THE ROLE OF ZOOPLANKTON IN THE PELAGIC FOOD WEBS OF TROPICAL LAKES

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By

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Dedication

This thesis is dedicated to the memory of my parents, Hasnah and Saeed.

The role of zooplankton in the pelagic food webs of tropical lakes

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Abstract

There is a general paucity of studies concerning trophic interactions between zooplankton and Cyanobacteria, and about the general role which zooplankton play in pelagic food webs in tropical saline lakes. Although the relative importance of allochthonous and autochthonous carbon resources to the diet of zooplankton in temperate lakes is well understood, significant knowledge gaps remain in tropical systems.

This thesis addresses three principal questions: (1) What are the principal trophic interactions between zooplankton and Cyanobacteria in tropical lakes, with a specific focus on the lakes of the East African Rift Valley?; (2) Is there potential for competition between zooplankton and lesser flamingos in the Rift Valley lakes?; (3) What is the relative importance of allochthonous versus autochthonous carbon sources for aquatic consumers in tropical lakes? These questions were answered by analysing the compositions and trophic interactions in the pelagic food webs of four contrasting East African lakes (Naivasha, Baringo, Bogoria and Sonachi). The lakes were sampled over two campaigns in different seasons. The planktonic compositions and size distributions were assessed by microscopic identification of individual planktonic taxa. Fish and flamingos were also sampled. The trophic levels and potential dietary interactions of each identified taxa were then evaluated using natural abundance stable isotope analyses ($\delta^{13}C$ and $\delta^{15}N$). The potential contribution of other carbon sources, such as terrestrial particulate organic carbon, was also assessed.

In Chapter 3, observations from Lake Sonachi suggest that the pico-alga *Synechococcus* sp. was the dominant food item for the principal zooplankton taxon (the large calanoid *Lovenula* sp.). This finding differs from reports in other in tropical lakes which had suggested that large calanoids mainly consume colonies of *Microcystis sp*. The findings from Lake Bogoria, presented in Chapter 4, suggest a pronounced seasonality in the occurrence of *Moina* sp. and *Cyclotella* sp. This was predominantly a consequence of lake level rise and associated freshening during the wet season. These organisms do not appear to be utilised as a significant food source by flamingos in this lake. This suggests that seasonal shifts in the planktonic food web structure are not beneficial for flamingos in this lake. The results also suggest that rotifers may compete with flamingos for their main food item, the Cyanobacterium *Arthrospira* sp. In Chapter 5, stable isotope abundance and C/N ratio data from Lakes Baringo and Naivasha suggest that pelagic zooplankton in both lakes were largely dependent on autochthonous carbon in both sampling seasons, despite potentially large catchment sediment fluxes. This challenges previous suggestions that allochthonous carbon is an important basal resource for pelagic food webs in many lakes. Such assumptions, as derived from temperate lake systems may not always apply to tropical lake systems, as sampled in this study.

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Table of Contents

List of Tables

List of Figures

List of Appendices

List of Plates

CHAPTER ONE: INTRODUCTION AND LITERATURE REVIEW

1.1 General Introduction

Zooplankton are important components in the pelagic food webs of lakes (Villaescusa *et al.*, 2016; Leoni, 2017). These organisms play an essential role in linking the base of the food web with consumers at higher trophic levels (Grey *et al.*, 2000). Several studies have examined the trophic links between zooplankton and the wider food web (e.g. Grey and Jones, 1999; Grey *et al.*, 2001; Matthews and Mazumder, 2006; Rautio *et al.*, 2011). However, the trophic interactions of zooplankton are sometimes oversimplified, neglecting the facts that zooplankton are very diverse (Heneghan *et al.*, 2016) and that the feeding strategies of these organisms differ between and within their main groups (Cladocera, cyclopoids, calanoids and rotifers) (Fernando, 2002; Barnett *et al*., 2007; Berggren *et al.*, 2014; Prowe *et al.*, 2018). Different taxa occupy different ecological niches and influence ecosystem processes in different ways (Schulze *et al.*, 1995). The ability to discriminate between different food particles, sizes of zooplankton and modes of feeding are key traits that affect zooplankton function (Hébert *et al*., 2016; Aranguren-Riaño *et al*., 2018) (Table 1.1; Figure 1.1).

Table 1.1 Differences between the main groups of zooplankton, modified from Fernando (2002).

Some important characteristics	**Cladocera**	**Calanoida**	**Cyclopoida**	**Rotifera**
Common adult length	0.3- 3.0 mm	1-2 mm	<1mm	0.2-0.6 mm
Feeding's mode	Filter feeder by appendages on thorax.	Filter feeder	Grasp food by maxillae	Suspension feeder by using cilia on corona.
Filtration rate	High	Low	None	Very low
Predation effect by fish	High	Low	Low	Very low
Predation effect by invertebrate	Moderate	Variable, moderate to high	Variable, moderate to high	High

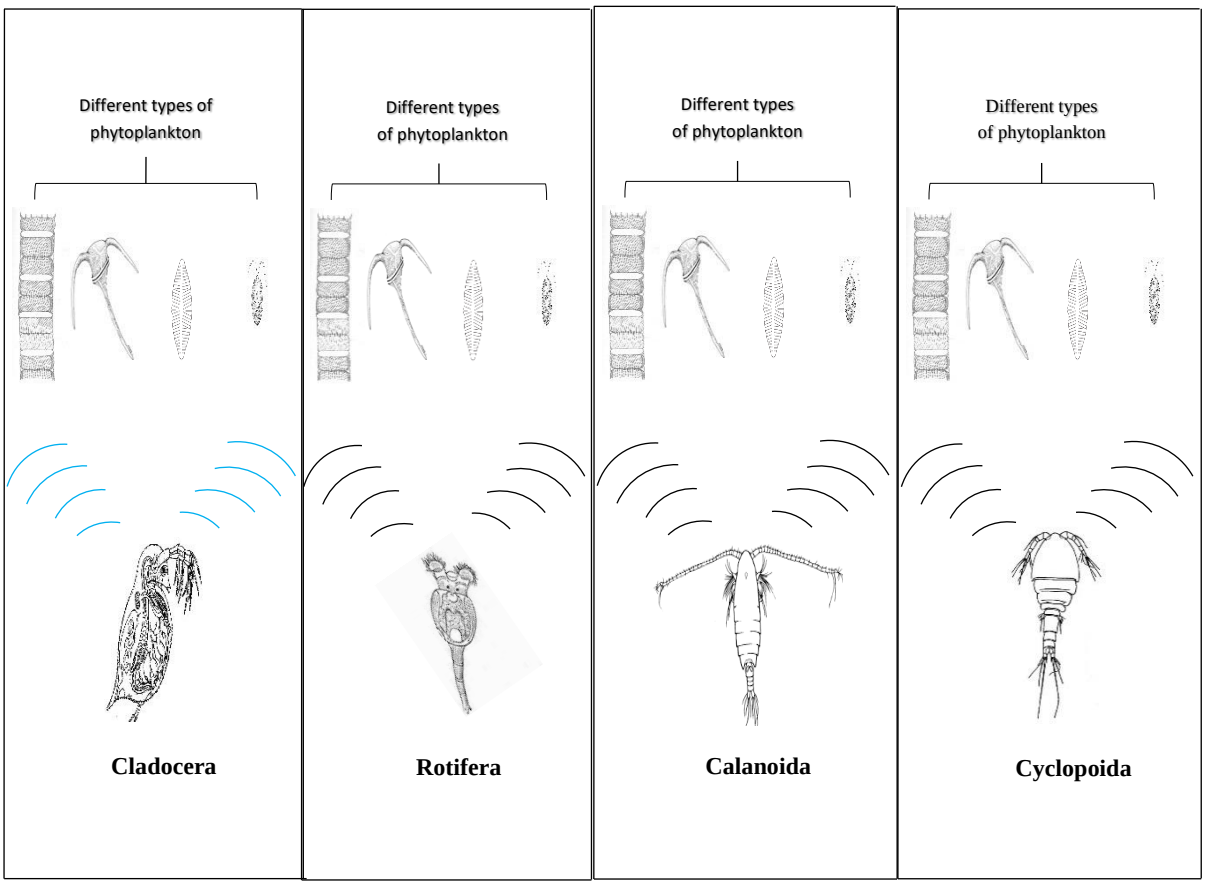

Figure 1.1 Differences among different groups of zooplankton (Rotifera, Cladocera, Calanoida and Cyclopoida) in detectability of food particles. A high detectability is represented by black curved lines and limited detectability is represented by blue curved lines.

Each zooplankton taxon has a different (and often plastic) feeding behaviour (Kiørboe, 2011; Giering *et al.*, 2018) which will influence the dominant sources of carbon that are utilised (Tanentzap *et al.*, 2017). Carbon resources are often distinguished between those that are allochthonous (i.e. carbon fixed in the terrestrial catchment and transported to the aquatic ecosystem) and those that are autochthonous (i.e. primary production inside the aquatic ecosystem) (Grey and Jones, 1999; Berggren *et al.*, 2014). Allochthonous carbon includes dissolved organic matter (DOM), leaf litter and POM (particulate organic matter) (Cole *et al.*, 2006). Furthermore, some species of zooplankton can switch their mode of feeding from suspension to ambush (Saiz and Kiørboe,1995), or switch from herbivory to carnivory when phytoplankton are deficient (Landry, 1981).

Assimilation of allochthonous and autochthonous carbon sources by zooplankton also depends on trophic state of lakes (e.g. oligotrophic, mesotrophic, eutrophic and hypertrophic lakes) (Grey *et al.*, 2000). Lakes vary in their primary productivity and are surrounded by catchments with different characteristics (Tanentzap *et al.*, 2017). Much of the literature on zooplankton shows that the specific mechanisms by which available carbon sources are used by zooplankton are still unclear (Perga *et al*., 2006; Berggren *et al*., 2015; Tanentzap *et al*., 2017). Tanentzap *et al.* (2014) showed that allochthonous sources can represent important contributions to the aquatic food web, particularly in lakes with strong hydrological and physical links with their catchments (Tanentzap *et al.*, 2017). However, Grey *et al.* (2000) suggest that allochthonous carbon sources decrease in importance when there is an increase in the primary production of high-quality carbon sources (e.g. phytoplankton). Allochthonous carbon resources often have lower nutritional values than phytoplankton (autochthonous resources). They are often poorer in essential fatty acids (DHA (docosahexaenoic acid) and EPA (eicosapentaenoic acid)) compared to most phytoplankton (Brett *et al*., 2012). On the other hand, allochthonous materials can reduce photosynthesis due to shading effects, which may increase utilization of allochthonous sources by aquatic consumers (Jones *et al.*, 2012).

The feeding behaviour of zooplankton is, in part, controlled by the characteristics of available food items (Burian *et al.*, 2013). For example, the traits of phytoplankton (e.g. morphological features and toxicity of Cyanobacteria) (Pančić and Kiørboe, 2018), can shape their trophic interactions with zooplankton (Ger *et al.*, 2014), thus affecting the use of carbon sources by these consumers. However, the impacts of those traits on the trophic interactions between Cyanobacteria and zooplankton are still unclear (Wilson *et al.*, 2006; Ger *et al.*, 2014). This is probably because most research on this subject has primarily examined trophic interactions between Cyanobacteria and Cladocera (Ger *et al.*, 2011). Less attention has been paid to trophic interactions between Cyanobacteria and Copepoda (Ger *et al.*, 2011). Conclusions based on Cladocera may limit our understanding because of differences in feeding behaviour between Copepoda and Cladocera (Fulton and Paerl, 1987; Ger *et al.*, 2011). Furthermore, our knowledge of the feeding behaviour of zooplankton is largely based upon empirical studies derived from temperate regions. Such studies are relatively rare in the tropics (Hart,1998).

Tropical regions are characterised by high mean temperatures, lower seasonal variability in solar irradiance, and higher phytoplankton production in general compared to

temperate regions (Lewis, 1996; Lewis, 2000). In addition, cyanobacterial blooms tend to be shorter-lived in temperate lakes than in eutrophic tropical lakes, where blooms are often semi-permanent (Ger *et al*., 2016). Furthermore, trophic interactions between zooplankton and Cyanobacteria in temperate regions are usually seasonal, continuing for limited periods (Ger *et al*., 2016). Generalisations based on temperate lakes may therefore restrict our understanding about trophic interactions between these organisms. Our understanding, therefore, of the role of zooplankton in the pelagic food webs of tropical lakes still needs improvement.

Global climate change and increased anthropogenic activities (e.g. intensification of agriculture), may increase allochthonous input of carbon, nitrogen and phosphorus into some lakes. This may be linked to a rise of cyanobacterial blooms across the world (Evans *et al.*, 2005; Rahel and Olden, 2008; Schindler and Lee, 2010; Paerl and Paul, 2012; O'neil *et al.*, 2012; Jackson *et al.*, 2017). Knowledge of these processes is key for developing more successful management strategies and for restoring impacted lakes (Urrutia-Cordero *et al.*, 2016; Mantzouki *et al.*, 2016; Kamenova *et al.*, 2017).

1.2 What is the role of zooplankton in the pelagic food web?

Zooplankton are central to the aquatic food web (Sommer and Stibor, 2002; Mimouni *et al.,* 2015) as illustrated by Figure 1.2. They consume bacteria, flagellates, ciliates phytoplankton, particulate organic matter (POM) and are, themselves, a primary food source for fish and some birds (Heneghan *et al.,* 2016; Emily *et al.,* 2017). Zooplankton can also reduce food availability (e.g. phytoplankton) for other primary consumers (e.g. birds that feed by filtration (e.g. lesser flamingo) (Robinson, 2015; Childress *et al*., 2008), and for certain invertebrates (De Stasio *et al.,* 2018). In addition, zooplankton can feed directly on phytoplankton and POM derived from autochthonous sources, including algal detritus (Grosbois *et al.,* 2017).

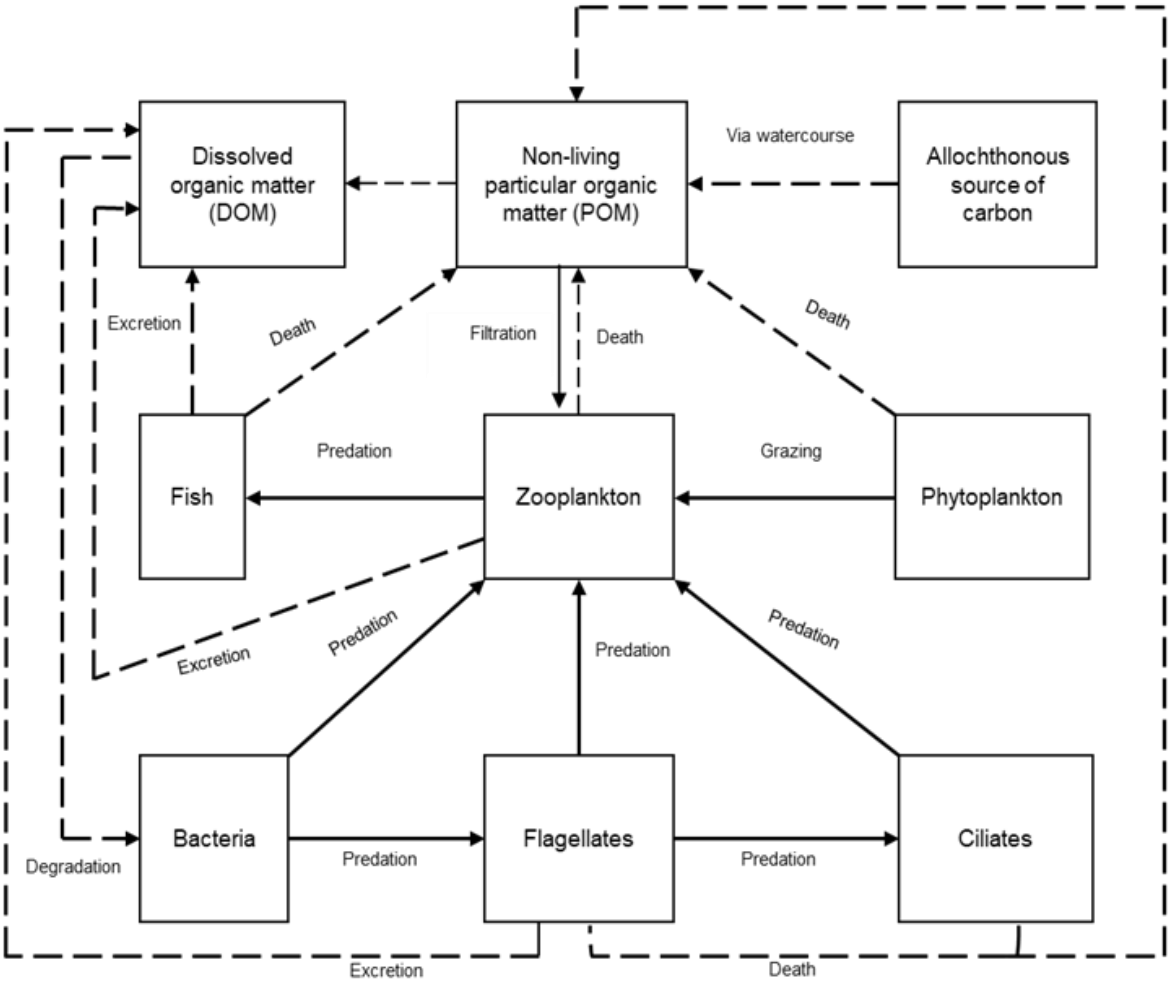

Figure 1.2 Schematic illustration of the central role of zooplankton in the aquatic food web of a lake. Trophic pathways are represented by arrows, dashed arrows illustrate flow of POM (particulate organic matter) and DOM (dissolved organic matter).

1.3 Main zooplankton groups

The main groups of zooplankton are crustacea (Cladocera and Copepoda) and Rotifera (Suthers and Rissik, 2009).

Cladocera are in the class Branchiopoda (Dole-Olivier *et al.,* 2000). Most Cladocera are small crustaceans. Their size typically ranges between 0.2 and 6 mm (Forró *et al.*, 2008). Cladocera have thoracic limbs (appendages) that are used for collecting food items and transferring them towards the mouth opening (Suthers and Rissik, 2009). Cladocera include four orders with twelve families and about 450-600 species in freshwater ecosystems (Dole-Olivier *et al.,* 2000). Cladocera are also found in marine and hypersaline ecosystems (Dumont and Negrea, 1996; Forró *et al.*, 2008). It is reported that Cladocera such as *Daphnia pulex*, *D. galeata mendotae*, *D. ambigua*, *D. magna* and *Ceriodaphnia dubia*, are unable to discriminate between food items which vary in quality (Kirk, 1991), although some studies (e.g. Gliwicz and Siedlar 1980; Sterner,1989; Pagano, 2008), suggest that cladocerans such as *D. magna*, *D. cucullata*, *D. hyaline* and *Moina micrura* are in fact selective feeders (e.g. they can detect and select food items with different sizes and qualities).

Copepoda are a sub class of Maxillopoda (Dole-Olivier *et al.,* 2000), which can comprise over 50 % of total zooplankton in some lake systems (Likens, 2010). In contrast to most Cladocera, it is generally acknowledged that Copepoda are selective feeders (DeMott, 1988) that make food choices on the basis of size and quality. Copepoda have chemical and mechanical receptors to detect food items (Kiørboe, 2011; Heuschele and Selander, 2014). For example, their mouthparts can be used to handle or reject food particles (Paffenhöfer *et al.,* 1982) increasing their ability to discriminate between food types (Kleppel,1993; Goncalves and Kiørboe, 2015). Calanoid and cyclopoid copepods are the main groups. The length of calanoids is about 1-2 mm, while cyclopoids are usually less than 1 mm in length (Suthers and Rissik, 2009). Most calanoids feed on bacteria (Wroblewski, 1980), phytoplankton (Calbet *et al.,* 2000) and particulate organic matter (POM) (Suthers and Rissik, 2009), while adult stages of cyclopoids are often predators, feeding on rotifers and small Cladocera (Brandl, 2005). Cyclopoids often consume larger food particles than calanoids (Thorp and Covich, 2009). Nauplii (the larval stages of Copepoda) vary in their feeding behaviour in comparison with adult copepods (Helenius and Saiz, 2017). Nauplii of cyclopoids and calanoids are largely herbivores (Matthews

and Mazumder, 2007). The feeding selectivity of nauplii is usually lower than in adults (Paffenhöfer and Lewis, 1989).

Rotifera form a small phylum of about 2000 species, living in all types of freshwater ecosystems and saline lakes (Likens, 2010). The length of rotifers usually ranges between 0.1 and 0.5 mm (Suthers and Rissik, 2009). The mouths of rotifers are surrounded by cilia, forming a structure called the corona. Both the feeding and swimming of rotifers rely on the movement of cilia in the corona to create currents (Ricci and Balsamo, 2000). The corona contains chemosensory neurons that are used by some species (such as *Brachionus* sp.) to discriminate between food particles (Snell, 1998). Rotifers can be carnivores (Ricci *et al.,* 2001), herbivores and bacterivores. Heterotrophic bacteria can comprise up to 40 % of diet (Arndt, 1993).

1.4 Biotic and abiotic factors affecting zooplankton in the pelagic food web of lakes

The role of zooplankton in pelagic food webs is shaped by a wide range of different interacting factors. The most important are those related to the catchment, water chemistry, climate and ecosystem characteristics. A complete review of the physical and biological interaction between zooplankton taxa and their environment is beyond the scope of this section. However, the most important factors are presented and discussed (largely following discussions by e.g. Gliwicz and Pijanowska, 1989; Mavuti, 1990; Williamson *et al*., 2002; Schallenberg *et al*., 2003; Lampert and Sommer, 2007; Richardson, 2008; Donohue and Garcia Molinos, 2009; Ekau *et al*., 2010; Kratina *et al*., 2012; Carrasco *et al*., 2013; Burian *et al*., 2013 and Tanentzap *et al*., 2017).

1.4.1 Seasonality

Previous work has shown that seasonality in the abundance and behaviour of tropical plankton is mainly driven by rainfall rather than by temperature, as is the case in temperate zones (Lewis, 1996; Mavuti and Litterick, 1981; Nilssen, 1984; Hamilton and Lewis, 1987). The relationship between the density of zooplankton and rainfall is clearly not direct but linked to nutrient loading from the lake catchment, which often increases after rainfall and which can promote algal production. This, then, increases grazing and zooplankton production (Mavuti, 1990). Mixing of the water column is also promoted during the rainy season. This redistributes nutrients and makes them more available to primary producers (e.g. phytoplankton), which can support zooplankton (Ghidini *et al*.,

2009). Hence, both phytoplankton and zooplankton abundance tend to be higher in the wet season compared with the dry season (Mavuti, 1990; Sanders, 2016), although, this is not always the case because the feeding behaviour of zooplankton is also controlled by the characteristics of food items (Burian *et al*., 2013) (see 1.4.9 Characteristics of food - Chapter 1).

Sometimes mixing can lead to an increased concentration of suspended solid particles in the water column. This could have negative impacts on light penetration and, thus, primary production (Odada *et al*., 2006; Omondi *et al*., 2015; Okech *et al*., 2018). In addition, high fine suspended solids concentrations can negatively impact zooplankton feeding, (e.g. by preventing the efficient identification of food items) (Kirk, 1991). Dejen *et al*. (2004) found that the density of some zooplankton taxa (Cladocera and Copepoda) in Lake Tana, (Ethiopia) was higher during the dry season (with low turbidity) than in the rainy season (with high turbidity). Although, many studies have examined the effects of seasonality on plankton compostion (e.g. Talling, 1986; Mavuti, 1990 and Mbogo, 2002) in East African lakes, far too little attention has been paid to seasonal changes in the importance of allocthonous and autocthonous carbon to zooplankton in these lakes.

1.4.2 Temperature

Temperature exerts an important control over aquatic organisms and can change trophic interactions between organisms within food webs (Lewandowska *et al*., 2015). The high temperatures typical experienced in tropical regions (Lewis, 1996; Lewis, 2000) and potentially high nutrient loading [particularly phosphorus] from the surrounding catchment due, for example, to seasonally high rainfall (Taipale *et al*., 2019), could play a role in the proliferation of inedible Cyanobacteria (Yamamoto *et al*., 2011; O'Neil *et al*., 2012). Larger cyanobacterial taxa (e.g. colonies of *Microcystis* sp.) are difficult to consume by tropical zooplankton (Kâ *et al*., 2012) and, thus, may affect food availability.

Increased temperatures tend to reflect high available energy at the surface, which promotes high rates of evaporation. This can lead to a decrease in water levels in some lakes, if evaporative losses and outflow are not replaced, as is common in semi-arid and arid regions (Williams, 2001). As a consequence, salinity can increase. Increased salinity may lead to reduced richness of the total zooplankton in lakes (Green and Mengestou, 1991).

1.4.3 Geology

The chemistry and biology of a lake is controlled by the geology of the lake basin and its catchment (Derry *et al*., 2003; Nõges *et al*., 2003). Lakes receive different materials from their catchments through chemical weathering and erosion (Nõges *et al*., 2003; Schagerl, 2016). For example, the dominant ions in saline-alkaline lakes in Africa are bicarbonate and sodium, which are derived from the surrounding geological formations of these lakes (Njuguna, 1982; Ballot *et al.*, 2005; Schagerl and Renaut, 2016). In such lakes, the diversity of organisms (for example zooplankton) decreases due to high salinity (Hammer, 1993).

The supply of chemicals derived from the surrounding rocks has a direct impact on the buffering capacity. Low buffering capacity can enhance lake acidification (via atmospheric precipitation: Carter *et al*., 1986) which can affect ecosystem composition (Havens *et al*., 1993). Acidification often leads to low diversity of zooplankton and a dominance of acid-tolerant taxa (e.g. cladocerans *Bosmina obtusirostris* and *Holopedium gibberium* in small lakes in mountain Tundra: Vandysh, 2002).

1.4.4 Lake geometry

Lake level exerts a strong influence on zooplankton density and succession, particularly in shallow lakes (Mavuti, 1990). During the dry season, lakes typically decease in surface area and depth (Twombly and Lewis, 1987). Shallower lakes tend to mix more thoroughly, resulting in more uniform physical and chemical parameters (e.g. dissolved oxygen and temperature) through the water column (MacIntyre and Melack, 1984). In contrast, during high water stands (e.g. due to an excess of rainfall or river inputs over losses), lake area and depth can increase (Twombly and Lewis, 1987). Furthermore, high nutrient inputs into lakes from their catchments can enhance phytoplankton productivity, which supports zooplankton production (Mavuti, 1990). Thus, the catchment area to lake volume ratio can also be important because it can affect water residence times (i.e. the ratio of volume to inflow or outflow rate). Changes in phytoplankton composition also change available food items for zooplankton. In deeper lakes, increases in lake level can promote stratification (MacIntyre and Melack, 1984) which can influence vertical distribution of phytoplankton and zooplankton in the water column (Thackeray *et al*., 2006).

Variations in lake area are often connected with changes in lake level. However, lake surface area can also be an independent control over lake ecology (Søndergaard *et al*., 2005). There has been an increasing interest in understanding the effects of spatial gradients on the structure of biological communities (Wellborn *et al*., 1996). The differentiation between small and large lakes is difficult to establish without an obvious delimitation (Wellborn *et al*., 1996), however many factors suggest that the two types of lakes are different (Søndergaard *et al*., 2005). Small lakes are often more isolated than large ones, which often have larger catchments with higher associated inputs of water, organic resources and nutrients (Søndergaard *et al*., 2005).

A decrease in basin size tends to enhance coupling between pelagic and benthic habitats, which can increase recycling of nutrients (Tessier and Woodruff, 2002). Strong coupling between pelagic and benthic habitats might explain why algal communities have been observed to be less influenced by phosphorus limitation in small lakes (Lim *et al*., 2001).

1.4.5 Hydrological sensitivity of lakes

Lake ecosystems are influenced by their catchment area via groundwater inflow, surface and subsurface runoff and by chemical weathering, which affect nutrient fluxes, water chemistry and hydrodynamics (Morales-Baquero and Conde-Porcuna, 2000; Crowe *et al*., 2008; Noges, 2009). These factors then control trophic state (Szyper and Gołdyn, 2002). Morales-Baquero *et al*. (1999) found that dissolved N:P ratios in the epilimnion of lakes in the Sierra Nevada in Spain increased with catchment size, suggesting that P deficiency increased with catchment size (Morales-Baquero and Conde-Porcuna, 2000). The available N:P ratio affects phytoplankton, zooplankton structure and biomass (Dillon *et al*., 1991; Morales-Baquero and Conde-Porcuna, 2000). Ferrão-Filho *et al*. (2003) observed that tropical *Moina micrura* (which has a higher P content than many temperate Cladocera: DeMott *et al*., 2001) performed poorly when feeding on P-deficient phytoplankton. P is essential for synthesis of nucleic acids and metabolism of energy storage (e.g. ATP) (Ferrão-Filho *et al*., 2003).

1.4.6 Salinity

Salinity affects the osmoregulation of aquatic organisms (Schallenberg *et al.*, 2003). It is one of the most important factors affecting zooplankton density and survival (Thorp and Covich, 2009; Aladin, 1991). Therefore, changes in salinity play an important role in

changing the composition of zooplankton communities (Jeppesen *et al.,* 2007; Gonçalves *et al.,* 2007).

Tropical soda lakes exhibit a very high salinity (Wood and Talling, 1988) and their ecosystems are sensitive to changes in the quantity of freshwater inputs (Scheffer and Jeppesen, 2007). Hypersaline lakes are characterised by the existence of organisms that are adapted to high osmolarities (Cooper and Wissel, 2012). It is expected therefore, that any reduction in salinity in hypersaline ecosystems will have a negative impact on the endemic biota of these systems. For example, zooplankton communities in Kenyan soda lakes (e.g. Lake Bogoria) are typically dominated by the rotifer *Brachionous* sp. (Burian *et al.,* 2013), because *Brachionous* sp. is a tolerant genus to high osmolarities (Epp and Winston, 1977). Experimentally, the density of *Brachionous* has been observed to decrease during periods of deceased salinity (Fielder *et al.,* 2000).

Increases in salinity in brackish ecosystems can also lead to a decrease in density and diversity of zooplankton (Schallenberg *et al.,* 2003). An increase in salinity led to a decrease in richness of the total zooplankton in nine lakes in North Africa (Ramdani *et al.,* 2001), rotifers in 30 lakes in Ethiopia (Green and Mengestou, 1991), Cladocera in 167 water bodies in South Africa and 67 in southern Australia (Frey, 1993) and Copepoda in 38 lakes in East Africa (Green, 1993). Jeppesen *et al.* (2007) found that *Daphnia* sp. was replaced by Rotifera and Copepoda in a shallow brackish lagoon (Lake Kogleaks, North Jutland, Denmark) under increased salinity.

Changes in salinity might also facilitate the appearance of new taxa in lakes as well as altering the relative abundance of endemic taxa. An increase in salinity level can lead to biological invasion by new zooplankton that favour high salinity (Kamenova *et al.,* 2017). Such invasions will, almost certainly have an impact on the trophic interactions of permanent biota by making novel trophic links (Jackson *et al.,* 2017).

Under most climate change scenarios, the East African Rift Valley is predicted to get wetter (De Wit and Stankiewicz, 2006; Thomson *et al*., 2018). This could make the East African lakes fresher, particularly during lake level rise. However, relatively little is known about the effects of changes in salinity on food web structure in these lakes. Modern inter-annual variation of salinity in some of the East African lakes (e.g. Lake Bogoria) allows this to be considered in more detail (see Chapter 4).

1.4.7 Turbidity

Turbidity is one of most important factors affecting aquatic food webs, including trophic interactions between consumers and their prey (Carter *et al.*, 2010), primary production of phytoplankton (Blottière *et al.*, 2017), prey selection by fish (Carter *et al.*, 2010), feeding of zooplankton (Carrasco *et al.*, 2013), and zooplankton structure (Donohue and Garcia Molinos, 2009). High concentrations of suspended solid particles can lead to the dominance of a small zooplankton over large ones (Jiang *et al.*, 2010) due, for example, to the negative effect on feeding and growth of Cladocera (Hart, 1988; Hart, 1992). Carrasco *et al.* (2013) found that a high level of turbidity led to an increase in mortality of the copepod calanoid *Acartiella natalensis.* Some species of zooplankton have a high degree of tolerance to turbidity (e.g. the cladoceran *Moina*: Kirk and Gilbert, 1990; Lougheed and Chow-Fraser, 1998). High concentrations of suspended particles, either from the catchment or from internal resuspension of sediment, affect Cladocera by decreasing ingestion of high-quality food in the presence of those particles (Kirk, 1988). This is probably due to the fact that most Cladocera are non-selective feeders. Rotifers are less affected by suspended sediment (Kirk, 1990), because rotifers tend to be more selective than Cladocera (Gilbert and Bogdan, 1984; Lenz *et al.*, 1997), and can avoid feeding on mineral particles. Turbidity can reduce production of phytoplankton by limiting light availability that is necessary for photosynthesis (Parkhill and Gulliver, 2002) and, thus, decrease the availability of autochthonous resources for zooplankton (Gasparini *et al.*, 1999).

Turbidity also affects visually planktivorous fish (e.g. fish depending on sight for grazing) by affecting their vision (Vinyard and O'Brien, 1976; Yasindi *et al.*, 2013). This has been suggested as one reason behind the low density of *Oreochromis niloticus* in Lake Baringo, Kenya (Omondi *et al.*, 2014a).

Few previous studies have examined the impact of turbidity and the input of allochthonous particles on the role of zooplankton in pelagic food webs in tropical lakes, particularly in terms of the effects of turbidity on the relative importance of autochthonous and allochthonous carbon sources for zooplankton and fish. An understanding of this is important because it can clarify how the dependence of aquatic consumers on these resources will change with turbidity. High turbidity in some East African lakes, such as Lake Baringo (Johansson and Svensson, 2002; Odada *et al*., 2006)

allows this to be examined via comparison with less turbid Lakes (e.g. Lake Naivasha),in otherwise comparable environmental settings (see Chapter 5).

1.4.8 Dissolved oxygen (DO)

Oxygen is one of the key factors that affects pelagic organisms (Ekau *et al.,* 2010). High concentrations of dissolved oxygen (supersaturation) can be produced by increasing primary production during conditions of high solar radiation, particularly in water rich in nutrients (Lampert and Sommer, 2007). In such conditions, oxygen saturation might reach 200 % or higher during the day. Although there are a number of benefits to high oxygen concentrations, supersaturation can also have adverse influences on some components of the aquatic food web (Lampert and Sommer, 2007). For instance, gas bubbles of oxygen can attach to the external structure (carapace) of Cladocera, causing enhanced buoyancy and an accumulation of these zooplankton on the surface where they are more prone to predation (Lampert and Sommer, 2007).

Zooplankton differ in their ability to tolerate different levels of oxygen concentration. The lower tolerance of many zooplankton ranges from 1 to 2 mg L^{-1} (Vanderploeg *et al.,* 2009). Low DO values can have adverse effects on zooplankton, for example values between 0.5 and 1.0 mg L^{-1} can be lethal for the cladoceran *Daphnia pulex* (Weider and Lampert,1985). Copepod calanoids on the other hand are more tolerant to these low DO concentrations (Stalder and Marcus,1997). Similarly, the cladoceran *Moina micrura* cannot adapt to such deficiencies of oxygen; their filtration process is stopped when DO concentrations reach 0.7-0.8 mg L^{-1} (Ekau *et al.,* 2010).

Anoxic layers in stratified lakes can be used as a refuge by zooplankton to avoid fish predation (Vanderploeg *et al.,* 2009), because many fish are not able to access these layers. Differences between zooplankton in terms of their adaptation for lower or higher concentrations of dissolved oxygen in the water column might, therefore, have an impact on feeding and survival of zooplankton and trophic interactions with fish. These interactions will ultimately affect carbon transfer pathways in lakes.

1.4.9 Characteristics of food

Different zooplankton taxa have different feeding behaviours (Fernando, 2002). This behaviour is affected by features of their food items (Burian *et al.*, 2013). Characteristics such as toxicity (Lampert and Sommer, 2007; Leitão *et al.*, 2018), taste (DeMott, 1986), size (Bern, 1994; Leitão *et al.*, 2018; Gebrehiwot *et al.*, 2019), morphology(Gebrehiwot *et al.*, 2019), ingestion (DeMott and Gulati, 1999; Anderson, 1992), quality and origin (allochthonous or autochthonous) (Brett *et al.*, 2009; Brett *et al.*, 2017), as well as the concentration of food particles in the water column (Mitra and Flynn, 2007) can all influence feeding and, thus, their role in channelling carbon to higher trophic levels.

For example, the cyanobacterium *Microcystis* is toxic to many zooplankton taxa. This is a type of defence mechanism against predation (DeMott and Moxter, 1991), which inhibits the function of the digestive enzymes of zooplankton during feeding (Rohrlack *et al.*, 2004). The calanoid *Eudiaptomus gracilis* has been observed to selectively avoid feeding on *Microcystis* (Ger *et al.*, 2016), probably because they can detect *Microcystis* and have evolved to avoid it (Ger *et al.*, 2011).

Cladocera (such as *Daphnia*) lack a mechanism for food selection by taste (Leoni, 2017). Their ability to select mainly depends on the size of food particles (DeMott, 1986). The size of food particles is also important for the rotifer *Brachionus* (Rothhaupt, 1990). The preferred size range of food particles for *Brachionus* in temperate regions is between 6.5 μm and 12.9 μm with an optimum of 8.3 μm (Hansen *et al.*, 1997). In contrast, in the tropics, *Brachionus plicatilis* was found to feed on *Arthrospira fusiformis* (large filamentous cyanobacterium with an average trichome length of 421 μm) in tropical Lake Nakuru, Kenya (Burian *et al.*, 2014; Ogato and Kifle, 2014). In contrast, food selection by Copepoda is based on mechanical and chemical detection (Kiørboe, 2011). Copepod cyclopoids can feed on filamentous phytoplankton. *Thermocyclops* was found to be able to ingest filamentous algae after fragmenting them (Gebrehiwot *et al.*, 2019). In contrast, Cladocera appear not to be able to feed on large filamentous algae due to interference with their filtration apparatus (Gliwicz and Lampert, 1990). It is also possible that the mucous layer of some Cyanobacteria might reduce the feeding rate of zooplankton (Gebrehiwot *et al.*, 2019). The mucous layer of Cyanobacteria can resist ingestion and digestion by zooplankton (Reynolds, 2007). Although many studies have been conducted on trophic interactions between zooplankton and Cyanobacteria, much uncertainty still exists about these interactions. In part, this is due to the fact that most information is still

derived from temperate lake systems. There continues to be, therefore, a particular need to improve our understanding of these trophic links in tropical lakes (Hart,1998; Leitão *et al*., 2018).

Considering alternative food sources, inland waters receive considerable amounts of allochthonous carbon that can act as an alternative carbon resource for zooplankton (Brett *et al.,* 2017). The importance of these allochthonous resources relative to autochthonous carbon for zooplankton food webs is generally well understood for temperate lakes. However, important knowledge gaps remain in tropical lake systems (e.g. Cole *et al*., 2011; Taipale *et al.,* 2016 a).

1.4.10 Competition

Competition regulates the structure and dynamics of all ecosystems and lakes are no exception (Lampert and Sommer, 2007). Competition between two species might ultimately exclude one of the competitors when they are competing for the same food resource (Tilman *et al.,* 1981). Coexistence can occur, however, if the inter-specific competition is lower than intra-specific competition (Begon *et al.,* 1986). Competition could occur between native species and invasive ones, potentially leading to the exclusion of the native species (Dick *et al.,* 2017).

Pelagic zooplankton (Copepoda, Cladocera and Rotifera) often show competition for food resources (Brandl, 2005). Such competition might be depressed under conditions of high food availability where many species can coexist (Nandini and Sarma, 2002). However, when food becomes scarce competition is likely to be more important.

Cladocera and rotifers are similar in their mode of reproduction (predominantly parthenogenesis) and they lack larval stages during their development to adults (Xi and Hagiwara, 2007). Such similarities may result in some niche-overlap. Large Cladocera are generally considered as a superior competitor (Kirk and Gilbert, 1990), in part, due to the fact that they can produce high-speed currents that can lead to rapid collection of food items (Brooks and Dodson, 1965; Gilbert, 1985). Furthermore, small rotifers such as *Brachionous* sp. can be physically damaged by these currents (Gilbert, 1988; Likens, 2010). Gama-Flores *et al.* (2006) report that *B. calyciflorus* was outcompeted by *Moina macrocopa* in a laboratory experiment, (Gama-Flores *et al.,* 2006). In contrast, small Cladocera tend to have less suppressive impact on rotifers (Gilbert, 1988).

