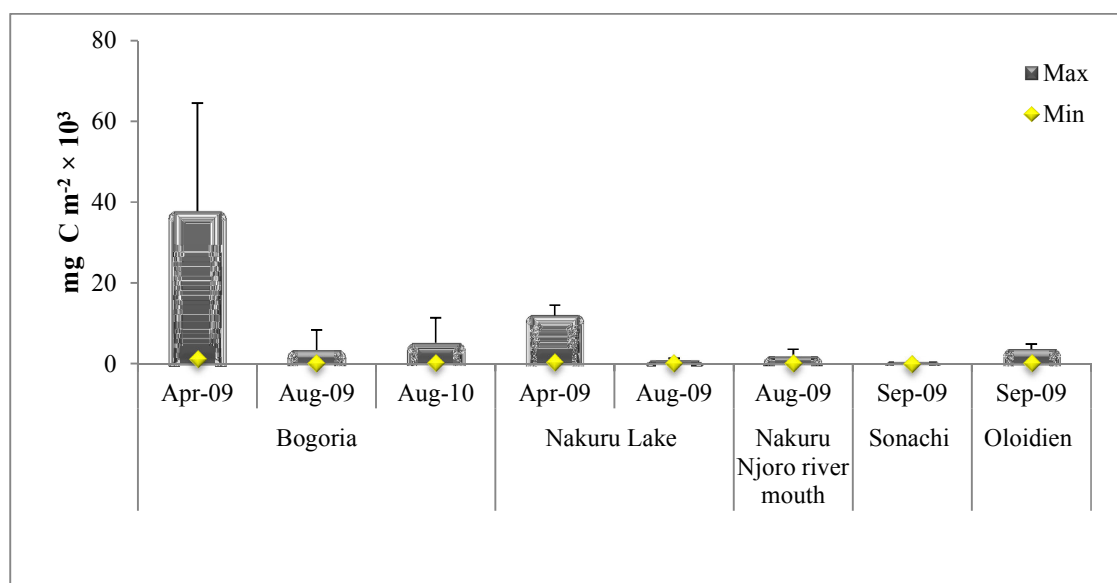


Fig. 4.1: Mean (\pm se) standing crop of planktonic food resource in the study lakes.

Table 4.3: Mean (\pm se) standing crop of the suspended epipellic community.

Site	Month/year	Max mg C m ⁻² ($\times 10^3$)	Min mg C m ⁻² ($\times 10^3$)	se($\times 10^3$)	n
Elementeita	Aug-09	0.66	0.02	0.16	6
Natron lagoon	Dec-09	0.79	0.02	0.48	7
Natron marsh	Dec-09	4.29	0.13	1.97	11

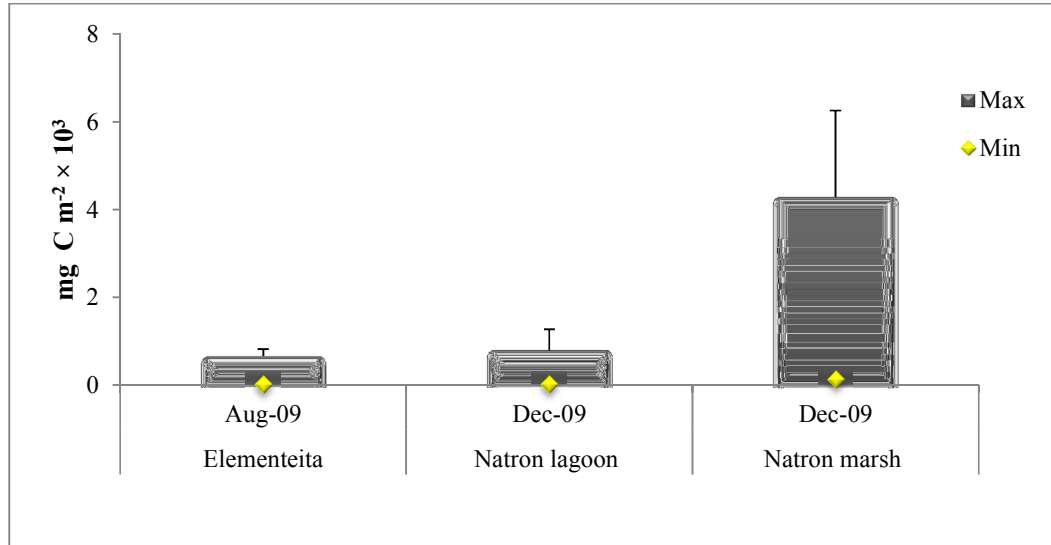


Fig. 4.2: Mean (\pm se) standing crop of suspended epipellic food resource in the study lakes.

4.3.2. Standing crop of sedimented *Arthrospira fusiformis* and the epipellic food resource

A decline in the sedimented *A. fusiformis* was recorded at Bogoria (Table 4.4; Fig. 4.3) and the pattern corresponded to the decline in planktonic standing crop at Bogoria observed between April 2009 and August 2010 (Fig. 4.1). Within this period, sedimented *Arthrospira* declined from 17.24×10^3 to 3.85×10^3 mg C m⁻². The highest mean epipellic standing crop was recorded at Lake Nakuru in April 2009, ranging between $67.67 - 30.36 \times 10^3$ mg C m⁻² with a mean of 46.7×10^3 mg C m⁻². The lowest recorded in Lake Nakuru was at the Njoro River mouth with a mean of 2×10^3 mg C m⁻².

Lake Natron recorded high epipellic standing crop compared to Lake Elementeita which was significantly lower than all measurements at Lake Natron's Lagoon and Marsh ($p < 0.01$). Some of the standing crop measurements of the sedimented *A. fusiformis* at Lake Bogoria (April 2009), epipellic and lake shore mud value at Lake Natron's Marsh in April 2009 and December 2009 varied highly. The results suggest that values of at least $55.9 - 95.6 \times 10^3$ mg C m⁻² were achieved for some measurements resulting in high mean standing crop (Table 4.5; Fig. 4.4).

Table 4.4: Mean (\pm se) standing crop of the sedimented *Arthrospira fusiformis*.

Site	Month/year	Max mg C m ⁻² ($\times 10^3$)	Min mg C m ⁻² ($\times 10^3$)	se ($\times 10^3$)	n
Bogoria	Apr-09	17.24	0.52	11.25	12
	Aug-09	4.25	0.13	5.79	40
	Aug-10	3.85	0.12	2.45	18

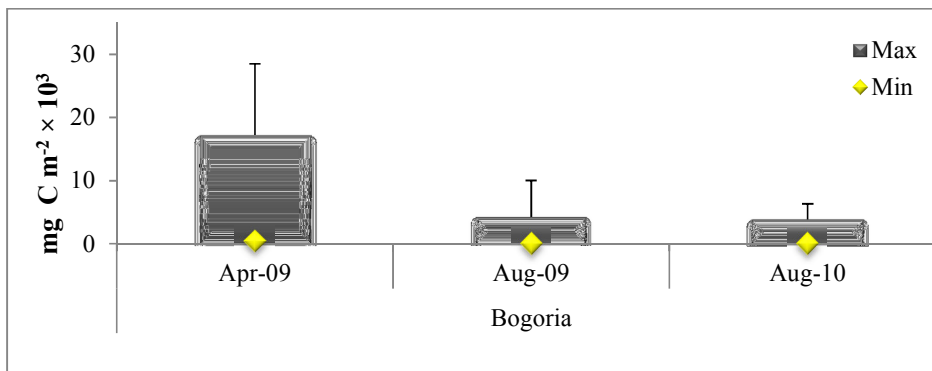


Fig. 4.3: Mean (\pm se) standing crop of sedimented *A. fusiformis* at Lake Bogoria.

Table 4.5: Mean (\pm se) standing crop of the epipellic community.