Copepoda often exhibit more complex trophic interactions (Nandini and Sarma, 2002). Cyclopoids (generally predators) can prey on calanoids (Nandini and Sarma, 2002). Calanoids are mainly herbivores but may compete with cyclopoid nauplii in feeding on edible algae and consequently reduce the density of cyclopoids (Soto and Hurlbert, 1991).

Despite, growing insights on the interactions which occur between different zooplankton, the effect of competition between different groups of zooplankton on carbon pathways is rarely considered in the literature, even though this is an important control on the functioning of the aquatic food web.

In addition, zooplankton can compete with other organisms such as birds (e.g. lesser flamingo) for specific food items (such as *Arthrospira* sp.) in African saline lakes. Relatively little is known about the potential competition that might exist between flamingos and zooplankton in these lakes.

1.4.11 Predation

Predation by fish and invertebrates is considered one of the main factors affecting zooplankton composition and density (Gliwicz and Pijanowska, 1989). The effects of predation on zooplankton composition and abundance are captured by the size efficiency hypothesis (Brooks and Dodson, 1965). This hypothesis predicts that rotifers will be abundant when visually-planktivorous fish are present (due to size- selective predation of these fish on large Cladocera). As a consequence, Cladocera will be dominated by smaller species under such conditions. In contrast, when fish are absent, large Cladocera will be more abundant. This, in turn, tends to reduce the density of rotifers.

Predation by fish and invertebrates can also affect zooplankton migration. It is widely established that zooplankton use diel vertical migration (e.g. through the water column) or horizontal migration (e.g. from open water to the littoral zone of shallow lakes) to avoid predators (Dodson, 1990; Gonzalez Sagrario *et al*., 2010). However, other physical and chemical parameters such temperature, light intensity, dissolved oxygen concentration and feeding strategies can also control migration behaviour (Mavuti, 1992; Omondi *et al*., 2014b). Omondi *et al*. (2014b) reported that light and feeding strategies control vertical migration of zooplankton taxa in Lake Baringo, Kenya; during the day these organisms remain close to the surface, feeding on phytoplankton and are able to avoid fish (sight predators) due to the high turbidity. During the night zooplankton migrated to the mid and bottom layers (Omondi *et al*., 2014b).

Few studies have examined effects of predation by fish on zooplankton size in East African lakes. This might be expected to reduce the size of large zooplankton. Furthermore, to the author's knowledge, no studies have reported predation on zooplankton by lesser flamingo in East African saline Lakes.

1.5 Methods for food web analysis

Historically, food web structure has been examined using several methods, including gut content analysis and direct observation of feeding behaviour in the laboratory and in the field (Pasternak and Schnack-Schiel, 2001; Bouvy *et al*., 2001; Michener and Lajtha, 2008). These methods have helped us to understand trophic interactions between the components of aquatic food webs. However, these methods have some significant limitations (Michener and Lajtha, 2008). Although they provide information on which food particles are consumed, they do not necessarily indicate the nature of long-term food assimilation (Makoto and Tsutomu, 1984; Omorii and Ikeda, 1984). Direct observation is often prevented by the aquatic environment (Grey, 2006). Gut content analysis requires a high level of taxonomic knowledge about the organisms present in an animal's gut (Michener and Lajtha, 2008) and is not possible in zooplankton taxa less than 1 millimetre in length (Michener, 1994) or in organisms with very rapid digestion rates (Feller *et al*., 1979). Furthermore, gut content analysis typically only reveals the most recent diet (last 24 hours) which could lead to bias (Newton, 2001).

The determination of patterns of resource assimilation by organisms over long-term periods requires chemical analysis (Bowes and Thorp, 2015). This includes fatty acid/ lipid analysis (Ruess *et al*., 2004; Perga *et al*., 2006) and natural abundance stable isotope analysis (SIA) (Makoto and Tsutomu, 1984; Post, 2002; Fry, 2006; Boecklen *et al*., 2011). Both techniques are useful for identifying dietary sources, which may not be detected by gut content analysis (Grey, 2006; Michener and Lajtha, 2008). An additional advantage of SIA is that it allows small organisms in the food web (i.e. many planktonic organisms) to be included, as long as sufficient material can be separated and prepared for analysis (Grey *et al*., 2001).

1.6 Stable isotope ecology

Variations in the natural abundance of stable isotopes (SI) are widely used in ecology (Boecklen *et al*., 2011) to trace carbon flows and to understand complex trophic interactions (DeNiro and Epstein, 1978; Ambrose and DeNiro, 1986; Hobson and Welch, 1992; Hobson *et al*., 1994; Grey, 2006; Linnebjerg *et al*., 2016). Specifically, the relative abundance of stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes can elucidate aspects of the structure and function of planktonic food webs (e.g. Grey *et al.*, 2001; Fry, 2006; Brett *et al.*, 2017). Carbon (C) and nitrogen (N) are both key elements in all forms of life and both have stable isotopes that can help reveal important food web characteristics, such as the potential food sources and trophic levels of different taxa (Wada, 2009).

The name isotope is derived from the Greek, meaning equal place. An isotope is a variant of an element with the same number of protons and the same chemical properties, but with a different number of neutrons. Stable isotopes are not subject to radioactive decay (Fry, 2006). The delta (δ) notation is used to express stable isotope ratios (i.e. the relative abundance of two isotopes of the same element: Zanden and Rasmussen, 1999). The ratio may be higher or lower than that of a standard. A sample is said to be enriched when it has a higher ratio of the rarer stable isotope to the most abundant isotope, compared to the standard. A sample is considered depleted when the rare isotope is less abundant in the sample relative to its abundance in the standard.

When stable isotopes are subjected to a mass-dependant process, isotope fractionation occurs. This process is kinetic isotope fractionation. Equilibrium isotope fractionation occurs in chemical equilibria reactions and is a temperature dependant process. Fractionation occurs because different stable isotopes undergo chemical reactions at slightly different rates (Tieszen and Boutton 1989). Trophic fractionation causes trophic enrichment in $\delta^{15}N$ and $\delta^{13}C$ at each trophic level along the food web (Zanden and Rasmussen, 2001; Post, 2002). $\delta^{15}N$ normally increases by approximately 3 ‰ (per mil) between prey and consumer, while $\delta^{13}C$ increases by about 1 ‰ from prey to consumer (Figure 1.3) (DeNiro and Epstein, 1978; DeNiro and Epstein, 1981; Minagawa and Wada, 1984; Hobson and Welch, 1992). Post (2002) has suggested that $\delta^{15}N$ increases by 3.4 ± 1 ‰ and $\delta^{13}C$ does not increase significantly (0 ± 1.3‰) between prey and consumer (Figure 1.3). Preferential excretion of ^{12}C and ^{14}N by the consumer can be responsible for enrichment in $\delta^{15}N$ and $\delta^{13}C$ in consumers (Fry and Arnold, 1982; Rau *et al*., 1983; Ponsard and Averbuch, 1999). The δ space for an example plot of $\delta^{13}C$ and $\delta^{15}N$ can

provide information about trophic niches of organisms within the food web (Ambrose and DeNiro, 1986; Fry, 2006). An area in the δ space with isotopic signatures of $\delta^{13}C$ and $\delta^{15}N$ that represents potential ecological links with other organisms is often referred to as the ‘‘isotopic niche’’ (Newsome *et al.*, 2007). Since distinctive enrichment in $\delta^{15}N$ occurs at successive trophic levels, $\delta^{15}N$ is usually used to provide details about the trophic position of consumers (Vander Zanden and Rasmussen, 1999). $\delta^{13}C$ can be used to trace carbon flow through food webs because there is only a slight enrichment from prey to consumer at each trophic level and because different carbon sources have clearly different $\delta^{13}C$ values (DeNiro and Epstein, 1978; Fry and Arnold, 1982). Thus, $\delta^{15}N$ is usually used to indicate trophic level while $\delta^{13}C$ is used to indicate potential dietary links between organisms at different trophic levels (Figure 1.3).

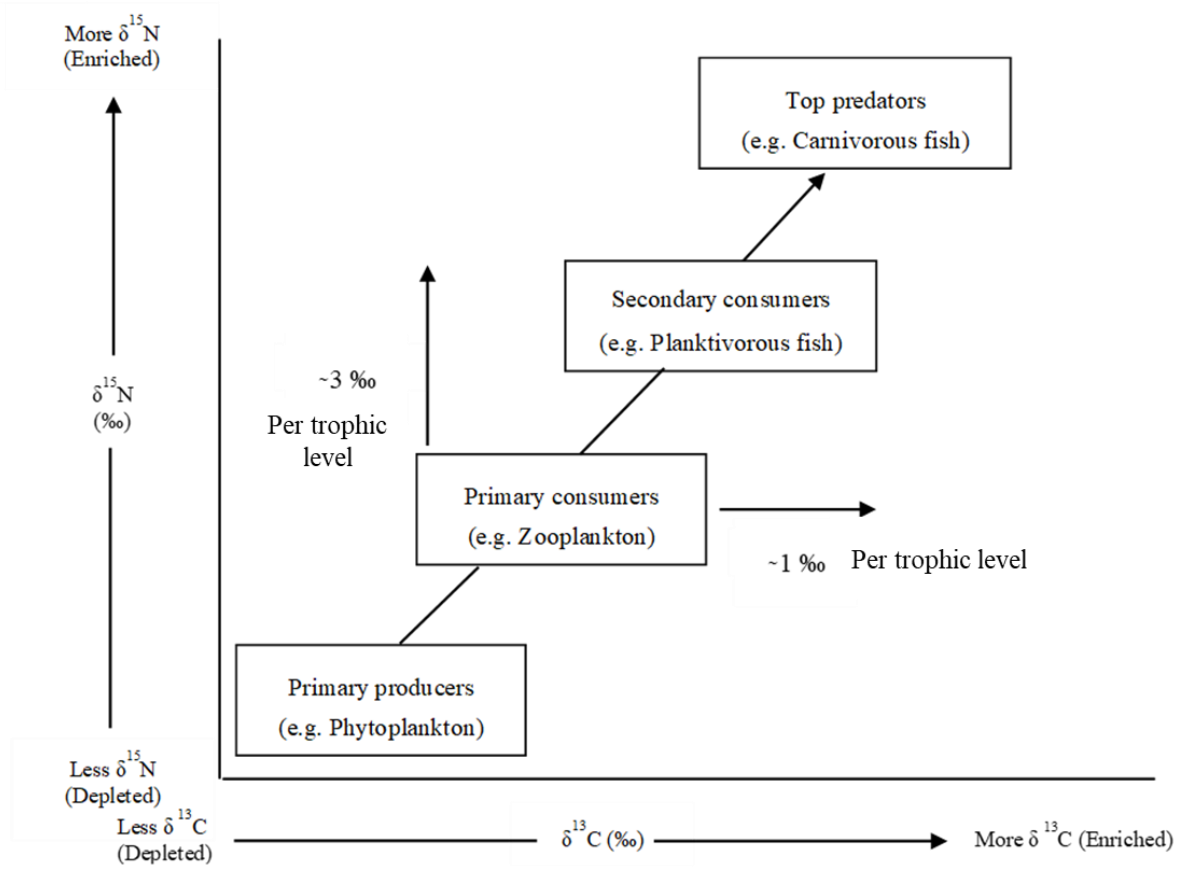

Figure 1.3 Conceptual illustration of the enrichment in $\delta^{15}N$ and $\delta^{13}C$ across trophic levels. Modified from Muñoz (2007).

There are several sources of variation in the degree of enrichment of ^{15}N in consumers (Vanderklift and Ponsard, 2003). One of the most important factors is food quality (Minagawa and Wada, 1984; Zanden and Rasmussen, 2001). A diet of zooplankton with a low nitrogen content might lead to significant enrichment in $\delta^{15}N$ (Adam and Sterner, 2000). The difference between $\delta^{15}N_{consumer}$ and $\delta^{15}N_{diet}$ is known as $\Delta\ \delta^{15}N$. This can range between 0 ‰ and 7 ‰ (Mizota and Yamanaka, 2011). The enrichment in $\delta^{15}N$ may also differ between species (DeNiro and Epstein, 1981; Hobson and Clark, 1992) possibly due, in part, to differences in the biochemical form of N excretion between different organisms (Vanderklift and Ponsard, 2003). Ammonotelic taxa which excrete mostly ammonia generally show lower $\delta^{15}N$ enrichment than ureotelic species (Vanderklift and Ponsard, 2003).

A prerequisite for the application of stable isotope analysis to food webs is that the available basal resources exhibit sufficiently robust and distinct isotopic signatures to allow tracing of carbon flow in a particular system (del Giorgio and France, 1996; Grey and Jones, 1999; Grey *et al*., 2001). For example, the $\delta^{13}C$ signatures of C_3 and C_4 plants are very different and can easily be distinguished (Smith, 1972) (Figure 1.4). Allochthonous carbon sources derived from plants in arid ecosystems tend to show variation in $\delta^{13}C$ values in the range -10 to -34 ‰, reflecting the mixed presence of C_3 and C_4 plants in such environments (O'Leary, 1988). An approximate $\delta^{13}C$ value for C_3 plants is -28‰, while C_4 plants typically have $\delta^{13}C$ value of about -13 ‰ (Figure 1.4). Such differences exist principally because these plants have different photosynthetic pathways (Fry, 2006).

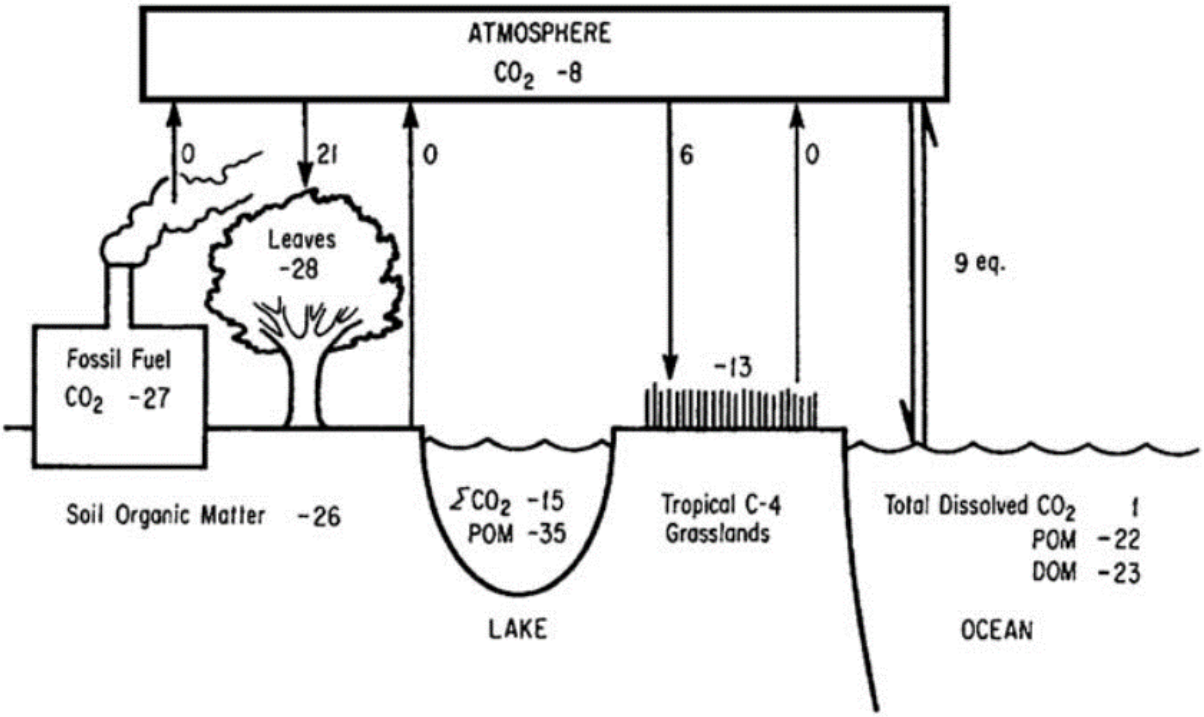

Figure 1.4 $\delta^{13}C$ distributions in different ecosystems. Double arrows indicate equilibrium isotope fractionation. Single arrows represent CO_2 flows. Numbers for different pools signify the carbon isotope signatures per mil (‰). Numbers for the arrows represent the isotopic fractionation per mil during transfers. The Figure is taken from Fry (2006).

The $\delta^{13}C$ signatures of phytoplankton can vary by over 20 ‰ (e.g. Yoshioka *et al*., 1994; Gu *et al*., 1994; Taipale *et al*., 2016 b). This depends on the uptake mechanisms of inorganic carbon, either via CO_2 or bicarbonate (Maberly *et al.,* 1996). The $\delta^{13}C$ of HCO_3^- tends to be higher than that of CO_2 (Wang *et al.,* 2013), by approximately 8.4 ‰ and 12 ‰ at 30 °C and 0 °C, respectively (Mook *et al*., 1974). The $\delta^{13}C$ of photosynthates tend to be more depleted in comparison with inorganic sources of carbon (Fry, 2006). For example, the $\delta^{13}C$ of Chlorophyta was reported to be -27.3 ‰ compared with dissolved inorganic carbon that was used by these phytoplankton which had a value of -8.9 ‰ (Taipale *et al*., 2016b). Cyanobacteria tend to have high values of $\delta^{13}C$ (more enriched) (Wang *et al.,* 2013; Vuorio *et al.,* 2006) due to an active carbon concentrating mechanism (CCM) in these organisms (Price *et al.,* 2011) (Figure 1.5). This results in an efficient uptake of HCO_3^-, which is converted to CO_2 by using carbonic anhydrase (CA: Wang *et al.,* 2013).

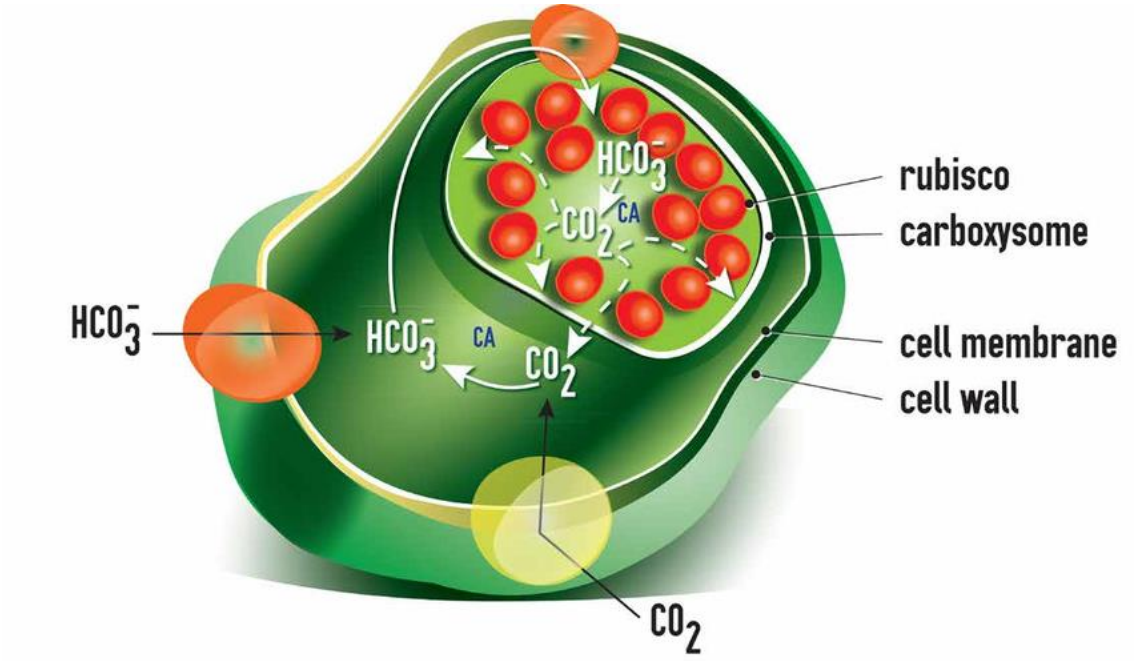

Figure 1.5 The Carbon concentration mechanism in Cyanobacteria (CCM). The figure is taken from Mackey *et al.* (2015).

These mechanisms lead to organic carbon that is less depleted in comparison with other algae, such as Bacillariophyceae, which depend on CO_2 uptake by passive diffusion (Smyntek *et al.*, 2012). The isotopic values of phytoplankton may not only differ between due to differences in physiology, but also between lakes because the latter differ in catchment geology and basin morphometry (Grey *et al*., 2000).

Phytoplankton are difficult to isolate from other detritus (Grey *et al*., 2000). Therefore, POM (e.g. mixture of bacteria, microplankton, detritus from different origins) is routinely used as surrogate for the isotopic signatures for phytoplankton. Unfortunately, this can mask the real phytoplankton isotopic value and can lead to misinterpretations of trophic relationships (del Giorgio and France, 1996). A significant fraction of POM is often derived from allochthonous sources. It is, therefore, expected to have a carbon isotopic signature close to those for terrestrial C_3 plants (Jones *et al*., 1998). This, of course, depends on availability of C_3 plants compared with other resources in the ecosystem. The $\delta^{13}C$ signature of phytoplankton is typically lower than this terrestrial signature, whilst for littoral plants it is higher (Grey *et al*., 2000). Grey *et al*. (2000) found that the $\delta^{13}C$ values of POM from eutrophic and mesotrophic lakes were -26.6 ‰ and -26.2 ‰, respectively, which were close to the $\delta^{13}C$ signatures of soil organic matter (-26 ‰) and terrestrial C_3 plants (-28 ‰) (Peterson and Fry,1987). The $\delta^{13}C$ values of POM from hypertrophic lakes was reported to be more enriched (-21.6 ‰: Grey *et al*., 2000).

Shifts in the contributions of allochthonous resources and phytoplankton to POM along gradients of trophic states (e.g. oligotrophic, mesotrophic, eutrophic and hypertrophic lakes) can be assessed by differences in carbon isotope signatures between POM and algae (Grey *et al*., 2000). However, sometimes these fail to discriminate the origin of POM due to overlaps in $\delta^{13}C$ values between terrestrial and littoral vegetation and phytoplankton. Therefore, other complementary methods such as microscopic observations and C/N ratios can be used to supplement stable isotope analyses. The origin of POM can be assessed by microscopic examination of POM (Sarvala *et al*., 2003), to understand the relative contribution of terrestrial vegetation and phytoplankton. POM can also be categorised by its C/N ratio (Savoye *et al*., 2003). The C/N ratio for phytoplankton typically ranges between 6 and 10 (Montagnes *et al*., 1994; Creach, 1995). It is generally larger than 12 for organic matter of terrestrial origin (Thornton and McManus, 1994), and it commonly ranges from 3 to 6 for bacteria and zooplankton (Gorsky *et al*., 1988; Fagerbakke *et al*., 1996).

Although stable isotope analysis can provide a lot of information about food web structure, there are some issues with its use in aquatic studies (Bowes and Thorp, 2015), and these should be considered whenever it is used. Stable isotope analysis yields a signal for assimilated food items over relatively long-time periods. However, differences in the rate of isotopic turnover, due to differences in metabolic rate between organisms, could be reflected in the isotopic expression in organism tissues (Grey, 2006). Thus, errors or misinterpretations can be made when samples are collected at one point in time in systems where there is significant temporal variability in one or more of the organisms sampled (Grey, 2006). Organisms that grow fast tend to have rapid turnover (Fry and Arnold, 1982). For example, a shift in the isotopic signature of phytoplankton could occur faster than in zooplankton because of the rapid turnover of phytoplankton cells. As a result, the recorded signature of a grazer could reflect a previous diet (Grey and Jones, 1999). It has been suggested that the fast response of the $\delta^{13}C$ signature to changes in the $\delta^{13}C$ signal in food sources of the cladoceran *Daphnia* sp. in comparison with Copepoda might reflect the rapid turnover rate of *Daphnia*, due to its high reproduction rate (mainly parthenogenesis) and short lifespan (Jones *et al*., 1998). The tissue turnover rates of larger consumers range from months to years (Hesslein *et al*., 1993). Therefore, their isotopic signature tends to reflect assimilated diet over these longer periods (Post, 2002).

Despite their tremendous potential, there are some methodological problems with using SIA. For example, it is difficult to obtain a pure phytoplankton sample without other living and non-living particles (e.g. bacteria and dead organic matter: Taipale *et al*., 2016 b). In addition, it is difficult to isolate zooplankton whose size overlaps with other plankton, which can lead to difficulties in obtaining sufficient weight and pure sample for stable isotope analysis (Burian *et al*., 2014).

Techniques to obtain a sufficient quantity and purity of a particular taxon of zooplankton for SIA include hand-picking using a fine pipette under a microscope (a time-consuming process), sedimentation, buoyancy, phototaxis (e.g. separation based on light) (Grey *et al*., 2000; Grey *et al*., 2001; Vuorio *et al*., 2006; Burian *et al*., 2014). The success of the separation method adopted depends on the number-density of zooplankton in the sample, as a substantial quantity of material can be lost during separation process (Burian *et al*., 2014). A large number of zooplankton can often be collected from lakes by repeated net hauls even when the number density of plankton is relatively low (Burian *et al*., 2014).

The gut and lipid contents of organisms can affect carbon and nitrogen isotope ratios. Specific tissues of larger organisms are, therefore, routinely dissected to reduce the errors introduced by the gut content (Feuchtmayr and Grey, 2003; McCutchan *et al*., 2003). However, tissue separation or gut removal from small-bodied organisms (e.g. zooplankton) is inapplicable (Feuchtmayr and Grey, 2003). Although attempts have been made (e.g. Grey and Jones, 1999; Grey *et al*., 2001; Burian *et al*., 2014) to evacuate zooplankton guts, Feuchtmayr and Grey (2003) suggested that gut content did not have a significant impact on isotopic signatures of Cladocera (e.g. *Daphnia*). Lipids are normally more depleted in $\delta^{13}C$ values than carbohydrates and proteins (DeNiro and Epstein, 1977). Therefore, $\delta^{13}C$ signals are likely to be more depleted for samples with high lipid contents than samples with low lipid contents (McCutchan *et al*., 2003). Therefore, $\delta^{13}C$ values could be more depleted for organisms (like fish) analysed whole, in comparison with consumers analysed for muscle tissue, which has a low lipid content (McCutchan *et al*., 2003).

1.6.1 Mixing Models and Resource Polygons

Mathematical isotopic mixing models can help to determine the fraction of a consumer organisms' diet derived from different food sources (Deniro and Epstein, 1976; Fry, 2006; Phillips, 2012; Phillips *et al*., 2014). They are based on the principle of the "isotopic niche" in which prey items are primarily derived from one trophic level below that of the consumer (defined by differences in $\delta^{15}N$), with the relative contribution of different food items assessed via differences in their $\delta^{13}C$ signals (Newsome *et al.,* 2007). This potential contribution space is also sometimes referred to as a diet or resource polygon (a graphical representation of the relationship between a consumer and its prey on a plot of $\delta^{13}C$ versus $\delta^{15}N$: e.g. Fry, 2013). In this thesis, resource polygons have been defined using the trophic enrichment reported in the literature for $\delta^{15}N$ 3.4 ± 1 ‰ and for $\delta^{13}C$ 0.4 ± 1.3 ‰ (Post, 2002).

It is important to understand that choosing a mixing model in food web studies is largely dependent on the ecological question, and that it is important to be aware of the limitations of the model employed. Most mixing models are linear combinations based on a simple mass balance equation (Layman *et al*., 2012), which can be used to determine the relative contribution of each food source in a system with a few potential food items (Layman *et al*., 2012). This approach has been used in this thesis. For example to ascribe the potential contribution of phytoplankton and POM to pelagic zooplankton in Lakes Sonachi and Bogoria and the relative importance of allochthonous and autochthonous carbon to zooplankton and fish (see Chapter 2 for details). However, in complex food webs with numerous potential food sources or in situations where different food sources have indistinct isotopic signatures, the ability of mixing models to accurately quantify food contributions to consumers can be limited (Phillips *et al*., 2005; Layman *et al*., 2012). Interpretations can also be challenging if there are differences in the sampling timeframe for prey items and consumers and the time needed to synthesise consumer tissue, or if data are missing for some significant prey items. More sophisticated modelling tools such as the IsoSource model (Phillips and Gregg, 2003) have been proposed to overcome some of these issues (e.g. by grouping similar sources). IsoSource cannot generate exact numbers for the relative contributions of each source but can provide possible source contributions. Briefly, the first step of this model is to generate each potential combination of food source proportions. Secondly, the predicted isotopic signatures for the consumer are calculated for each one of these combinations. Then,

these predicted signatures for the consumer are compared with the observed signatures of the consumer. If they are within slight tolerance (e.g. 0.2 ‰), or equal (slightly higher signatures to include sampling-variability effects are permitted), then this mixture of food source proportions can provide a reasonable solution which satisfies mass balance. The lower and higher signatures for each food source define the range of potential contributions of these sources.

Another limitation of mixing models is that they cannot incorporate variations in the trophic enrichment factor (TEF) within food sources (i.e. variations in the separation of prey from consumer via their $\delta^{15}N$ values). To try to account for this, Bayesian mixing models have been proposed (Parnell *et al*., 2013). These models attempt to adjust the probability of the relative contribution of different food items to a consumer using prior information (e.g. from the literature) about isotopic values of food sources or consumers (Parnell *et al*., 2013; Layman *et al*., 2012).

In this thesis, stable isotope analysis is used to look at trophic interactions in the pelagic food webs particularly those at the base of the food web in East African lakes (e.g. Naivasha, Baringo, Bogoria and Sonachi). The difficulties in sampling and sample preparation of diverse plankton for SIA may have led to oversimplification of lower trophic levels of the food web in many studies (e.g. Burian *et al*., 2014) particularly in the tropics (Hart,1998).

1.7 Introduction of the East African Lakes (Naivasha, Baringo, Bogoria and Sonachi)

In this study, four contrasting East African Lakes (Naivasha, Baringo, Bogoria and Sonachi) were investigated. These lakes were selected because they are good model systems for exploring the ecological role of tropical zooplankton in tropical lakes. East African lakes range in size and have highly varied water chemistries (saline to freshwater) (Odada and Olago, 2006). As such, they show considerable differences in zooplankton and phytoplankton composition (Green, 1993; Schagerl, 2016). The aquatic food webs in these lakes range in complexity from relatively simple systems in the most saline lakes (Harper *et al*., 2003; Sanders, 2016) to more complex and diverse ones in the freshwater lakes (Omondi *et al*., 2017). Historically, the saline Lake Bogoria has been dominated by the cyanobacterium *Arthrospira* sp. and the rotifer *Brachionious* sp. (Vareschi and

Jacobs, 1985; Harper *et al.*, 2003). The saline Lake Sonachi has been primarily dominated by the rotifer *Brachionus dimidiatus*, the calanoid *Paradiaptomus africanus* (De Beauchamp, 1932; Beadle, 1932; Lowndes, 1936), the cyanobacterium *Synechococcus bacillaris* and *Arthrospira fusiformis* (Melack, 1981; Verschuren *et al.*, 1999; Ballot *et al.*, 2005; Robinson, 2015). Analyse of a range of lake characteristics allows different abiotic factors (e.g. salinity, altitude, lake size) to be investigated. Furthermore, saline lakes such as Lake Bogoria and Lake Sonachi are sometimes eutrophic and are characterised by high abundances of phytoplankton. This may reduce the effects of seasonal changes in food abundance on zooplankton dynamics (Burian, 2016). In addition, these lakes have different catchment characteristics that can affect their ecosystems. For example, Lake Baringo receives much higher loads of suspended sediment than Lake Naivasha (Hickley *et al.*, 2004). This is mainly due to soil erosion from the catchment (Johansson and Svensson, 2002; Eric *et al.*, 2006), trigged by unstructured soils and probably exacerbated by more intensive grazing and deforestation (Johansson and Svensson, 2002; Hickley *et al.*, 2004). Lake Baringo also has a larger catchment area (8655 km^2) than Lake Naivasha (3267 km^2) (Hickley *et al.*, 2004; Kallqvist, 1987), which promotes higher loads of allochthonous particles into this lake (Snelder and Bryan, 1995). This is likely to affect lake ecology and, specifically, the role of zooplankton.

1.8 The relative importance of the planktonic component of the food web in shallow lakes (Naivasha, Baringo, Bogoria and Sonachi).

East African Lakes are important habitats for dense populations of birds (Ward, 2015). For example, Lakes Bogoria and Sonachi are an important habitat for lesser flamingos (*Phoeniconaias minor*: Krienitz *et al*., 2003; Krienitz *et al*., 2010; Robinson, 2015), which are largely dependent on the pelagic planktonic cyanobacterium *Arthrospira* sp. (Vareschi, 1978; Burian *et al*., 2013; Krienitz *et al.*, 2013). However, during shortages of planktonic resources (e.g. *Arthrospira* sp.), lesser flamingos can feed on benthic and littoral diatoms as an alternative food item (Tuite, 2000; Robinson, 2015). Lakes Naivasha and Baringo are both relatively shallow and support fisheries (e.g. tilapia: Britton and Harper, 2008), which contribute food and income for local communities (Odada *et al*., 2006; Omondi *et al*., 2017). Plankton in the pelagic zone are important

food for many fish (Mavuti, 1990; Britton *et al*., 2007). For example, Britton *et al.* (2009) found that tilapia (*Oreochromis niloticus baringoensis*) was dependent on planktonic basal resources in Lake Baringo. Similarly, in Lake Naivasha, zooplankton have been documented as important dietary items for fish (e.g. *Barbus* sp. and *Oreochromis* sp.) (Muchiri, 1990; Otieno *et al*., 2014). In Lake Baringo, *O. niloticus* (which comprises about 80 % of the fish community in this lake: Aloo, 2002), largely feeds on pelagic zone plankton (Omondi *et al*., 2013). However, fish communities in Lakes Naivasha and Baringo also rely on littoral and benthic resources. For example, benthic invertebrates such as oligochaetes, chironomids and small crayfish are known to be utilised by carp in Lake Naivasha (Britton *et al*., 2007). Similarly, Omondi *et al*. (2013) found that *Protopterus aethiopicus* in Lake Baringo was largely dependent on molluscs in the benthic zone.

In addition to the importance of pelagic and benthic habitats to fish in shallow lakes, the littoral zones are also important for fish feeding and breeding (Omondi *et al*. 2016). Hickley *et al*. (1993) found that the largemouth black bass (*Micropterus salmoides*) tends to prey on free-living animals in the littoral zone of Lake Naivasha. Differences in the relative importance of pelagic plankton compared to littoral or benthic resources in different lakes are, to some extent, governed by differences in the feeding habits of the fish. For example, planktivorous fish (e.g. the tilapia *O. niloticus*) is likely to rely more heavily on pelagic plankton than benthic feeders such *Protopterus aethiopicus* (Omondi *et al*., 2013).

The importance of plankton relative to benthic resources is likely to be different in shallow and deeper lakes. For example, in Lake Malawi (maximum depth: 785 m), stable isotope analysis showed that 17 of 20 fish species were largely dependent on benthic resources, while only 3 fish taxa had pelagic dominated diets (Bootsma *et al*., 1996). Such differences may be due to differences between fish in feeding habits (as explained above) or due to the fact that the benthic habitats of deeper lakes appear to support more diverse and complex biological communities than in pelagic zones (Hecky and Hesslein, 1995; Schindler and Scheuerell, 2002).

1.9 Key knowledge gaps about the role of zooplankton in pelagic food webs.

Information about the trophic interactions between zooplankton and Cyanobacteria is inconclusive and the literature contains contradictory findings about these interactions (Wilson *et al.,* 2006; Ger *et al.,* 2014). Furthermore, most studies on the trophic links between zooplankton and Cyanobacteria are based upon empirical studies from temperate regions. Such studies are rare in the tropics (Hart, 1998; Leitão *et al*., 2018). In addition, there are a number of studies of trophic interactions between Cladocera and Cyanobacteria, but relatively few on trophic interactions between Cyanobacteria and Copepoda (Ger *et al.,* 2011). More studies, therefore, are needed to examine trophic interactions between Cyanobacterial taxa and copepods particularly in tropical regions (Kâ *et al.,* 2012).

Relatively little is known specifically about the role of zooplankton in pelagic food webs in tropical saline lakes, particularly the potential for dietary competition between zooplankton and the lesser flamingo in these systems. In addition, many tropical saline lakes across Africa have shown periodic appearances of freshwater Cladocera (Frey, 1993). To the author's knowledge, no studies that examined the role of these organisms in these lakes.

Although the relative importance of allochthonous and autochthonous resources to the diet of zooplankton in temperate lakes is well understood, significant knowledge gaps remain in tropical systems (e.g. Cole *et al*., 2011; Galloway *et al*., 2014; Taipale *et al*., 2016 a). These are important because they can help to understand mechanism which are responsible for changes in the relative importance of allochthonous and autochthonous carbon to zooplankton in tropical lakes.

In these East African lakes, such information could help to develop better management strategies and assist in restoring key ecosystem services provided by zooplankton, such as support to fisheries, control of cyanobacterial blooms or restoration of services provided by terrestrial resources delivered from the lake catchment, which can support food web components in lakes.

1.10 Aim

The principal aim of this thesis was to improve our understanding of the role of zooplankton in the pelagic food webs of tropical lakes. Specifically, the thesis addresses

three main questions: (1) What are the trophic interactions between zooplankton and Cyanobacteria?; (2) Is there potential competition between zooplankton and the lesser flamingo? and (3) What is the relative importance of allochthonous and autochthonous carbon sources for aquatic consumers (particularly zooplankton)? These questions were addressed by investigating the composition and structure of the pelagic food webs in four contrasting East African lakes (Naivasha, Baringo, Bogoria and Sonachi) over two sampling campaigns conducted in different seasons. This involved sampling and subsequent detailed analysis of the taxa present and their relationships with one another, primarily established using SIA, supplemented by C/N ratios. Each question was answered by focussing on a single lake or via comparison between lakes as detailed below:

1.10.1 Lake Sonachi

Aim: To examine the feeding preference of calanoids in a saline lake and to specifically determine the relative contribution of different Cyanobacterial taxa (*Synechococcus* sp. and *Microcystis* sp.) to the calanoid diet.

Objectives:

- Elucidate the relative abundance of different zooplankton and phytoplankton taxa.
- Determine the fractional contribution of potential food item to the diet of the zooplankton.

1.10.2 Lake Bogoria

Aim: To examine the potential competition between zooplankton and the lesser flamingo in a saline lake.

Objectives:

- Elucidate the relative abundance of different zooplankton and phytoplankton taxa.
- Reconstruct the food web structure via stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) for each taxon.

- Determine the fractional contribution of different food items to the diet of zooplankton using a simple mixing model, with a focus on establishing (and explaining) differences between the wet and dry seasons.

1.10.3 Lake Naivasha and Lake Baringo

Aim: To determine the relative importance of allochthonous and autochthonous carbon sources to aquatic consumers (particularly zooplankton and fish) in tropical freshwater lakes. It was hypothesised that zooplankton and fish in the more turbid Lake Baringo would have a higher dependence on allochthonous carbon sources compared to those sampled from the less turbid Lake Naivasha.

Objectives:

- Elucidate the relative abundance of different zooplankton and phytoplankton taxa in Lakes Naivasha and Baringo.
- Identify and separate the major carbon pools (e.g. phytoplankton, POM, terrestrial and littoral aquatic plant leaves and periphyton) which could act as food resources for zooplankton.
- Reconstruct the food web of each lake via stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) of each separate material or taxon, supplemented with an analysis of the C/N ratios for these food web components.
- Determine the fractional contribution of different food items to the diet of the principal zooplankton and fish taxa present using a simple mixing model.

CHAPTER TWO: METHODS

2.1 Lakes of the East African Rift Valley

The Great Rift Valley system is split into two branches (Figure 2.1), both of which form the East African Rift System (Ward, 2015). The Eastern branch divides Kenya from north to south (Ward, 2015). A chain of lakes runs through three countries (Ethiopia, Kenya and Tanzania) incorporating the Eastern branch (Yuretich, 1982). These lakes were formed by volcanic and tectonic activities during the formation of the Rift Valley (Odada and Olago, 2006).

All field sampling campaigns were conducted in four lakes of the East African Rift Valley (Lakes Naivasha, Baringo, Bogoria and Sonachi). The locations and satellite images of these lakes are shown in Figure 2.2.

The East African Rift Valley lakes are generally shallow (Odada and Olago, 2006), and range in salinity from freshwater dominated systems such as Lake Naivasha and Lake Baringo, to hypersaline systems, such as Lakes Bogoria, Sonachi, Nakuru, Elementeita, Oloidien, Natron, Magadi and Logipi (Odada and Olago, 2006; Ward, 2015).

The lakes vary markedly in their ecology and hydrology, ranging in depth from just 15 cm in some parts of Lake Natron to more than 16 m in the deepest parts of Lake Bogoria (Robinson, 2015). The deeper saline lakes (e.g. Lake Bogoria) are characterised by high electrical conductivities, which range between 25,000 and 77,000 µS cm^{-1} (Harper *et al*., 2003). In contrast, the conductivity of surface water in shallow saline lakes (e.g. Lake Natron) ranges between 6000-160,000 µS cm^{-1} (Robinson, 2015).

All these lakes have experienced fluctuations in water levels and ecological condition in the last hundred years (Verschuren, 2001).The main factor that affects the hydrological budget of all the East African lakes is rainfall (Ward, 2015; Gebrechorkos *et al*., 2019), which has contributed to flood and drought events (Barros and Field, 2014; Tierney *et al*., 2015). Climate diagrams for the study lake systems are shown in Figures (2.3 and 2.4). Clearly, there is a prononced seasonality in rainfall, whilst, temperature remains relatively constant over the year. The total rainfall in Kenya is a result of the movement of the inter-tropical convergence zone (Rao *et al*., 2011; Ward, 2015). Typically all the study lakes have two rainy seasons: a long one between April and August and a shorter one between October and November (Odada *et al.*, 2006; Jirsa *et al*., 2013; Omondi *et*

al., 2017). However, the climate of East Africa is characterised by erratic rainfall (Odada *et al.*, 2006; Rao *et al*., 2011).

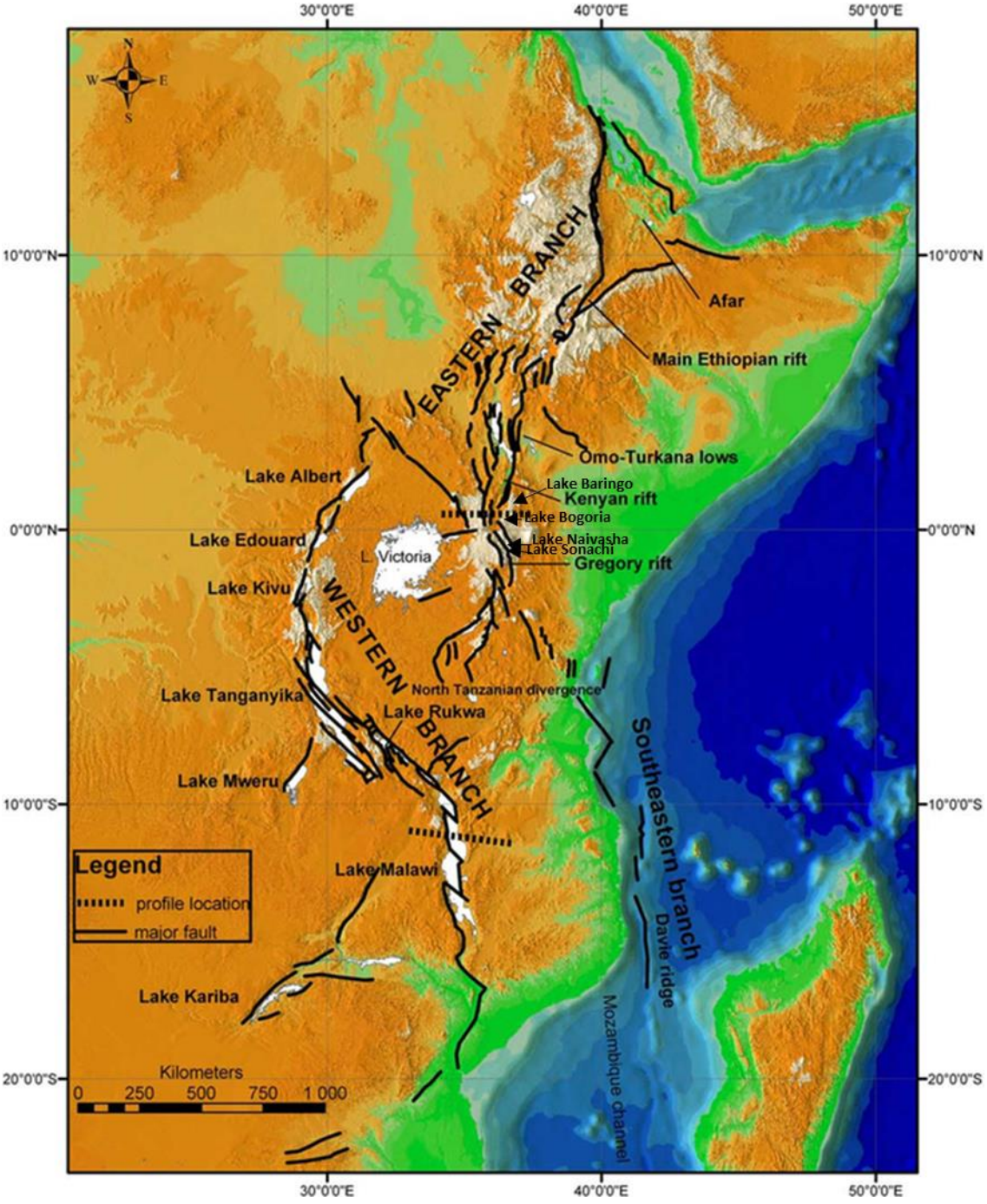

Figure 2.1 Map of the East African Rift system, modified from (Source: http://structuralgeologyof.weebly.com/extensional/the-east-african-rift-system.

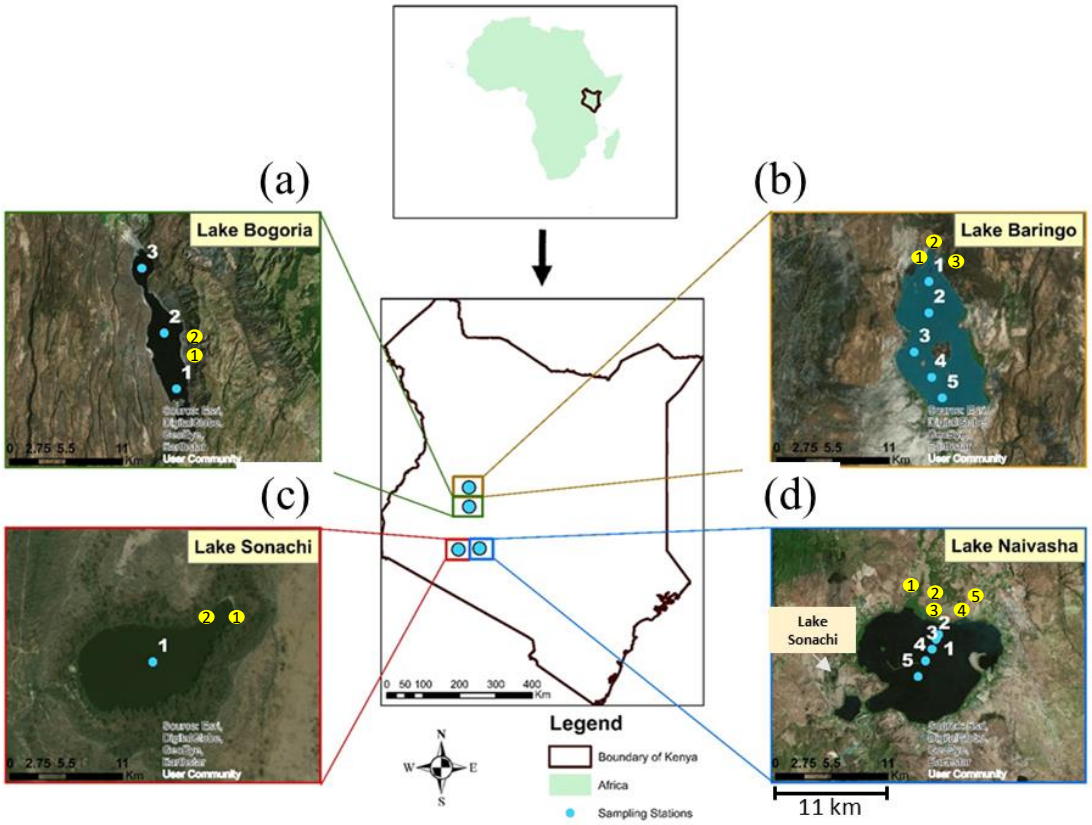

Figure 2.2 Map showing Africa and Kenya and the pelagic sampling stations for Lake Naivasha (1, 2, 3, 4 and 5), Lake Baringo (1, 2 , 3, 4 and 5), Lake Bogoria (1, 2 and 3) and Lake Sonachi (1), and the approximate locations of littoral and terrestrial samples (yellow circles). Source: Esri, DgitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USGS, AeroGRID,IGN, and the GIS User Community.

Samples and physico-chemical data in this study were collected in two field campaigns:

(1) between 15/11/2016 and 24/11/2016 for Lake Naivasha and Lake Sonachi, and for Lake Baringo and Lake Bogoria between 01/12/2016 and 06/12/2016. Samples were collected later from lakes Bogoria and Baringo due to heavy rain in November 2016, which made access unsafe.

(2) between 01/03/ 2018 and 20/03/ 2018 from all four lakes.

These date ranges were chosen to be approximately representative of the wet and dry seasons, respectively and, therefore, to capture seasonal influences on lake condition and ecosystem state.

Lake Naivasha and Lake Sonachi are close togather (ca. 3 km), and thus have the same general climate. Similarly, Lake Baringo and Lake Bogoria are relatively close together (~24 km) and can be regarded as climatologically similar.

These lakes were selected because they are good model systems with which to explore the role of zooplankton in tropical lake pelagic food webs in general and because they allow us to address the specific knowledge gaps outlined in Chapter 1. They vary significantly in their important ecological characteristics, allowing different questions to be addressed (Table 2.1). For more details see Chapter 1).

Table 2.1 Differences in the key ecological characteristics of the sampled East African Lakes (Naivasha, Baringo, Bogoria and Sonachi). Data from Beadle, 1932; Melack, 1981; Tiercelin *et al*., 1987; Njuguna, 1988; Uku and Mavuti, 1994; Verschuren, 1996; Verschuren *et al*., 1999; Schagerl and Oduor, 2003; Harper *et al*., 2003; Harper and Mavuti, 2004; Ballot *et al*., 2005; Omondi *et al*., 2015; Sanders, 2016; Stoof-Leichsenring *et al*., 2012; Omondi *et al*., 2017.

Characteristics	**Saline Lake Sonachi**	**Saline Lake Bogoria**	**Freshwater Lake Naivasha**	**Freshwater Lake Baringo**
Surface electrical conductivity	3,000 to 14,940 μScm^{-1}	25,000 to 77,000 $\mu S\ cm^{-1}$	250 to 400 $\mu S\ cm^{-1}$	578 $\mu S\ cm^{-1}$
Catchment area	1 km^2	930 km^2	3267 km^2	8655 km^2
Complexity of food web	Simple	Simple	Complex	Complex
Dominated zooplankton	Calanoids	Rotifers	Cladocera, Cyclopoids and Rotifera	Cladocera, Cyclopoids and Rotifera
Dominated phytoplankton	Cyanobacterium *Synechococcus* sp. and *Microcystis* sp.	Cyanobacterium *Arthrospira* sp.	Diatom *Aulacoseira* sp.	Green algae, diatoms and Cyanobacteria

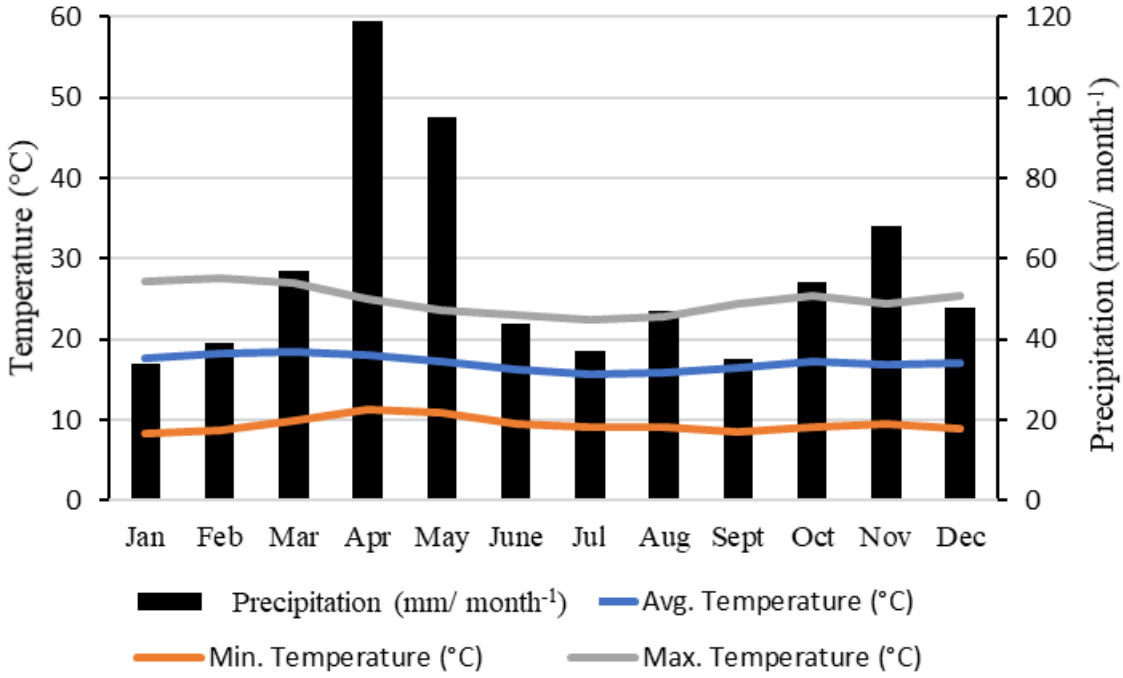

Figure 2.3 Annual precipitation (mm) and minimum, average and maximum temperature in Lake Naivasha (source: climate-data.org). Due to their proximity, these data are also relevant for Lake Sonachi.

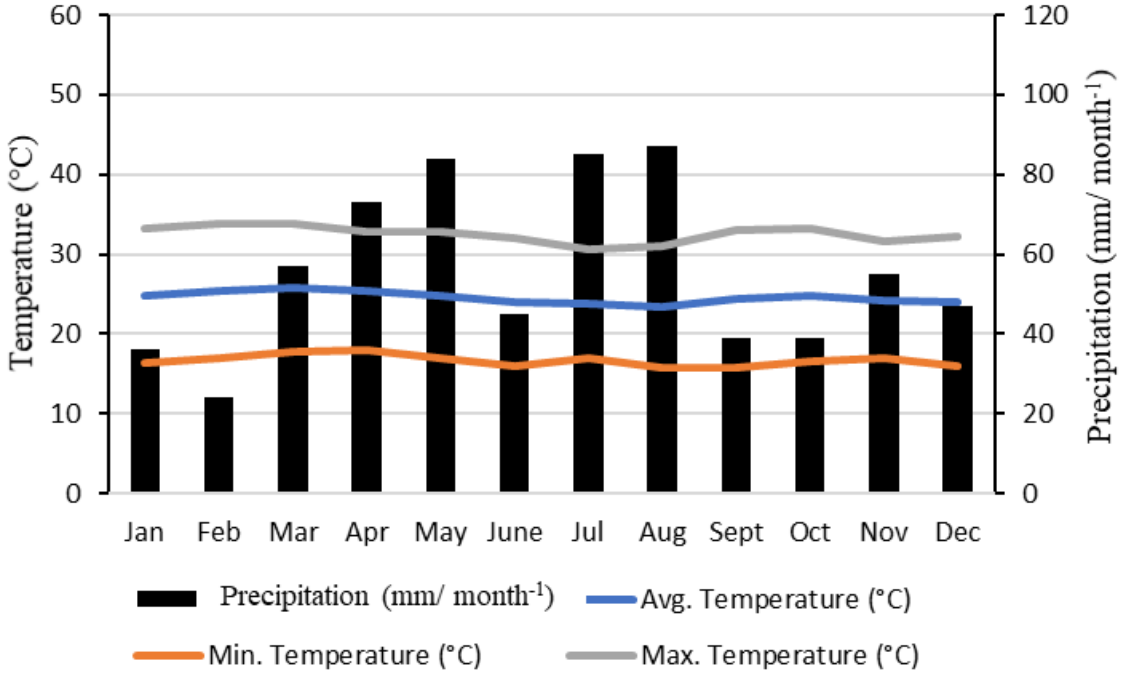

Figure 2.4 Annual precipitation (mm) and minimum, average and maximum temperature in Lake Baringo (source: climate-data.org). Due to their proximity, these data are also relevant for Lake Bogoria.

2.2 General description of methods

Terrestrial, littoral, benthic and pelagic carbon sources can all support consumers in aquatic food webs (Grey *et al*., 2001; Vander Zanden and Vadeboncoeur, 2002; De Kluijver *et al*., 2015). Therefore, a range of carbon sources from these habitats were collected to evaluate their relative contributions to pelagic zooplankton and other consumers of the pelagic food webs. Samples of zooplankton, phytoplankton, birds, fish, fractions of particulate organic matter (POM), dissolved organic matter (DOM), soil, sediments, terrestrial and littoral aquatic plant leaves and periphyton derived from aquatic plants were collected, identified, enumerated (Table 2.2, See sections 2.3 and 2.4 for details). All were subject to stable isotope and C/N ratio anayses. Body sizes of zooplankton and phytoplankton were measured. Chlorophyll a was also measured (Table 2.3).

In all cases, pelagic samples were collected from a boat. In Lake Bogoria (See Figure 2.2, a) samples were collected from three stations that approximately cover the length of the lake. In Lakes Baringo and Naivasha (See Figure 2.2,b and d, respectively), samples were collected from five stations. Again, these were selected so as to be approximately representative of the lake area. However, in Lake Naivasha (See Figure 2.2), sample locations did not cover the whole length of the lake due to poor weather conditions at time of sampling. In Lake Sonachi, samples were collected from only one station in the centre, due to the small size of this lake (See Figure 2.2, c).

Inputs of allochthonous OM from rivers could have systematically influenced the data collected at specific locations in all the lakes sampled, except Lake Sonachi (because it does not have river inflows). Stable isotope anlayses were therefore only performed on samples from one locale (the central pelagic zone), which was assumed to be most representative of the whole system. This assumption was underpinned by the fact that the central station had physical and chemical parameters which were approximately equal to the mean values at other stations (Appendices 2.1, 2.2, 2.3, 2.4, 2.5 and 2.6). The composition of the plankton communities at the central station were also approximately representative of the communities at the other stations (Appendices, 2.7, 2.8, 2.9, 2.10, 2.11 and 2.12).

Samples of zooplankton, phytoplankton and POM fractions were collected in both sampling campaigns from all four lakes. Other samples (lesser flamingo feathers from

Lake Bogoria, fish samples from Lake Naivasha and Lake Baringo), DOM, soil, sediment, terrestrial and aquatic plant leaves and periphyton were collected during the first sampling campaign in 2016, but were not collected in the 2018 campaign for logistical reasons (limited time and resources for sampling).

Table 2.2 Data collected from the four lakes during the two sampling campaigns, along with sampling times.

Data type	Day time/Year	Lakes
Zooplankton	8 a.m.-1 p.m./ 2016 and 2018	Naivasha, Baringo, Bogoria and Sonachi
Phytoplankton	8 a.m.-1 p.m./ 2016 and 2018	Naivasha, Baringo, Bogoria and Sonachi
Bird feathers	8 a.m.-1 p.m./ 2016	Bogoria
Fish	8 a.m.-1 p.m./ 2016	Naivasha and Baringo
Benthic invertebrates	8 a.m.-1 p.m./ 2016	Naivasha
POM (0.7-25 μm)	8 a.m.-1 p.m./ 2016	Naivasha, Baringo, Bogoria and Sonachi
POM (0.7-2 μm)	8 a.m.-1 p.m./ 2018	Naivasha, Bogoria and Sonachi
POM (2-20 μm)	8 a.m.-1 p.m./2018	Naivasha, Baringo, Bogoria and Sonachi
POM (20-48 μm)	8 a.m.-1 p.m./2018	Naivasha, Baringo, Bogoria and Sonachi
(48 μm < POM)	8 a.m.-1 p.m./2018	Baringo
Dissolved organic matter (DOM)	8 a.m.-1 p.m./ 2016	Naivasha, Baringo, Bogoria and Sonachi
Sediment	8 a.m.-1 p.m./ 2016	Naivasha, Baringo, Bogoria and Sonachi
Soil	8 a.m.-1 p.m./ 2016	Naivasha, Bogoria and Sonachi
Terrestrial plant leaves	8 a.m.-1 p.m. 2016	Naivasha, Baringo, Bogoria and Sonachi
Aquatic plants	8 a.m.-1 p.m. 2016	Naivasha and Baringo
Periphyton	8 a.m.-1 p.m. 2016	Naivasha and Baringo

Table 2.3 Physical and chemical variables measured in the four lakes during the two sampling campaigns, along with sampling times.

Variables	Time of measurement	Lakes
pH	8 a.m.-1 p.m. (2016 and 2018)	Naivasha, Baringo, Bogoria and Sonachi
Dissolved oxygen (DO)	8 a.m.-1 p.m. (2016 and 2018)	Naivasha, Baringo, Bogoria and Sonachi
Biological oxygen demand (BOD)	In the lab (2016 only)	Baringo, Bogoria and Sonachi
Water temperature	8 a.m.-1 p.m. (2016 and 2018)	Naivasha, Baringo, Bogoria and Sonachi
Water conductivity	8 a.m.-1 p.m. (2016 and 2018)	Naivasha, Baringo, Bogoria and Sonachi
Secchi depth	8 a.m.-1 p.m. (2016 and 2018)	Naivasha, Baringo and Bogoria
Depth	8 a.m.-1 p.m. (2016 and 2018	Naivasha, Baringo, Bogoria and Sonachi
Total Alkalinity	In the lab (2016 only)	Naivasha, Baringo, Bogoria

2.3 Sample collection and preparation of major aquatic food web components for stable isotope analysis

2.3.1 Zooplankton and phytoplankton

Plankton samples were collected 10 cm below the water surface from the central pelagic zone of each lake using haul nets with meshes of 150 and 80 μm for zooplankton and phytoplankton, respectively. The nets were washed after each sampling to avoid contamination of collected samples from previous tows, and to prevent clogging (Goswami *et al.,* 2004).

Zooplankton were preserved in 50% ethanol for isotopic analysis. All these ethanol-preserved samples were kept at 4 °C immediately after returning to the camp equipped with a refrigerator and a freezer. Except during transit back to the UK, when samples were kept in an insulated cool box containing frozen blocks, samples were kept at 4 °C. Previous work has shown that ethanol has no significant effect on the stable isotope ratios of zooplankton and phytoplankton (Feuchtmayr and Grey, 2003; Francis *et al.,* 2011; Montoya and McCarthy, 1995; Carabel *et al.,* 2009).

Zooplankton and phytoplankton were hand-picked from samples using a fine glass pipette under a dissecting microscope. In the first sampling campaign, no preservation was used for phytoplankton samples. The samples were separated into their taxa at the lab in Kenya. In the second sampling campaign, phytoplankton samples were preserved in 50% ethanol and separated later. This was due to logistical issues, which hindered on-site separation of phytoplankton as in the second camapign. Instead, samples were separated after samples had been transported back to the lab at the University of Leicester. Zooplankton were separated into their main groups (Cyclopoida, Cladocera, Rotifera and Calanoida) in sufficient numbers of individuals for isotopic analysis. Phytoplankton samples from Lake Bogoria and Lake Sonachi were separated to different taxa for stable isotope analysis, while the phytoplankton samples for stable isotope analysis in Lakes Naivasha and Baringo were prepared in bulk. The isolated samples were then rinsed with deionised water. Purity was checked by examining subsamples under a Nikon-DS-Fi2 microscope. The separated samples of zooplankton (from the two sampling campaigns) and the separated samples of phytoplankton (from the second sampling campaign) were then freeze-dried (approximately 18 hours). The separated samples of phytoplankton from the first sampling campaign were dried at 60 °C for 24 hours in an oven and stored in labelled vials prior to isotopic analysis.

Subsamples of isolated phytoplankton (*Microcystis* sp. from Lake Sonachi, *Arthrospira* sp. from Lake Bogoria and bulk phytoplankton from Lake Naivasha) were acidified with HCl (10%) (drop-by-drop) for $\delta^{13}C$ analysis. These acidified samples were rinsed and then dried. Samples of phytoplankton (*Cyclotella* sp. from Lake Bogoria and bulk phytoplankton from Lake Baringo) were not acidified and were only rinsed and dried, due to the low quantities available, which precluded the possibility of having both acidified and non-acidified aliquots. Then, all samples were ground using an agate mortar and pestle.

Acidification is an important step for removing dissolved inorganic carbon from samples. This is especially important when mechanical removal of carbonate is impossible (Schlacher and Connolly, 2014), such as is the case for sediments (Fernandes and Krull, 2008) and POM (Lorrain *et al*, 2003), as well as plankton (zooplankton and phytoplankton) rich in carbonate and crustaceans with a calcareous structure (Jacob *et al*., 2005; Carabel *et al*., 2006). Inorganic carbon often reflects the isotopic signature of the surrounding environment rather than assimilated organic carbon in plant and animal

tissues. It therefore introduces bias into $\delta^{13}C$ values (Yokoyama *et al*., 2005; Schlacher and Connolly, 2014). Acidification can also lead to bias in $\delta^{13}C$ and $\delta^{15}N$ signatures, for example by modifying the chemical composition of samples (Fernandes and Krull, 2008: Brodie *et al.*, 2011; Schlacher and Connolly, 2014). However, if acidification is necessary for carbon isotope samples, $\delta^{13}C$ signatures should be obtained from acidified samples, while $\delta^{15}N$ values should be obtained from unacidified samples (Schlacher and Connolly, 2014). Parallel acidified and unacidified samples were, therefore, prepared and analysed (when quantities allowed) to recognise the effect of acidification on isotopic signatures of samples. Acidified samples were rinsed and dried at 60°C to remove HCl (Jaschinski *et al.*, 2008).

The difference in $\delta^{13}C$ and $\delta^{15}N$ values before and after acidification was examined in some zooplankton samples and in POM fractions (Table 2.4). A t-test showed that there was no significant difference between $\delta^{13}C$ signatures between acidified and non-acidified for the calanoid *Lovenula* sp. from Lake Sonachi in November in 2016 (Table 2.4, Appendix 2.13 and Appendix 3.3). However, there was a significant difference in $\delta^{15}N$ signature between acidified and non-acidified samples of *Lovenula* sp. (Table 2.4, Appendix 2.14 and Appendix 3.3). A t-test showed that there was a significant difference in both the $\delta^{13}C$ and $\delta^{15}N$ signatures between acidified and non-acidified samples for the cladoceran *Moina* sp. sampled from Lake Bogoria in December in 2016 (Appendices 2.15, 2.16 and 4.9). However, t differences were relatively small (e.g. <1‰ for $\delta^{13}C$ and~ 1‰ for $\delta^{15}N$). Therefore, the $\delta^{13}C$ and $\delta^{15}N$ signatures of acidified *Moina* sp. and *Lovenula* sp. were not used (see Appendix 3.3 and Appendix 4.9).

Table 2.4 p values for two tailed t-tests for the differences between $\delta^{13}C$ and $\delta^{15}N$ in acidified and nonacidified samples in different lakes. Values of $p < 0.05$ are sequential at the 95% confidence level. N/A= not determined.

	Lake Sonachi		Lake Bogoria		Lake Naivasha		Lake Baringo	
	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
Lovenula sp.	0.41	0.02	N/A	N/A	N/A	N/A	N/A	N/A
Moina sp.	N/A	N/A	0.005	0.02	N/A	N/A	N/A	N/A
POM 0.7-25 μm	0.01	N/A	0.0001	N/A	0.71	N/A	0.10	N/A
POM 0.7-2 μm	0.0001	N/A	0.0001	N/A	N/A	N/A	N/A	N/A
POM 2-20 μm	N/A	N/A	0.0003	N/A	0.0001	N/A	N/A	N/A
POM 20-48 μm	N/A	N/A	0.09	N/A	0.0008	N/A	N/A	N/A
48 μm < POM	N/A	N/A	N/A	N/A	N/A	N/A	0.02	N/A

Comparisons were made between $\delta^{13}C$ of acidified and non-acidified POM samples for different lakes (Table 2.4, Appendices 2.17, 2.18, 3.3, 2.19, 2.20, 2.21, 2.22, 4.9, 2.23, 2.24, 5.23, 2.25, 2.26, 2.27 and 5.24). The differences between acidified and non-acidified POM fractions in many cases were high and statistically significant (e.g. between 10 and 12 ‰ for $\delta^{13}C$). Therefore, the $\delta^{13}C$ signatures of acidified POM were reported in this study.

2.3.2 Bird Feathers

Freshly-shed feather samples of lesser flamingo (*Phoeniconaias minor*) (three replicates) were collected from the shore of the middle basin of Lake Bogoria in December 2016. These feathers were collected to the understand dietary record of these birds using stable isotope analysis. Flamingos replace their feathers approximately annually (Shannon, 2000). During feather growth, carbon and nitrogen isotopes are assimilated and integrated into the structure of the feather's keratin. Therefore, feathers represent a fixed record of the animal's diet during the period of growth (Kelly *et al*., 1998). Samples were rinsed with deionised water and freeze-dried for 24 hours. The feather samples were ground to a fine powder using a ball mill. The powder samples were stored in labelled vials in a desiccator prior to analysis.

The isotopic signature of feathers could differ from that of muscle tissue because the latter has a relatively high turnover rate (due to relatively high metabolic rate). Muscle could, therefore, reflect the isotopic signature of relatively recently assimilated food, whereas feathers probably reflect the diet of animals over the longer term (Hobson and Clark, 1992; Knoff *et al*., 2001). Although muscle tissue would, therefore, probably be more appropriate than feathers for the interpretation isotope data from plankton, it is much more difficult to sample and process. In any case, linking the isotopic signatures of feather samples to those in the planktonic food web has been done before (e.g. Sanders, 2016) and is considered to be a valid, if not ideal, comparison.

2.3.3 Fish

Common fish genera were purchased from fishermen near the shores of Lakes Naivasha and Baringo in November and December 2016, after sampling of the pelagic zone in each lake. Fish are not present in Lakes Bogoria and Sonachi. The fish samples were used to examine fish feeding and potential trophic interactions with phytoplankton, zooplankton and POM. The fish samples (three replicate of each genus- see Tables 2.5 and 2.6 for Lake Naivasha and Lake Baringo, respectively) were washed and sorted to genus level. The length and weight of each purchased fish was also measured (Tables 2.5 and 2.6 for Lake Naivasha and Lake Baringo, respectively). Muscle tissues of the fish were taken from all identified adults from behind the pectoral fin. The samples were rinsed with distilled water and dried at 60 °C (Britton *et al.*, 2007). The sampled tissues were ground using a ball mill and then put in labelled vials. All vials were kept in a desiccator in the lab.

Table 2.5 Taxon, length and weight of fish samples from Lake Naivasha during the first sampling campaign in November 2016.

Scientific names	Length (cm)	Weight (grams)
Cyprinus (1)	65	3500
Cyprinus (2)	34.5	500
Cyprinus (3)	36	580
Large *Oreochromis* (1)	33	480
Large *Oreochromis* (2)	31	530
Large *Oreochromis* (3)	34	610
Small *Oreochromis* (1)	21.5	200
Small *Oreochromis* (2)	23.5	225
Small *Oreochromis* (3)	22	175
Clarias (1)	42	500
Clarias (2)	59.5	1500
Clarias (3)	48.5	950

Table 2.6 Taxon, length and weight of fish samples from Lake Baringo during the first sampling campaign in December 2016.

Scientific names	Length (cm)	Weight (grams)
Heterobranchus (1)	52	800
Heterobranchus (2)	52	660
Heterobranchus (3)	48	460
Clarias (1)	25	125
Clarias (2)	40	780
Clarias (3)	42	78
Barbus (1)	23	88
Barbus (2)	22	78
Barbus (3)	24	101
Oreochromis (1)	7	69
Oreochromis (2)	8	85
Oreochromis (3)	7	63

2.3.4 Macroinvertebrates

An Ekman grab sampler was used to collect sediment samples from the centre of Lakes Naivasha and Baringo. The sediment samples were sieved through a 1 mm mesh in the lab. Macroinvertebrates were collected from the sediment using forceps and then put in filtered water for 24 hours for gut evacuation (Hershey *et al*., 2006), followed by drying at 60 °C for 24 hours in an oven and storage in labelled vials until isotopic analysis. The macroinvertebrate samples were used to examine potential trophic interactions with fish. Unfortunately, the sediment samples from Lake Baringo did not contain macroinvertebrates.

Crayfish (*Procambarus* sp.) were purchased from fishermen near the shore of Lake Naivasha in November 2016 after sampling of the pelagic zone in this lake. No crayfish were sampled from the other lakes. The collected samples of crayfish were washed and muscle tissues were taken from tails, after removing these from the exoskeleton. These were then dried in the oven for 24 hours (Hicks *et al.,* 1997) at 60 °C.

2.4 Sampling of major carbon pools

2.4.1 Fractions of particulate organic matter (POM)

In the wet season, water samples were collected for extraction of POM fractions on the same date as the samples were collected for zooplankton and phytoplankton, from all four

lakes. The 0.7<25 μm POM fraction was collected by passing a one litre water sample through a 25 μm sieve on the boat. The filtrate (<25 μm) was then passed through a pre-combusted and pre-weighed (450 °C) GF/F filter (0.7 μm). Filters were dried at 60 °C in an oven and stored inside vials and kept in desiccators.

In the dry season, different POM fractions (20-48 μm, 2-20 μm and 0.7-2 μm) were collected for stable isotope analysis to examine the importance of these as carbon sources to pelagic zooplankton. Changes were made to the POM size fractions investigated between sampling periods. This was based on an analysis of data from the 2016 campaign, which suggested that some zooplankton taxa (*Moina* sp. from Lake Bogoria and *Lovenula* sp. from Lake Sonachi) were mainly feeding on small phytoplankton. This highlighted the importance of smaller particulate carbon fractions for these zooplankton. Changing the POM size fractions measured was, therefore, intended to reveal specific details of the feeding preferences of different groups of zooplankton. Water samples were taken 10 cm below the water surface from the central pelagic zone of each lake and filtered through a 48 μm sieve. The <48 μm fraction, was size-fractionated in the lab using 2 and 20 μm nylon filters and a vacuum pump to obtain different POM size classes: (i) 20-48 μm, (ii) 2-20 μm and (iii) <2 μm. For the smallest size fraction (0.7-2μm) a pre-combusted GF/F filter (0.7μm) was employed.

Each nylon filter (20μm and 2μm) was rinsed separately in different beakers by spraying the filter with filtered water from the same lake using a squirt bottle. Contents of the different beakers for (20-48 μm and 2-20 μm) were also passed through pre-combusted GF/F filters (0.7μm) to retain different POM size classes (20-48 μm and 2-20 μm). All samples were dried at 60 °C for 24 hours in an oven (Burian *et al.,* 2014). The samples were put in labelled vials, which were stored in desiccators until isotopic analysis. Subsamples of POM fractions (crushed GF/F filters) for carbon isotope analysis were acidified with HCl (10%) (drop-by-drop), until no CO_2 bubbles were noticeable.

The (0.7-2 μm) POM fraction was not collected from Lake Baringo due to difficulty in filtering to this fractional size highly turbid lake water. Other fractions of particulate organic matter 2-20 μm and 20-48 μm were collected normally, as well as the < 48 μm POM.

2.4.2 Dissolved organic matter (DOM)

Water samples for dissolved organic matter (DOM) analysis were taken 10 cm below water surface from the central part of each lake. A 1 litre filtered sample (< 0.7 μm) was frozen and brought back to the UK in a cool box. DOM was collected from each sample using a rotating evaporator (Persaud and Dillon, 2011) and dried in an oven at 60 °C (Burian *et al.,* 2014). Subsamples of DOM for $\delta^{13}C$ analysis were acidified with HCl (10%) (drop-by-drop), until no bubbles were visible. Subsamples of DOM were kept without acidification for δ^{15} N measurement to avoid the effect of acidification on $\delta^{15}N$.

2.4.3 Sediments

An Ekman grab was used to collect triplicate samples of sediments from the centre of each lake. The upper 1cm of sediments were scraped off using a metal spatula (De Kluijver *et al.,* 2012) to remove undesirable particles. The samples were placed directly inside labelled glass jars (Chemoiwa *et al.,* 2015). Samples were then dried at 60 °C for 24 hours in an oven. These samples were used to measure $\delta^{15}N$. Subsamples were acidified with HCl (10%) (drop-by-drop) for $\delta^{13}C$ measurements. The acidified samples were rinsed, then dried and kept in labelled vials.

2.4.4 Soil

Samples of soil were collected from the catchment of each lake, excluding Lake Baringo. Soil samples from Lake Naivasha were collected near the Malewa and Gilgil rivers, while samples from Lakes Bogoria and Sonachi were collected from the catchment of both lakes at approximately the same locations as the terrestrial plant leaves samples were taken (Figure 2.2). Samples were collected with a trowel to about 2 cm depth excluding surface debris and dead leaves (Mortillaro *et al.,* 2011). Soil was dried at 60 °C for 48 hours in an oven prior to δ^{15} N measurement (Ponsard and Arditi, 2000). Subsamples of soil were acidified with HCl (10%) (drop-by-drop) for $\delta^{13}C$ analysis. These acidified samples were rinsed and then dried and stored in labelled vials until isotopic analysis.

2.4.5 Terrestrial and aquatic plant leaves and periphyton

Three replicate fresh leaves from each common terrestrial plant, were collected from the catchment of each lake at approximately the same locations as the soil samples were taken. Samples from Lakes Baringo, Bogoria and Sonachi were collected close to the lake shores, while from Lake Naivasha were collected close to the lake shore and near the Malewa and Gilgil rivers (see Appendix 5.24). Samples of leaves were sorted to genus

and species level. Samples were washed with distilled water, cut to threads and dried at 60 °C for 48 hours.

Samples of fresh leaves from each species of aquatic plant present in Lakes Naivasha and Baringo were collected from their littoral zones. No aquatic plants grow in the soda lakes. The fresh leaves were identified to species level. Samples were rinsed with distilled water and dried at 60 °C for 48 hours in an oven (De Kluijver *et al.*, 2015). Periphyton were collected from replicates of aquatic plants using a nylon brush and the samples were placed in trays which contained distilled water (De Kluijver *et al.*, 2015). All visible particles were removed, and samples were passed through a plastic sieve with a mesh size of 100 μm. The samples were then filtered through pre-combusted (4 hours at 450 °C) GF/F filters (0.7μm) (De Kluijver *et al.*, 2015). Samples then were dried at 60 °C for 48 hours. All samples of terrestrial and aquatic plants and periphyton were ground to a fine powder using a ball mill prior to analysis.

2.5 Chemical and physical parameters

In parallel with sampling plankton in each lake, various ecological variables were measured. Dissolved oxygen (DO) was measured *in situ* using a handheld DO probe (YSI instruments, Ohio, USA); pH, conductivity and temperature were also measured *in situ* using portable probes on the same instrument. Total alkalinity was measured using titration for water samples by phenolphthalein and bromocresol green indicators, in the laboratory (APHA, 2012). Water turbidity was measured using a Secchi disk. Water depth was measured using a weighed line. BOD_5 was measured according to APHA (1999). The following equation was used

$$BOD_5 = DO_1 - DO_2 \quad (1)$$

where DO_1 is the concentration of dissolved oxygen before incubation (mg/L), and DO_2 is the concentration of dissolved oxygen after incubation at 20 °C for five days in the dark (mg/L).