Site	Month/year	Max mg C m ⁻² ($\times 10^3$)	Min mg C m ⁻² ($\times 10^3$)	se ($\times 10^3$)	n
Elementeita	Aug-09	4.92	0.15	3.23	9
Nakuru Lake	Apr-09	46.67	1.40	13.66	7
	Aug-09	5.81	0.17	7.31	6
Nakuru Njoro river mouth	Aug-09	2.41	0.07	2.50	18
Natron lagoon	Apr-09	12.74	0.38	10.28	40
	Dec-09	20.69	0.62	6.66	27
Natron marsh	Apr-09	32.93	0.99	14.91	8
	Dec-09	26.68	0.80	22.03	12
Sonachi	Sep-09	3.12	0.09	2.72	6
Oloidien	Sep-09	3.12	0.09	2.63	8

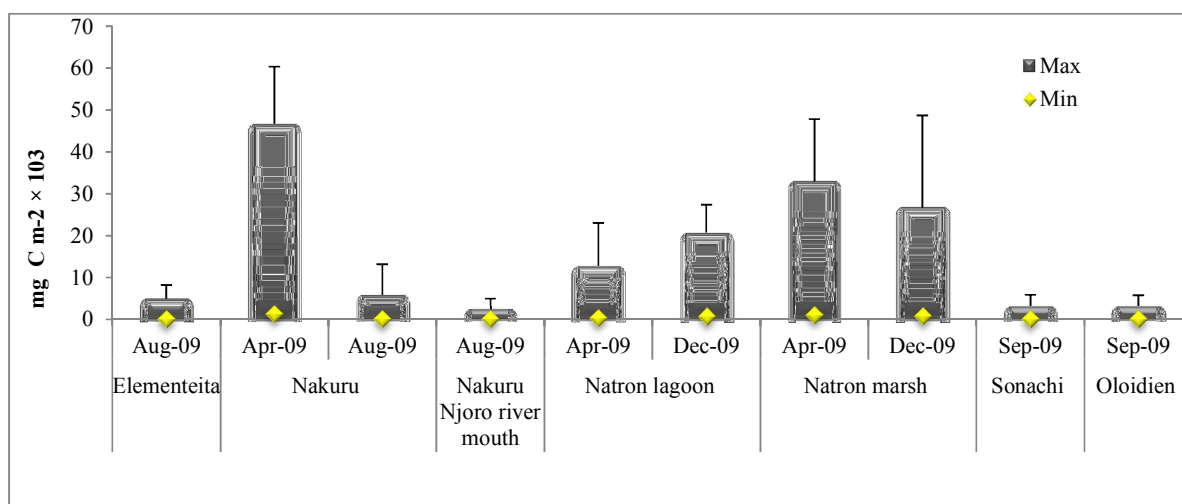


Fig. 4.4: Mean (\pm se) standing crop of epipellic food resource in the study lake.

4.3.3. Standing crop of lake shore mud food resource

The highest lake shore mud standing crop was recorded at Lake Bogoria in April 2009 with a mean of $55.46 \times 10^3 \text{ mg C m}^{-2}$ and the lowest at Lake Bogoria in August 2010 with a mean of $0.53 \times 10^3 \text{ mg C m}^{-2}$ (Fig. 4.5). Lake Elementeita's standing crop was significantly lower than that of Lake Natron's lagoon and marsh with $p < 0.01$.

Considering only the month of August 2009, the lake shore mud algae standing crop was highest at Lake Nakuru with a mean of $14 \times 10^3 \text{ mg C m}^{-2}$ compared to Lakes Elementeita and Bogoria. The standing crop at Lake Natron lagoon declined slightly between April and December 2009 from $22 \times 10^3 \text{ mg C m}^{-2}$ to $16 \times 10^3 \text{ mg C m}^{-2}$ while the Natron Marsh maintained its standing crop at $44 \times 10^3 \text{ mg C m}^{-2}$.

Table 4.6: Mean (\pm se) standing crop of the lake shore mud algae.

Site	Month/year	Max $\text{mg C m}^{-2} (\times 10^3)$	Min $\text{mg C m}^{-2} (\times 10^3)$	se ($\times 10^3$)	n
Bogoria	Apr-09	55.46	1.66	6.86	2
	Aug-10	0.53	0.02	–	1
Elementeita	Aug-09	2.83	0.09	2.86	6
Nakuru Lake	Aug-09	14.27	0.43	17.07	2
Nakuru Njoro river mouth	Aug-09	0.62	0.02	1.48	4
Natron lagoon	Apr-09	22.97	0.69	14.65	14
	Dec-09	16.73	0.50	5.50	8
Natron marsh	Apr-09	44.08	1.32	26.40	7
	Dec-09	44.90	1.35	24.44	12
Sonachi	Sep-09	6.08	0.18	0.08	2
Oloidien	Sep-09	3.91	0.12	0.25	3

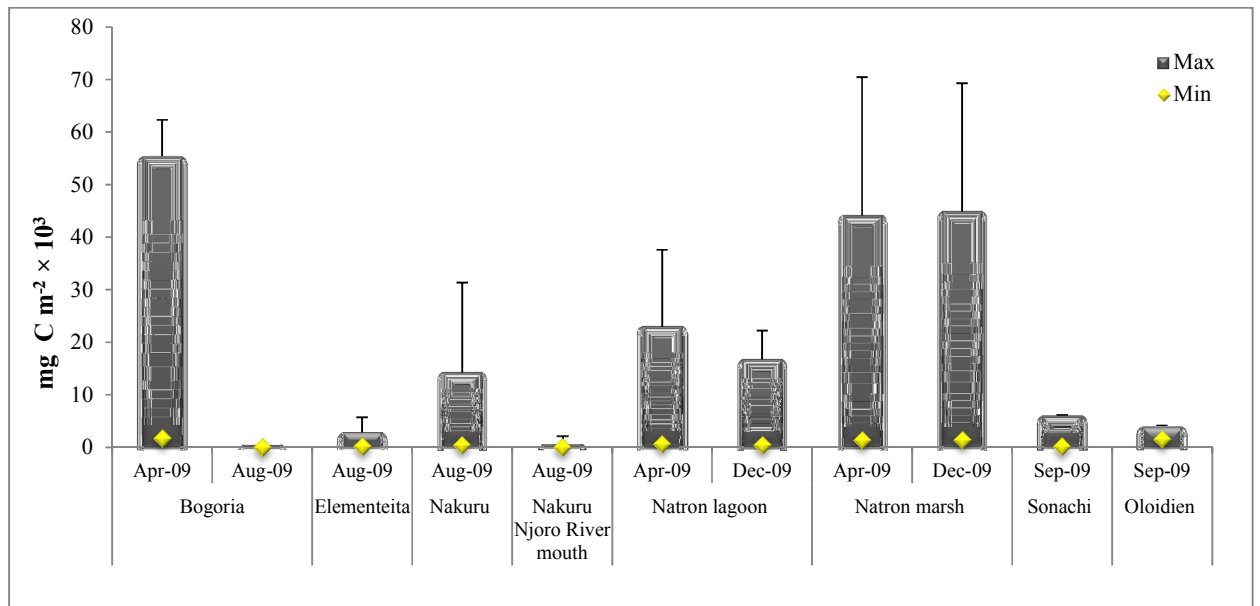


Fig. 4.5: Mean (\pm se) standing crop of lake shore mud algae in the study lakes.

4.4. Effect of water depth on standing crop of the various food resources

The Spearman's rank-order correlation indicated a weak negative association between the standing crop of the planktonic algae and water depth (Fig. 4.6). There a general decrease in was a significant negative correlation between water depth and the epipellic standing crop of $r_s = - 0.297$ ($p < 0.01$) (Fig. 4.7).