2.6 Density and classification of plankton

2.6.1 Zooplankton

Samples were taken 10 cm below the water surface of the pelagic zones, from three stations in Lake Bogoria, five stations in Lakes Naivasha and Lake Baringo and one

station in Lake Sonachi. Using several stations was intended to ensure collection of representative samples. All samples were preserved in the field in 70% ethanol and stored in labelled plastic bottles. Samples of pelagic zooplankton were collected using a plankton net haul with a mesh size of 150 μm. Zooplankton were examined and counted using a Sedgewick-Rafter counting chamber under a Nikon-DS-Fi2 microscope. The density of zooplankton was expressed as the number of individuals per litre. Identification was based on the standard keys of Fernando (2002) and Korinek (1999).

2.6.2 Phytoplankton

Phytoplankton samples were collected at the same time as sampling zooplankton using a plankton net haul with a mesh size of 80 μm. Samples were preserved in the field by adding a few drops of Lugol's solution. 45 mL of unfiltered lake water from the central station was preserved with formaldehyde (2 %: Pirlot *et al.,* 2005). Phytoplankton was examined and counted using a Sedgewick-Rafter counting chamber under a Nikon-DS-Fi2 microscope. The abundances of the most dominant phytoplankton taxa were expressed as numbers per litre. Identification was based on the standard keys of van Vuuren *et al.,* (2006) and John *et al*., (2011).

Zooplankton and phytoplankton were classified to genus level. The densities of zooplankton and phytoplankton were expressed according to (Edmondson and Winberg, 1971; Arimoro *et al.,* 2008; Omondi *et al.,* 2015)

$$P = N/V \quad (2)$$

where P is the density of plankton (L^{-1}), N is the number of individuals in the sample, V is the volume of water filtered = $\pi r^2 d$, where r is radius of mouth of net (15cm for zooplankton and 10 cm for phytoplankton), d is distance or length of tow.

2.7 Chlorophyll-a measurement

Water samples for chlorophyll-a were taken from the same depths and locations as the plankton samples collected in 2016. The spectrophotometric method described by Pechar (1987) was used in the local laboratory.

Each sample of lake water (known volume) was passed through a Whatman Glass fibre filter (GF/F) with a diameter of 45 mm. Filters were then put into labelled tubes wrapped in aluminium foil to avoid light penetration and kept frozen overnight. Next day, acetone/methanol (5:1) (volume: volume) was added. The samples were heated in a water

bath at 65 °C for two minutes. Hand centrifugation was applied for samples at approximately 500 rpm for 5 minutes. The supernatant was then transferred by pipette into a cuvette. Absorbance was measured on a spectrophotometer against an acetone/methanol (5:1) blank, at 664 and 750 nm before acidification. Samples were acidified and remeasured at 664 and 750 nm. The cuvette was washed with acetone/methanol (5:1) and left to dry before the next measurement.

Four replicates were collected from each of the five stations on Lake Naivasha and Lake Baringo, four replicates were collected from each of the three stations on Lake Bogoria, and eight replicates were collected from the single pelagic station on Lake Sonachi.
The chlorophyll-a concentration was calculated using the equation of Lorenzen (1967), taken from Vollenweider *et al.* (1974):

$$C = 11.9[2.43(D_b - D_a)].\frac{Ve}{Vf}.L \qquad (3)$$

where D_b is the absorbance before acidification, D_a is the absorbance after acidification, V_e is the volume of acetone/methanol (5:1) used for extraction (ml), L is the path length of cuvette (cm), V_f is the volume of filtered water (L), 11.9 is the absorption coefficient of chlorophyll-a, 2.43 is the factor used to equate the reduction in absorbance to initial chlorophyll concentration, and C is the chlorophyll-a concentration (μgL^{-1}).

2.8 Size measurements of plankton

For size measurements of individual taxa, a digital camera (Nikon-DS-Fi2) interfaced to a light microscope (Nikon-eclipse-Ci), was used. Measurements of length of various genera of zooplankton and phytoplankton were made with imaging software (Nis-Elements, D4.10.00, 64 bit). An average of approximately 20 individuals of plankton were used to calculate sizes.

2.9 Stable isotope analysis

$\delta^{13}C$ and $\delta^{15}N$ determinations were made in the Environmental Isotope laboratory at the University of Leicester. Samples were combusted at 1010 °C in the presence of oxygen in an Elemental Analyzer (SERCON ANCA GSL) coupled to a continuous-flow isotope

ratio mass spectrometer (SERCON Hydra 20-20 MS). Values of stable isotope ratios are expressed according to the following equation:

$$\boldsymbol{\delta^{13}C \text{ or } \delta^{15}N = \left[\left(R_{sample}/R_{standard}\right) - 1\right] \times 1000} \quad (4)$$

where R_{sample} is the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$, and $R_{standard}$ for ^{13}C is the international standard of Vienna Pee Dee Belemnite (VPDB), and $R_{standard}$ for ^{15}N is atmospheric nitrogen.

A minimum sample mass of 40 µg was used for nitrogen and 100 µg for carbon measurements. The system's detection limits for $\delta^{13}C$ and $\delta^{15}N$ were 12 µg and 7 µg for nitrogen and carbon respectively. The precision of the isotope measurements was 0.1 ‰ for $\delta^{13}C$ and 0.2 ‰ for $\delta^{15}N$. Molar C:N ratio data for each sample analysed were derived from the isotopic analysis data. The precision for C was 0.2 and for N was 0.03.

2.10 Data analyses

t-tests were used to assess if there were statistically significant differences between: (1) phytoplankton biomass (with chlorophyll-a as a proxy for standing stock) in Lakes Naivasha and Baringo in 2016; (2) the total zooplankton abundance in Lakes Baringo and Naivasha; (3) $\delta^{13}C$ and $\delta^{15}N$ signatures for acidified and non-acidified samples of zooplankton; (4) $\delta^{13}C$ signatures of acidified and non-acidified POM fractions.

For analyses and interpretations of the stable isotope data, trophic enrichments of 3.4 ± 1 ‰ for $\delta^{15}N$ and 0.4±1.3 ‰ for $\delta^{13}C$ between trophic levels were assumed (Post, 2002). The percentage of carbon assimilated by zooplankton was estimated using a two component mixing model (based on a simple mass balance equation) with putative carbon sources for pelagic zooplankton of (i) phytoplankton and (ii) bulk POM (see Grey *et al*., 2001). As such the model is of the form:

$$\delta^{13}C_{ZOO} = \delta^{13}C_{POM} \cdot Fr_{POM} + \delta^{13}C_{Phyto} \cdot Fr_{Phyto} \quad (5)$$

where $\delta^{13}C_{zoo,}$ $\delta^{13}C_{Phyto}$ and $\delta^{13}C_{POM}$ are the isotope signals of zooplankton, phytoplankton and POM, respectively, and Fr_{POM} and Fr_{Phyto} are the fractional contributions from POM and phytoplankton, respectively (assuming no isotope fractionation between food and

consumer). We have two unknowns (Fr $_{POM}$ and Fr $_{Phyto}$) but only one equation. However, we can assume

$$Fr_{POM} + Fr_{Phyto} = 1 \quad (6)$$

$$Fr_{Phyto} = 1 - Fr_{POM} \quad (7)$$

Substituting in (5), we get

$$\delta^{13}C_{ZOO} = \delta^{13}C_{POM} \cdot Fr_{POM} + \delta^{13}C_{Phyto} \cdot (1 - Fr_{POM}) \quad (8)$$

$$\delta^{13}C_{ZOO} = \delta^{13}C_{POM} \cdot Fr_{POM} + \delta^{13}C_{Phyto} - \delta^{13}C_{Phyto} \cdot Fr_{POM} \quad (9)$$

$$\delta^{13}C_{ZOO} - \delta^{13}C_{Phyto} = \delta^{13}C_{POM} \cdot Fr_{POM} - \delta^{13}C_{Phyto} \cdot Fr_{POM} \quad (10)$$

$$\delta^{13}C_{ZOO} - \delta^{13}C_{Phyto} = Fr_{POM} \cdot \left(\delta^{13}C_{POM} - \delta^{13}C_{Phyto}\right) \quad (11)$$

$$Fr_{POM} = \frac{\delta^{13}C_{ZOO} - \delta^{13}C_{Phyto}}{\delta^{13}C_{POM} - \delta^{13}C_{Phyto}} \quad (12)$$

We can also include an isotope fractionation (*F*) between food and consumer of 0.3 ‰ for δ^{13}C for invertebrates (McCutchan *et al*., 2003). This value is in line with value suggested by Grey *et al*. (2001) which was (0.43 ‰) for crustacean zooplankton.

$$Fr_{POM}\% = \frac{\left(\delta^{13}C_{ZOO} - F - \delta^{13}C_{Phyto}\right)}{\left(\delta^{13}C_{POM} - \delta^{13}C_{Phyto}\right)} \times 100 \quad (13)$$

This model (Equation 13) was used to quantify the relative importance of phytoplankton and POM to zooplankton diet in Lakes Sonachi, Naivasha and Baringo when δ^{13}C signatures of phytoplankton and POM were distinct from each other and the δ^{13}C value of the zooplankton fells between the δ^{13}C values of these two food sources.

The following model (Equation 14) was used to quantify the relative importance of phytoplankton (e.g. *Arthrospira* sp. and *Cyclotella* sp.) to zooplankton diet (e.g. the cladoceran *Moina* sp.) in Lake Bogoria. The δ^{13}C and δ^{15}N of these food sources and those of *Moina* sp. suggest they were the most important carbon sources to the cladoceran. These sources were, therefore, the only ones included in the model. The relative importance of these algal items to rotifers in this lake was not quantified since both the

$\delta^{13}C$ values of *Arthrospira* sp. and *Cyclotella* sp. were slightly lower than that of the rotifers. It was, therefore, not possible to apply a mixing model (which requires that the $\delta^{13}C$ values of food items straddle that for the putative consumer).

$$Fr_{Cyclo.}\% = \frac{\left(\delta^{13}C_{Moi.} - F - \delta^{13}C_{Arthro.}\right)}{\left(\delta^{13}C_{Cyclo.} - \delta^{13}C_{Arthro.}\right)} \times 100 \qquad (14)$$

where $\delta^{13}C_{Moi.,}$ $\delta^{13}C_{Arthro.}$ and $\delta^{13}C_{Cyclo.}$ are the isotope signals of *Moina* sp., *Arthrospira* sp. and *Cyclotella* sp., respectively, $Fr_{Cyclo.}$ is the fractional contribution from *Cyclotella* sp., and *F* represents the isotope fractionation between food sources and consumer. This is assumed to be 0.3 ‰ for $\delta^{13}C$ (after McCutchan *et al*., 2003).

The relative importance of autochthonous and allochthonous carbon to zooplankton was also assessed using a similar mixing model as follows:

$$Fr_{\text{Auto.}}\% = \frac{\left(\delta^{13}C_{Zoo} - F - \delta^{13}C_{Allo.}\right)}{\left(\delta^{13}C_{Auto.} - \delta^{13}C_{Allo.}\right)} \times 100 \qquad (15)$$

where $\delta^{13}C_{Zoo,}$ $\delta^{13}C_{Auto.}$ and $\delta^{13}C_{Allo.}$ are the isotope signals of zooplankton, autochthonous and allochthonous carbon, respectively, $Fr_{Auto.}$ is the fractional contribution from autochthonous carbon and *F* is an isotope fractionation factor. Again, this was assumed to be 0.3 ‰ for $\delta^{13}C$ (after McCutchan *et al*., 2003). The $\delta^{13}C$ values of phytoplankton were used to provide a better representation of the $\delta^{13}C$ signatures of autochthonous carbon in comparison with other sources (e.g. aquatic plants and periphyton) in the mixing model. The terrestrial plants were used in this model as one source (i.e. average foliar $\delta^{13}C$ was taken) to represent $\delta^{13}C$ signature of allochthonous carbon. The average $\delta^{13}C$ value of pelagic Cladocera and Cyclopoida (mixed) was used to better represent the $\delta^{13}C$ signatures of zooplankton. This allowed the relative importance of autochthonous and allochthonous carbon to zooplankton in both lakes (Baringo and Naivasha) to be estimated.

The relative importance of littoral resources and planktonic components of the food web to *Barbus* sp. was assessed using the following mixing model:

$$Fr_{\text{Plank.}}\% = \frac{\left(\delta^{13}C_{Bar.} - F - \delta^{13}C_{Litto.}\right)}{\left(\delta^{13}C_{Plank..} - \delta^{13}C_{Litto.}\right)} \times 100 \quad (16)$$

where $\delta^{13}C_{Bar.}$, $\delta^{13}C_{Plank.}$ and $\delta^{13}C_{Litto.}$ are the isotope signals of *Barbus* sp., planktonic components (pelagic Cladocera, pelagic mixed Cyclopoida, pelagic adult Cyclopoida, pelagic copepodites, pelagic nauplii and phytoplankton) and littoral resources (*E. crassipes* and periphyton), $Fr_{Plank.}$ is the fractional contribution from planktonic resources and *F* is an isotope fractionation factor between food sources and consumer. This was assumed to be 0.4 ‰ for $\delta^{13}C$ following Post (2002).

The following model (Equation 17) was used to quantify the relative importance of the pelagic zooplankton and benthic sources (sediment) to fish. Other carbon sources (e.g. periphyton and terrestrial plants) were not included in this model as the goal was to compare the relative importance of pelagic zooplankton and benthic carbon sources to fish. In the case of zooplankton, a mean $\delta^{13}C$ signature of mixed Cladocera and Cyclopoida was used here. This model was successfully applied to quantify these sources to fish (e.g. *Claris* sp. in Lake Baringo and *Cyprinus* sp. and *Clarias* sp. in Lake Naivasha). It should be noted that the contributions of these sources to some fish genera were not assessed here because either (i) the $\delta^{13}C$ values of the zooplankton and fish (e.g. *Oreochromis* sp. *Barbus* sp. and *Heterobranchus* sp.) were not sufficiently distinct from each other to allow relative contributions to be assessed or (ii) due to the fact that the $\delta^{13}C$ value of the fish did not fall between the $\delta^{13}C$ values of the two food sources (zooplankton and sediment) (Phillips, 2012; Layman *et al*., 2012). Otherwise, different fractionation factors are needed to make the model fit in this situation (i.e. to obtain positive values of source contribution) (Phillips, 2012).

$$Fr_{Zoo}\% = \frac{\left(\delta^{13}C_{Fish} - F - \delta^{13}C_{Sedi.}\right)}{\left(\delta^{13}C_{Zoo} - \delta^{13}C_{Sedi.}\right)} \times 100 \quad (17)$$

where $\delta^{13}C_{zoo}$ and $\delta^{13}C_{Sed.}$ are the isotope signals of zooplankton and sediment, respectively and Fr_{ZOO} is the fractional contribution from zooplankton and *F* is an isotope fractionation factor between food sources and consumer. This was assumed to be 0.4 ‰ for $\delta^{13}C$ following Post (2002).

The relative importance of autochthonous and allochthonous carbon to fish was assessed using the following mixing model:

$$Fr_{\text{Auto.}}\% = \frac{\left(\delta^{13}C_{Fish} - F - \delta^{13}C_{Allo.}\right)}{\left(\delta^{13}C_{Auto.} - \delta^{13}C_{Allo.}\right)} \times 100 \qquad (18)$$

Under the assumption that both autochthonous and allochthonous carbon sources can be potentially important carbon sources for fish, $\delta^{13}C$ values of phytoplankton were used to represent primary production (autochthonous C) in the pelagic zone and the average $\delta^{13}C$ signature for terrestrial plants were used to represent of allochthonous carbon. The average $\delta^{13}C$ of all fish types was assumed to represent the top consumers. This allowed the relative importance of autochthonous and allochthonous carbon to fish in both lakes (Baringo and Naivasha) to be estimated.

The C:N data were used to help disentangle the specific origin of POM in these lakes because the $\delta^{13}C$ values between terrestrial and littoral vegetation and phytoplankton sometimes overlap which can lead to difficulties in discriminating the origin of lake POM.

Resource polygons (Figure 2.5) have been defined using the trophic enrichment reported in the literature of $\delta^{15}N$ 3.4±1 ‰ and for $\delta^{13}C$ 0.4±1.3 ‰ (Post, 2002). These polygons were used to define trophic niches of zooplankton in Lake Sonachi (Chapter 3), Lake Bogoria (Chapter 4) and Lakes Baringo and Naivasha (Chapter 5) in the wet and dry seasons.

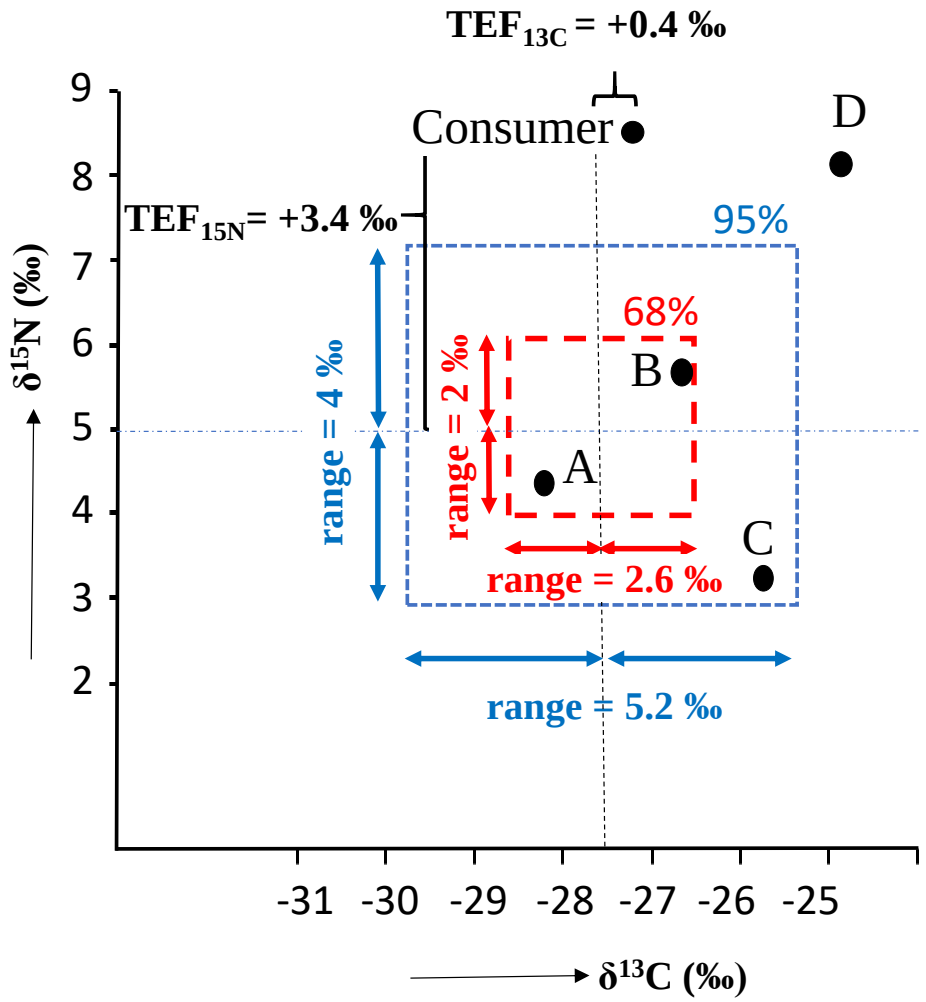

Figure 2.5 Schematic illustration of the isotopic resource polygon for a hypothetical consumer. The height and width of the resource polygon is defined using TEFs as reported by Post (2002). The mean trophic enrichment in $\delta^{15}N$ is 3.4 ‰ ± 1 ‰ and for $\delta^{13}C$ is 0.4 ‰ ± 1.3 ‰ the range is fixed based on 1 standard deviation representing a confidence interval of 68% as indicated by the red box. A 95% confidence level interval of 95% is represented by the blue box as defined by 2 standard deviations, meaning 95% of the food items are fall within these boundaries. For the purpose of this thesis, we define the resource polygon that captures 95% of the food sources, applying this rule food sources A, B and C fall within the boundaries of the resource polygon for the consumer, while food source D can be excluded based on a 95 % confidence level.

CHAPTER THREE: TROPHIC LINKS BETWEEN ZOOPLANKTON AND CYANOBACTERIA IN A TROPICAL SODA LAKE (SONACHI, KENYA).

3.1 Introduction

Cyanobacterial blooms are a common occurrence globally, especially saline-alkaline lakes of high pH (Kâ *et al.,* 2012; Ger *et al.,* 2016). Such blooms can have serious negative impacts on freshwater lake ecosystem function (Sukenik *et al.,* 2015). They are controlled by nutrient availability and light conditions (Conley *et al*., 2009), but their development can also be controlled by herbivores, including herbivorous taxa of zooplankton (Boon *et al*., 1994).

Many studies have been conducted to understand the feeding behaviour and role of zooplankton during cyanobacterial blooms (Boon *et al*., 1994; Bouvy *et al*., 2001; Kâ *et al.,* 2012; Hong *et al*., 2013; Ger *et al*., 2014). Different factors have been suggested that may determine trophic interactions between zooplankton and Cyanobacteria (Kâ *et al.,* 2012). The feeding of zooplankton on Cyanobacteria can be controlled by toxicity, taste and by the morphological features of the cyanobacterial prey (DeMott, 1986; Bern, 1994; Lampert and Sommer, 2007; Leitão *et al.,* 2018; Gebrehiwot *et al.,* 2019). Much uncertainty still exists however, about trophic interactions between zooplankton and Cyanobacteria (Wilson *et al.,* 2006; Ger *et al.,* 2014); the literature contains contradictory findings about their interactions. Some studies have reported that the toxicity of filamentous and colonial forms of Cyanobacteria can hamper feeding of Cladocera (Gliwicz and Lampert,1990; Rohrlack *et al.,* 2004), rotifers (Rothhaupt, 1991) and copepods (Koski *et al*., 1999). In contrast, other studies have shown that many zooplankton taxa are able to consume different taxa of Cyanobacteria. For example, in experimental studies, Work *et al*. (2003) found colonial and filamentous Cyanobacteria (e.g. *Microcystis auerginosa, Oscillatoria* sp. *Anabaena* sp.) in the guts of zooplankton (the cladoceran *Daphnia* sp. and the calanoid *Diaptomus dorsalis*). DeMott and Moxter (1991) observed, under a microscope, that copepods were feeding on the filamentous cyanobacterium *Oscillatoria* sp., but that whole filaments of that cyanobacterium were not consumed. Finally, Vareschi and Jacobs (1984) found that calanoids were able to feed on Cyanobacteria in Lake Nakuru, Kenya.

Another source of uncertainty arises from the fact that most previous studies have focused on trophic interactions between Cladocera and Cyanobacteria (Ger *et al*., 2011), with less attention paid to trophic interactions between Copepoda and Cyanobacteria (Ger *et al.,* 2011). Generalisations based on Cladocera thereofre restrict our overall understanding given to clear differences in feeding mechanisms between Cladocera and Copepoda (Fulton and Paerl, 1987; Ger *et al.*, 2011). In addition, our knowledge of the feeding responses of zooplankton to cyanobacterial blooms is largely based upon empirical studies derived from temperate zones (Ger *et al*., 2016). Cyanobacterial blooms tend to be shorter in temperate regions than in eutrophic lakes in the tropics, where blooms are usually semi-permanent (Ger *et al*., 2016). As such, more studies are needed to understand the feeding responses of Copepoda to cyanobacterial blooms in the tropical lakes (Kâ *et al.*, 2012).

The present study was conducted in Lake Sonachi, a saline lake in the Kenyan Rift Valley. Lake Sonachi was selected because saline lakes have simple food webs. This means that they are excellent model systems for examining the trophic interactions between zooplankton and Cyanobacteria (Burian, 2016). In addition, cyanobacterial blooms are common in this lake (Melack, 1981; Njuguna, 1988; Verschuren *et al.*,1999). The pelagic food web in this lake is principally composed of calanoids and cyanobacterium *Synechococcus* sp. and *Microcystis* sp.

3.2 Aim

The aim of the work described in this Chapter was to examine the feeding preference in calanoids in a saline lake and to specifically determine the relative contribution of different Cyanobacterial taxa (*Synechococcus* sp. and *Microcystis* sp.) to the calanoid diet.

3.3 Objectives

- Elucidate the relative abundance of different zooplankton and phytoplankton taxa.
- Determine the fractal contribution of different potential food items to the diet of the zooplankton.

3.4 Study site

Lake Sonachi (Figure 3.1), previously known as Naivasha Crater Lake (Beadle, 1932) is a saline-alkaline lake (MacIntyre and Melack, 1982), about 3 km from Lake Naivasha (Verschuren *et al.,* 1999). The surface area of the lake is 0.14 km^2 (Verschuren *et al.,* 1999). The average depth of the lake is approximately 5 m (Njuguna, 1988).

The lake is at an altitude of about 1884 m above sea level (Cocquyt and De Wever, 2002), in a semi-arid region (Verschuren *et al.,* 1999). The average annual rainfall is about 680 mm (MacIntyre and Melack, 1982), and the average annual evaporation rate is 1865 mm (Ase *et al.,* 1986). The catchment area of the lake is only about 1 km^2 (Ballot *et al.,* 2005). The lake is sheltered from the effects of wind by *Acacia xanthophloea* and a high crater rim that sits between 30 and 115 m above the water level (MacIntyre and Melack, 1982).

The lake has no riverine surface inflow or outflow (Ballot *et al.,* 2005), and its water level is controlled by a combination of groundwater flow from Lake Naivasha and rainfall. The main water loss is via evaporation (MacIntyre and Melack, 1982). The dominant ions in Lake Sonachi are bicarbonate and sodium, as in most other saline-alkaline lakes in Africa, and it has a pH of 10-10.4 (Njuguna, 1982; Ballot *et al.,* 2005). The lake is meromictic (does not show vertical mixing for several years: MacIntyre and Melack, 1982), and exhibits a chemocline which usually starts at 4 m from the surface (Verschuren *et al.,* 1999). Electrical conductivity at the surface ranges between 3,000 and 11,550 µS cm^{-1} (Verschuren, 1996), and conductivity of the monimolimnion is between 8,270 and 14,940 µS cm^{-1} (Njuguna, 1988).

The zooplankton community is known to have limited species diversity (Verschuren *et al.,* 1999). The rotifer *Brachionus dimidiatus* was present in 1929 (De Beauchamp, 1932), as was the calanoid *Paradiaptomus africanus* (Lowndes, 1936) at a high density (Beadle, 1932). The other important invertebrates in Lake Sonachi are chironomids; their community is composed taxa such as *Kiefferulus disparilis, Microtendipes sp., Chironomus alluaudi, Tanytarsus sp., Microchironomus deribae* and *Chironomus formosipennis* (Verschuren *et al.,* 1999). The phytoplankton community has historically been dominated by Cyanobacteria (Njuguna, 1988), particularly *Synechococcus bacillaris* (Melack, 1981; Verschuren *et al.*,1999) and *Arthrospira fusiformis* (Ballot *et al.,* 2005; Robinson, 2015). The shoreline of the lake is rich in the C_3 plants such as

Acacia sp. *and Vernonina* sp., and the C_4 plant *Cyperus laevigatus* (Mwaniki *et al*., 2019) (see Figure 3.2).

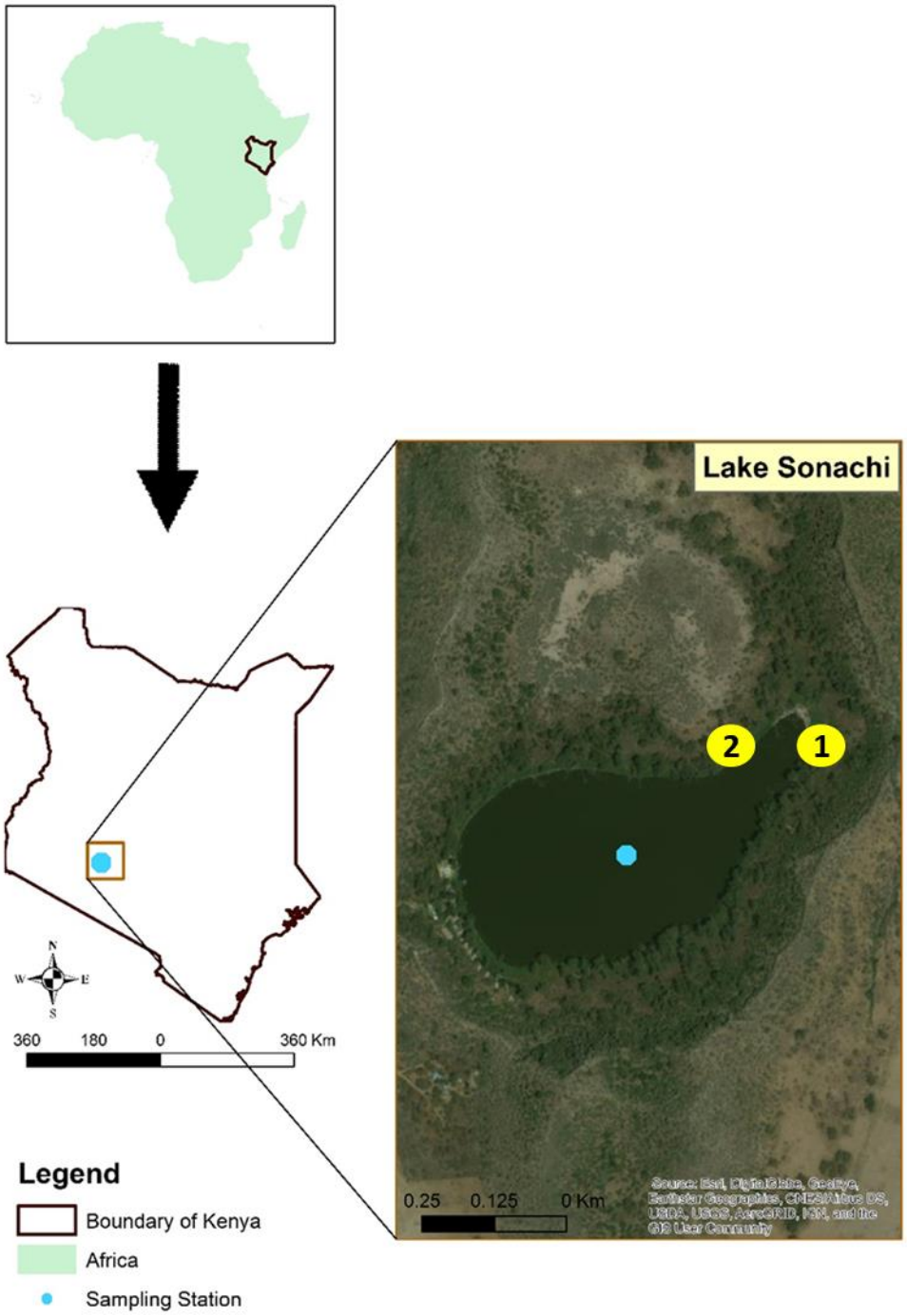

Figure 3.1 Map showing Africa and Kenya and the pelagic sampling station (1) of Lake Sonachi and the approximate locations of littoral and terrestrial samples (yellow circles). Source: Esri, DgitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USGS, AeroGRID,IGN, and the GIS User Community.

Figure 3.2 The shoreline of Lake Sonachi. Photo taken by Ahmed Al-Budeiri

3.5 Methods

Samples of the main components of the pelagic food web and from the major terrestrial carbon sources were collected from Lake Sonachi in November 2016 and March 2018. These include zooplankton, phytoplankton, POM, soil, sedments and terrestrial leaves. Individual plankton taxa were identified, enumerated and analysed for stable isotope analysis and C/N ratio analysis (see Chapter 2). In addition, chlorophyll a and a range of physical and chemical parameters were determined.

3.6 Results

3.6.1 Physiochemical and biological features

Basic water quality variables and biological characteristics measured are shown in Table 3.1. Depth profiles of some physiochemical parameters are in Appendix 3.1 and Appendix 3.2. The lake displayed stratification in dissolved oxygen and during both sampling campaigns.

Table 3.1 Water quality and biological variables at the pelagic station in Lake Sonachi for the two sampling campaigns. The number of replicates for chlorophyll-a measurements was 8.

Variables	Wet season (November 2016)	Dry season (March 2018)
Depth (m)	5.6	4.0
Surface pH	9.7	9.7
Surface dissolved oxygen (DO) mg L^{-1}	11.8	8.5
Surface water conductivity µS cm^{-1}	8028	11270
Surface water temperature °C	21.0	23.7
Density of *Synechococcus* sp. L^{-1}	7.8×10^{9}	$2.56\times10^{8}\pm7.7\times 10^{7}$
Density of *Microcystis* sp. L^{-1}	3.5×10^{7}	Not present
Chlorophyll a µgL^{-1}	41.7±7.4	Not determined
Secchi depth cm	23	Not determined
Biological oxygen demand (BOD) mg L^{-1}	6.8	Not determined

In the wet season (November 2016), the dominant cyanobacterial taxa were *Synechococcus* sp. and colonies of *Microcystis* sp. The average length of *Synechococcus* is shown in Table 3.3. In the dry season (March 2018), *Synechococcus* sp. was the dominant cyanobacterium, but its density was lower than in the wet season. *Microcystis* sp. was not present in the March 2018 campaign.

3.6.2 Zooplankton density, composition and length

The zooplankton community in Lake Sonachi was composed exclusively of the calanoid *Lovenula* sp. in both November 2016 and March 2018. Copepodites and nauplii of that calanoid were only present in November 2016 (Table 3.2). The average length of adult *Lovenula* sp. is shown in Table 3.3.

Table 3.2 Zooplankton density in the pelagic zone of Lake Sonachi in the dry and wet seasons. Indiv. = individuals, SD = standard deviation, number of replicates = 3.

Group	Taxon	Wet season (November 2016) (Indiv. L^{-1}) Mean ± SD	Dry season (March 2018) (Indiv. L^{-1}) Mean ± SD
Calanoida	*Lovenula* sp.	5.0 ± 1.5	2.9 ± 1.1
	Copepodites	0.2 ± 0.2	Not present
	Nauplii	0.1 ± 0.06	Not present
Total density of zooplankton		**5.3**	**2.9**

Table 3.3 Average length of zooplankton and Cyanobacteria in the pelagic zone of Lake Sonachi. N= **20 individuals of each species.**

Group	Taxon	Average length ±SD
Cyanobacteria	*Synechococcus* sp.	2 ± 0.15 μm
Calanoida	*Lovenula* sp.	1.6 ± 0.18 mm

3.6.3 Stable isotopic compositions and C/N ratios

$\delta^{13}C$ and $\delta^{15}N$ of the living and non-living components in the samples collected from Lake Sonachi are plotted in Figure 3.3 for the wet season (November 2016) and Figure 3.4 for the dry season (March 2018). Data are shown in Appendix 3.3. The $\delta^{13}C$ and $\delta^{15}N$ signatures of the potential food sources of the calanoid *Lovenula* sp. provide the coordinates defining diet polygons for this consumer in the wet and dry seasons (Figures 3.3 and 3.4, respectively). In the wet season (November 2016), the $\delta^{13}C$ value of the *Lovenula* sp. was similar to that of 0.7-25 μm POM. The $\delta^{15}N$ for *Lovenula* sp. was approximately 7.2 ‰ higher than that of 0.7-25 μm POM, suggesting that the 0.7-25 μm POM fraction may have been a carbon source for calanoids.

In November 2016, the C/N ratio of POM 0.7-25 μm was 7.3 (Table 3.4); in March 2018, C/N ratios of POM fractions (0.7-2 μm, 2-20 μm) ranged between 7 and 8.5. It is likely that the contribution of phytoplankton to POM is *Synechococcus* sp., which was the dominant phytoplankton taxon in both seasons. The C/N ratios of soils were 8.4 (Table 3.4), however, the $\delta^{13}C$ signatures of soil were different from those of the 0.7-25 μm POM fraction suggesting that POM was not derived from soil.

The $\delta^{13}C$ signatures of *Lovenula* sp. in November 2016 (wet season) were 5.5 ‰ lower than colonies of *Microcystis* sp. In addition, the $\delta^{15}N$ signatures of *Lovenula* sp. were 9 ‰ enriched relative to *Microcystis* sp. (Figure 3.3). This difference is typical of approximately two trophic levels and suggests that *Microcystis* sp. is probably unimportant for the diet of the pelagic calanoid *Lovenula* sp. That said, in the present study, the trophic enrichment of $\delta^{15}N$ in calanoids relative to their food sources (Figure 3.3) appeared to be greater than the typical enrichment for aquatic ecosystems (3.4 ‰: Post, 2002). In the dry season (March 2018), the nitrogen enrichment between *Lovenula* sp. and the POM fractions (0.7-2 μm, 2-20 μm and 20-48 μm) was 7.1, 6.0 and 5.6 ‰

respectively (Figure 3.4). High enrichment (5.5 ‰) was also reported by Grey *et al*. (2001) for mixed zooplankton in Loch Ness, UK. Some studies have suggested that quality of diet can affect enrichment of $\delta^{15}N$ (Adam and Sterner, 2000; Mizota and Yamanaka, 2011). In a laboratory experiment, Adam and Sterner (2000) found that a strong increase in $\delta^{15}N$ of *Daphnia* sp. was associated with reduced N content of their food items (e.g. phytoplankton). The results reported here for Lake Sonachi do not appear to support this idea, as the C/N ratios of POM fractions, dominated by the *Synechococcus* (which are likely to be a major food item) were relatively low (between 7 and 8.5). Unfortunately, the specific mechanisms which are responsible for variations in $\delta^{15}N$ enrichment are still unclear (Vanderklift and Ponsard, 2003). Schmidt *et al*. (1999) found no effect of diet on $\delta^{15}N$ enrichment.

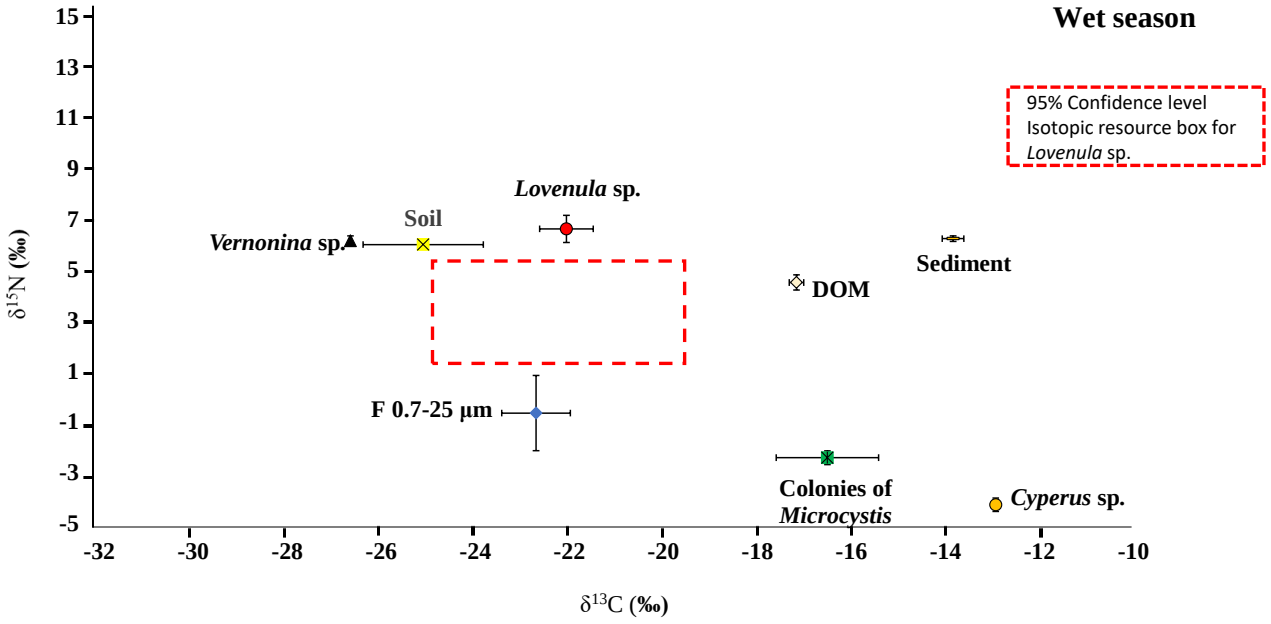

Figure 3.3 Mean (±1SD) values of $\delta^{13}C$ plotted against $\delta^{15}N$ for the potential food sources of *Lovenula* sp. in Lake Sonachi during the wet season (November 2016). The diet polygon for mean (±2SD) values of $\delta^{13}C$ plotted against $\delta^{15}N$ for the *Lovenula* sp. is represented by dashed red rectangle. F= Fraction. Note: the principal food source for *Lovenula* sp. (POM 0.7-25 µm) falls outside of the 95% confidence level isotopic resource box. However, we do consider this to be the main food source and the observation may be explained by a higher than normal mean trophic enrichment factor of nitrogen for *Lovenula* sp. Examples of this have been reported in many experimental and field studies (e.g. Adam and Sterner, 2000; Grey *et al*., 2001; Vanderklift and Ponsard, 2003; Mizota and Yamanaka, 2011).

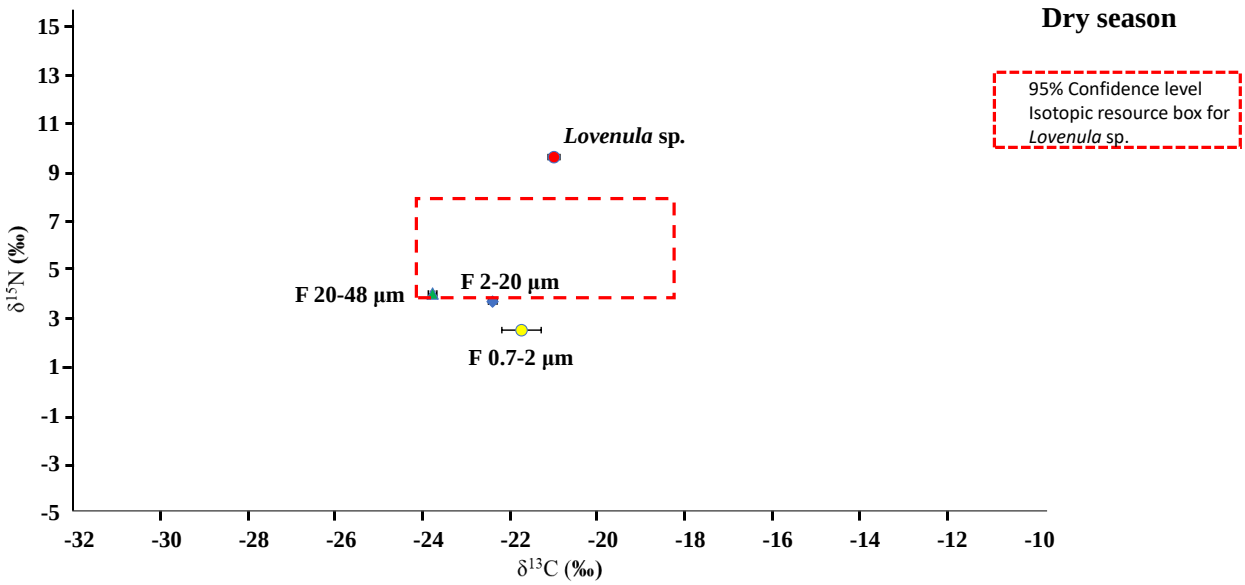

Figure 3.4 Mean (±1SD) values of $\delta^{13}C$ plotted against $\delta^{15}N$ for the potential food sources of *Lovenula* sp. in Lake Sonachi during the dry season (March 2018). F= Fraction. The diet polygon for mean (±2SD) values of $\delta^{13}C$ plotted against $\delta^{15}N$ for the *Lovenula* sp. is represented by dashed red rectangle. Note: one of the principal food sources for *Lovenula* sp. (0.7-2 µm POM fraction) falls outside of the 95% confidence level isotopic resource box. However, we do consider this to be also potential food source and the observation may be explained by a higher than normal mean trophic enrichment factor of nitrogen for *Lovenula* sp. Examples of this have been reported in many experimental and field studies (e.g. Adam and Sterner, 2000; Grey *et al.*, 2001; Vanderklift and Ponsard, 2003; Mizota and Yamanaka, 2011).

Table 3.4 Molar C/N ratios of the main food web components in Lake Sonachi and from the major terrestrial resources during the wet season (November 2016) and the dry season (March 2018). Note that different size fractions of POM were determined in March 2018 compared to November 2016.

Taxon/ Group	Time of sampling	Number of replicates for carbon (C)	Number of replicates for nitrogen (N)	C/N (S.D)
Lovenula sp.	November 2016	3	3	9.5±2.42
Lovenula sp.	March 2018	3	3	4.7±0.42
POM 0.7-25 μm	November 2016	3	3	7.3±0.11
POM 0.7-2 μm	March 2018	3	1	7
POM 2-20 μm	March 2018	1	1	8.5
POM 20-48 μm	March 2018	1	1	8.5
Microcystis sp.	November 2016	3	1	6.1
DOM	November 2016	3	3	69.4±0.26
Soil	November 2016	3	3	8.4±0.01
Sediments	November 2016	3	3	8±0.05
Vernonina sp.	November 2016	3	3	13.8±0.15
Cyperus sp.	November 2016	3	3	38.4±0.15

The $\delta^{13}C$ signature of DOM was considerably higher than that of *Lovenula* sp., suggesting that DOM was probably not an important carbon source for that calanoid. The $\delta^{13}C$ signatures of leaves of *Vernonia* sp. and *Cyperus* sp. also suggest that inputs of these allochthonous materials are not important dietary items for *Lovenula* sp.

In the dry season (March 2018), the $\delta^{13}C$ signature of *Lovenula* sp. was similar to that of the POM fractions (0.7-2 μm and 2-20 μm). The $\delta^{15}N$ signature for the pelagic calanoids was higher than those of the POM fractions (0.7-2 μm and 2-20 μm), indicating that calanoids may feed significantly on these POM fractions, which are likely to be dominated by phytoplankton according to their C/N ratios (Table 3.4). The comparison

between $\delta^{13}C$ and $\delta^{15}N$ signatures of *Lovenula* sp. with those of 20-48 μm POM, suggests that *Lovenula* sp. does not feed significantly on 20-48 μm POM.

The percentage of carbon assimilated by *Lovenula* sp. which was derived from 0.7-25 μm POM and *Microcystis* sp. was estimated using a simple mixing model (Equation 13). The explanation and justification for using this mixing model and for including these two potential carbon sources or for not including the other carbon sources in this model can be found in Chapter 2 (see 2.10 Data analyses for details). The mixing model suggests that in the wet season (November 2016), the carbon derived from the 0.7-25 μm POM fraction (dominated by *Synechococcus* sp.) accounts for 93.5 % of *Lovenula* sp. carbon, while carbon derived from *Microcystis* sp. contributed only 6.5 %. In the dry season (March 2018), *Lovenula* sp. was assumed to rely entirely on POM fractions due to the disappearance of *Microcystis* from the system at this time. It was not possible to estimate the contributions of the different POM fractions to *Lovenula* sp. in the dry season because the $\delta^{13}C$ signatures of the consumer and the different POM fractions were not sufficiently distinct from one other and the $\delta^{13}C$ values of the POM did not envelop that of the consumer.

3.7 Discussion

The cyanobacterium *Synechococcus* sp. is likely to have been the main source of carbon for the calanoid *Lovenula* sp. $\delta^{13}C$ signature of *Lovenula* sp. was enriched relative to small POM fractions (dominated by the pico-alga *Synechococcus*) by ~1 ‰. This is in line with Post (2002) who suggested that the trophic enrichment between consumer and food is 0.4 ± 1.3 ‰ for $\delta^{13}C$. The C/N ratios of these POM fractions suggest that phytoplankton predominantly contributed to the POM. The C/N ratios of phytoplankton normally ranges between 6 and 10 (Montagnes *et al*., 1994; Creach, 1995) which is in line with the present study. C/N ratios for organic matter derived from terrestrial materials is typically larger than 12 (Thornton and McManus, 1994). The C/N ratios for bacteria and zooplankton commonly range from 3 to 6 (Gorsky *et al*., 1988; Fagerbakke *et al*., 1996).

The tendency of the *Lovenula* sp. to principally feed on *Synechococcus* rather than colonies of *Microcystis* sp. in November 2016 (wet season) when both algal sources were present in the lake, is supported by the fact that the unicellular *Synechococcus* sp. is not

toxic (Wagner and Frost, 2012). This result is consistent with previous laboratory experiments on the feeding behaviour of calanoids (Vogt *et al.,* 2013), which found that *Pseudodiaptomus marinus* fed on *Synechococcus* sp. In an isotopic study, Yoshioka *et al*. (1994) found that the calanoid *Eodiaptomus japonicus* fed predominantly on non-toxic small food particles in Lake Suwa, Japan. It has been suggested that the feeding of zooplankton on *Microcystis* sp. can be limited by different factors: including, 1) The toxicity of *Microcystis* to many zooplankton species (Lampert and Sommer, 2007; Ger *et al.,* 2018); 2) The ability of *Microcystis* to secrete a gelatinous sheath (Omori *et al.,* 2018); 3) The fact that *Microcystis* can form large colonies (Yang *et al.,* 2008). Mucilaginous colonies of *Microcystis* can hamper filter feeding by calanoids; 4) Feeding selectivity by calanoids, for example, the calanoid *Notodiaptomus iheringi* avoids feeding on colonies and cells of the microcystin producing strain of *Microcystis,* which have diameter of less than 5 μm (Ger *et al*., 2016 b). The fact that *Lovenula* sp. has been shown to primarily feed on *Synechococcus,* rather than *Microcystis,* will have implications for the functioning of the pelagic food web, including the potential accumulation of *Microcystis*-derived photosynthate in the water column of this lake. As some strains of cyanobacterium *Microcystis* produce toxins, the accumulation of such toxic products in aquatic ecosystems can cause serious consequences for zooplankton production, insects, aquatic plants, birds and human (Malbrouck and Kestemont, 2006; Paerl and Otten, 2013).

The stable isotope data presented here differ from those reported by *in situ* experiments of Lampert and Taylor (1985) in Lake Schöhsee, in northern Germany and by laboratory studies of Lampert (1987). These studies suggested that relatively large Cladocera with body length of 1.75 mm (e.g. *Daphnia galeata*) feed more efficiently on *Synechococcus* than marine and freshwater calanoids as the cells of *Synechococcus* sp. are too small (1-2 μm) to be utilised by calanoids. It was found that the relatively large calanoid *Boeckella accidentalis* (body length approximately 1.65 mm) fed on large Cyanobacteria (> 10 μm) such as *Lyngbya, Ulothrix and Nodularia* in the tropical Lake Titicaca on the border of Bolivia and Peru (Haney and Trout, 1985; Haney, 1987; Burns and Xu, 1990). However, the results presented here differ from these studies: the similarly large calanoid *Lovenula* sp. (average length 1.6 mm) appeared to significantly feed on *Synechococcus* sp. The evidence from this study suggests that the idea that the limited control exerted by zooplankton on large Cyanobacteria in the tropics is due to the dominance of small

zooplankton (Havens *et al*., 1996; Lazzaro, 1997; Fernando, 1994; Fernando, 2002) may be not a generalised pattern in this region.

In addition, in gut content analysis, Work *et al*. (2003) found that filamentous and colonial forms of Cyanobacteria including *Microcystis auerginosa* were largely consumed by the cladoceran *Daphnia* sp. and the calanoid *Diaptomus dorsalis*. However, these studies, and most other information about the diets of zooplankton, are based on traditional methods (Jia *et al*., 2016) such as gut content analysis or laboratory observation of feeding behaviour (e.g. Pasternak and Schnack-Schiel, 2001; Bouvy *et al*., 2001). These methods provide information about ingested food particles but do not reflect the long-term nature of food items assimilated (Makoto and Tsutomu, 1984; Omorii and Ikeda, 1984). The present study shows that SIA is more effective for identifying the contribution of different food items to the diet of the zooplankton compared with traditional methods.

In East African saline lakes, changes in phytoplankton abundance are likely to occur seasonally. This was the case here where *Synechococcus* sp. and colonies of *Microcystis* sp. were observed in November 2016 (wet season) but only *Synechococcus* sp. was recorded in March 2018 (dry season). This was probably due to changes in physical and chemical conditions between the dry and wet seasons. The existence of *Microcystis* sp. in East African Soda Lakes is typically restricted to periods when electrical conductivity is low (Wood and Talling, 1988), so an increase in conductivity may explain the disappearance of *Microcystis* in the dry season. The seasonal changes in phytoplankton and zooplankton compositions are also explored in Lake Bogoria, another African saline lake in Chapter 4.

Overall, in Lake Sonachi, the results suggest that there was some dietary variation for the relatively large calanoid *Lovenula* sp. between seasons, with an apparent preference for POM fractions dominated by *Synechococcus*. The results of the present study provide evidence that the size of zooplankton in Lake Sonachi is not the key factor that enables them to feed on large Cyanobacteria.

CHAPTER FOUR: DO ZOOPLANKTON AND LESSER FLAMINGO COMPETE FOR RESOURCES IN LAKE BOGORIA?

4.1 Introduction

Lake Bogoria in East Africa is an alkaline-saline lake that is an internationally important habitat for lesser flamingos (*Phoeniconaias minor*) (Krienitz *et al*., 2010; Robinson, 2015; Krienitz *et al*., 2013). More than a million individuals of this bird have been recorded in this lake (Brown, 1959; Harper *et al*., 2003). Lesser flamingos mainly feed on the cyanobacterium *Arthrospira fusiforms* (Vareschi and Jacobs, 1985; Harper *et al*., 2003; Sanders, 2016) with benthic diatoms as an alternative food item at times with shortages of planktonic food (Tuite, 2000). Flamingos are very sensitive to changes in food concentration because of this specialisation (Krienitz and Kotut, 2010). In last few decades, the density of *Arthrospira* has been shown unpredictable fluctuations in saline lakes such as Lakes Simbi, Bogoria and Nakuru, Kenya (Melack, 1979; Schagerl and Oduor, 2008), affecting flamingo population density and location (Harper *et al*., 2016). Different explanations for fluctuations in the density of *Arthrospira* sp. have been put forward, including changes in water level, salinity, nutrient concentrations and cyanophage effects. (e.g. Melack, 1979; Melack, 1988; Schagerl and Oduor, 2008 Krienitz *et al*., 2013; Harper *et al*., 2016; Krienitz *et al*., 2016).

An additional factor of potential relevance to this issue is that relatively little is known about the resource competition between zooplankton and the lesser flamingo. In addition, any consideration thus far as to the potential role of zooplankton has been speculative due to lack of quantitative and comparative data. Zooplankton are one of most important biological factors affecting the structure and density of phytoplankton and hence, have significant potential to influence food availability for flamingos in saline lakes of East Africa (Childress *et al*., 2008). In recent years, lesser flamingos have also experienced occasional (and mysterious) die-offs in Lake Bogoria and other lakes in eastern Africa (Harper *et al.*, 2003; Krienitz and Kotut, 2010). Some authors have suggested there has been a long-term decline of African flamingo populations in last twenty years (Simmons. 1996; Simmons, 2000). In addition, flamingos are classified as 'near threatened' by IUCN (Childress *et al.*, 2007; IUCN, 2015). There is thus a significant conservation imperative to understand the functioning of food webs associated with flamingos in this region (Schagerl, 2016).

The typical pelagic food web in Lake Bogoria consists mainly of Cyanobacteria, dominated by *Arthrospira fusiforms* (Harper *et al.*, 2003; Burian *et al.*, 2014), and rotifers (mainly *Brachionious* sp.) (Nogrady, 1983; Green and Mengestou, 1991; Fontaneto *et al.*, 2006). Latterly, high lake levels throughout the Rift Valley have resulted in periodic connections between lakes. In 2013, the cladoceran *Moina* sp. was recorded in Lake Bogoria for the first time (Harper *pers. comm.*), possibly due to this increased connectivity. The periodic appearance of Cladocera in saline lakes has also been reported in waterbodies in South Africa and southern Australia (Frey, 1993). In experimental studies, *Moina* sp. feeds on filamentous and unicellular phytoplankton (Pagano, 2008; Kâ *et al*., 2012). The periodic appearance of Cladocera might therefore play an important role in changing food availability for lesser flamingo in Lake Bogoria.

This study examines whether there is potential competition between zooplankton taxa (Cladocera and rotifers) and the lesser flamingo for the principal food source for flamingos - *Arthrospira* - in Lake Bogoria. To the author's knowledge, this is the first study to examine the potential for competition between these primary consumers using stable isotope analysis in saline lakes.

4.2 Aim

The aim of this chapter is to examine potential resource competition between zooplankton and the lesser flamingo in a saline East African lake.

4.3 Objectives

The aim was achieved via the following objectives:

- Elucidate the relative abundance of different zooplankton and phytoplankton taxa.
- Reconstruct the food web structure via stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) for each taxon.
- Determine the fractional contribution of different food items to the diet of zooplankton using a simple mixing model, with a focus on establishing (and explaining) differences between the wet and dry seasons and assess whether this supports the hypotheisis that there may be competition between these zooplankton and flamingos.

4.4 Study site

Lake Bogoria (Figure 4.1) (previously known as Lake Hannington) is a saline-alkaline lake about 240 km north of Nairobi (Hickley *et al.,* 2003), in the Eastern Rift Valley. The surface area of the lake is 34 km^2 (Tiercelin *et al.,* 1987). The length and width of the lake are ~17 km and 3.5 km respectively (Jirsa *et al.,* 2013). The lake has three basins, with a mean depth of 5.4 m, athough some deep points reach beyond 10 m (Robinson, 2015).

The lake lies at an altitude of 975 m (Harper *et al.,* 2003), in a semi-arid area. The annual rainfall is 700 mm $year^{-1}$ with potential evapotranspiration about 2500 mm $year^{-1}$ (Ashley *et al.,* 2004). There is a high variability in annual rainfall (Jirsa *et al.,* 2013).

The total lake catchment is about 930 km^2 (Tiercelin *et al.,* 1987), and is principally underlain by volcanic rocks (McCall,1967). The catchment is occupied by a mixture of C_3 and C_4 plants (Harper *et al.,* 2003). Dominant are *Acatia tortilis, A. seyal, A. mellifera, Capparis* sp., *Salvadora persica* (Harper *et al.,* 2003), *Balanites* sp. and *Commiphora* sp. (Wetang'ula, 2013). The shoreline of the lake is rich in grasses (27 species), two of which are true halophytes: C_4 plants *Cyperus laevigatus* and *Sporobolus spicatus* (Harper *et al.,* 2003).

The lake hydrology is complicated by multiple hot springs and river inflows (Harper *et al.,* 2003). There are approximately 30-40 springs surrounding the lake, supplying about a quarter of the lake's water (Cioni *et al.,* 1992). The remaining water is provided by four rivers. The largest two rivers are seasonal and enter the lake in the north. There are also two small perennial, streams from freshwater springs to the south (Harper *et al.,* 2003).

Electrical conductivity of the lake water ranges between 25,000 and 77,000 µS cm^{-1} but is typically usually at the higher end of this range, and the pH is 10.1-10.2 (Harper *et al.,* 2003). Its alkalinity fluctuates between 1020 and 1500 meq l^{-1} (Harper *et al.,* 2003; Krienitz *et al.,* 2003). The total nitrogen and phosphorus concentrations are typically 1.4 and 5.4 mg L^{-1} respectively (Krienitz *et al.,* 2003).

The composition of this lake's food web has been studied by several authors at different times (e.g. Harper *et al.,* 2003; Schagerl *et al.,* 2015; Krienitz *et al.,* 2012). Frequent transitions in its structure have been reported (in terms of zooplankton, phytoplankton and macroinvertebrates). These temporal shifts in plankton communities are not fully understood (Schagerl and Oduor, 2008). Zooplankton above the size of rotifers are

typically absent (Harper *et al.*, 2003) with rotifers and protozoa dominant (Schagerl *et al.*, 2015). Few invertebrates have been recorded in the lake, including a single species of (unusually pelagic) chironomid *Tanytarsus minutipalpas* (Sanders, 2016). Phytoplankton have historically been dominated by *Arthrospira fusiforms* (Harper *et al.*, 2003), although, Krienitz *et al.* (2012) reported that *Picocystis salinarum* (>3 billion cells l^{-1}) was dominant in 2006.

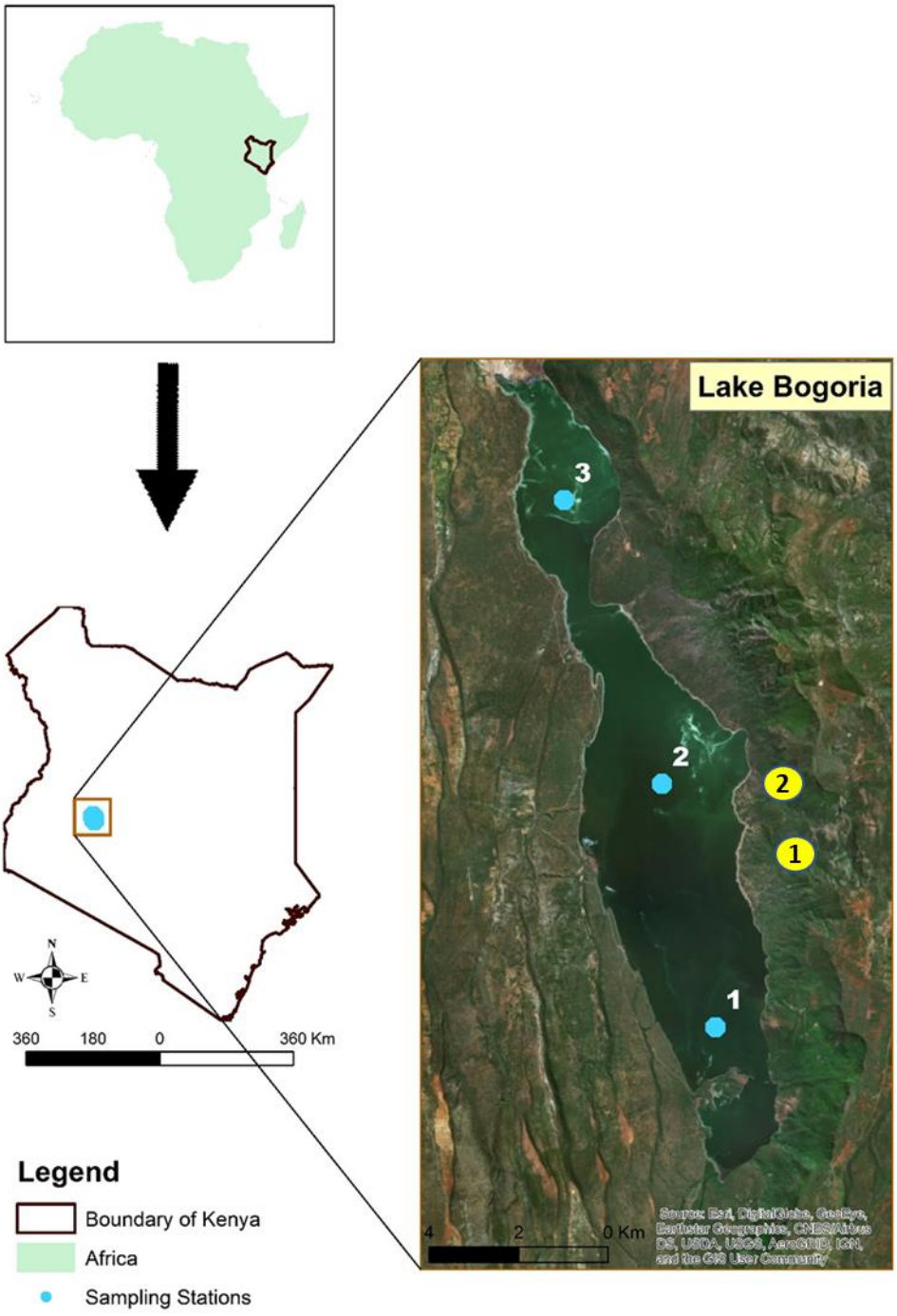

Figure 4.1 Map showing Africa and Kenya and the pelagic sampling stations (1, 2 and 3) of Lake Bogoria and the approximate locations of terrestrial samples (yellow circles). Source: Esri, DgitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USGS, AeroGRID,IGN, and the GIS User Community.

4.5 Methods

Samples of the main components of the pelagic food web, including the major terrestrial carbon sources, were collected from Lake Bogoria in December 2016 and March 2018. These included zooplankton, phytoplankton, lesser flamingo feathers, POM, soil, sedments and terrestrial leaves. Individul plankton taxa were identified, enumerated and analysed for stable isotope and C/N ratio analyses (see Chapter 2). In addition, chlorophyll a concentration, and a range of physical and chemical parameters were determined.

4.6 Results

4.6.1 Physiochemical and biological features

Water quality variables and biological characteristics measured during the sampling campaigns are shown in Table 4.1. Depth profiles of some physiochemical parameters were recorded (Appendices 4.1, 4.2, 4.3, 4.4, 4.5, 4.6, 4.7 and 4.8). The lake displayed stratification in dissolved oxygen and conductivity in December 2016, but only appeared to be stratified for dissolved oxygen in March 2018. Conditions in the two sampling campaigns were quite different. In particular, lake level was higher and conductivity was much lower in the wet season. The concentration of dissolved oxygen was also lower and Secchi depth much higher in the wet season (Table 4.1).

Table 4.1 Water quality and biological variables in Lake Bogoria during the sampling campaigns. SD= standard deviation. n=number of replicates. (i.e. one replicate for each station except chlorophyll a which was five replicates for each station and *Cyclotella* sp. which was three replicates for the central station).

Variables	N	Wet season December 2016 Mean±(SD)	Dry season March 2018 Mean±(SD)
Depth (m)	3	14.7±0.4	11.3±0.5
pH	3	10±0.05	9.9±0.05
Surface dissolved oxygen (DO) mg L^{-1}	3	4.3±0.9	23.2±18.2
Surface water conductivity µS cm^{-1}	3	38628±516	42080±161
Surface water temperature °C	3	26.2±0.4	27±2.3
Secchi depth cm	3	43.6±5.7	15±0
Density of *Arthrospira* sp. coil ml^{-1}	3	$2.06\times10^3\pm3.4\times10^2$	$5.22\times10^3\pm4.84\times10^3$
Density of *Cyclotella* sp. ml^{-1}	3	$2.79\times10^3\pm1.1\times10^2$	Not detected
Chlorophyll a µgL^{-1}	15	27.4±15.4	Not determined
Biological oxygen demand (BOD) mg L^{-1}	3	1.7±2.6 mg L^{-1}	Not determined

The diatom *Cyclotella* sp. and the cyanobacterium *Arthrospira* sp. coexisted in the wet season (Table 4.1), but in the dry season *Arthrospira* sp. dominated and *Cyclotella* sp. (Plate 1, c), appeared to have disappeared. The average length of sampled *Cyclotella* sp. is shown in Table 4.3.

4.6.2 Zooplankton density, composition and length

The zooplankton community was dominated by the cladoceran *Moina* sp. (Plate 1, a) in the wet season (Table 4.2) with rotifers (Plate 1, b) at lower density (Table 4.2). *Brachionus* dominated in the dry season when *Moina* sp. seemed to have disappeared completely from all three pelagic stations. The average lengths of *Moina* sp. and rotifers is shown in Table 4.3.

Table 4.2 Zooplankton density in the pelagic zone of Lake Bogoria for the dry and wet seasons. Indiv.= individuals, SD= standard deviation. Number of replicates=9 (i.e. three replicates for each station).

Group	**Taxon**	**Wet season Dec. 2016** (Indiv. L^{-1}) Mean±SD	**Dry season Mar. 2018** (Indiv. L^{-1}) Mean±SD
Cladocera	*Moina* sp.	24.4±31.2	Not present
Total density of Cladocera		24.4±31.2	Not present
Rotifers			
	Brachionus sp.	2.2± 1.2	1062± 1191
	Lecane sp.	0.2±0.4	Not present
	Hexarthra sp.	0.6 ± 0.8	Not present
	Synchaeta sp.	Not present	25.3± 42.6
Total density of rotifers		3±2.4	1087±1234
Total density of zooplankton		**27.4**	**1087**

Table 4.3 Average length (±SD) of zooplankton and phytoplankton in the pelagic zone of Lake Bogoria. The average was calculated from approximately 20 individuals.

Group	**Taxon**	**Average length** ±SD
Diatoms	*Cyclotella* sp.	10±0.4 µm
Cladocera	*Moina* sp.	900±60 µm
Rotifera	Rotifers	350±34 µm

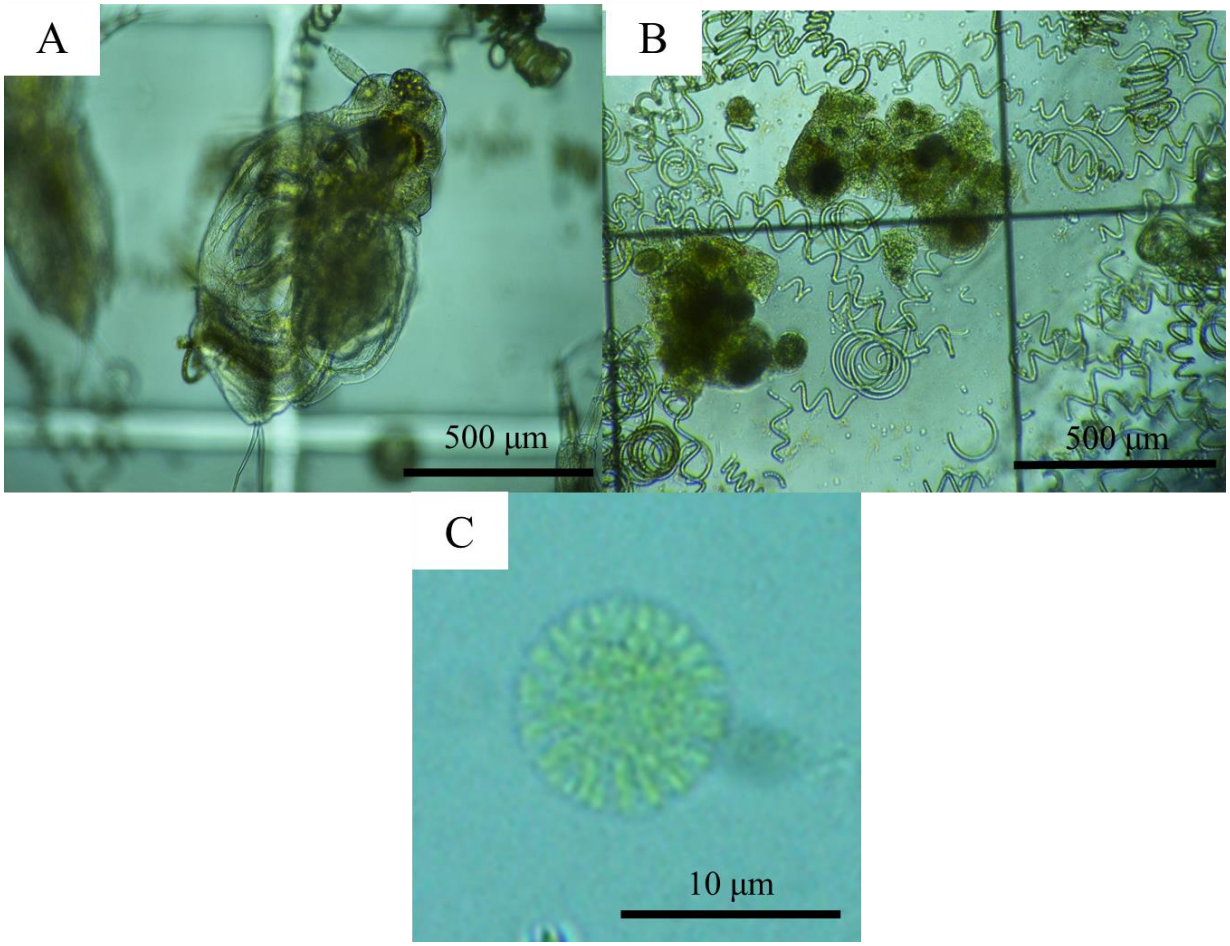

Plate 1: Photographs of A: *Moina* sp., B: Rotifers and *Arthrospira* sp. and C: *Cyclotella* sp., from Lake Bogoria. All photographs taken under a light microscope by Ahmed Al-Budeiri.

4.6.4 Stable isotope compositions and C/N ratios

$\delta^{13}C$ and $\delta^{15}N$ of different living and non-living components in the samples collected from Lake Bogoria are plotted in Figure 4.2 for the wet season (December 2016) and in Figure 4.3 for the dry season (March 2016). Data are fully reported in Appendix 4.9. C/N ratios of these components are shown in Table 4.4. The $\delta^{13}C$ and $\delta^{15}N$ signatures of potential food sources provide the coordinates for the potential diet polygon of the cladoceran *Moina* sp. in the wet season (Figures 4.2).

In the wet season, *Cyclotella* sp. appeared to be an important carbon source for *Moina* (Figure 4.4). The simple linear mixing model (Equation 14) suggests that the carbon derived from *Cyclotella* accounted for 87 % of *Moina* carbon, while *Arthrospira* sp. made a 13% contribution to *Moina* carbon. The explanation and justification for using this mixing model and for including these carbon sources (and for excluding the other potential sources) in this model can be found in Chapter 2 (see 2.10 Data analyses for details). DOM was not considered an important as a carbon source for *Moina* sp.

The $\delta^{13}C$ of pelagic rotifers was close to that of *Arthrospira*, suggesting that rotifers may feed on *Arthrospira* (Figure 4.4). Since both the $\delta^{13}C$ values of *Arthrospira* sp. and *Cyclotella* sp. were slightly lower than that of the rotifers, it was not possible to apply a mixing model. Both could represent dietary sources for the rotifers, but the isotopic values suggested that *Cyclotella* sp. was not important as a carbon source for rotifers. The isotopic values of the lesser flamingo imply that they feed predominantly on *Arthrospira* sp. (Figure 4.4). Similarity in the isotope signatures of rotifers and flamingos suggests that these taxa may be competing for *Arthrospira* sp. The carbon isotope signatures of *Cyclotella* sp. and lesser flamingo, suggest that the former was not utilised by flamingos (Figure 4.4).

In the present study, the trophic enrichment of $\delta^{15}N$ in *Moina* sp. and rotifers relative to their likely food sources was greater than the trophic enrichment which is often used in food web studies (approximately 3.4 ‰: Post, 2002). In the wet season (December 2016), the average nitrogen enrichment between the *Moina* sp. and food sources (*Cyclotella* sp. and *Arthrospira* sp.) was 5.7 and 6.3 ‰ respectively (Figure 4.2). In the dry season (March 2018), the average nitrogen enrichment between the rotifers and *Arthrospira* and the POM fraction (20-48 μm) were 4.7 and 4.1‰, respectively (Figure 4.3). The possible

reasons behind such high enrichment are discussed in Chapter 3 (see 3.6.3 Stable isotopic compositions and C/N ratios).

In the dry season, $\delta^{13}C$ and $\delta^{15}N$ signatures of rotifers and *Arthrospira* sp. suggested that *Arthrospira* sp. was an important carbon source for rotifers. The $\delta^{15}N$ of pelagic rotifers, 0.7-2 µm POM and 2-20 µm POM were similar, suggesting that POM fractions were not important dietary items for rotifers. This is supported by the fact that the $\delta^{13}C$ of rotifers is significantly lower than those for POM fractions. The $\delta^{13}C$ and $\delta^{15}N$ signatures of potential food sources and the consumer provide coordinates that define the diet polygon for that consumer in the dry season (March 2018) (Figures 4.3). Contributions of the POM fraction 20-48 µm and *Arthrospira* sp. to rotifer diet in the dry season (March 2018) were not quantified because the $\delta^{13}C$ signatures of rotifers and *Arthrospira* sp. were not sufficiently distinct. The $\delta^{13}C$ signatures for 20-48 µm POM were too far from those of pelagic rotifers to suggest that POM was significantly used either compared to *Arthrospira* sp. (Figure 4.3).

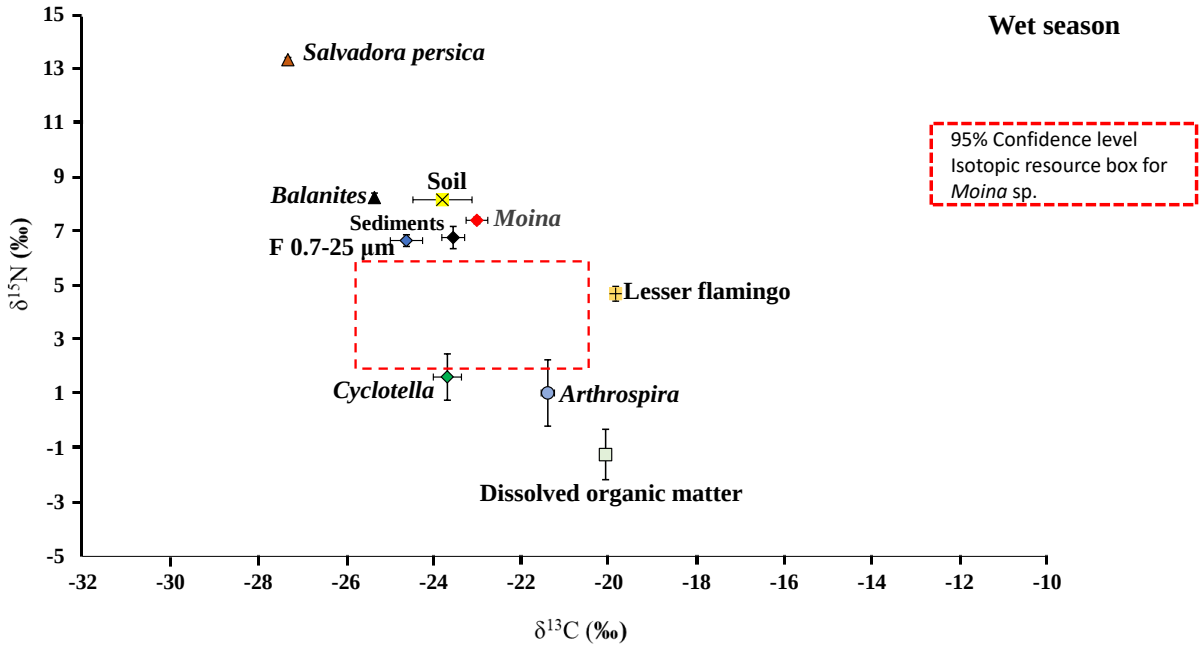

Figure 4.2 Mean (±1SD) values of $\delta^{13}C$ plotted against $\delta^{15}N$ for the main components of the pelagic food web in Lake Bogoria and the dominant terrestrial carbon sources in the wet season (December 2016). The diet polygon for mean (±2SD) values of $\delta^{13}C$ plotted against $\delta^{15}N$ for the cladoceran *Moina* sp. is represented by dashed red rectangle. F= Fraction. Note: the principal food sources for *Moina* sp. (*Cyclotella* sp. and *Arthrospira* sp.) fall slightly outside of the 95% confidence level isotopic resource box. However, we do consider these to be potential food sources and the observation may be explained by a higher than normal mean trophic enrichment factor of nitrogen for *Moina* sp. Examples of this have been reported in experimental and field studies (e.g. Adam and Sterner, 2000; Grey *et al.*, 2001; Vanderklift and Ponsard, 2003; Mizota and Yamanaka, 2011).