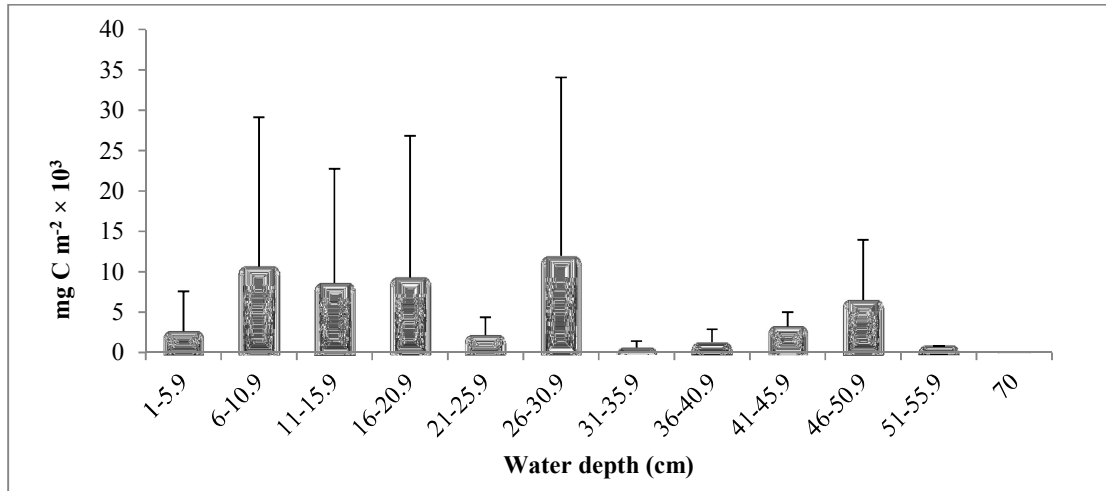


Fig. 4.6: Mean (\pm se) planktonic standing crop at varying water depths of all the study lakes.

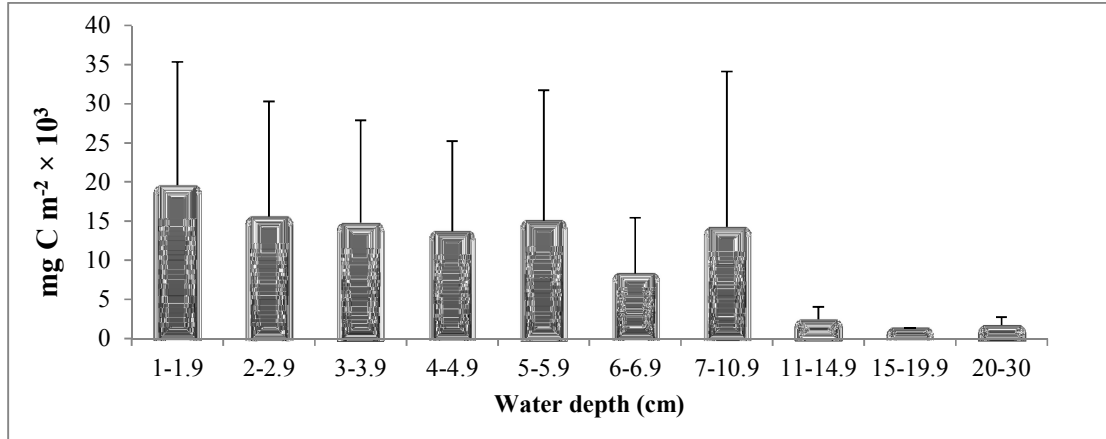


Fig. 4.7: Mean (\pm se) epipellic standing crop at varying water depth of the study lakes.

The standing crop of both the planktonic and sedimented *A. fusiformis* at Lake Bogoria (Fig. 4.8) increased slightly from a depth of 1- 10.9 cm of water depth and decreased to a water depth of 25.9 cm. It was highest at 26-30.9 cm water depth and thereafter decreased up to a depth of 50.9 cm water depth where the sedimented became higher than planktonic from 51-70 cm water depth.

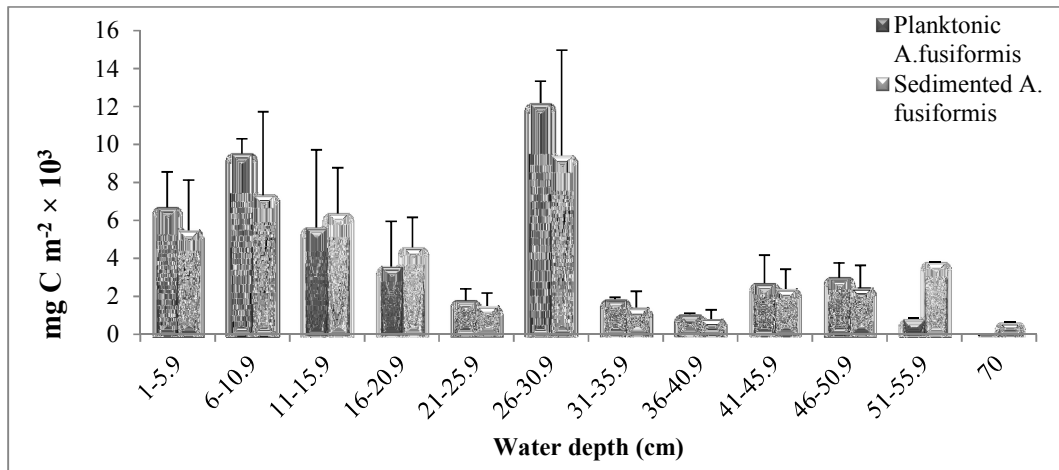


Fig. 4.8: The comparison between the mean planktonic and sedimented *A. fusiformis* biomass at Lake Bogoria at different water depths.

The shallow lakes; Lake Natron and Lake Elementeita, whose depth did not exceed 10cm, were characterized by high biomass of benthic diatoms. There was a general decrease in both the epipelagic and suspended epipelagic standing crop as observed in figure 4.9 with a weak positive Spearman's rank-order correlation ($r_s=0.176$). The suspended epipelagic biomass was higher than the epipelagic biomass only at a water depth of 1-1.9 cm and thereafter the epipelagic biomass was higher.

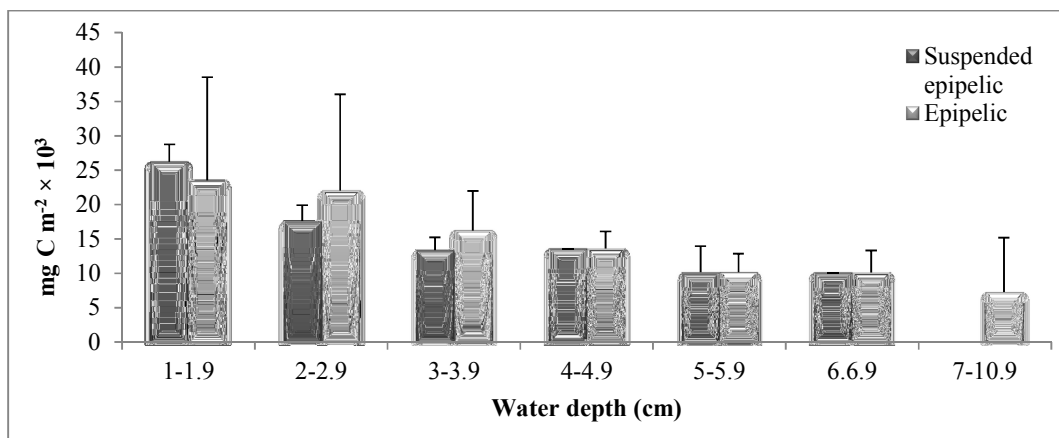


Fig. 4.9: Comparison between the mean suspended epipelagic and epipelagic biomass of Lake Natron and Lake Elementeita at different water depths.

4.5. *P. minor* population estimates and standing crop of the different food resources

The greatest *P. minor* population of 516,979 was recorded at Lake Bogoria in August 2010 (Table 4.7) from estimates carried out by the National Museums of Kenya waterfowl census in July 2010. The Spearman's rank-order correlation showed a positive but weak relationship between *P. minor* population estimates and the planktonic standing crop ($r_s=0.571$) but indicated a negative correlation with epipellic standing crop ($r_s=-0.190$) and lake shore mud standing crop ($r_s=-0.286$).

Table 4.7: Mean (\pm se) standing crop of different food resources and *P. minor* population estimates. (NMK= National Museums of Kenya national waterfowl census).