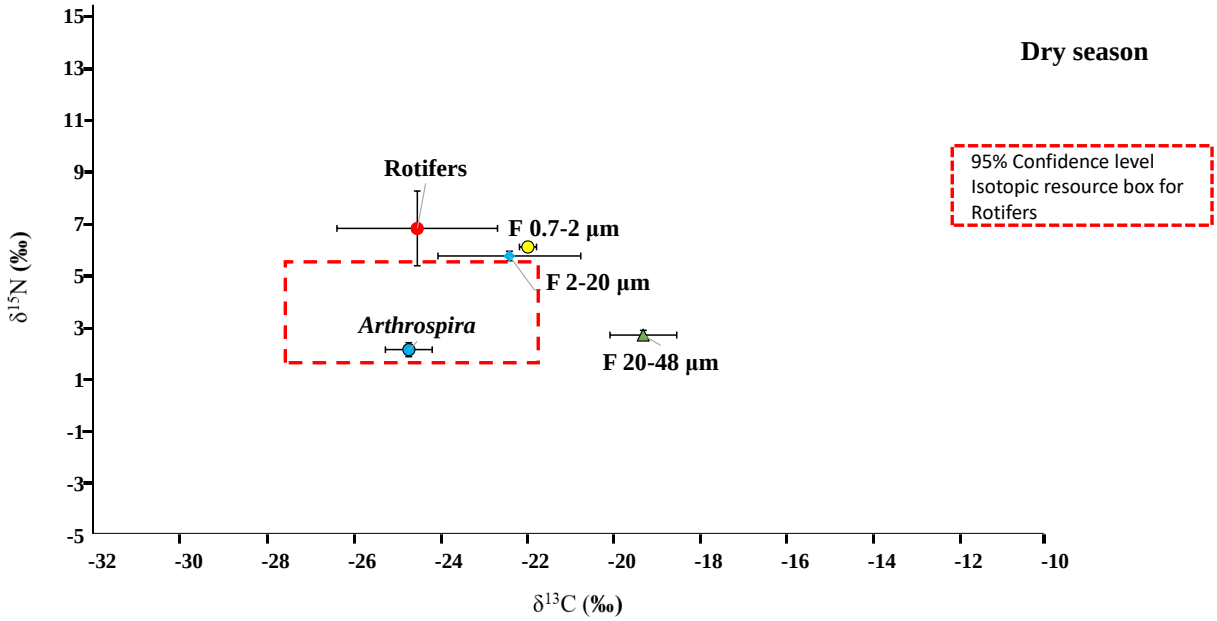

Figure 4.3 Mean (±1SD) values of $\delta^{13}C$ plotted against $\delta^{15}N$ for the potential food sources of rotifers in Lake Bogoria in the dry season (March 2018). The diet polygon for mean (±2SD) values of $\delta^{13}C$ plotted against $\delta^{15}N$ for the rotifers is represented by dashed red rectangle. F= Fraction.

Table 4.4 Molar C/N ratios of the main food web components in Lake Bogoria and from the major terrestrial resources during the wet season (December 2016) and the dry season (March 2018). Note that different size fractions of POM were determined in March 2018 compared to December 2016.

Taxon/ Group	Time of sampling	Number of replicates for carbon (C)	Number of replicates for nitrogen (N)	C/N (S.D)
Moina sp.	December 2016	3	3	4.37±6.0
Rotifers	March 2018	3	3	3.74±8.5
Arthrospira sp.	December 2016	3	3	6.17±0.72
Arthrospira sp.	March 2018	3	3	4.57±0.62
Cyclotella sp.	December 2016	1	1	5.20
Lesser flamingo	December 2016	3	3	4.09±11.35
POM 0.7-25 µm	December 2016	3	3	4.5±0.04
POM 0.7-2 µm	March 2018	3	1	4.62
POM 2-20 µm	March 2018	3	1	16
POM 20-48 µm	March 2018	3	1	5.4
DOM	December 2016	3	3	208±0.12
Soil	December 2016	3	3	4.28±0.02
Sediments	December 2016	3	3	9.6±0
Balanites sp.	December 2016	3	3	11.5±0.04
Salvadora persica	December 2016	3	3	9.4±0.08

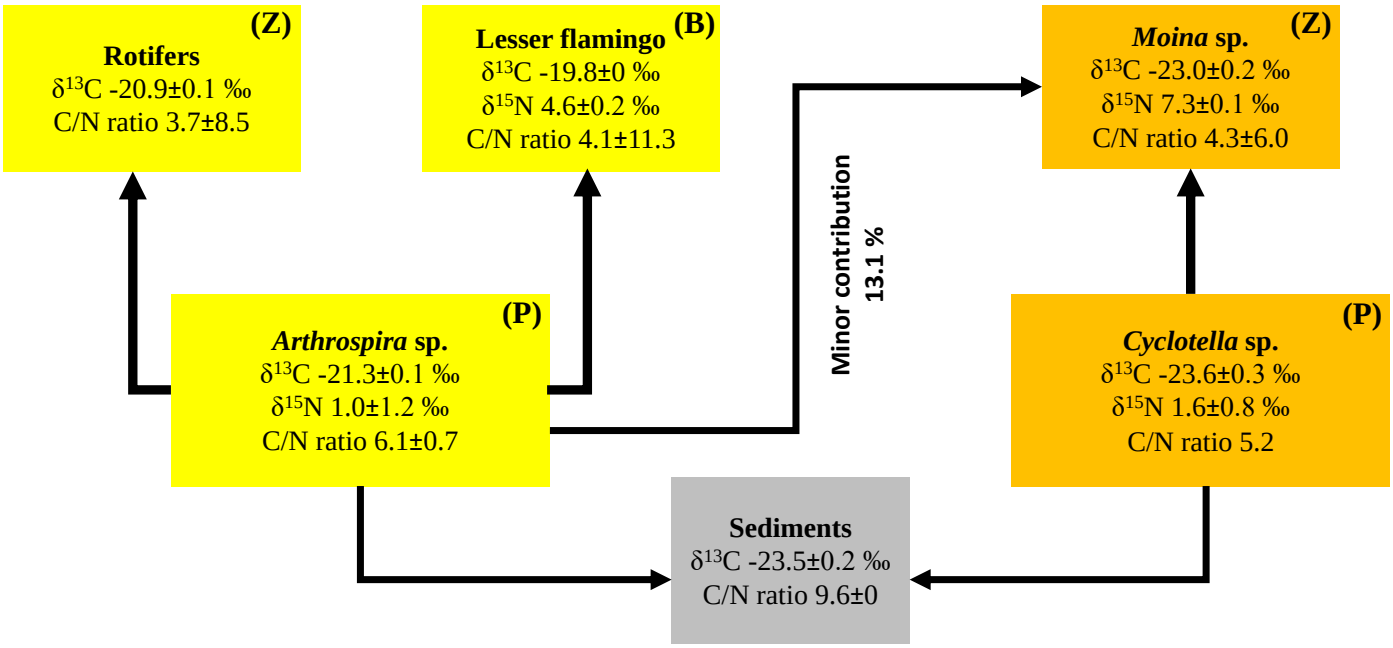

Figure 4.4 Schematic illustration showing the main carbon pathways in the pelagic food web in Lake Bogoria in the wet season (December 2016). Carbon pathways are represented by black solid arrows. Z= zooplankton, P=phytoplankton, B= bird.

4.7 Discussion

4.7.1 Seasonal composition of plankton communities in Lake Bogoria.

Lake conditions during the wet season (low conductivity and deeper water) suggest that the salinity in the epilimnion was much lower than in the dry season. This may have been responsible for the dominance of *Moina* sp. *M. micura* is a successful inhabitant of lower salinity lakes, such as the Cabiúnas lagoon in Brazil (Santangelo *et al.*, 2008). The appearance of *Cyclotella* sp. in the wet season can also be attributed to decreased salinity at this time. Melack (1979) suggested that in saline lakes, temporal variation in algal communities can be related to changes in physiochemical conditions. Rainfall is the main seasonal driver affecting salinity (via dilution), suspended sediment (via runoff from the terrestrial catchment) and nutrient redistribution affecting growth of phytoplankton in African lakes (Talling, 1986; Dumont *et al*., 1994). Other factors such as wind patterns (which can cause near-surface turbulence and mixing), ionic composition and alkalinity could also play a role (Hecky and Kilham, 1973; Talling, 1986).

Paleolimnological evidence suggests that lake level variation and associated changes in salinity can drive changes in zooplankton and phytoplankton communities in Lake

Sonachi, another African saline lake (Verschuren *et al*., 1999). Such lakes are characterised by specialised organisms with a tolerance for high osmolarities (Hecky and Kilham, 1973; Cooper and Wissel, 2012). For example, the rotifer *Brachionous plicatilis* can tolerate high salinity, but is unable to survive at lower osmolarities (Pennak, 1945; Epp and Winston, 1977; Thorp and Covich, 2009). Thus, the decreased salinity in the wet season can contribute to the decrease in the density of rotifers observed in Lake Bogoria.

In the dry season (March 2018), the phytoplankton community in Lake Bogoria consisted only of *Arthrospira* with no observed record of *Cyclotella* sp. This may have been caused by the decreased in lake level and increased surface salinity at this time. *Moina* sp. also seemed to have disappeared. This may have been a direct effect of the increase in salinity at this time, but is also likely to have been a consequence of the loss of *Cyclotella* sp. (the main dietary item for *Moina* sp. in the wet season). Furthermore, the high density of *Arthrospira* sp. in this season in Lake Bogoria may have interfered with the filtration process of *Moina* sp. The availability and characteristics of available food items (e.g. morphology and quality) for zooplankton are known to affect feeding in zooplankton (Jeppesen *et al.,* 2007; Gonçalves *et al.*, 2007; Thorp and Covich, 2009; Burian *et al.,* 2013).

4.7.2 Trophic interactions in the pelagic food web

In the wet season (December 2016), *Cyclotella* sp. is likely to have been the main source of carbon for *Moina* sp. or perhaps *Cyclotella*-derived carbon via the microbial chain. Experimentally, tropical *Moina micrura* can feed on a range of particle sizes from unicellular picophytoplankton to large phytoplankton (≥40 μm) (Pagano, 2008). However, substantial feeding of *Moina* sp. on the filamentous *Arthrospira* sp. is unlikely to have occurred because these algae appear to interfere with the food filtration process employed by *Moina* sp. Similarly, it has been reported that feeding of the cladoceran *Daphnia* was inhibited by filamentous Cyanobacteria clogging their filtration device (DeMott *et al.,* 2001). Instead, *Moina* sp. have probably evolved to feed on smaller food items such as unicellular *Cyclotella* sp. This was confirmed by a simple two pool isotope mixing model which showed that *Arthrospira* sp. is likely to have made a minor contribution to carbon assimilation by *Moina* in the wet season (Figure 4.4).

Arthrospira sp. did appear to be the main food source for pelagic rotifers in Lake Bogoria in both seasons sampled. In an isotopic study, Burian *et al*. (2014) found that *Arthrospira fusiformis* was an important food source for *Brachionus plicatilis* in Lake Nakuru, a saline lake in Kenya. Rotifers can feed on large phytoplankton due to their ability to enlarge their body size and ingest single colonies. *B. plicalitis* tended to be smaller when feeding on small items such as yeast, and larger when feeding on the large filamentous cyanobacterium *Schizothrix* sp. (Snell and Carrillo, 1984). *Arthrospira* is considered as a low-quality food for rotifers due to the fact that Cyanobacteria have low concentrations of the unsaturated fatty acids DHA (docosahexaenoic acid) and EPA (eicosapentaenoic acid), which are required for growth of zooplankton (Reitan *et al*., 1997; Brett *et al.,* 2009). However, appears that *Brachinous sp.* was still able to survive on an *Arthrospira*-dominated diet in Lake Bogoria. Burian *et al.* (2014) indicated that *B. plicalitis* might be able to use *Arthrospira* sp. as a food source by increasing rates of feeding and decreasing gut transition time. In contrast, the isotopic data collected for this thesis suggest that *Cyclotella* was not an important food item for rotifers, possibly due to competition from *Moina*.

The isotopic data suggest that lesser flamingo fed predominantly on *Arthrospira* in the wet season, as expected. This is consistent with other studies (e.g. Harper *et al.,* 2003; Krienitz *et al.,* 2013; Sanders, 2016), which support the idea that *Arthrospira* is a primary food item for lesser flamingo in Lake Bogoria and other soda lakes. Isotopic values for *Arthrospira* reported by Sanders (2016) for Lake Bogoria ranged from -21 to -21.8 ‰ for $\delta^{13}C$ and from 2.9 to 4.8 ‰ for $\delta^{15}N$ in the wet and dry seasons, respectively. Sanders (2016) also reported isotopic values for feather detritus from flamingos which ranged from -15.9 to -18 ‰ for $\delta^{13}C$ and from 4.5 to 8.4 ‰ for $\delta^{15}N$, in the wet and dry seasons, respectively. In the present study, the $\delta^{13}C$ signatures of *Arthrospira* ranged from -21.3 to -24.9 ‰ for $\delta^{13}C$ and from 1 to 2.1 ‰ for $\delta^{15}N$ in the wet and dry seasons, respectively. The $\delta^{13}C$ and $\delta^{15}N$ signatures of feathers of lesser flamingo in the present study were -19.8 ‰ and 4.6 ‰, respectively. The isotope signatures of *Arthrospira* and of the feathers of lesser flamingo in both the present study and in the study of Sanders (2016) suggest that *Arthrospira* is an important food item for lesser flamingos in this lake. Unfortunately, we did not collect lesser flamingo feathers in the dry season, which would have been useful. Hence, the present study is restricted to the wet season in terms of linking the isotope signature of feathers to the planktonic food web. The isotopic signature of

plankton reflects a specific period of time, while feathers reflect diet of the birds over a longer period (Hobson and Clark, 1992). There is, therefore, a need to put more effort into sampling of plankton over longer time periods which are consistent with feather formation in order to avoid misleading interpretations.

The fact that both the lesser flamingo and rotifers were feeding significantly on *Arthrospira* in the wet season, suggests that they were in potential competition. To the author's knowledge, this is the first study to highlight this as a potential phenomenon using stable isotope analysis in saline lakes. However, the extent to which consumption of *Arthrospira* by rotifers critically influences food availability for flamingos will depend on the size of the rotifer population and its feeding rate, relative to the abundance of *Arthrospira*. This could be influenced by a range of other limiting factors, including rotifer fecundity, predation and the effects of lake water quality. Some rotifers (for example *Brachionous calyciflorus*) have the highest reproductive rates for metazoans (Bennett and Boraas, 1989). The development time of rotifers is short which means that they can reach high abundance in short periods when environmental conditions are favourable for reproduction and growth (Kostopoulou *et al*., 2012). High densities of rotifers will ultimately lead to high *Arthrospira* consumption rates. The density of rotifers in the dry season was high, suggesting they may indeed have affected the food availability for lesser flamingos at this time. In the wet season, rotifers probably had a lower impact on *Arthrospira* due to their lower density at that time. Although, the density of *Arthrospira* in the wet season was half that in the dry season, the density in both seasons was low relative to reports by Harper *et al*. (2003) in the same lake. They reported that the densities of *Arthrospira* in Lake Bogoria varied from 3375 coil ml^{-1} in 2000 to 20826 coil ml^{-1} in 2003 (See also Table 4.2). Note that it was not possible to compare the *Arthrospira* density data collected here (measured as coil ml^{-1}) directly with all other studies because different researchers employed different units. For example, Kihwele *et al*. (2014) used filaments ml^{-1}, and Krienitz and Kotut (2010) used mg L^{-1}. Kihwele *et al*. (2014) found a positive relationship between populations of lesser flamingo and the density of *Arthrospira* sp. in Lake Manyara, Tanzania. Krienitz and Kotut (2010) suggested that a reduction in *Arthrospira* sp. density might be a reason for weakening of flamingos, making them more vulnerable to infection by bacteria such as *Pseudomonas aeruginosa* and *Mycobacterium avium* (Njuguna and Owuor, 2006; Krienitz and Kotut, 2010). These combined factors (i.e. starvation with infection) were suggested to be a

possible reason for massive flamingo die-off in Lake Nakuru in 1974 (Sileo *et al*., 1979). Die-off of flamingos was also reported at Lake Bogoria in 1993 and 2000 (Harper *et al*., 2003). Besides the problem with starvation, the weakening of flamingos can also result from other factors such as ingestion of cyanotoxins and agrochemicals. The latter is more likely in other lakes such as Nakuru, which drain catchments containing urban areas and intensive farmland (Njuguna and Owuor, 2006; Krienitz and Kotut, 2010). Other factors that influence the density of *Arthrospira* in Lake Bogoria include periods of lower salinity which could promote the growth of green algae that compete with *Arthrospira* (Ward, 2015). Krienitz *et al.* (2012) also found that the green alga *Picocystis salinarum* ($>3\times10^9$ cells l^{-1}) replaced *Arthrospira* sp. in Lake Bogoria in 2006. In addition to changes in water level and salinity, factors such as nutrient concentrations and the presence of cyanophages (viruses which infect Cyanobacteria) could influence the population of *Arthrospira* sp. (Melack, 1988; Peduzzi *et al*., 2014; Harper *et al.*, 2016; Amer *et al*., 2018).

Although, it is known that lesser flamingo mainly feed on *Arthrospira*, they may also feed on other food sources such littoral, shallow and benthic diatoms, as well as small zooplankton (Tuite, 2000; Robinson, 2015). Tuite (2000) observed that flamingos can switch to feeding on benthic diatoms during a reduction in *Arthrospira* density. However, the $\delta^{13}C$ and $\delta^{15}N$ signatures of flamingo's feather were closely associated with the base of the food web (e.g. *Arthrospira*) in Lake Bogoria, suggesting that other dietary items sampled from this lake (e.g. zooplankton and other phytoplankton) do not make substantial contributions to the diet of the lesser flamingo (Figure 4.4). Although, rotifers can be captured by filtering device of flamingos, the results do not support this connection. Rotifers may have developed mechanisms to escape from predation by lesser flamingo; such as vertical migration deeper in the water column (Ohman, 1988; Gliwicz, 1986; Boeing *et al*., 2006; Garcia *et al*., 2007).

However, it should also be noted that the sample lesser flamingo feathers may have formed when the flamingo not resident at this lake. However, the isotopic values of flamingo's feather are a closely associated with those measured for with *Arthrospira* in this lake, and are in reasonable agreement with existing data for this lake (Sanders 2016), implying that feathers were likely formed a resident lesser flamingo at the lake.

The isotopic results presented here suggest that *Cyclotella* sp. was not an important dietary item for flamingos, probably due to their small size. The isotope data also suggest that *Moina* sp. do not contribute significantly to the diet of the lesser flamingo. This is

probably due to the large size of *Moina*. Lesser flamingos filter food particles from 200 μm (Jenkins, 1936) to 800 μm (Vareschi, 1978). Their filtering devices contain excluders that protect the delicate filtering apparatus from damage by preventing larger particles (Vareschi, 1978; Robinson, 2015) from entering the filtering pathway (Jenkin, 1957).

A key context for these findings is that Lake Bogoria shows continued increasing lake levels (Kiage and Douglas, 2020). Such changes may have potentially severe consequences for the biodiversity of the East African saline lakes (Kiage and Douglas, 2020). This also might lead to decreases in the population of the flamingos in these lakes (IPCC, 2007: Kiage and Douglas, 2020). The results of this study have suggested a pronounced seasonality in the occurrence of *Moina* sp. and *Cyclotella* sp. in Lake Bogoria that can be linked to changing seasaonal salinity. Extending such variability over longer timescales, the lake may increasingly became much fresher during the wet season. The data presented here indicate that these organisms are not utilised by flamingos in this lake. Therefore, such seasonal/climaticially induced changes in planktonic food web structure of Lake Bogoria presents a potential long-term challenge for lesser flamingos in terms of food availability in Lake Bogoria.

The climate of the East African Rift Valley is predicted to get wetter in the near future due to the influence of increased Greenhouse gas concentrations in the atmosphere (De Wit and Stankiewicz, 2006; Thomson *et al*., 2018). Under this scenario, flamingos which typically rely on a narrow range of planktonic food items (primarily *Arthrospira* sp.) may be more exposed to climatic perturbations, because the convertion of saline lakes to a much fresher state is likely to have a negative impact on endemic plankton in these lakes, which are adapted to high osmolarities (Cooper and Wissel, 2012).

Additonally, the isotopic results suggest that the cladoceran *Moina* sp. does not significantly feed on *Arthrospira* sp. in the wet season. However, the data do suggest that rotifers feed on *Arthrospira* sp. in both seasons. This may result in competition between rotifers and lesser flamingo for food - particularly in the dry season, which may influence flamingo abundance. This study is limited the collection of samples at only two points in time. This is clearly not adequate to draw firmer conclusions about seasonal patterns. Additional (and more frequent) fieldwork is needed to confirm the relationships postulated here.

CHAPTER FIVE: THE IMPORTANCE OF AUTOCHTHONOUS AND ALLOCHTHONOUS RESOURCES IN THE PELAGIC FOOD WEBS OF TWO TROPICAL FRESHWATER LAKES: INSIGHTS FROM STABLE ISOTOPE ANALYSIS AND C/N RATIOS.

5.1 Introduction

Biological communities in lakes are supported by different carbon sources. These can be either autochthonous (e.g. primary production that is produced inside the aquatic ecosystem) or allochthonous (e.g. terrestrial photosynthate from the surrounding catchment which is transported to the aquatic ecosystem via hydrological or aeolian pathways) (Grey *et al.,* 2000; Tanentzap *et al.,* 2014).

The relative importance of allochthonous and autochthonous carbon sources will vary in different aquatic food webs (Grey *et al,* 2000; Grosbois *et al.,* 2017). Allochthonous carbon will usually make more significant contributions to zooplankton and other components of the food web in lakes that receive high inputs of those sources (Tanentzap *et al.,* 2017) and have strong hydrological and physical connections with their catchments (Babler *et al.,* 2011; Tanentzap *et al.,* 2014; Tanentzap *et al.,* 2017). Taipale *et al.* (2016 a) suggest that the importance of terrestrial carbon sources to freshwater zooplankton increases when there is a decrease in phytoplankton production, caused by, for example, an increase in allochthonous inputs which can trigger shading effects (Brett *et al.*, 2012). However, Galloway *et al*. (2014) suggest that autochthonous sources are more important to lake zooplankton, even in lakes with high allochthonous inputs. Differences in feeding selectivity between zooplankton groups can also change the degree of utilisation of allochthonous and autochthonous carbon sources (Berggren *et al.,* 2015; Kiørboe, 2011; Giering *et al.,* 2018). For example, Cladocera are non-selective feeders and, therefore, may assimilate more autochthonous carbon if this becomes more abundant in the pelagic zone (Barnett *et al.,* 2007; Berggren *et al.,* 2015). Zooplankton also differ in carbon use efficiency (i.e. C assimilated / C consumed) depending on food quality and availability (Koussoroplis *et al.,* 2013). This can lead to differences in the relative uptake of allochthonous and autochthonous carbon (Matthews and Mazumder, 2003). There is disagreement in previous studies as to whether the relative importance of allochthonous and autochthonous carbon to lacustrine food webs reflects differences in the nature of lake catchments, the characteristics of the zooplankton present or variations in lake

productivity (which drives the availability of photosynthate). Information on the relative contribution of different carbon sources is especially poor for tropical lakes, particulary in the context of information derived from stable isotope studies (Kupfer *et al*., 2006; Fetahi *et al*., 2018). Additional research is, therefore, needed in tropical systems to reconcile these different findings (Tanentzap *et al*., 2017).

In this chapter an attempt is made to disentangle the relative contributions of different carbon sources to zooplankton in two tropical freshwater lakes. The study was conducted in Lakes Naivasha and Baringo in the Kenyan Rift Valley. Both lakes are designated Ramsar sites (Harper *et al*., 2011; Omondi *et al*., 2015). Both have high biological diversity (Omondi *et al.*, 2017) and support important fisheries (Hickley *et al.*, 2004; Omondi *et al.*, 2017). In addition, they provide water for irrigation, wildlife and livestock and they attract many people for tourism (Odada *et al*., 2006; Otiang'a-Owiti and Oswe, 2007). Both lakes face threats from increasing human populations (Omondi *et al*., 2017). The combined human population in the two lake catchments is about 900,000 (Kenya Republic, 2010). Almost all of this is in the catchment for Lake Naivasha, which has major towns and a strong agricultural industry. In contrast, the catchment for Lake Baringo is dominated by rural pastoralism. The increasing human population in the catchments of these lakes has led to an increase in the demand for agricultural and urban development land (Omondi *et al*., 2017).

The immediate riparian zone of Lake Niavasha is largely used for horticultural and floricultural industries (Hickley *et al.*, 2004; Otiang'a-Owiti and Oswe, 2007). Such intensive activities are accompanied by high usage of pesticides and fertilisers, significant water extraction, and growing demands for housing and latrines for workers (Enniskillen, 2002). In addition, large areas of the wider lake catchment are dedicated to rain-fed agriculture (Otiang'a-Owiti and Oswe, 2007). Runoff of waste water effluent, nutrients and pesticides are believed to have a significant impact on the lake waters (Hubble and Harper, 2001; Omondi *et al*., 2017).

The most noticeable characteristic of Lake Baringo is its high turbidity. This is believed to be a recent phenomenon that reflects high rates of soil erosion from the catchment (Johansson and Svensson, 2002; Odada *et al*., 2006), caused by naturally unstructured soils that have been disturbed by deforestation and grazing (Johansson and Svensson, 2002; Hickley *et al.*, 2004). Large numbers of livestock (e.g. approximately 300,000

cattle, 200,000 sheep and 900,000 goats) are kept in the catchment and these animals are believed to degrade the soil and vegetation (Hickley *et al.*, 2004; Omondi *et al*., 2017). The high turbidity of Lake Baringo may be responsible for its lower algal production compared to Lake Naivasha, (Kallqvist, 1987; Schagerl and Oduor, 2003). Lake Baringo also has a larger catchment area (8655 km^2) than Lake Naivasha (3267 km^2) (Hickley *et al.*, 2004; Kallqvist, 1987). The differences in the size and character of the two catchment areas may result in a higher transport of allochthonous particles to Lake Baringo than to Lake Naivasha (Berggren *et al*., 2010), depending how catchment sediment yield scales with catchment area. Both lakes are at risk of losing ecosystem services and functions (Odada *et al*., 2006; Otiang'a-Owiti and Oswe, 2007). An analysis of the impacts of these differing allochthonous inputs upon these two lake food webs is therefore highly pertinent as it speaks to key issues concerning human impact on aquatic ecoystem goods and services in this region.

5.2 Aim

The main aim of the study is to determine the relative importance of allochthonous and autochthonous carbon sources to aquatic consumers (particularly zooplankton and fish) in Lake Baringo (which is relatively turbid) and Lake Naivasha (which is less turbid).

5.3 Objectives

- Elucidate the relative abundance of different zooplankton and phytoplankton taxa in Lakes Naivasha and Baringo.
- Identify and separate the carbon pools (e.g. phytoplankton, POM, terrestrial and littoral aquatic plant leaves and periphyton) that can act as food resources for zooplankton.
- Reconstruct the food web of each lake via stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) of each separate material or taxon, supplemented with an analysis of the C/N ratios for these food web components.
- Determine the fractional contribution of different food items to the diet of the principal zooplankton and fish taxa present using a simple mixing model.

It was hypothesised that zooplankton and fish in the relatively turbid Lake Baringo would have a higher dependence on allochthonous carbon sources compared to those sampled from the less turbid Lake Naivasha.

5.4 Study sites

5.4.1 Lake Naivasha

Lake Naivasha (Figure 5.1) is a freshwater lake (Harper and Mavuti, 2004) situated in a semi-arid region just south of the equator approximately 80 km north west of Nairobi (Hubble and Harper, 2001) in the eastern part of the Kenyan Rift Valley. It lies approximately 1885 m above sea level (water level fluctuates by ~5 m) (Harper *et al.*, 1990). Its surface area ranges from 100 to 150 km^2 due to these fluctuations (Harper and Mavuti, 2004). Mean depth ranges between 3 and 6 m (Harper *et al.*, 2011). Its freshness is due to runoff inputs via rivers and seepage losses (Gaudet and Melack, 1981), despite the local evaporation rate being typically greater than local rainfall (Harper *et al.*, 1995). The average air temperature is 21 °C (Hickley *et al.*, 2004) all year round.

The soils in the catchment are of volcanic origin (Odongo *et al.*, 2016), derived from ash and olivine basalts (Odongo *et al*., 2014). Catchment vegetation (Figure 5.2) includes forest, bush and wooded grasslands (Hubble, 2000), dominated mainly by C_3 plants (Grey and Harper, 2002). *Acacia* spp. are the dominant trees in the catchment (Harper and Mavuti, 2004). Most tend to come into leaf during the wet seasons and shed leaves during the dry seasons (Odongo *et al.*, 2016). The shoreline is dominated by *Cyperus papyrus* (Omondi *et al.*, 2017). *Cyperus papyrus* has the ability to reduce the impacts of catchment soil erosion by preventing the translation of fine particles into the lake (Boar and Harper, 2002). There are also floating rafts dominated by *Eichhornia crassipes* and *Salvinia molesta* (Harper *et al.*, 1995).

Water inflow is principally via two perennial rivers, the Malewa and the Gilgil (Harper *et al.*, 1990), and one seasonal river, the Karati (Omondi *et al.*, 2016). These rivers enter the lake from the north (Stoof-Leichsenring *et al*., 2011). The combined discharge of the Gilgil and the Karati is lower than in the Malewa (Tarras-Wahlberg *et al.*, 2002). The estimated average flow of the Malewa is 153 million m^3 annually (i.e. an average of 4.85 $m^3\ s^{-1}$), the estimated average flow of Gilgil is 24 million m^3 annually (i.e. an average of 0.76 $m^3\ s^{-1}$) while the flow of Karati is ephemeral and uncertain (Ase and Sernbo, 1986; Ase, 1987). The Gilgil river often contains higher concentrations of finer suspended sediment particles (fine clay and silt) than the Malewa and Karati rivers. This may be due to flow conditions or the propensity for erosion in the contributing catchments (Tarras-Wahlberg *et al.*, 2002). The Malewa River is the main source of suspended sediment load

due to its higher discharge and higher sediument yields in its catchment (Hubble, 2000). Accumulated sediment in the lake is mainly from the Malewa and Gilgil rivers (Rupasingha, 2002). The suspended sediment flux is estimated to be more than 7.07×10^6 tonnes from 1957 to 2001 (Rupasingha, 2002). In addition to suspended mineral particles these rivers contain particulate and dissolved organic matter and nutrients (e.g. N and P) (Hubble, 2000; Rupasingha, 2002; Kitaka *et al*., 2002).

Allochthonous inputs to both lakes will be enhanced during rainfall and wind events (Grey and Harper, 2002; Ndungu, 2014; Hubble, 2000). Nutrient inputs from the catchment may enhance phytoplankton production in the lake (Hubble and Harper, 2002). Aeolian and fluvial erosion can also transport allochthonous materials from the catchment into the lake (Grey and Harper, 2002; Hicks, 2012; Ndungu, 2014; Boar and Harper, 2002). Furthermore, animals such as hippos (*Hippopotamus amphibious*) can transport allochthonous organic matter into Lake Naivasha through their dung (Grey and Harper, 2002).

The electrical conductivity of the water in Lake Naivasha ranges between 250 µS cm^{-1} and 400 µS cm^{-1} (Harper and Mavuti, 2004) with pH ranging from 8 to 9 (Harper *et al.*, 1993). Total phosphorus and nitrogen concentrations range from 0.07 to 0.20 mg P L^{-1} and from 0.5 to 2.4 mg N L^{-1}, respectively, with an average Secchi depth of 50 cm in the late 2000s (Ballot *et al.*, 2009).

Phytoplankton has typically been dominated by the diatom *Aulacoseira* sp. (Hubble and Harper, 2002; Bergner and Trauth, 2004; Stoof-Leichsenring *et al*., 2012). The zooplankton community is composed of Cladocera, Copepoda and Rotifera (Mavuti, 1990; Green, 1993; Uku and Mavuti, 1994); dominant species are *Diaphanosoma excisum, Ceriodaphnia cornuta* (Cladocera) and *Thermocyclops oblongatus* (Copepoda) (Uki and Muvati, 1994). Copepoda and Cladocera are important dietary sources for fish (Britton *et al.*, 2007). Different fish species were reported in the lake, such as *Tilapia zillii, Oreochromis leucostictus, Cyprinus carpio, Barbus amphigranna*, *Micropterus salmoides* and *O. niloticus* (Harper *et al.*, 1990; Britton *et al*., 2007; Omondi *et al.*, 2017). There is a diverse community of water-dependent birds with a large population of fish eagles *Haliaeetus vocifer* (Harper *et al.*, 2002; Omondi *et al.*, 2017). The lake is also an important habitat for riparian mammals, mainly *H. amphibius* (Harper *et al.*, 2011).

5.4.2 Lake Baringo

Lake Baringo (Figure 5.1) is a freshwater lake just north of the equator, about 250 km north of Lake Naivasha (Omondi *et al.*, 2017). It is situated in the eastern part of the Kenyan Rift Valley at an altitude of 975 m (Omondi *et al.*, 2015), in a semiarid region (Britton *et al.*, 2009). The annual rainfall ranges between 600 and 900 mm a^{-1} and mean annual potential evaporation is 2600 mm a^{-1} (Tarits *et al.*, 2006). The average air temperature is 25°C (Kiage and Liu, 2009). Its surface area is about 130 km^2 (Lwenya and Yongo, 2010), with a maximum length and width of 21 km and 13 km, respectively (Tarits *et al.*, 2006). The mean water depth is 5.7 m, but the maximum depth can be 9.5 m during elevated water levels (Omondi *et al.*, 2014 a). Lake Baringo, like Lake Naivasha, has relatively low salinity despite the fact that evaporation is higher than precipitation, due to groundwater seepage out (Ngaira, 2006).

The geology of the lake catchment is volcanic, and the area is still tectonically active (Tarits *et al.*, 2006; Dunkley *et al.*, 1993). Soils are rich in clay and silt (Hickley *et al.*, 2004). The vegetation in the lake catchment (Figure 5.3) is dominated by C_3 perennial bushes such as *Acacia gerardii* and *Balanites aegyptiaca* (Wetang'ula, 2013). Littoral aquatic plants are less developed around the lake than Naivasha (Hickley *et al.*, 2004). The shoreline is dominated by *Sesbania sesban* (Harper, *pers. comm*.).

There are two perennial rivers - the Molo and the Perkerra - and many seasonal rivers that supply the lake, including the Ol Arabel, Endao, Mukutan, Chemeron, Ndau, Kutwa and Kapthurin (Tarits *et al*., 2006; Omondi *et al.*, 2015). The northern zone of the lake receives fewer riverine inputs than in the south (Tarits *et al*., 2006; Ouma and Mwamburi, 2014). The inflow of the Molo River in 1973 was 126×10^6 m^3 annually (i.e. an average discharge of 4 m^3 s^{-1}) while the inflow of the Perkerra was 39×10^6 m^3 annually (ca. 1.14 m^3 s^{-1}) (Ojany and Ogendo, 1973). The Molo and the Perkerra are also the main sources of suspended sediment loads from eroded catchment soils to the lake (Tarits *et al*., 2006). This load includes sediment-associated organic matter and suspended nutrients (Ouma and Mwamburi, 2014; Omondi *et al*., 2011; Onyando *et al*., 2005). The high inputs of allochthonous materials via these rivers are more pronounced in the rainy seasons (Ngaira, 2006). The larger catchment area of Lake Baringo makes it more exposed to wind erosion than Lake Naivasha especially in dry periods (Kiage and Liu, 2009; Ouma and Mwamburi, 2014). Additional quantities of allochthonous materials enter the lake via aerial deposition particularly in the afternoon and evening on northeast winds (Ouma and

Mwamburi, 2014). As in Lake Naivasha, hippos can also transport allochthonous resources into Lake Baringo through their dung.

The electrical conductivity of lake water was measured as 578 µS cm^{-1} (Omondi *et al.*, 2017) with pH ranging between 8.5 and 10.5 (Oduor *et al.*, 2003). The lake has limited light penetration (Okech *et al.*, 2018) as a result of high turbidity (Odada *et al.*, 2006; Omondi *et al.*, 2015). The average Secchi depth in Lake Baringo between 2008 and 2013 was between 35 cm and 40 cm. This can decrease significantly in rainy seasons, to as little as 7 cm (Omondi *et al.*, 2014 a).

The phytoplankton community is dominated by Cyanobacteria, green algae and diatoms (Schagerl and Oduor, 2003). The zooplankton community is typically composed of Cladocera, Copepoda and Rotifera (Omondi *et al.*, 2015). Zooplankton, especially the cladocerans *Diaphanosoma excisumm* and *Moina micrura* are important food items for fish (Omondi *et al.*, 2013). The fish community is dominated by five species: *Oreochromis niloticus*, *Barbus intermedius*, *Protopterus aethiopicus*, *Clarias gariepinnus* and *Labeo cylindericus* (Aloo, 2002). Aloo (2002) reported that *O. niloticus* comprised about 80 %. The lake is also an important habitat for birds such as *Falco naumanni*, *Anhinga rufa*, *Ardeola ralloides*, *Circus macrourus*, *Podiceps cristatus* and *Ardea alba*), crocodiles (*Crocodylus niloticus*), lizards (*Varanus* sp.), frogs (*Rana* sp.) and *H.amphibius* populations (Omondi *et al.*, 2017).

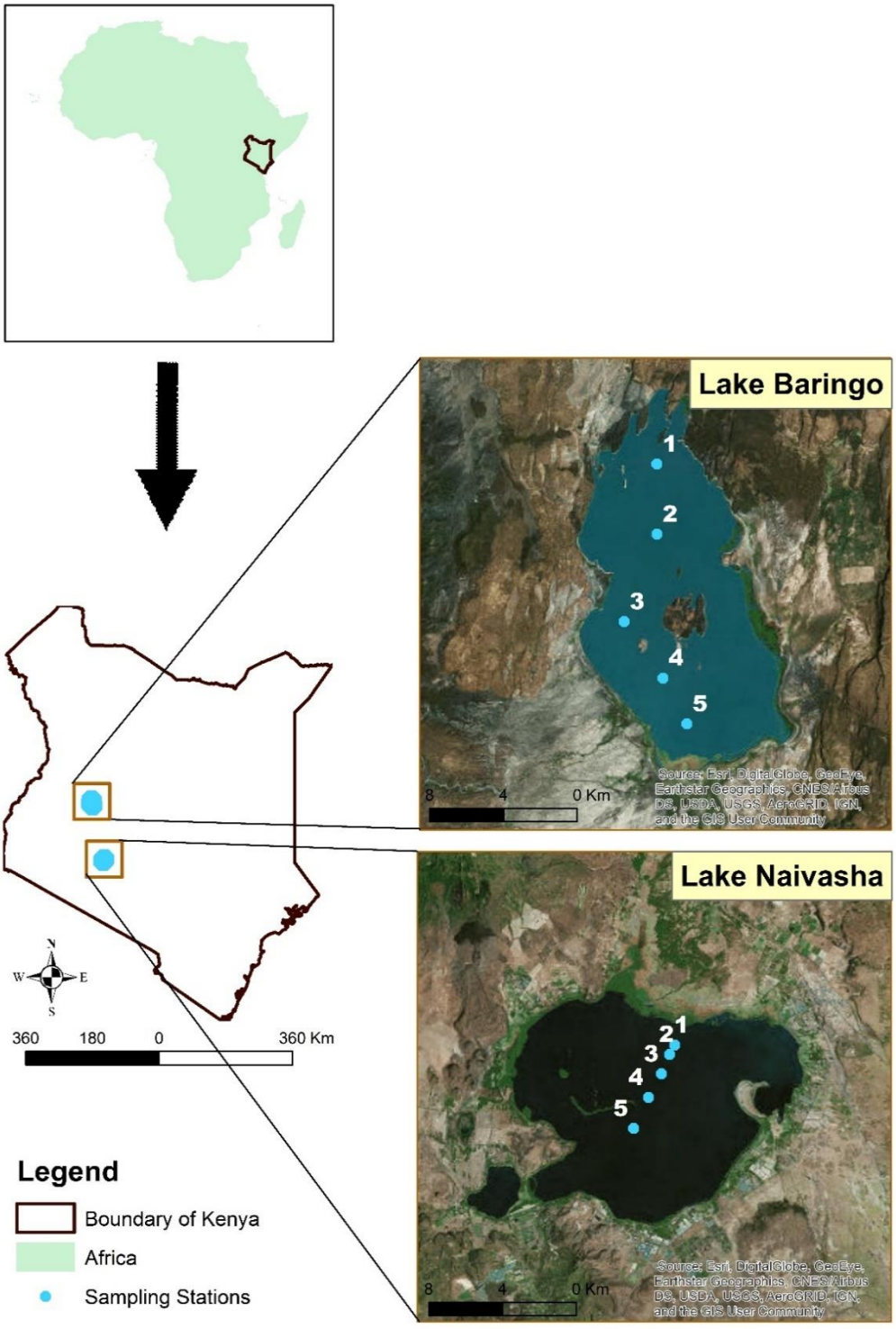

Figure 5.1 Map showing the African and Kenyan context and the pelagic sampling stations (1,2,3,4 and 5) on Lake Naivasha and Lake Baringo. Sources: Esri, DgitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USGS, AeroGRID,IGN, and the GIS User Community. Lake Baringo Looks different from Lake Naivasha due to its high light reflectance (because of high turbidity).