SCmax	Month-year	Planktonic mg C m ⁻² × 10 ³	Epipellic mg C m ⁻² × 10 ³	Lake shore mud mg C m ⁻² × 10 ³	<i>P. minor</i> population	<i>P. minor</i> population estimated by
Bogoria	April-2009	37.74	17.24	55.46	128,515	NMK January-2009
	August-2009	3.24	4.25	0.53	12,929	NMK July-2009
	August-2010	5.17	3.85	0.66	516,979	NMK July-2009
Elementeita	August-2009	0.66	4.92	2.83	6,325	NMK July-2009
Nakuru	April-2009	11.97	46.66	–	250,000	This study
	August-2009	0.90	5.81	14.27	255,294	NMK July-2009
Natron lagoon	April-2009	–	12.74	22.97	6,038	This study
Natron lagoon	Dec-2009	0.79	20.69	16.73	11,268	This study

4.6. Primary productivity of the various communities.

High primary productivity was indicated by extremely high dissolved oxygen concentration reaching super-saturation levels of over 300% with concentrations of 25 mg O₂ L⁻¹ at Lake Bogoria. Tables 4.8 – 4.11 and Figures 4.10 – 4.13 below summarize the primary productivity and respiration values of the study lakes during the periods of study.

4.6.1. Primary productivity of the planktonic and the suspended epipellic community

The highest hourly planktonic net primary productivity (NPP) was recorded at Lake Bogoria in April 2009 with a mean value of 204.6 mg C m⁻² hr⁻¹ (Table 4.8, Fig. 4.10). This corresponded with the highest planktonic standing crop of 37.7 × 10³ mg C m⁻². High primary productivity values were recorded in April with a significant decline (p<0.01) recorded at Lake Bogoria between April 2009 and August 2010. Lake Oloidien, which had the second highest NPP of planktonic standing crop 143.81 mg C m⁻² hr⁻¹ and a standing crop of 3.63 × 10³ mg C m⁻². The lowest planktonic standing crop of 0.56 × 10³ mg C m⁻² recorded at Sonachi was comparable with low planktonic NPP of 29.67 mg C m⁻² hr⁻¹. Sonachi recorded the highest community respiration of 117 mg C m⁻² hr⁻¹. Lake Nakuru recorded high standing crop of 1.41 × 10³ mg C m⁻², but the productivity was not measured due to failure of the oxygen meter.

Lake Elementeita's suspended epipellic community recorded high NPP of 60.82 mg C m⁻² hr⁻¹ although it was only 30% in comparison to the productivity of the planktonic community at Lake Bogoria. The suspended epipellic community at Lake Natron's lagoon recorded negative net primary productivity values with a mean of -33 mg C m⁻² hr⁻¹ in April 2009. Lake Natron marsh which had high standing crop of 4.29 × 10³ mg C m⁻² recorded negative NPP of -20.27 mg C m⁻² hr⁻¹ (Table 4.9, Fig. 4.11).

Table 4.8: Mean (\pm se) primary productivity and respiration of the plankton community. (NPP= Net primary productivity, GPP= Gross primary productivity, Resp = Respiration).

Lake	Month-Year	NPP mg C m ⁻² hr ⁻¹			GPP mg C m ⁻² hr ⁻¹			Resp mg C m ⁻² hr ⁻¹		
		Mean	sd	n	Mean	sd	n	Mean	sd	n
Bogoria	Aug-08	61.73	89.25	68	115.18	117.86	68	53.43	72.42	68
	Apr-09	204.60	67.24	10	208.67	54.68	10	4.07	24.95	10
	Aug-10	15.49	119.90	22	37.55	127.66	22	22.06	34.65	22
Sonachi	Sep-09	29.67	44.43	6	146.67	81.32	6	117.00	43.91	6
Oloidien	Sep-09	143.81	166.71	7	178.10	110.80	7	34.29	108.56	7

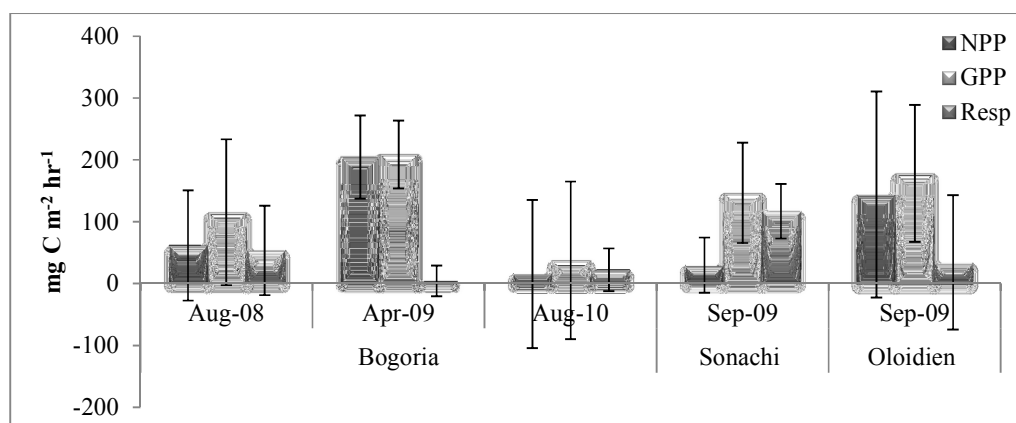


Fig. 4.10: Mean (\pm se) net and gross primary productivity and respiration of the planktonic community of the lakes studied. (NPP= Net primary productivity, GPP= Gross primary productivity, Resp = Respiration).

Table 4.9: Mean (\pm se) primary productivity and respiration of the suspended epipelagic community. (NPP= Net primary productivity, GPP= Gross primary productivity, Resp = Respiration).

Lake	Month-Year	NPP mg C m ⁻² hr ⁻¹			GPP mg C m ⁻² hr ⁻¹			Resp mg C m ⁻² hr ⁻¹		
		Mean	sd	n	Mean	sd	n	Mean	sd	n
Elementeita	Aug-08	60.82	43.19	13	81.74	57.62	13	20.97	27.81	13
Natron Lagoon	Apr-09	-33.00	53.39	8	0.00	37.03	8	33.00	54.89	8
	Dec-09	-23.88	38.52	11	146.42	430.11	11	170.36	426.74	11
Natron Marsh	Dec-09	-20.27	38.62	10	-11.60	22.60	10	8.67	51.48	10

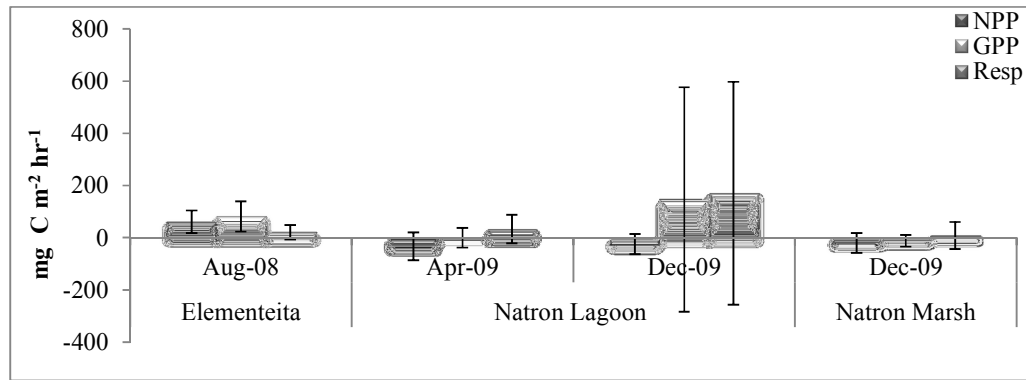


Fig. 4.11: Mean (\pm se) net and gross primary productivity and respiration of the suspended epipellic community of the lakes studied. (NPP= Net primary productivity, GPP= Gross primary productivity, Resp = Respiration).

4.6.2. Primary productivity of the sedimented *A. fusiformis* and epipellic community

The sedimented *Arthrospira fusiformis* of Lake Bogoria (August 2008) recorded high net productivity with a mean of 103.01 mg C m⁻² hr⁻¹ (Table 4.10). By August 2010, Lake Bogoria's net productivity recorded a significant decline ($p < 0.001$) with 60% less than the value recorded in August 2008 (Fig. 4.12).

The highest net primary productivity of the epipellic community was recorded at Lake Elementeita with 72.9 mg C m⁻² hr⁻¹ (Table 4.11, Fig. 4.13). This was only 70% in comparison to the sedimented *A. fusiformis* at Lake Bogoria. The lowest net primary productivity values were recorded at Lake Natron's marsh in December 2009 with mean of 3.71 mg C m⁻² hr⁻¹. High standing crop at Natron did not translate into high productivity. A standing crop of 20.69×10^3 mg C m⁻² at Natron Lagoon had a net productivity of 21.62 mg C m⁻² hr⁻¹ compared to Bogoria 4 times less biomass had twice the productivity at 41.38 mg C m⁻² hr⁻¹.

Table 4.10: Mean (\pm se) primary productivity and respiration of the sedimented *Arthrospira fusiformis*. (NPP= Net primary productivity, GPP= Gross primary productivity, Resp = Respiration).

Lake	Month-Year	NPP mg C m ⁻² hr ⁻¹			GPP mg C m ⁻² hr ⁻¹			Resp mg C m ⁻² hr ⁻¹		
		Mean	se	n	Mean	se	n	Mean	se	n
Bogoria	Aug-08	103.01	35.10	24	126.61	37.40	24	23.60	20.43	24
	Aug-10	41.38	74.33	15	58.70	61.06	15	17.32	31.19	15

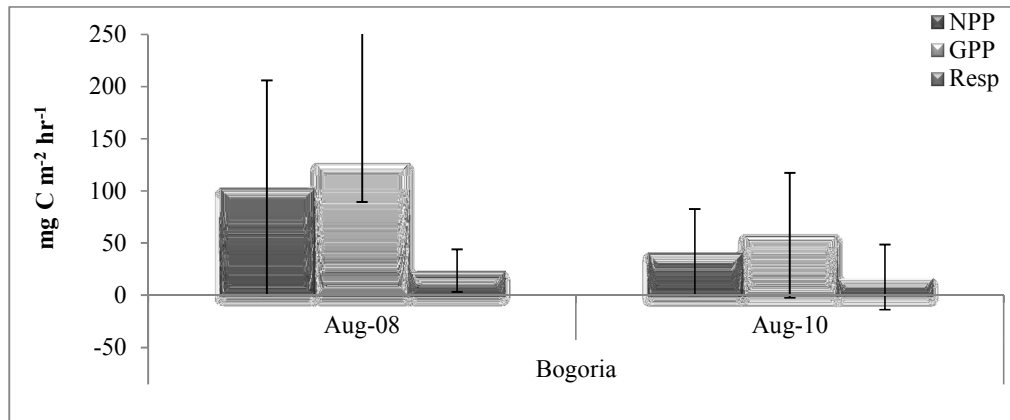


Fig. 4.12: Mean (\pm se) net and gross primary productivity and respiration of the sedimented *Arthrospira fusiformis* at Lake Bogoria. (NPP= Net primary productivity, GPP= Gross primary productivity, Resp = Respiration).

Table 4.11: Mean (\pm se) primary productivity and respiration of the epipellic community. (NPP= Net primary productivity, GPP= Gross primary productivity, Resp = Respiration).

Lake	Month-Year	NPP mg C m ⁻² hr ⁻¹			GPP mg C m ⁻² hr ⁻¹			Resp mg C m ⁻² hr ⁻¹		
		Mean	se	n	Mean	se	n	Mean	se	n
Elementeita	Aug-08	72.98	45.92	14	96.01	55.30	14	23.03	14.29	14
Natron lagoon	Apr-09	14.37	20.90	42	10.00	15.35	42	24.37	23.34	42
	Dec-09	21.62	10.89	11	55.97	27.81	11	34.35	28.46	11
Natron Marsh	Apr-09	28.32	15.13	11	40.33	21.23	11	12.01	10.95	11
	Dec-09	3.71	11.92	12	19.42	17.58	12	15.71	14.16	12

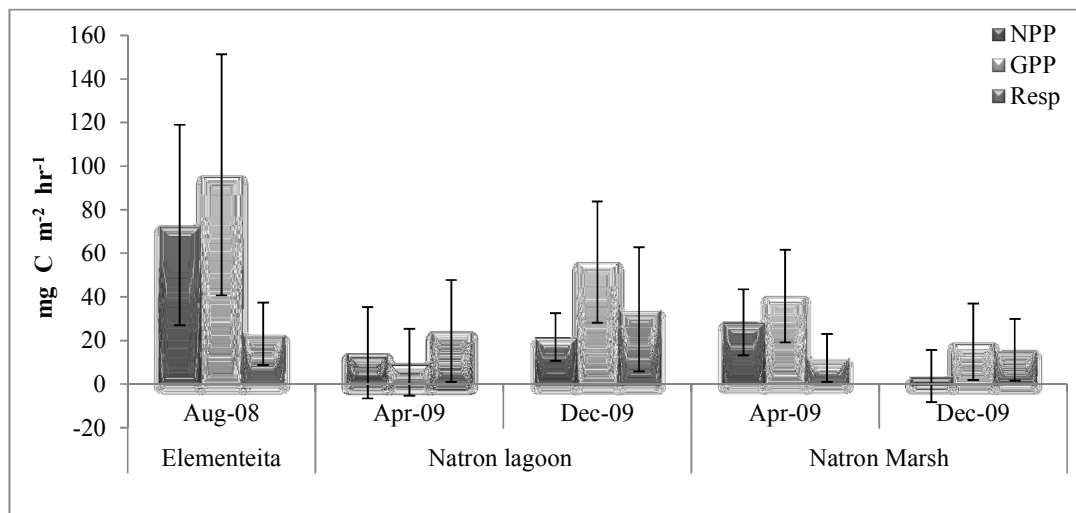


Fig. 4.13: Mean (\pm se) net and gross primary productivity and respiration of the epipellic community of the studied lakes. (NPP= Net primary productivity, GPP= Gross primary productivity, Resp = Respiration).

CHAPTER FIVE

DISCUSSION CONCLUSION AND RECOMMENDATIONS

5.1. Energy budget by *P. minor*

An adult lesser flamingo weighs $1,730 \pm 40$ g and has to feed on 72 ± 6.5 g of dry weight day^{-1} , equivalent to 314 ± 28 kcal day^{-1} which is 181.5 kcal kg^{-1} of body weight day^{-1} (Vareschi, 1978). In August 2010 Lake Bogoria had the highest recorded lesser flamingo population of 516,979. The planktonic biomass on the shallow edges of the lake was 5.17×10^3 mg C m^{-2} (45.09 kcal m^{-2}). Assuming that the measured planktonic biomass was even over the whole lake, a lesser flamingo population of 516,979 would feed on 18.6 tons of C day^{-1} ($162,331$ tons of calories day^{-1}). This is only 92% of the total planktonic biomass of 20.15 tons C day^{-1} (lake area 34 km^2). This makes the lesser flamingo a major primary consumer on the saline lakes.

The remaining biomass is fed on by other important primary consumers such as the zoobenthic chironomid midge larvae, which occurs at a density of 4×10^4 organisms m^{-2} at Lake Bogoria (Harper *et al.*, 2003). Other consumers of planktonic biomass include protozoa, rotifers, and copepods. In lakes Nakuru, Elementeita and Natron the resident alkaline water fish *Alcolapia alcalicus grahmi*, is an important primary consumer. A mean annual fish yield of $2,436$ kg wet weight $\text{ha}^{-1} \text{yr}^{-1}$ was recorded at Lake Nakuru in 1974 (Vareschi, 1978). With a production rate of 20.15 tons C day^{-1} and a consumption rate of 18.6 tons of C day^{-1} , it seems likely that the consumption may exceed production. During this period the lake regenerated at a rate of 2 tons C hr^{-1} by considering both the planktonic and sedimented *A. fusiformis*. The high consumption actually facilitates in the regeneration of the cyanobacteria as 'cropping/pruning' by the consumers provides more space for growth.

At the shallow lakes, Lake Natron and Lake Elementeita, where the epipellic algae was suspended the lesser flamingo depended on the epipellic and lake shore mud food resources. Lake Natron lagoon had low suspended epipellic biomass which could only provide 6.89 kcal m^{-2} (0.79×10^3 mg C m^{-2}) of the required 314 kcal. The epipellic and lake shore mud recorded 20.7×10^3 mg C m^{-2} (180.68 kcal m^{-2}) and 16.7×10^3 mg C m^{-2} (145.9 kcal m^{-2}) respectively, could be able to meet this need. In this way, the different food resources, (i.e. the planktonic, epipellic and lake shore mud) are therefore able to complement each other to sustain the flamingo population in this system.