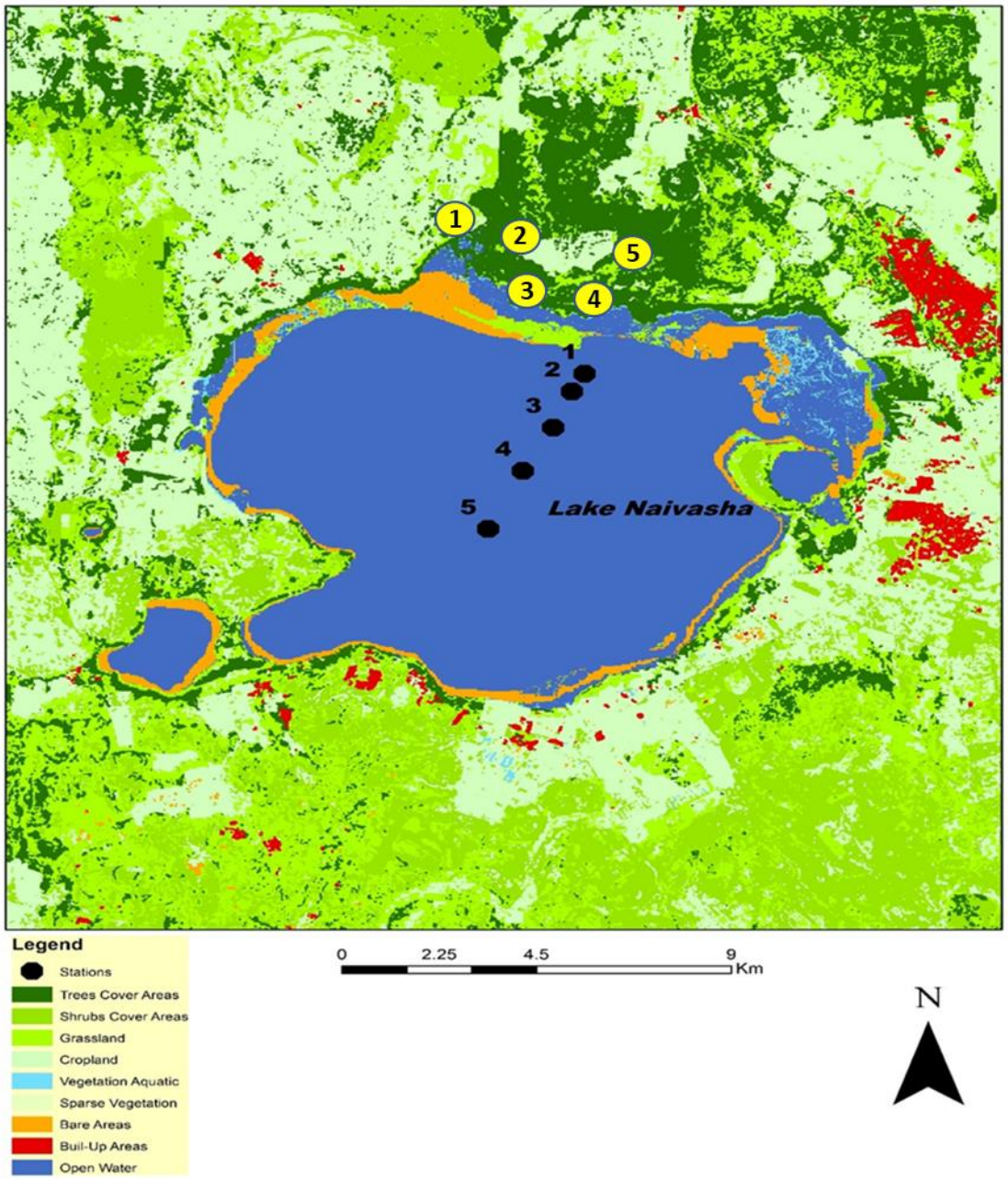

Figure 5.2 Map of Lake Naivasha showing the vegetation of the terrestrial environs, the location of pelagic sampling stations and the approximate locations of terrestrial and littoral samples (yellow circles). Source: Esri, DgitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USGS, AeroGRID,IGN, and the GIS User Community.

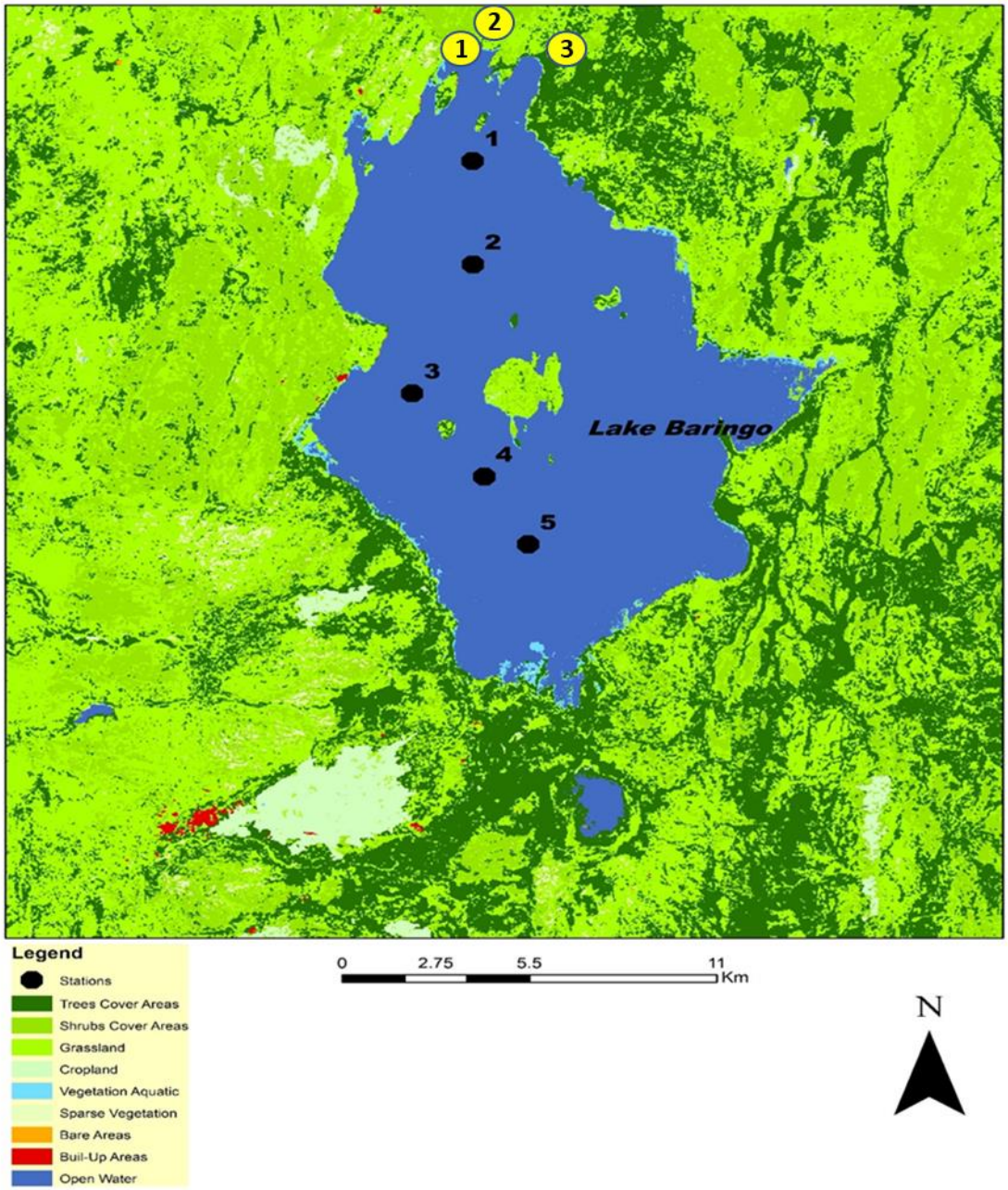

Figure 5.3 Map of Lake Baringo showing the vegetation of the terrestrial environs, the location of pelagic sampling stations and the approximate locations of terrestrial and littoral samples (yellow circles). Source: Esri, DgitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USGS, AeroGRID,IGN, and the GIS User Community.

5.5 Methods

Detailed methods are described in Chapter 2. Briefly, samples of the main components of the pelagic food web and from the major terrestrial and littoral carbon sources were collected from Lake Naivasha (November 2016 (considered the wet season)) and March 2018 (dry season) and from Lake Baringo (December 2016 and March 2018). Samples of zooplankton, phytoplankton, fish, fractions of particulate organic matter (POM), soil, sedments, terrestrial and littoral aquatic plant leaves and periphyton derived from aquatic plants were identified, enumerated and analysed for stable isotope and C/N ratios. Chlorophyll a as well as several physical and chemical parameters were also measured.

5.6 Results

5.6.1 Physiochemical and biological features

Basic water quality variables and biological characteristics measured during the two sampling campaigns are shown in Table 5.1. Depth profiles of some physiochemical parameters measured (Appendices 5.1, 5.2, 5.3, 5.4, 5.5, 5.6, 5.7, 5.8, 5.9, 5.10, 5.11, 5.12, 5.13, 5.14, 5.15, 5.16). Neither lake showed any stratification during the sampling campaigns.

Table 5.1 Water quality and biological variables at the study sites during the two sampling campaigns. SD= standard deviation. n=number of replicates (i.e. one replicate for each station except chlorophyll a which was four replicates for each station).

		Lake Baringo			**Lake Naivasha**	
Variables	n	Wet season Dec. 2016 mean±SD	Dry season Mar. 2018 mean±SD	n	Wet season Nov. 2016 mean±SD	Dry season Mar. 2018 mean±SD
Depth (m)	5	9.6±0.7	8.3±0.2	5	6.4±0.6	4.9±0.5
Surface pH	5	8.7±0	8.6±0.08	5	8.4±0.05	8.5±0.2
Surface dissolved oxygen (DO) mg L^{-1}	5	7.0±0.2	8.5±0.6	5	6.7±0.4	8.8±0.9
Surface water conductivity µS cm^{-1}	5	477±1.5	543.4±3.9	5	262.6±0.5	331.8±1.3
Surface water temperature °C	5	26.3±1.0	26.9±1.3	5	20.2±0.1	22.4±1.0
Secchi depth cm	5	45.4±7.7	49±21.3	5	69.4±14.2	44.6±5.0
Density of phytoplankton L^{-1}	5	29.0×10^3 $\pm 17\times 10^3$	8.6×10^3 $\pm 2.5\times 10^3$	5	2.57×10^5 $\pm 13.4\times 10^3$	6.34×10^4 $\pm 6.5\times 10^3$
Chlorophyll a µgL^{-1}	20	3.0±0.9	-	20	6.6±2.7	-

Phytoplankton density in Lake Naivasha was significantly higher than that in Lake Baringo in both the wet and dry seasons ($p < 0.05$, Appendices 5.17 and 5.18). The algal community in Lake Baringo was dominated by *Aulacosiera* sp., *Closterium* sp. and *Microcystis* sp. In Lake Naivasha, *Aulacosiera* sp. was also a dominant taxon. Secchi depth in Lake Naivasha was significantly larger than that in Lake Baringo in the wet season (t-test $p < 0.05$, Figure 5.4., Appendix 5.19), but not in the dry season ($p > 0.05$, Figure 5.5., Appendix 5.20). In the dry season, the values of Secchi depth of Lake Baringo were slightly higher than in the wet season but the difference was not significant (Table 5.1). Secchi depth in Lake Naivasha was significantly lower in the dry season than in the wet season.

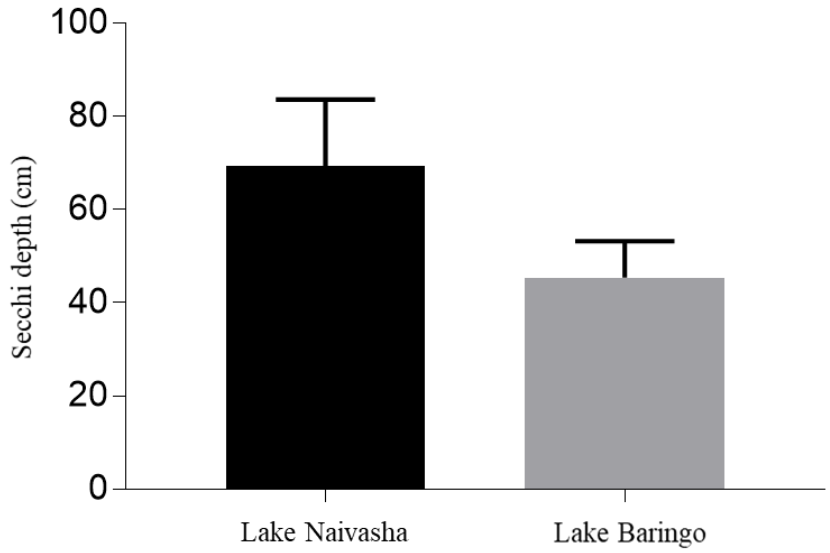

Figure 5.4 Mean (±SD) values of Secchi depth (cm) in Lake Baringo and Lake Naivasha during the wet season in 2016. Number of replicates was 5 (i.e. one replicate for each station).

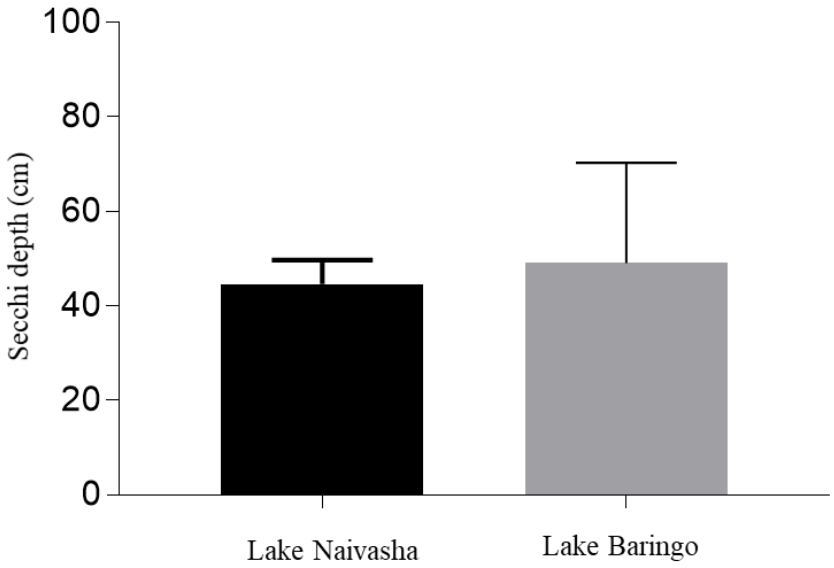

Figure 5.5 Mean (±SD) values of Secchi depth (cm) in Lake Baringo and Lake Naivasha during the dry season in 2018. Number of replicates was 5 (i.e. one replicate for each station).

5.6.2 Zooplankton density, composition and length

The density of different zooplankton taxa is shown for the two sampling campaigns in Table 5.2. In Lake Baringo, zooplankton were dominated by Cladocera (*Moina* sp.) in both seasons, which co-occurred with Copepoda and Rotifera in December 2016 (Table 5.2). Rotifers were not present in Lake Baringo in the dry season (March 2018). In Lake Baringo, the density of zooplankton in the dry season was higher than in the wet season (Table 5.2).

There were important differences in the abundance of different zooplankton taxa between the two sampling campaigns in Lake Naivasha. In the wet season (November 2016), Copepoda density was higher than that of Cladocera and Rotifera (Table 5.2). However, in the dry season (March 2018), Cladocera were dominant (especially *Diaphanosoma* sp.), with Copepoda and Rotifera less abundant. The total abundances of zooplankton in Lake Naivasha in the wet season were lower than in the dry season (Table 5.2).

Table 5.2 Zooplankton density in the pelagic zone of both lakes during the two sampling campaigns., Indiv.= individuals, SD= standard deviation. Number of replicates was 15 (i.e. three replicates at each station).

		Wet season	**Dry season**
Group	Taxon	Dec. 2016 (Indiv. L^{-1}) Mean±SD	Mar. 2018 (Indiv. L^{-1}) Mean±SD
Lake Baringo			
Cladocera	*Moina* sp.	0.5 ±0.3	12.1± 13.6
	Diaphanosoma sp.	0.3±0.2	2.3 ± 3.2
	Ceriodaphnia sp.	0.1± 0.1	Not present
	Chydorus sp.	0.001±0.003	Not present
	Macrothrix sp.	0.01±0.008	Not present
	Daphnia sp.	0.002±0.005	0.05± 0.10
Total density of Cladocera		1.0±0.4	14.5 ± 16.1
Copepoda			
	Thermocyclops sp.	0.05±0.04	Not present
	Cyclops sp.	0.003±0.006	2.1 ± 2.8
	Pseudodiaptomus sp.	0.003±0.006	Not present
	Mesocyclops sp.	Not present	0.04± 0.09
Total density of Copepoda		0.06±0.04	2.1 ± 2.8
Rotifers			
	Brachionus sp.	0.007±0.010	Not present
	Synchaeta sp.	0.003±0.006	Not present
Total density of Rotifera		0.01±0.008	
Total density of zooplankton		**1.1**	**16.7**
Group	Taxon	Nov. 2016 (Indiv. L^{-1}) Mean±SD	Mar. 2018 (Indiv. L^{-1}) Mean±SD
Lake Naivasha			
Cladocera	*Diaphanosoma* sp.	2.9±2.1	193.2± 99.4
	Chydorus sp.	0.09±0.14	Not present
	Ceriodaphnia sp.	0.03 ± 0.06	Not present
	Alonella sp.	0.03± 0.08	Not present
Total density of Cladocera		3.0 ± 2.2	193.2±99.4
Copepoda			
	Mesocyclops sp.	2.3 ± 3.4	0.2±0.3
	Thermocyclops sp.	1.6 ± 1.2	0.08± 0.18
	Cyclops sp.	Not present	3.4 ± 1.6
	Nauplii	0.054± 0.07	Not present
	Copepodites	0.06±0.14	Not present
Total density of Copepoda		4.0 ± 4.7	3.7 ±1.8
Rotifers			
	Asplanchna sp.	0.2± 0.1	Not present
	Brachionus sp.	0.1 ± 0.1	2.2± 1.9
	Lecane sp.	0.1±0.1	Not present
	Keratella sp.	0.03±0.08	Not present
	Trichocera sp.	0.03±0.08	Not present
	Euchinus sp.	Not present	0.08 ± 0.18
Total density of Rotifera		0.5 ±0.2	2.3±1.8
Total density of zooplankton		**7.7**	**199.3**

Total zooplankton abundances in both samplings of Lake Baringo were significantly lower than in Lake Naivasha ($p < 0.05$, Figures 5.6 and 5.7, Appendices 5.21 and 5.22). However, the Copepoda composition in Lake Naivasha was similar to that of Lake Baringo. The average lengths of Cladocera and Cyclopoida in Lake Baringo were lower than those in Lake Naivasha (Table 5.3).

Table 5.3 Average length (±SD) of zooplankton in the pelagic zone of Lake Naivasha and Lake Baringo. The average was calculated from approximately 20 individuals.

Lake Naivasha	Group	Average length ±SD
	Cladocera	853.0±162.4 µm
	Cyclopoida	1096.0±273.0 µm
Lake Baringo	Cladocera	596.2± 141.0 µm
	Cyclopoida	888.3±94.2 µm

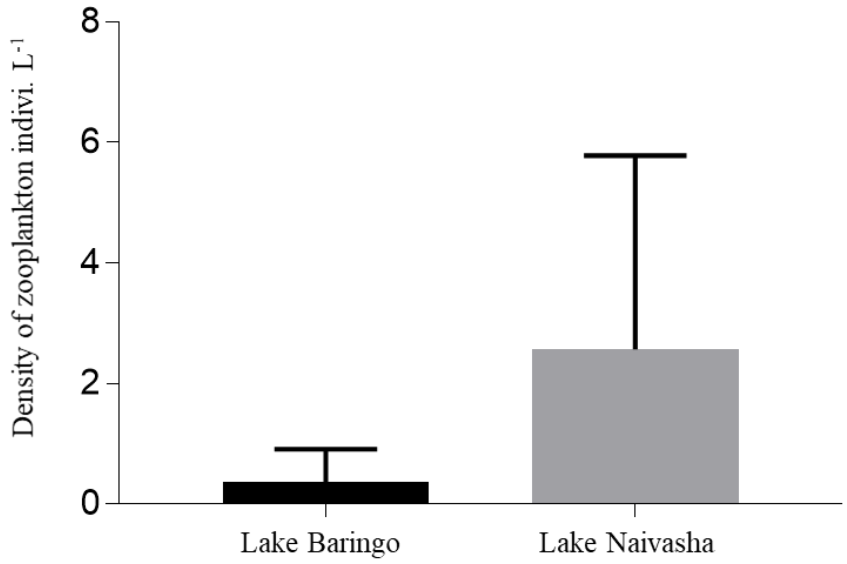

Figure 5.6 Mean (±SD) values of zooplankton density in Lake Baringo and Lake Naivasha during the sampling campaign in 2016. Number of replicates was 15 (i.e. three replicates for each station).

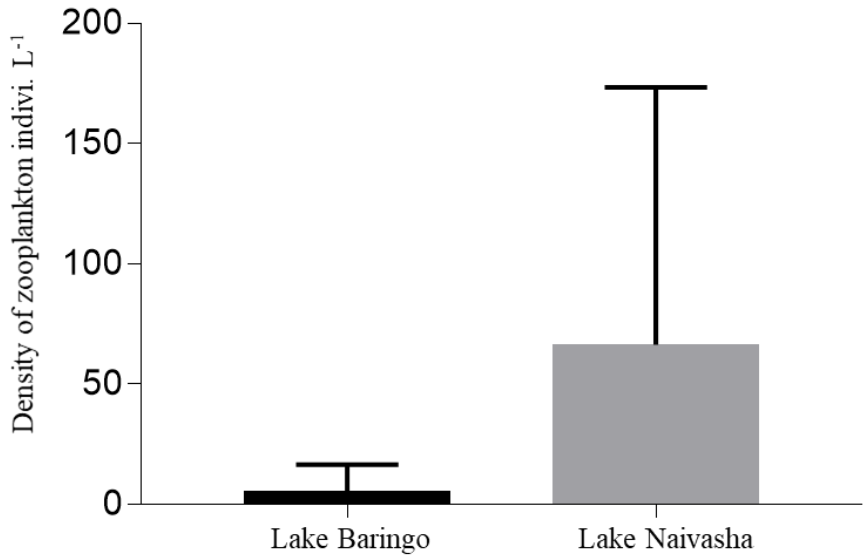

Figure 5.7 Mean (±SD) values of zooplankton density in Lake Baringo and Lake Naivasha during the sampling campaign in 2018. Number of replicates was 15 (i.e. three replicates for each station).

5.6.3 Stable isotope compositions and C/N ratios

The measured values of $\delta^{13}C$ and $\delta^{15}N$ of different taxa are summarised in Appendix 5.23 for Lake Baringo and in Appendix 5.24 for Lake Naivasha. The data are plotted in Figure 5.8 for the wet season and Figure 5.9 for the dry season for Lake Baringo and Figure 5.10 for the wet season and Figure 5.11 for the dry season for Lake Naivasha. The $\delta^{13}C$ and $\delta^{15}N$ signatures of different consumers in Lakes Baringo and Naivasha for the two sampling campaigns, together with those of their potential food sources are shown in Figures 5.8, 5.9, 5.10 and 5.11. Resource (or diet) polygons for selected zooplankton are also shown in these figures. These define the theoretical range of isotope ratios expected for the food consumed by each zooplankton taxon (see Section 2.10 Data analyses and Figure 2.5 for an explanation of how these polygons were constructed).

5.6.3.1 Trophic niches of zooplankton in different lakes

5.6.3.1.1 Lake Baringo

The $\delta^{13}C$ and $\delta^{15}N$ signatures of phytoplankton in the wet season (December 2016) suggest that phytoplankton may have made an important contribution to the diet of pelagic Cladocera. The $\delta^{13}C$ and $\delta^{15}N$ signatures of pelagic Cladocera and the 0.7-25 μm POM fraction, suggest that the latter may also have utilised by cladocerans. The mixing model (Equation 13) suggests that the carbon derived from phytoplankton accounts for 92 % of Cladocera carbon, while carbon derived from POM contributed 8 %. The explanation and justification for using this mixing model and for including these carbon sources (and for not including the other sources) in this model can be found in Chapter 2 (see 2.10 Data analyses for details).

The small difference in $\delta^{15}N$ signatures between pelagic Cladocera (6.2±0.7‰) and the periphyton (5.6±0.4‰) and aquatic plants (*Eichhornia crassipes*: 5.9±0.4‰) indicate that these carbon sources were probably not important food sources. The $\delta^{13}C$ values of pelagic zooplankton were lower than those of DOM. This suggests that DOM is not an important carbon source for zooplankton.

The $\delta^{13}C$ and $\delta^{15}N$ values of pelagic mixed Cyclopoida and pelagic adult cyclopoids were similar and appeared to suggest a high dependence on the 0.7-25 μm POM fraction. The $\delta^{13}C$ signatures of these consumers were also close to those of phytoplankton and the $\delta^{15}N$ values of these zooplankton were higher than those of the phytoplankton, indicating that phytoplankton are a potential carbon source for these zooplankton. Since both the $\delta^{13}C$ values of phytoplankton and POM were slightly lower than that of the zooplankton, it was not possible to apply a mixing model. Both could represent food sources for the zooplankton.

The mixing model (Equation 15) suggests that the carbon derived from autochthonous carbon accounts for 82% of the carbon in pelagic Cladocera and Cyclopoida. Carbon derived from allochthonous carbon contributed 18% of zooplankton carbon (see 2.10 Data analyses for details).

The stable isotope ratios for pelagic Cladocera in the dry season (March 2018) and (<48 μm POM) suggest that POM may be an important dietary source for pelagic Cladocera. The small difference in $\delta^{15}N$ between pelagic Cladocera (4.7±0.1‰) and the other two

POM fractions (2-20: 4.3±0.4‰ and 20-48 μm: 3.5±0.4‰) indicates that these POM were probably not important. The isotope data suggest that pelagic Cyclopoida may have been feeding on pelagic Cladocera in 2018, also 2-20 μm POM and 20-48 μm POM, may have contributed. The $\delta^{13}C$ values of terrestrial plant leaves (*Acacia tortilis* and *Sesbania sesban*) in the wet season were very close to the $\delta^{13}C$ values of phytoplankton in the wet and dry seasons, and to the 0.7-25 μm POM fraction in the wet season, <48 μm POM, 2-20 μm POM, 20-48 μm POM in the dry season; their overlapping isotopic signatures were difficult to distinguish from each other. The C/N ratios of allochthonous carbon sources (*A. tortilis* and *S. sesban*) were 12.55 and 14.34 respectively (Table 5.4); C/N ratio of 0.7-25 μm POM was 10.5 in the wet season. The C/N ratios of <48 μm POM, 2-20 μm POM, 20-48 μm POM were 7.2, 9 and 11, respectively in the dry season (Table 5.4). The C/N ratios of phytoplankton were 5.99 and 8.75 in the dry and wet seasons respectively (Table 5.4). These data suggested that phytoplankton made an important contribution to the POM fractions.

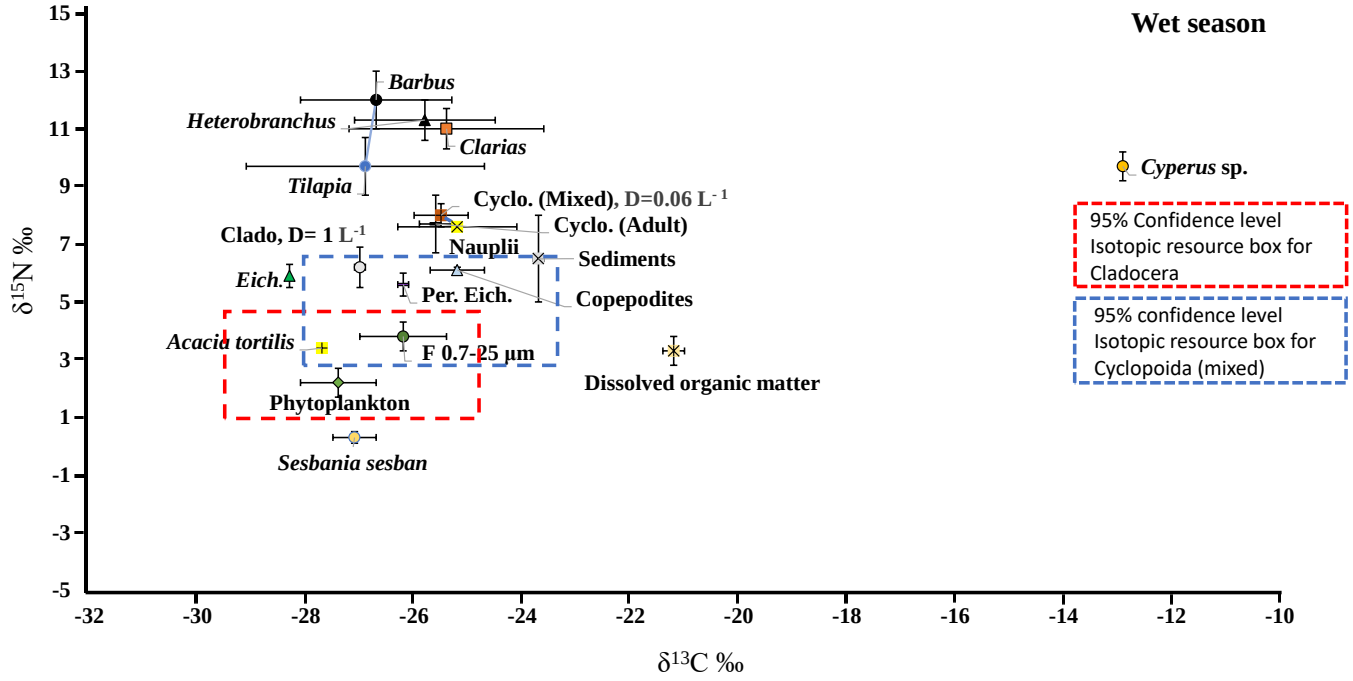

Figure 5.8 Mean (±1SD) values of $\delta^{13}C$ plotted against $\delta^{15}N$ for the main components of the pelagic food web in Lake Baringo and from the major terrestrial and littoral carbon sources in the wet season (December 2016). The diet polygons for mean (±2SD) values of $\delta^{13}C$ plotted against $\delta^{15}N$ for zooplankton are represented by dashed red rectangle for Cladocera and dashed blue rectangle for Cyclopoida, with densities (D) of major groups of zooplankton (Cladocera, Cyclopoida). F= POM fraction, Peri. =Periphyton., Eich=*Eichhornia crassipes*, Clado.=Cladocera and Cyclo.=Cyclopoida.

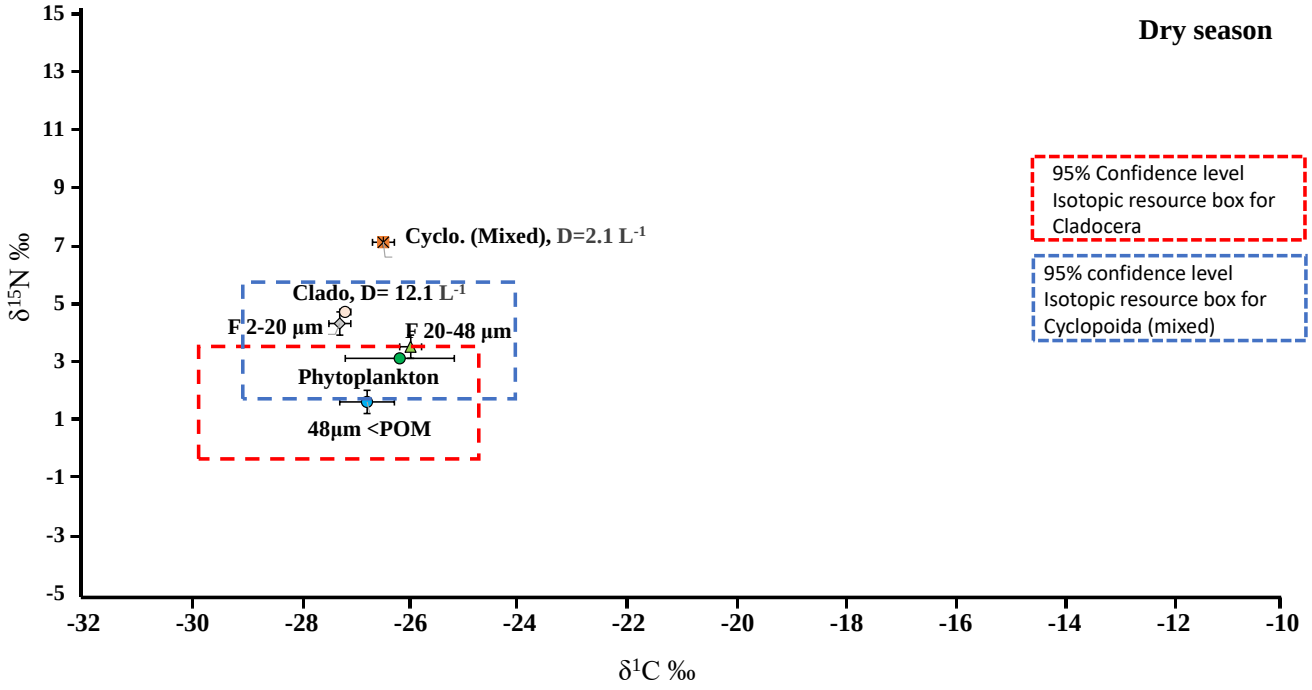

Figure 5.9 Mean (±1SD) values of $\delta^{13}C$ plotted against $\delta^{15}N$ for the potential food sources for zooplankton in Lake Baringo, with densities (D) of major groups of zooplankton (Cladocera, Cyclopoida) in the dry season (March 2018). The diet polygons for mean (±2SD) values of $\delta^{13}C$ plotted against $\delta^{15}N$ for zooplankton are represented by dashed red rectangle for Cladocera and dashed blue rectangle for Cyclopoida. F= POM fraction, POM=particulate organic matter, Clado.=Cladocera and Cyclo.=Cyclopoida.

Table 5.4 Molar C/N ratios of the main food web components and the major terrestrial and littoral resources in Lake Baringo during the wet season (December 2016) and the dry season (March 2018). Note that different size fractions of POM were determined in March 2018 compared to December 2016.

Taxon/ Group	Time of sampling	Number of replicates for carbon (C)	Number of replicates for nitrogen (N)	Mean C/N (S.D)
Pelagic Cladocera (mixed)	December 2016	3	3	11.09±0.28
Pelagic Cyclopoida (mixed)	December 2016	3	3	5.50±10.76
Pelagic Cladocera (mixed)	March 2018	3	3	3.92±1.10
Pelagic Cyclopoida (mixed)	March 2018	3	3	4.04±0.30
Pelagic Cyclopoida (adult)	December 2016	4	4	5.53±10.40
Phytoplankton	December 2016	1	1	8.75
Phytoplankton	March 2018	2	2	5.99±1.65
Barbus	December 2016	3	3	3.77±1.96
Oreochromis	December 2016	3	3	3.57±0.24
Clarias	December 2016	3	3	3.87±0.91
Heterobranchus	December 2016	3	3	3.68±3.06
Periphytopn from *Eichhornia*	December 2016	3	3	14.54±0.1
POM 0.7-25 µm	December 2016	3	3	10.5±0
POM 2-20 µm	March 2018	1	1	9
POM 20-48 µm	March 2018	1	1	11
48 µm <POM	March 2018	3	1	7.2
Sediments	December 2016	3	3	5.21±0.02
Cyperus sp.	December 2016	3	3	50.78±0.26
Sesbania sesban	December 2016	6	6	14.34±0.33
Acacia tortilis	December 2016	3	3	12.55±0.19
Eichhornia	December 2016	3	3	22.58±0.03

5.6.3.1.2 Lake Naivasha

The isotope ratios of both pelagic Cladocera and pelagic Cyclopoida in Lake Naivasha in the wet season (November 2016)**,** suggest that both these zooplankton taxa feed on phytoplankton. The difference between $\delta^{15}N$ for pelagic Cladocera and Cyclopoida is small (4.2±0.5‰ and 4.4±0.4‰, respectively), which suggests little if any predatory feeding of Cyclopoida on Cladocera. The $\delta^{15}N$ data for littoral periphyton (*E. crassipes* and *S. molesta*), were too close to those of pelagic zooplankton to indicate that these resources were significantly utilised. The $\delta^{13}C$ and $\delta^{15}N$ values of *E. crassipes* and *S. molesta* suggest that these taxa were not important carbon sources for pelagic zooplankton ($\delta^{13}C$ values too low and $\delta^{15}N$ values too high) either. The $\delta^{13}C$ values of pelagic zooplankton were lower than those of DOM suggesting that the latter is also not a major carbon source for zooplankton. The $\delta^{15}N$ data for sediment collected from the Gilgil and Malewa rivers were also too close to those of pelagic Cladocera and Cyclopoida to suggest that inputs of organic matter from these rivers were significantly utilised. The $\delta^{13}C$ values of the 0.7-25 μm POM and phytoplankton, were not sufficiently distinct from each other to allow the relative contribution of these carbon sources to zooplankton to be assessed using the mixing model (Phillips, 2012; Layman *et al*., 2012). The $\delta^{15}N$ signatures for 0.7-25 μm POM were too close to those of pelagic Cladocera and Cyclopoida to suggest that POM was significantly used compared to phytoplankton. The mixing model (Equation 15) suggests that the carbon derived from autochthonous carbon (e.g. phytoplankton) accounts for 100% of pelagic zooplankton carbon (pelagic Cladocera and Cyclopoida). This means that there was little, if any, allochthonous carbon contribution to zooplankton (see 2.10 Data analyses for details).

The isotope data suggest that both pelagic Cladocera and Cyclopoida may have been feeding on phytoplankton in the dry season (March 2018). Pelagic Cladocera and Cyclopoida may also have been feeding on 20-48 μm POM. In addition, 0.7-2 μm POM may have been utilised by Cladocera and Cyclopoida. C/N ratios of 20-48 μm POM and 0.7-2 μm POM were 5.8 and 11.5 respectively which suggests that POM had an algal provenance (Table 5.5). Neither pelagic Cladocera nor Cyclopoida appear to be using 2-20 μm POM. Since both the $\delta^{13}C$ values of phytoplankton and POM were slightly lower than that of the Cladocera, it was not possible to apply a mixing model. Both could represent dietary sources for the Cladocera, along with potentially other uncertain items such as protozoa.

The percentage of carbon assimilated by cyclopoids was estimated using Equation 13 (see 2.10 Data analyses in Chapter 2 for details). POM fractions (20-48 µm and 0.7-2 µm) and phytoplankton were used in the model to estimate their contributions to cyclopoids. The model suggests that the carbon derived from the POM accounts for 29 % of cyclopoid carbon and carbon derived from phytoplankton contributed 71 %.