Though the food biomass calculation here takes into account the cyanobacteria (Plate 4.1) and algal (Plate 4.2) food components only, the diet of the lesser flamingo is also enriched with protein from several species of protozoa and rotifers (see Plate 4.3).

5.2. Primary producer community categories

Three primary producer communities can be recognized in saline lakes (Tuite, 1981). The three are categorized according to the dominant photo-synthesizers; 1. *Arthrospira* dominated phytoplankton, 2. Non-*Arthrospira* dominated phytoplankton and 3. benthic diatoms. From the results, the first type of primary producer community was represented in Lake Bogoria, Lake Oloidien and Lake Sonachi. Bogoria was characterised by high primary productivity by both the planktonic and sedimented *Arthrospira* (204.60 and 103 mg C m⁻²hr⁻¹ respectively). The second state was represented by Lake Nakuru where *Arthrospira* did not reach dominance level during the study period but other cyanobacteria species of *Anabaenopsis magna* and *A. abijatae*. However, it is important to note that the lake may transition between type 1 and 2. In fact *Arthrospira* has been recorded by Vareschi (1978) to dominate Nakuru's phytoplankton at times when the lake level is high.

Primary productivity that is dominated by benthic diatoms system was represented by lakes Natron and Elementeita, where there was very low planktonic standing crop 0.21×10^3 mg C. Primary production was totally supported by benthic diatom productivity. At Lake Natron benthic diatoms contributed 100% of the productivity considering that productivity measurements of the suspended epipelagic community gave negative values of up to $-33 \text{ mg C m}^{-2} \text{ hr}^{-1}$, due probably due to high respiratory demands obtained. Diatoms did not achieve dominance at lakes where *Arthrospira spp.* dominated like lakes Bogoria, Nakuru, Oloidien and Sonachi, but dominated in the epipelagic community of Lake Natron and Lake Elementeita. At the shallow lakes, Lake Natron and Lake Elementeita, protozoan and rotifer species were exceptionally scarce compared to the deeper lakes like lakes Bogoria, Nakuru and Oloidien.

5.3. Production rate of lesser flamingo food

High levels of primary productivity were recorded in the six lakes and Talling *et al.*, (1973) proposed that these high rates were due to a combination of high tropical temperatures, stability of the solar illumination in the tropics and high dissolved inorganic phosphorus resulting in high phytoplanktonic primary productivity. High net primary productivity of $103 \text{ mg C m}^{-2} \text{ hr}^{-1}$ was measured for sedimented *A. fusiformis* at Lake Bogoria. Although it is expected that surface photo-inhibition would result in low production through self shading by the population. In some cases, the cyanobacteria species can adapt to relatively low light intensities (Wetzel, 2001) at the deeper layers resulting to higher photosynthetic rates than at the water surface as evidenced by the high productivity of the sedimented *A. fusiformis*.

Negative net primary productivity was recorded for the planktonic community of Lake Natron was due to high respiration by the whole planktonic community. Models estimating net primary productivity by Oduor and Schagerl (2007) showed negative values on certain days for lakes Bogoria and Nakuru. This situation was attributed to high respiration of the community or as a result of ecological conditions under cloud cover.

From a comparison of productivity values generated from this study and other previous measurements, showed that some of the previous measurements are at least 5 times higher (Table 5.1) than the values from this study but are within the expected range for tropical lakes. At Lake Bogoria, Melack (1981) measured a NPP of $320 \text{ mg C m}^{-2} \text{ h}^{-1}$ while this study estimated a NPP of $72 \text{ mg C m}^{-2} \text{ h}^{-1}$ similarly, at Lake Sonachi, Melack (1981) measured a NPP of $146 \text{ mg C m}^{-2} \text{ h}^{-1}$ while this study estimated a NPP of $29 \text{ mg C m}^{-2} \text{ h}^{-1}$. These variations could be attributed mainly to the use of different methods in different studies. These results could also have been influenced by changes within the lakes ecology and chemistry human activities within the catchment

Diatoms contributed the highest biomass in shore mud samples for lakes where *P. minor* were observed feeding on mud at the lake shore. These lakes were Lake Elementeita and Lake Natron. The birds foraged in the shallow water where they would shuffle their legs in the water to suspend the epipellic food resource growing on the sediment. Occasionally they were observed feeding at the lake edge on diatoms growing on the shore mud. Epipellic and lake shore mud communities

contributed significantly to the food resources of lesser flamingos and the primary productivity of the lakes especially on shallow lakes.

Table 5.1: Comparison of primary productivity values measured during this study with others from previously published work from different locations.

Location	Lake	Planktonic NPP mg C m ⁻² h ⁻¹	Epipellic NPP mg C m ⁻² h ⁻¹	Reference
Kenya	Bogoria	93.94	72.2	This study
	Bogoria	320.00	-	Melack , 1981
	Bogoria	2.27	-	Odour and Schagerl, 2007
	Nakuru	216.67	-	Melack , 1981
	Nakuru	89.00	-	Melack and Kilham , 1974
	Nakuru	3.57	-	Odour and Schagerl, 2007
	Elementeita	60.82	72.98	This study
	Elementeita	166.67	-	Melack , 1981
	Elementeita	2.83	-	Odour and Schagerl, 2007
	Sonachi	29.67	-	This study
	Sonachi	146.67	-	Melack , 1981
Tanzania	Natron Lagoon	-28.44	18	This study
	Natron Marsh	-20.27	16.02	This study
	Reshitani	667	-	Melack , 1981
Ethiopia	Kilotes	266.67	-	Talling et al, 1973
	Aranguadi	665.00	-	Talling et al, 1973
United States of America	Borax	-	480	Hammer 1981

5.4. Foraging options

All animals feed for growth, maintenance and reproduction. A lesser flamingo requires a daily maintenance food ration of 72 ± 6.5 g of dry weight day⁻¹, equivalent to 314 ± 28 kcal day⁻¹ (Vareschi, 1978), this is the food needed by an adult bird to be in a state of constant body composition. The flamingo population estimates were weakly correlated with values of planktonic biomass. For most of the lakes the planktonic biomass would be unable to sustain the flamingo population without the flamingos depending on both the epipellic and lake shore mud resources. Correlation of flamingo population with epipellic and lake shore mud food biomass indicated a weak negative correlation.

As food resources become limited in a lake e.g. at Lake Elementeita (see Table 4.7.) where low food biomass is accompanied by low population, the energy gain is expected to gradually decrease as it takes more time to obtain the daily maintenance food ration. This also would require more energy to acquire the food. An ultimate point/peak point is reached where the energy cost in acquiring food is greater than energy gained from the food. This implies that the food available cannot sustain the population. At this point lesser flamingo will choose to stop feeding and start moving to the next site. They choose instead to conserve energy for travel to the next feeding site. In so doing they risking to lose energy in travelling as they do not know whether the next site will have adequate food supply.

The fundamental choice that a lesser flamingo has to make is how long to stay at a feeding site, when and where to move in search for the optimal feeding site among the widely scattered soda lakes of on the eastern rift valley. In a situation where food declines at Lake Nakuru and the flamingos would have to move. They have several choices of lakes that are within a radius of 70 km, Lake Bogoria, to the North and Lakes Elementeita, Oloidien and Sonachi to the south. When the time comes for them to move, a few flamingos start flying in a circle above the lake as the sun sets. The group becomes larger as more birds join and just as it becomes dark they fly off to the next lake. Though they move as a group it is the decisions of the individual birds that seem to coincide with the group's interests. The decision has to ensure the highest probability of finding a high quality and quantity food supply that justifies the energy spent travelling there. To make good decisions the assumption is that flamingos have acquired perfect knowledge and information about their environment, to make reliable decisions that have eventually ensured the survival of the species in the millions of years they have been on earth.

5.5.Conclusion

The study builds on the works of Tuite (1981) and Vareschi (1978) who were first to explore the importance of epipellic and lake shore mud food resources as flamingo food and their importance to the lake's ecology as they support the food chains. From this study, it can be appreciated that both the epipellic and lake shore mud algae play an important role in providing nutrition for the lesser flamingo. The lesser flamingo population is not just sustained on *Arthrospira fusiformis* but may

from time to time rely exclusively on the epipelagic algae especially when the birds are on the shallow lakes. The epipelagic algae is also important ecologically as it provides energy to the other trophic levels that includes consumers such as protozoa and rotifers which also enrich the *P. minor* diet. Time spent feeding would depend on the species type of the food resource and its biomass. *P. minor* displays a great ability to adapt to change in food availability by adapting their feeding behaviour to acquire the most food such as diving in the water at Lake Bogoria to feed on the sedimenting *A. fusiformis*.

5.6.Recommendations

5.6.1. Further research actions

I propose that further research should be carried out to determine the time lesser flamingos spend feeding on the different food resources and the nutritional value of the various food resources. Studies should be designed that can investigate any differentiation in the food requirements and intake between birds of different ages, the immature and the adult flamingos. The cause of sedimentation of *A. fusiformis* should be investigated. The hydrology of the lakes and the rivers and springs that sustain these lakes needs to be well established including the effects of human land use practices within the catchment. For the effective management and conservations of flamingos, the lesser flamingo population numbers and trends and the cause of mortality need to be further studied. There is a need to establish how local ecological changes contribute to the changes in saline lake ecosystems and the resilience of flamingos and saline lake to these changes.

5.6.2. Conservation and management actions

Habitat connectivity of habitats used by flamingos should be ensured by protecting all the habitats that serve as main feeding or breeding sites including the other small lakes that are infrequently utilized by flamingos. Any management interventions should emphasise on the protection and ensuring the biological diversity and sustaining lake ecosystem functioning instead of focusing on single species.

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APPENDICES

Appendix 1: Standing Crop

Appendix 1.a: Mann-Whitney U Test results for planktonic standing crop.

	Bogoria April 2009	Bogoria August 2009	Bogoria August 2010	Nakuru April 2009	Nakuru Njoro River August 2009	Nakuru August 2009	Sonachi September 2009	Oloidien September 2009
Bogoria April 2009		0.000**	0.000**	0.243	0.002**	0.000**	0.004**	0.000**
Bogoria August 2009			0.019*	0.017*	0.338	0.781	0.206	0.016*
Bogoria August 2010				0.035*	0.011*	0.009**	0.011*	0.758
Nakuru April 2009					0.025*	0.007**	0.034*	0.012*
Nakuru Njoro River August 2009						0.681	0.142	0.019*
Nakuru August 2009							0.443	0.021*
Sonachi September 2009								0.020*
Oloidien September 2009								

* = significant at $p < 0.05$

**= significant at $p < 0.01$

Appendix 1.b: Mann-Whitney U Test results for the standing crop of the suspended epipellic community.

	Elementeita August 2009	Natron Lagoon December 2009	Natron Marsh December 2009
Elementeita August 2009		0.668	0.001**
Natron Lagoon December 2009			0.001**
Natron Marsh December 2009			

* = significant at $p < 0.05$

**= significant at $p < 0.01$

Appendix 1.c: Mann-Whitney U Test results for standing crop of the sedimented *Arthrospira fusiformis*.

	Bogoria April 2009	Bogoria August 2009	Bogoria August 2010
Bogoria April 2009		0.000**	0.005**
Bogoria August 2009			0.151
Bogoria August 2010			

* = significant at $p < 0.05$

**= significant at $p < 0.01$

Appendix 1.d: Mann-Whitney U Test results for standing crop of the epipellic community.

	Elementeita August 2009	Nakuru April 2009	Nakuru. Njoro River August 2009	Nakuru August 2009	Natron Lagoon April 2009	Natron Lagoon December 2009	Natron Marsh April 2009	Natron Marsh December 2009
Elementeita August 2009		0.001**	0.637	0.027*	0.010*	0.000**	0.001**	0.001**
Nakuru April 2009			0.003*	0.000**	0.000**	0.000**	0.132	0.022*
Nakuru Njoro River August 2009				0.257	0.040*	0.002**	0.007**	0.009**
Nakuru August 2009					0.000**	0.000**	0.000**	0.000**
Natron Lagoon April 2009						0.000**	0.000**	0.017*
Natron Lagoon December 2009							0.008**	0.855
Natron Marsh April 2009								0.217
Natron Marsh December 2009								

* = significant at $p < 0.05$

**= significant at $p < 0.01$

Appendix 1.e: Mann-Whitney U Test results for standing crop of the lake shore mud community.

	Bogoria April 2009	Bogoria August 2009	Elementeita August 2009	Nakuru Njoro River August 2009	Nakuru August 2009	Natron Lagoon April 2009	Natron Lagoon December 2009	Natron Marsh April 2009	Natron Marsh December 2009	Sonachi September 2009	Oloidien September 2009
Bogoria April 2009		0.221	0.046*	0.121	0.064	0.026*	0.037*	0.380	0.465	0.121	0.554
Bogoria August 2009			0.617	0.221	1.000	0.105	0.121	0.127	0.109	0.221	0.157
Elementeita August 2009				0.505	0.201	0.002**	0.002**	0.003**	0.001**	0.182	0.020*
Nakuru Njoro River August 2009					0.165	0.634	1.000	0.143	0.100	1.000	0.076
Nakuru August 2009						0.004**	0.007**	0.008**	0.004**	0.064	0.032*
Natron Lagoon April 2009							0.275	0.0378	0.016*	0.057	0.059
Natron Lagoon December 2009								0.015*	0.003**	0.037*	0.014*
Natron Marsh April 2009									0.933	0.040*	0.732
Natron Marsh December 2009										0.028*	0.563
Sonachi September 2009											0.076
Oloidien September 2009											

* = significant at $p < 0.05$

**= significant at $p < 0.01$

Appendix 2: Primary productivity

Appendix 2.a: Mann-Whitney U Test results for primary productivity of planktonic community.

Planktonic Productivity		Bogoria Aug.-2008			Bogoria April-2009			Bogoria Aug.-2010			Sonachi Sept.-2009			Oloidien Sept.-2009			
		GPP	Resp	NPP	GPP	Resp	NPP	GPP	Resp	NPP	GPP	Resp	NPP	GPP	Resp	NPP	
Bogoria Aug. 2008	GPP		0.000**	0.003**	0.004**	0.000**	0.005**	0.011*	0.000**	0.001**	0.337	0.714	0.056	0.140	0.153	0.971	
	Resp			0.527	0.000**	0.010*	0.000**	0.800	0.087	0.231	0.007**	0.015*	0.539	0.007**	0.906	0.115	
	NPP				0.000**	0.008**	0.000**	0.478	0.033*	0.101	0.020*	0.038*	0.434	0.012*	0.920	0.172	
Bogoria April 2009	GPP					0.000**	0.570	0.000**	0.000**	0.000**	0.128	0.012*	0.000**	0.524	0.001**	0.032*	
	Resp						0.000**	0.027*	0.100	0.132	0.001**	0.001**	0.254	0.005**	0.130	0.013*	
	NPP							0.000**	0.000**	0.000**	0.114	0.009**	0.000**	0.768	0.001**	0.086	
Bogoria Aug. 2010	GPP								0.136	0.313	0.012*	0.010*	0.737	0.011*	0.610	0.103	
	Resp										0.503	0.001**	0.000**	0.494	0.005**	0.210	0.028*
	NPP											0.003**	0.004**	0.892	0.005**	0.386	0.041*
Sonachi Sept.-2009	GPP												0.462	0.010*	0.520	0.062	0.667
	Resp													0.004**	0.315	0.106	0.943
	NPP														0.018*	0.429	0.133
Oloidien Sept. 2009	GPP															0.047*	0.337
	Resp																0.276
	NPP																

(NPP= Net primary productivity, GPP= Gross primary productivity, Resp = Respiration)

* = significant at $p < 0.05$

**= significant at $p < 0.01$

Appendix 2.b: Mann-Whitney U Test results for primary productivity of the suspended epipelagic community.

Planktonic Productivity		Elementeita Aug.-2008			Natron Lagoon April-2009			Natron Lagoon Dec.-2009			Natron Marsh Dec.-2009		
		GPP	Resp	NPP	GPP	Resp	NPP	GPP	Resp	NPP	GPP	Resp	NPP
Elementeita Aug 2008	GPP		0.003**	0.182	0.003**	0.080	0.001**	0.077	0.182	0.000**	0.001**	0.006**	0.001**
	Resp			0.006	0.103	0.561	0.004**	0.977	0.213	0.000**	0.005**	0.292	0.006**
	NPP				0.004**	0.146	0.001**	0.173	0.339	0.000**	0.000**	0.011*	0.000**
Natron Lagoon April-2009	GPP					0.256	0.202	0.170	0.020*	0.113	0.264	0.859	0.263
	Resp						0.030*	0.588	0.114	0.004**	0.016	0.419	0.041*
	NPP							0.020*	0.001**	1.000	0.754	0.167	0.788
Natron Lagoon Dec.-2009	GPP								0.234	0.004**	0.020*	0.307	0.026*
	Resp									0.000**	0.001**	0.041*	0.001**
	NPP										1.000	0.158	0.750
Natron Marsh Dec.-2009	GPP											0.343	0.909
	Resp												0.211
	NPP												

(NPP= Net primary productivity, GPP= Gross primary productivity, Resp = Respiration)

* = significant at p<0.05

**= significant at p<0.01

Appendix 2.c: Mann-Whitney U Test results for primary productivity of the sedimented *Arthrospira fusiformis*.

		Bogoria August 2008			Bogoria August 2010		
		GPP	Resp	NPP	GPP	Resp	NPP
Bogoria August 2008	GPP		0.000**	0.008**	0.000**	0.000**	0.000**
	Resp			0.000**	0.003**	0.419	0.053
	NPP				0.007**	0.000**	0.001**
Bogoria August 2010	GPP					0.008**	0.418
	Resp						0.029*
	NPP						

(NPP= Net primary productivity, GPP= Gross primary productivity, Resp = Respiration)

* = significant at p<0.05

**= significant at p<0.01

Appendix 2.d: Mann-Whitney U Test results for primary productivity of the epipelagic community.

		Elementeita August 2008			Natron Lagoon April 2009			Natron Lagoon December 2009			Natron Marsh April 2009			Natron Marsh December 2009		
		GPP	Resp	NPP	GPP	Resp	NPP	GPP	Resp	NPP	GPP	Resp	NPP	GPP	Resp	NPP
Elementeita August 2008	GPP		0.000**	0.154	0.009**	0.000**	0.000**	0.100	0.001**	0.000**	0.018*	0.000**	0.001**	0.000**	0.000**	0.000**
	Resp			0.002**	0.779	0.012*	0.105	0.001**	0.250	0.956	0.055	0.089	0.381	0.719	0.354	0.001**
	NPP				0.009**	0.000**	0.000**	0.622	0.025*	0.001**	0.112	0.000**	0.010**	0.001**	0.000**	0.000**
Natron. Lagoon. April 2009	GPP					0.001**	0.030*	0.001**	0.498	0.640	0.046*	0.055	0.626	0.574	0.217	0.003**
	Resp						0.288	0.000**	0.002**	0.005**	0.000**	0.399	0.001**	0.038*	0.102	0.052
	NPP							0.000**	0.019*	0.210	0.001**	0.901	0.027*	0.276	0.611	0.035*
Natron. Lagoon. December 2009	GPP								0.020*	0.001**	0.308	0.000**	0.008**	0.001**	0.000**	0.000*
	Resp									0.250	0.278	0.028*	0.818	0.242	0.096	0.001**
	NPP										0.093	0.052	0.224	0.622	0.355	0.001**
Natron Marsh. April 2009	GPP											0.001**	0.199	0.036*	0.016*	0.000**
	Resp												0.011*	0.295	0.460	0.027*
	NPP													0.268	0.056	0.000**
Natron Marsh. December 2009	GPP														0.564	0.006**
	Resp															0.009**
	NPP															

(NPP= Net primary productivity, GPP= Gross primary productivity, Resp = Respiration)

* = significant at p<0.05
 **= significant at p<0.01

Appendix 3: Energy calculations

Appendix 3.a: Energy calculations for standing crop and net primary productivity of the planktonic food resource.

Planktonic					
	Month-Year	Amount of available food $\text{mg C m}^{-2} \times 10^3$	Energy of available food k cal m^{-2}	Rate of regeneration by net primary productivity $\text{mg C m}^{-2} \text{hr}^{-1}$	Rate of energy input by net primary productivity $\text{Kcal m}^{-2} \text{hr}^{-1}$
Bogoria	Apr-09	37.74	329.18	204.60	1.79
Bogoria	Aug-09	3.24	28.26	-	-
Bogoria	Aug-10	5.17	45.09	15.49	0.14
Nakuru	Apr-09	11.97	104.41	-	-
Nakuru	Aug-09	0.9	7.85	-	-
Sonachi	Sep-09	0.56	4.88	29.67	0.26
Oloidien	Sep-09	3.63	31.66	143.81	1.25

Appendix 3.b: Energy calculations for standing crop and net primary productivity of the suspended epipellic food resource.

Suspended epipellic					
	Month-Year	Amount of available food $\text{mg C m}^{-2} \times 10^3$	Energy of available food k cal m^{-2}	Rate of regeneration by net primary productivity $\text{mg C m}^{-2} \text{hr}^{-1}$	Rate of energy input by net primary productivity $\text{Kcal m}^{-2} \text{hr}^{-1}$
Elementeita	Aug-08	-	-	60.82	0.53
Elementeita	Aug-09	0.66	5.76	-	-
Natron lagoon	Dec-09	0.79	6.89	-23.88	-0.21
Natron marsh	Dec-09	4.29	37.42	-20.27	-0.18

Appendix 3.c: Energy calculations for standing crop and net primary productivity of the sedimented *Arthrospira fusiformis* food resource.

Sedimented <i>Arthrospira fusiformis</i>					
mg C m^{-2}	Month-Year	Amount of available food $\text{mg C m}^{-2} \times 10^3$	Energy of available food k cal m^{-2}	Rate of regeneration by net primary productivity $\text{mg C m}^{-2} \text{hr}^{-1}$	Rate of energy input by net primary productivity $\text{Kcal m}^{-2} \text{hr}^{-1}$
Bogoria	Apr-09	17.24	150.37	-	-
Bogoria	Aug-09	4.25	37.07	-	-
Bogoria	Aug-10	3.85	33.58	41.38	0.36

Appendix 3.d: Energy calculations for standing crop and net primary productivity of the epipellic food resource.

Epipellic					
mg C m ⁻²	Month-Year	Amount of available food mg C m ⁻² × 10 ³	Energy of available food k cal m ⁻²	Rate of regeneration by net primary productivity mg C m ⁻² hr ⁻¹	Rate of energy input by net primary productivity Kcal m ⁻² hr ⁻¹
Elementeita	Aug-09	4.92	42.91	-	-
Nakuru	Apr-09	46.67	407.07	-	-
Nakuru	Aug-09	5.81	50.68	-	-
Natron lagoon	Apr-09	12.74	111.12	14.37	0.13
Natron lagoon	Dec-09	20.69	180.46	21.62	0.19
Natron marsh	Apr-09	32.93	287.22	28.32	0.25
Natron marsh	Dec-09	26.68	232.71	3.71	0.03

Appendix 3.e: Energy calculations for standing crop and net primary productivity of the lake shore mud community food resource.

Lake shore mud			
	Month-Year	Amount of available food mg C m ⁻² × 10 ³	Energy of available food k cal m ⁻²
Bogoria	Apr-09	55.46	483.73
Bogoria	Aug-10	0.53	4.62
Elementeita	Aug-09	2.83	24.68
Nakuru Lake	Aug-09	14.27	124.47
Nakuru Njoro river mouth	Aug-09	0.62	5.41
Natron lagoon	Apr-09	22.97	200.35
Natron lagoon	Dec-09	16.73	145.92
Natron marsh	Apr-09	44.08	384.48
Natron marsh	Dec-09	44.9	391.63
Sonachi	Sep-09	6.08	53.03
Oloidien	Sep-09	3.91	34.01