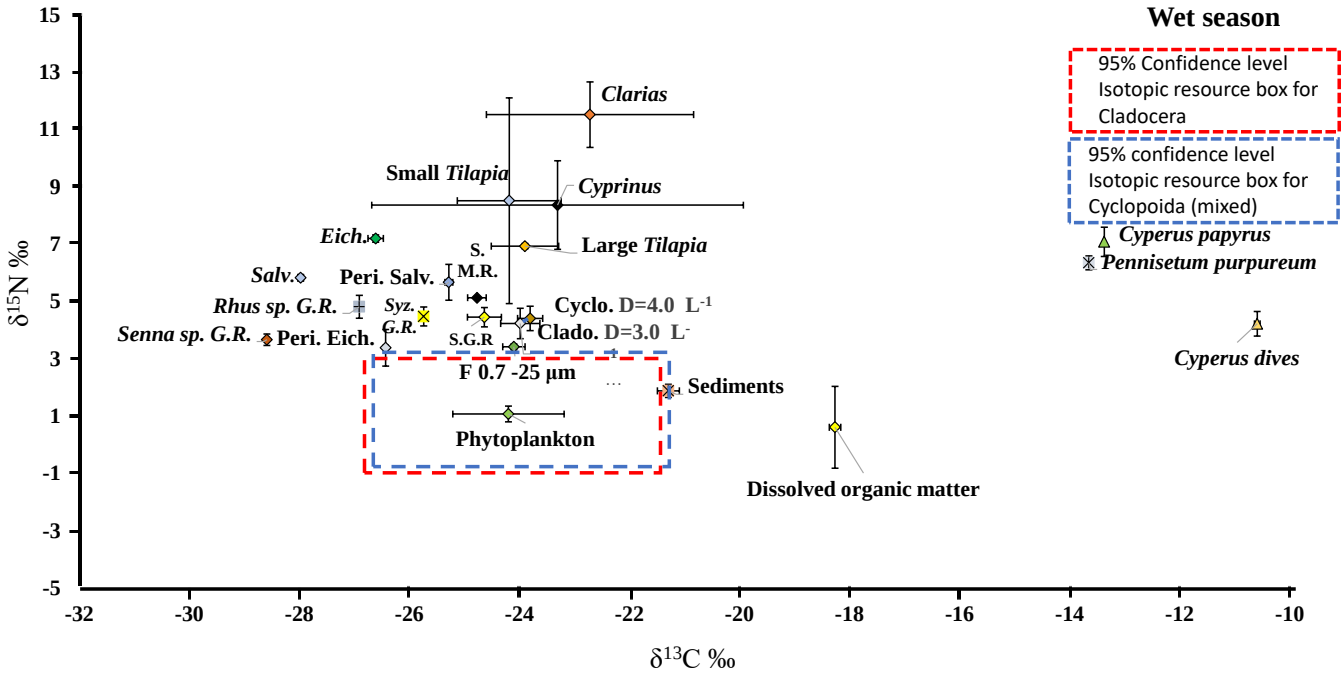

Figure 5.10 Mean (±1SD) values of δ ^{13}C plotted against δ ^{15}N for the main components of the pelagic food web in Lake Naivasha and from the major terrestrial and littoral carbon sources in the wet season (November 2016), with densities (D) of major groups of zooplankton (Cladocera, Cyclopoida) . The diet polygons for mean (±2SD) values of δ^{13}C plotted against δ^{15}N for zooplankton are represented by dashed red rectangle for Cladocera and dashed blue rectangle for Cyclopoida. F= POM fraction, Peri. =Periphyton., Eich=*Eichhornia crassipes*, Salv.=*Salvinia molesta*, Syz.= *Syzygium* sp., S.G.R=Soil of the Gilgi River, S.M.R.= Soil of the Malewa River, Clado.=Cladocera and Cyclo.= Cyclopoida.

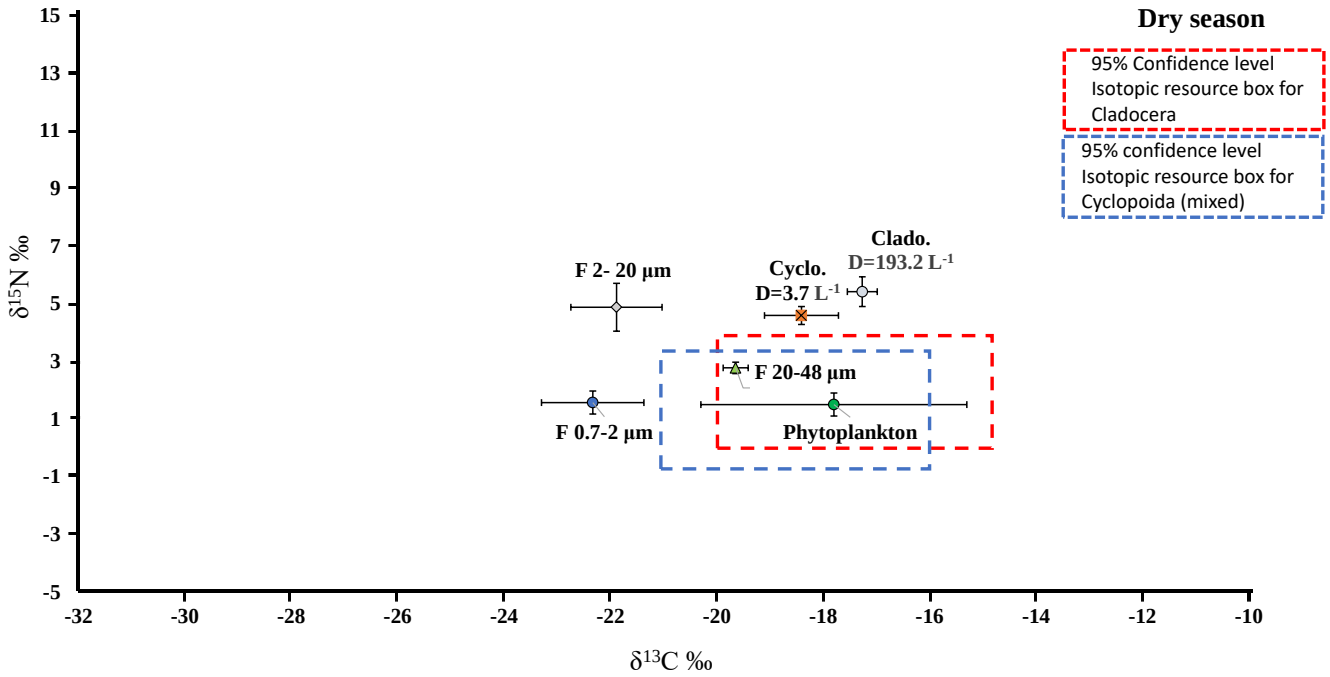

Figure 5.11 Mean (±1SD) values of $\delta^{13}C$ plotted against $\delta^{15}N$ for the potential food sources for zooplankton in Lake Naivasha, with densities (D) of major groups of zooplankton (Cladocera, Cyclopoida) in the dry season (March 2018). The diet polygons for mean (±2SD) values of $\delta^{13}C$ plotted against $\delta^{15}N$ for zooplankton are represented by dashed red rectangle for Cladocera and dashed blue rectangle for Cyclopoida. F= POM fraction, POM=particulate organic matter, Clado.=Cladocera and Cyclo.=Cyclopoida.

Table 5.5 Molar C/N ratios of the main food web components in Lake Naivasha and the major terrestrial and littoral resources during the wet season (November 2016) and the dry season (March 2018). Note that different size fractions of POM were determined in March 2018 compared to November 2016.

Taxon/ Group	Time of sampling	Number of replicates for carbon (C)	Number of replicates for nitrogen (N)	Mean C/N (S.D)
Pelagic Cladocera	November 2016	3	3	10.41±1.21
Pelagic Cyclopoida	November 2016	3	3	13.13±1.82
Pelagic Cladocera	March 2018	3	3	3.60±0.88
Pelagic Cyclopoida	March 2018	3	3	3.58±1.61
Phytoplankton	November 2016	3	3	8.56±1.84
Phytoplankton	March 2018	3	3	4.72±0.64
Cyprinus	November 2016	3	3	5.15±3.34
Small *Oreochromis*	November 2016	3	3	6.11±0.23
Large *Oreochromis*	November 2016	3	3	4.56±1.78
Clarias	November 2016	3	3	3.47±1.22
Procambarus	November 2016	2	2	3.98±0.13
Oligochaetes	November 2016	3	3	6±0
Periphyton from *Salvinia*	November 2016	3	3	10.88±0.06
Periphytopn from *Eichhornia*	November 2016	3	3	10.2±0
POM 0.7-25 µm	November 2016	3	3	8.2±0
POM 0.7-2 µm	March 2018	2	1	11.5
POM 2-20 µm	March 2018	3	3	6±0.02
POM 20-48 µm	March 2018	3	3	5.8±0
DOM	November 2016	3	3	65.34±0.55
Soil (Gilgil river)	November 2016	3	3	9.84±0.11
Soil (Malewa river)	November 2016	3	3	7.26±0.04
Sediments	November 2016	3	3	7.62±0.04
Juncus sp. (Gilgil river)	November 2016	3	3	30.62±0.16
Rhus sp. (Gilgil river)	November 2016	3	3	21.31±0.1
Syzygium sp. (Gilgil river)	November 2016	3	3	25.12±0.56
Senna didymobotrya (Gilgil river)	November 2016	3	3	12.5±0.22
Senna sp. (Gilgil river)	November 2016	3	3	12.17±0.19
Cyperus papyrus (Gilgil river)	November 2016	3	3	37.13±0.29
Dombeya burgessiae (Malewa river)	November 2016	3	3	8.58±1.66
Ficus sur (Malewa river)	November 2016	3	3	19.67±0.08
Pennisetum purpureum	November 2016	3	3	12.25±0.67
Cyperus dives	November 2016	3	3	72.87±0.24
Eichhornia crassipes	November 2016	3	3	19.38±0.08
Salvinia molesta	November 2016	3	3	24.72±0.30

5.6.3.2 Trophic interaction between fish and their potential carbon sources.

The number of fish samples used (three replicates of each fish) for stable isotopic analysis was low and the isotopic signatures of measured samples had a high standard deviation. This suggests a diversity in feeding habits of these fish in both lakes.

5.6.3.2.1 Lake Baringo

In December 2016, the stable isotope ratios of *Oreochromis* sp. suggest that these fish may feed on pelagic Cladocera, pelagic mixed Cyclopoida, pelagic adult Cyclopoida, pelagic copepodites and pelagic nauplii. They may also consume 0.7-25 μm POM. The close $\delta^{13}C$ signatures of phytoplankton with those of *Oreochromis* sp. indicate that phytoplankton may also have been consumed by these fish (Figure 5.8 and Appendix 5.23).

The $\delta^{13}C$ and $\delta^{15}N$ signatures of *Barbus* sp. and those of *E. crassipes* and periphyton suggest that these may have been important dietary sources for *Barbus*. The latter may also feed on pelagic Cladocera, pelagic mixed Cyclopoida, pelagic adult Cyclopoida, pelagic copepodites and pelagic nauplii. In addition, the $\delta^{13}C$ signatures of *Barbus* sp. was close to the 0.7-25 μm POM and phytoplankton, so it is possible that these two resources were also consumed by *Barbus* sp. Application of a simple mixing model (Equation 16) suggested that the carbon derived from planktonic resources account for 7.6 % of *Barbus* sp. carbon with the remainder (92.4 %) derived from littoral resources (see 2.10 Data analyses for details).

The $\delta^{13}C$ and $\delta^{15}N$ results for *Clarias* sp. and *Heterobranchus* sp. suggest that they may have been feeding on *Oreochromis* sp., and sediments. In addition, these fish may also consume other dietary items including phytoplankton, zooplankton, POM, *E. crassipes* and periphyton. Again, applying a simple two pool mixing model (Equation 17) suggests that the carbon derived from pelagic mixed Cladocera and Cyclopoida account for 88% of the *Claris* sp. diet with the remainder (12%) coming from sediment (see 2.10 Data analyses for details).

Applying Equation 18 leads to an estimated 83.7% of fish carbon derived from autochthonous sources in Lake Baringo with the remainder (16.3 %) coming from allochthonous sources (Figure 5.12). The explanation and justification for using this

mixing model and for including these carbon sources or not including the other sources in this model can be found in Chapter 2 (see 2.10 Data analyses for details).

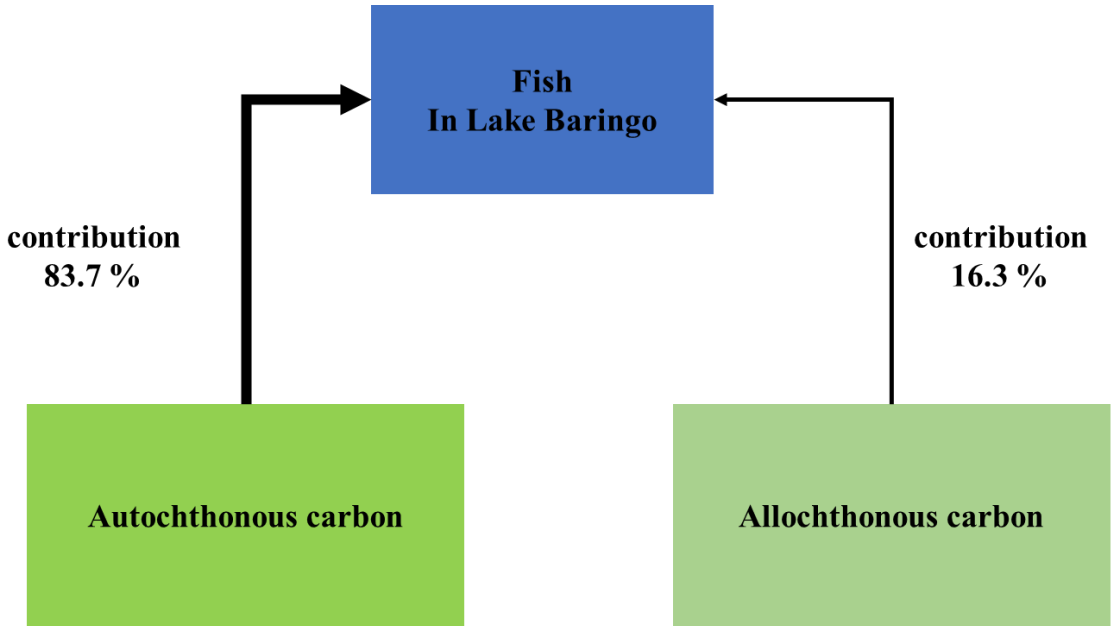

Figure 5.12 Illustration of the relative contribution of allochthonous and autochthonous carbon to fish in Lake Baringo estimated from a simple mixing model.

5.6.3.2.2 Lake Naivasha

In Lake Naivasha, the isotopic ratios of pelagic Cladocera, Cyclopoida and 0.7-25 µm POM suggest that they may be all be important dietary items for both large *Oreochromis* sp. and *Cyprinus* sp. Applying Equation 17 (see 2.10 Data analyses for details) suggests that the carbon derived from pelagic Cladocera and Cyclopoida account for 96% of carp sp. carbon with the remainder (~ 4%) probably coming from sediment. The $\delta^{13}C$ value of small *Oreochromis* sp. was similar to that of pelagic cyclopoids, Cladocera, 0.7-25 µm POM and phytoplankton. This suggests that small *Oreochromis* sp. may prey on these food items. The $\delta^{15}N$ signatures of small *Oreochromis* sp. confirm that this is likely. Employing a simple mixing model (Equation 17) suggested that the carbon derived from pelagic Cladocera and Cyclopoida may account for ~73% of the diet of *Clarias* sp. with the reaminder (27%) coming from sediment. However, we know that *Clarias* sp. can feed

on many items and there are several potential resources which have plausible $\delta^{13}C$ values which are separated by a plausible $\delta^{15}N$ trophic enrichment gap (i.e. lower than the consumer by approximately 4 ‰). Although, the typical trophic enrichment of $\delta^{15}N$ in literature is 3.4 ‰ (Post, 2002), this can range between 0 and 7 ‰ (Mizota and Yamanaka, 2011). The differences in $\delta^{15}N$ trophic enrichment can be caused by many factors which are described in Chapter 1 (1.6 Stable isotope ecology) and discussed in Chapter 6.

Employing Equation 18 suggests that the fish carbon derived from autochthonous and allochthonous sources in Lake Naivasha are in the region of 60% and 40%, respectively (Figure 5.13). An explanation and justification for including these carbon sources (or for omitting others) is given in Chapter 2 (see 2.10 Data analyses for details).

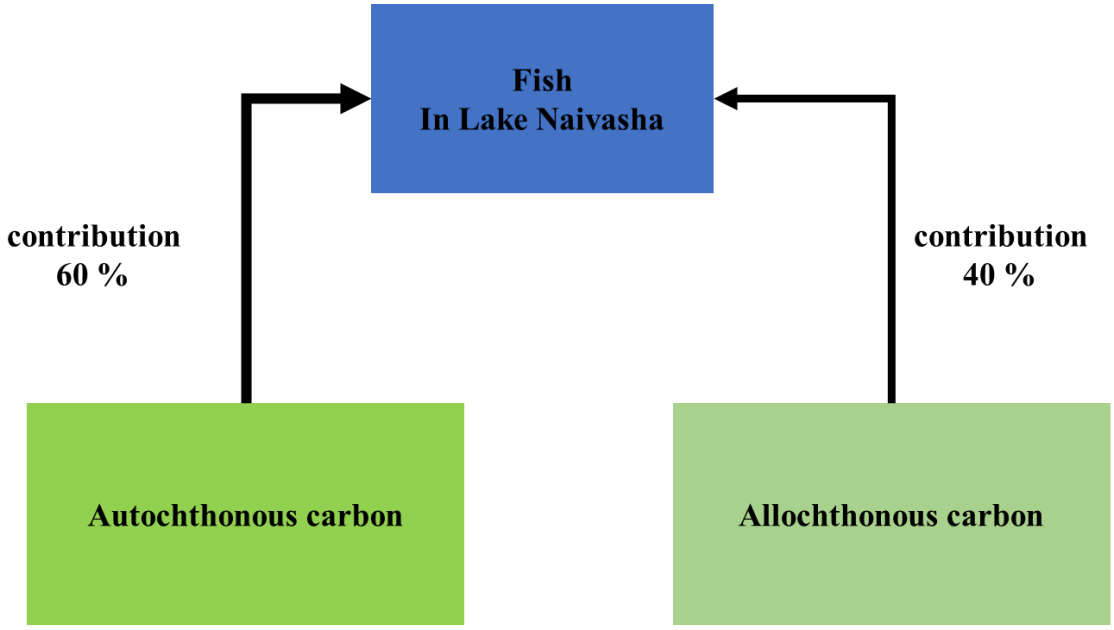

Figure 5.13 Illustration of the relative contribution of allochthonous and autochthonous carbon to fish in Lake Naivasha estimated from a simple mixing model.

The results suggest that in both lakes, autochthonous carbon contributed most to the diet of zooplankton and fish. The isotopic analysis also suggested that a range of different dietary items were consumed by the fish of both lakes, including zooplankton. The density of the latter in Lake Naivasha was significantly higher than in Lake Baringo.

5.7 Discussion

The study described in this Chapter aimed to examine the relative importance of allochthonous and autochthonous carbon sources to aquatic consumers in (turbid) Lake Baringo and in (less turbid) Lake Naivasha. These two lakes are of similar size but have quite different catchment characteristics and inputs.

Secchi depth in Lake Baringo was significantly lower than that of Lake Naivasha in the wet season, but that was not the case in the dry season when Secchi depths in both lakes were similar. Lake Naivasha might be more affected by wind shear than Lake Baringo due its shallower depth. In shallow lakes, wind can cause sediment resuspension and increase turbidity (Tarras-Wahlberg *et al*., 2002; Hubble, 2000). Self-shading of phytoplankton in Lake Naivasha was probably not the reason for the observed increase in turbidity in the dry season because phytoplankton densities in this season were too low to be a major contribution to high turbidity.

The mixing models and C/N ratios of the food webs of each lake revealed that pelagic zooplankton in both lakes in both seasons were mainly reliant on autochthonous carbon (phytoplankton and phytoplankton derived-POM). These results challenge the hypothesis that zooplankton in (typically more turbid) Lake Baringo would have a higher dependence on allochthonous carbon sources compared to zooplankton in (the less turbid) Lake Naivasha. Oduor *et al*. (2003) suggested that allochthonous inputs were principally responsible for the high turbidity in Lake Baringo and concluded that suspended solids were dominated by inorganic matter (90%). POM includes bacteria and protozoa which are also potential food sources for zooplankton (Jones *et al*., 1998). The C/N ratio of POM in Lake Baringo ranged from 7.2 to 11. This was similar to the C/N ratio of phytoplankton (which normally ranges between 6 and 10: Montagnes *et al*., 1994; Creach, 1995) suggesting that POM is largely derived from phytoplanktonic resources. Although, the C/N ratio of soil from Lake Naivasha ranged between 7.2 and 9.8, the $\delta^{13}C$ signatures of soil were different from those of the POM, suggesting soil does not make an important contribution to the POM in this lake. The fact that the $\delta^{13}C$ signatures of POM in both lakes were similar to those of phytoplankton suggests that POM was primarily derived from phytoplankton rather than catchment soils. The C/N ratio of organic matter derived from allochthonous origin is typically more than 12 (Thornton and McManus, 1994), as found in the present study. The C/N ratio for bacteria and zooplankton commonly ranges between 3 and 6 (Gorsky *et al*., 1988; Fagerbakke *et al*.,

1996). The findings of the present study are in line with Vuorio *et al*. (2006) who found that C/N ratios of POM in eutrophic Lake in south-west Finland ranged between 4.9 and 8.4, which was similar to the C/N ratios of phytoplankton (e.g. *Microcystis* sp.) which ranged between 5.1 and 9.8. This suggests that algae make a major contribution to POM in the studied lakes.

It is widely acknowledged that inputs of terrestrial organic matter into lakes can be utilised by zooplankton and other aquatic consumers, particularly in temperate zones (e.g. Grey *et al*., 2001; Cole *et al*., 2011; Rautio *et al*., 2011; Berggren *et al*., 2015). These resources can, hence, support ecosystem functions and services, forming an important link between the surrounding catchment and aquatic consumers such as zooplankton production and ultimately fish (Cole *et al*., 2011). However, in the case of tropical systems, such as Lake Baringo, it seems that high allochthonous inputs may not always make a significant contribution to the diet of aquatic consumers. This may be due to the fact that these inputs are poor in organic matter, as a result of the degraded nature of the soils in the Lake Baringo catchment. Vegetation cover in the catchment has decreased in recent decades due to deforestation, grazing and land clearance for human settlements (Johansson and Svensson, 2002; Hickley *et al.*, 2004; Wasonga *et al*., 2011; Omondi *et al*., 2017). This appears to have resulted in a decline in soil organic matter content and an increase in soil erosion – with largeler inorganic eroded particles delivered to the lake.

Rather than supporting zooplankton with extra resources, the high level of allochthonous inputs in Lake Baringo may negatively affect zooplankton density. The total zooplankton density in Lake Baringo was significantly lower than that in Lake Naivasha in both years, implying a lower contribution of zooplankton to fish in Lake Baringo. Lower zooplankton density in Lake Baringo may have been due to lower availability of autochthonous carbon (e.g. phytoplankton). Lake Baringo is well known to have a low production of phytoplankton, in part, due to high turbidity (Kallqvist, 1987; Schagerl and Oduor, 2003), which leads to light extinction in the water column. The higher turbidity in Lake Baringo compared to Lake Naivasha is visible in the satellite image shown in Figure 5.1.

The findings of the present study stress the need for better land management: improved vegetation cover should lead to increased soil carbon, which may increase allochthonous carbon inputs to receiving waters and, hence, provide resources for the aquatic ecosystem. The findings of earlier isotopic studies on Lakes Baringo and Naivasha (Britton *et al*.,

2007 and Britton *et al*., 2009) are consistent with those presented here. They also recommended increasing management efforts in the contributing catchments to reduce impact on the lakes (e.g. turbidity and the introduction of new fish species into these lakes).

A major problem for Lake Naivasha is high nutrient inputs from its catchment due to intensive agricultural activities (Hubble and Harper, 2001; Enniskillen, 2002; Hickley *et al.,* 2004). These inputs have led to an increase in phytoplankton production (Hubble and Harper, 2002) and, thus, an increase in the availability of autochthonous carbon sources for zooplankton. Lake Naivasha is moderately eutrophic (Hubble and Harper, 2002) which often benefits zooplankton initially. However, if eutrophication continues it can lead to the proliferation of inediable Cyanobacteria which decreases zooplankton biomass, as well as to a suppression of dissolved oxygen due to microbial decomposition of the algal necromass (Schindler, 2012; Taipale *et al*., 2019).

In both lakes, $\delta^{13}C$ and $\delta^{15}N$ values suggest that pelagic zooplankton were exploited by fish, either directly by planktivorous and omnivorous fish or indirectly via omnivorous fish feeding on planktivorous fish. Thus, zooplankton were indirectly and directly transfering autochthonous carbon to fish in both lakes. The results also suggest that there is a diversity in the feeding behaviour of fish in both lakes. Fish appear to access dietary items from planktonic, littoral, benthic and terrestrial resources. Application of simple mixing models revealed that autochthonous carbon contributed most to the diet of fish in both lakes (Figures 5.12 and 5.13). These results challenge the hypothesis that fish in (typically more turbid) Lake Baringo have a higher dependence on allochthonous carbon compared to fish in (the less turbid) Lake Naivasha.

In Lake Baringo, several components of the planktonic food web (e.g. cladocerans, cyclopoids and phytoplankton) were important dietary items for *Oreochromis* sp. Although, the isotopic dataset for fish feeding in the present study is limited to two "snapshots", these findings are consistent with those of Britton *et al.* (2009) for *Oreochromis niloticus baringoensis* in Lake Baringo. They found that this fish was largely dependent on planktonic resources over the course of the whole year. The mixing model of the present study revealed that littoral resources appeared to contribute most to the diet of *Barbus* sp.. This is consistent with the isotopic results of Britton *et al.* (2009) who also suggested that *Barbus* accessed different basal resources in Lake Baringo,

although they did not estimate the relative contributions of different resources. A previous study of the gut contents of *Barbus* from Lake Koka in Ethiopia (Dadebo *et al*., 2013) showed the occurrence of macrophytes, insects, zooplankton, phytoplankton and ostracods. The isotopic results of the present study suggest that *Clarias* sp. and *Heterobranchus* sp. also have a broad diet, including the consumption of littoral, benthic and pelagic resources. Previous gut content analyses for adult *Clarias gariepinus* from Lake Baringo, showed that *C. gariepinus* fed mainly on fish and zooplankton (Omondi *et al*., 2013). Dadebo *et al*. (2014) also found that *C. gariepinus* were omnivorous; feeding on fish, macrophytes, zooplankton, detritus, insects and phytoplankton in Lake Koka.

In Lake Naivasha, the isotopic results indicate that planktonic resources may be important dietary items for large and small *Oreochromis* sp. and *Cyprinus* sp. This is consistent with isotope data reported from Lake Koka in the Ethiopian Rift Valley, which suggests that *Oreochromis niloticus* feed mainly on zooplankton and POM (Fetahi *et al.*, 2018). Fetahi *et al.* (2018) suggested that zooplankton provide an important trophic link between basal resources and *Oreochromis* sp. In isotopic and stomach analysis, Britton *et al.* (2007) found that *Cyprinus* sp. in Lake Naivasha were feeding on zooplankton (Copepoda and Cladocera), benthic organisms (oligochaetes, chironomids) detritus, algae, small crayfish and fish. The results of the present study suggested that *Clarias* sp. (catfish) may prey on other fish. In gut content analysis, Meri *et al.* (2018) found that adult *Clarias* sp. (total length ≥ 40cm) in Lake Naivasha primarily fed on fish. The length of *Clarias* sp. samples in our study ranged from 42 to 59.5 cm suggesting that our samples were consistent with those collected by Meri *et al.* (2018). The results of the present study also suggested that *Clarias* sp. accessed different dietary items (e.g. crayfish, oligochaetes, POM, sediments, phytoplankton and zooplankton).

The larger size of the zooplankton individuals in Lake Naivasha compared with their counterparts in Lake Baringo may be due to the dominance of *O. niloticus* in Lake Baringo, which comprised about 80 % of fish community (Aloo, 2002). The juvenile stage of *O. niloticus* is a visual feeder, which means that it can be size-selective when grazing on zooplankton (Attayde and Menezes, 2008; Otieno *et al*., 2014). This could reduce the population size of large zooplankton by predation (Kerfoot and Lynch,1987).

In both lakes, $\delta^{13}C$ and $\delta^{15}N$ values and the C/N ratios of different food web components suggested that autochthonous carbon sources dominated zooplankton diets, thus

supporting fish directly and indirectly. However, the two pelagic food webs function in different ways. Both lakes are affected by continued human activities in their catchments (Hickley *et al*., 2004). Lake Baringo has higher levels of suspended sediment than Lake Naivasha, primarily due to increased soil erosion from the catchment (Johansson and Svensson, 2002), which can potentially affect photosynthesis. However, since the allochthonous inputs are mainly inorganic they do not appear to offer a significant source of carbon for zooplankton. In contrast to Lake Baringo, Lake Naivasha is eutrophic because it receives high nutrient loads from its surrounding catchment (Kitaka *et al*., 2002). These inputs have led to an increase in phytoplankton production (Hubble and Harper, 2002) and, thus, an increase in the availability of autochthonous carbon sources for zooplankton. Such differences in catchment characteristics affect the composition and function of the lake ecosystem – for example, maintaining a lower population of zooplankton in Lake Baringo than in Lake Naivasha. This, in turn, has an influence on the populations of fish and other top predators. This may explain why fish catches in Lake Naivasha have been higher than in Lake Baringo in recent years (Hickley *et al*., 2004). How the inputs of nutrients and other allochthonous materials will change in the future (e.g. with further changes in land use and catchment activities and with climate change) is an open question. Clearly, such changes could induce additional changes to the physico-chemical characteristics of each lake, which may have ecological consequences. Further work is needed to assess how these relationships develop going forward, building on the isotope and C/N data reported in this Chapter.

CHAPTER SIX: GENERAL DISCUSSION AND CONCLUSIONS

6.1 THESIS CONTEXT, AIMS AND STRUCTURE

Zooplankton have a central position in lacustrine pelagic food webs (Grey *et al.,* 2000; Mimouni *et al.,* 2015). These organisms can feed on phytoplankton, bacteria and particulate organic matter (POM), derived from both autochthonous and allochthonous sources (Grey *et al.*, 2001; Cole *et al.,* 2006; Cole *et al.,* 2011; Emery *et al.,* 2015; Grosbois *et al.,* 2017). They link these basal resources to organisms at higher trophic levels such as fish, invertebrates and some birds (Burian, 2010; Heneghan *et al.,* 2016; Emily *et al.,* 2017; De Stasio *et al.,* 2018). However, many knowledge gaps remain about their role. For example, there is contrasting evidence about trophic interactions between zooplankton and Cyanobacteria. Some studies have found that Cyanobacteria can cause negative effects on the feeding of zooplankton due to their toxicity and their size and shape which can make consumption difficult (see Chapter 1: 1.4.9 Characteristics of food) (Gliwicz and Lampert,1990; Rothhaupt, 1991; Koski *et al*., 1999; Rohrlack *et al.,* 2004). Others (e.g. Vareschi and Jacobs, 1984; Work *et al*., 2003; DeMott and Moxter, 1991) have found that zooplankton can be supported by both colonial and filamentous forms of Cyanobacteria. Studies on these interactions are rare in tropical regions, in contrast to the numerous studies in temperate regions (Hart, 1998; Leitão *et al*., 2018). Studies in temperate lakes to unravel trophic interactions between zooplankton and Cyanobacteria are largely based on generalist feeders such as the cladoceran *Daphnia* sp. (Ger *et al*., 2016). Such interactions in these regions are usually seasonal, continuing for limited periods (weeks or months: Ger *et al*., 2016). Generalisations based on temperate lakes may restrict our understanding about trophic interactions between tropical zooplankton and Cyanobacteria, because the generalist feeders such as *Daphnia* sp. are rare in tropical lakes (Fernando, 1994). In addition, cyanobacterial blooms tend to be shorter-lived in temperate lakes than in eutrophic tropical lakes, where blooms are often semi-permanent (Ger *et al*., 2016).

While many studies have been conducted to understand the relative importance of autochthonous and allochthonous carbon resources to the diet of zooplankton and fish in temperate systems (e.g. Galloway *et al*., 2014; Taipale *et al*., 2016 a; Tanentzap *et al*., 2014; Tanentzap *et al*., 2017), important knowledge gaps remain in tropical lakes (Kupfer *et al*., 2006; Fetahi *et al*., 2018).

Another uncertainty concerns the potential for competition between zooplankton and the lesser flamingo in saline lakes. The principal food resource for these birds is *Arthrospira fusiformis* (Krienitz and Kotut, 2010). Many studies (e.g. Melack, 1979; Schagerl and Oduor, 2008; Krienitz *et al*., 2012) have reported fluctuations in the density of *Arthrospira* sp., and these fluctuations have been linked with variations in lesser flamingo numbers in the lakes of eastern Africa (Harper *et al*., 2016). There have been several investigations into the causes of fluctuations in *Arthrospira* sp. numbers (e.g. Melack, 1988; Schagerl and Oduor, 2008 Krienitz *et al*., 2013). However, little attention has been paid to the role which zooplankton could play in terms of competition with lesser flamingo for *Arthrospira,* and hence the potential effect on food availability for flamingos.

The overall aim of this thesis was to address three principal questions: (1) What are the trophic interactions between zooplankton and Cyanobacteria in tropical lakes?; (2) Is there potential for competition between zooplankton and lesser flamingo? and (3) What is the relative importance of allochthonous and autochthonous carbon to aquatic consumers in two tropical lakes? This was achieved via detailed sampling, separation and analysis of food web components in four lakes in the Eastern Rift Valley of Kenya. According to Green (1993) the Eastern African lakes are model systems for comparisons of tropical food web studies because 1) they have a range of different sizes; 2) they have different water chemistries and 3) they have very different plankton communities. It has also been shown that they exhibit seasonal changes in ecological conditions (Mavuti, 1990; Sanders, 2016). Two sampling campaigns were conducted in Lakes Naivasha, Baringo, Bogoria and Sonachi. Differences in environmental conditions, the composition of the sampled food webs and the stable isotope compositions of food web components were observed in each lake. This work generated a number of novel insights into the role of zooplankton in these ecosystems, many of which are useful for understanding tropical lakes in general.

Chapter 3 explored features of the food web in Lake Sonachi with a focus on understanding dietary interactions between the calanoid *Lovenula* sp. (the principal zooplankton taxon) and different cyanobacterial taxa, specifically *Synechococcus* sp. and *Microcystis* sp. In Chapter 4, trophic interactions between the main components of the pelagic food web in Lake Bogoria were explored. Specifically, the interactions between zooplankton (the cladoceran *Moina* sp. and rotifers), phytoplankton (the diatom

Cyclotella sp. and the cyanobacterium *Arthrospira* sp.) and the lesser flamingo (*Phoeniconaias minor*) were assessed, with a focus on exploring potential competition between zooplankton and flamingos. In Chapter 5, the relative importance of different dietary sources (allochthonous and autochthonous) for zooplankton in Lakes Naivasha and Baringo was examined. These two freshwater lakes are similar in size, but have very distinct ecological conditions.

6.2 GENERAL DISCUSSION

Sampling of nano and picophytoplankton such as *Synechococcus* sp. and *Cyclotella* sp. and separation of planktonic taxa, which are often overlapping in sizes was a difficult task. The process of separation under the microscope was meticulous and time consuming. Although, there are automated methods for counting and identification of zooplankton such as the ZOOSCAN digital imaging system (Grosjean *et al*., 2004), there is no automated method for preparing pure samples of different zooplankton taxa which overlap in size. A combination of meticulous hand-picking and size fractionation was successfully employed in this study, but was time consuming. Another difficulty was obtaining sufficient amounts of planktonic taxa for stable isotope analysis. This depended on the densities of each taxa in each lake. Repeated haul nets were employed to ensure sufficient amounts of plankton were collected. It should be noted that these difficulties in sampling and sample preparation for lower trophic levels may have led to some oversimplification of the base of the food web (and associated understanding of trophic interactions), in common with other studies (e.g. Burian *et al*., 2014).

It is widely acknowledged that trophic enrichment in $\delta^{15}N$ between consumer and prey ranges between 2.4 and 4.4 ‰ (Post, 2002) with a mean of approximately 3 ‰ (DeNiro and Epstein, 1978; DeNiro and Epstein, 1981; Minagawa and Wada, 1984). However, the trophic enrichment in $\delta^{15}N$ for some zooplankton taxa relative to their most likely food sources in this thesis appeared to be above this average enrichment. This may have been due to (inter alia) the quality of diet, participation of microbial chains in carbon transfers to zooplankton and differences between species in the biochemical form of N excretion (e.g. Adam and Sterner, 2000; Grey *et al*., 2001; Vanderklift and Ponsard, 2003; Perga *et al*., 2006). Discrimination between the $\delta^{13}C$ signatures of POM, terrestrial plants and phytoplankton and understanding the trophic enrichment of $\delta^{15}N$ between trophic levels were more complex than anticipated. C/N ratios of different carbon sources were,

therefore, used as a complementary tool to understand the origin of carbon sources especially for those that had similar $\delta^{13}C$ signatures, as well as to understand the effects of food quality on the trophic enrichment of $\delta^{15}N$ for consumers. Stable isotope analysis is not an alternative for ecological knowledge, and it should always be combined with other tools to obtain a better understanding of aquatic ecology (Grey, 2006). For example, the stable isotope data in this study were integrated with the taxonomic identification of zooplankton and phytoplankton and the measurement of plankton density and the size of individuals.

Mixing models, combined with resource polygons, can help to estimate the relative contribution of each potential dietary item to a consumer. In this thesis, resource rectangles were constructed using the plausible range of $\delta^{15}N$ trophic enrichment with a plausible range of $\delta^{13}C$ variation in food items, to help identify the isotopic niche of each consumer (and hence identify the likely prey items utilised). Specific contributions were quantified, where possible, using simple mixing models. However, there are some challenges with applying mixing models. Most importantly, all potential food sources for a consumer should be known and sampled. If they are not, then significant errors will arise in mixing model predictions. Mixing models are most useful when there are two dominant food sources with sufficiently distinct isotopic ratios and when the $\delta^{13}C$ value of the consumer falls between the $\delta^{13}C$ values of the two food sources. Otherwise different fractionation factors are needed to make the mixing model fit (i.e. to obtain positive values of source contribution). Unfortunately, there appears to be no consistent way of assigning a value to this parameter. Such situations may indicate a potentially unknown dietary item. Ideally mixing models should use fractionation factors for similar taxa (McCutchan *et al*., 2003; Phillips *et al*., 2012) when these values are available in the literature, rather than using a general factor. However, to the author's knowledge, no specific fractionation factors already exist for the calanoid *Lovenula* sp., the cladoceran *Moina* sp. or for rotifers. An isotope fractionation factor of 0.3 ‰ for the $\delta^{13}C$ of invertebrates was, therefore, employed (McCutchan *et al*., 2003). A similar value (0.43 ‰) was suggested by Grey *et al*. (2001) for crustacean zooplankton. More research on variation in fractionation is required (Gannes *et al*., 1997; McCutchan *et al*., 2003), particularly since the applicability and power of mixing models largely depend on the validity of this factor (Phillips and Koch, 2002; Grey, 2006; Phillips *et al*., 2012).

This study focused principally on the trophic interactions between zooplankton and their food webs in the pelagic zone. Plankton and POM samples were only collected from the surface water layer. However, many zooplankton species can utilise food items in both the surface and deeper layers during their vertical migration (Matthews and Mazumder, 2006). This can complicate their trophic interactions and lead to some uncertainty about their carbon sources (Matthews and Mazumder, 2006). Lakes Naivasha and Baringo do not have persistent stratification (Hubble, 2000; Tarits *et al*., 2006) and the chemical and physical depth profiles sampled in this study suggested that they were not stratified at the time of sampling. Lack of stratification promotes continuous circulation of algal cells through the water column and homogenisation of food sources for zooplankton between the surface and deeper strata (Hubble, 2000; Oduor *et al*., 2003). This means that surface samples provide a good representation for the whole water column. Lakes Bogoria and Sonachi do show stratification, which may be long-lived (MacIntyre and Melack, 1982; Verschuren *et al.,* 1999; Harper *et al*., 2003; present study). Such stratification can create layers with different carbon sources for zooplankton (Matthews and Mazumder, 2006). Utilisation of these resources relies on the ability of zooplankton to access and feed in these layers, which have very different chemical and physical characteristics. For example, during stratification the epilimnion is usually oxygenated while the hypolimnion is anoxic (present study). The chemocline in these lakes usually starts between 1 and 2 m depth (Njuguna,1988; Harper *et al*., 2003; present study). In other studies, the calanoid *Lovenula* sp. has been shown to restrictively feed in oxygenated water in two crater lakes in Ethiopia (Lemma, 2009). Similarly, the filtration process of the cladoceran *Moina micrura* was observed to stop and swimming activity increase when dissolved oxygen concentrations fell to 0.5-0.6 mg L^{-1} (Ekau *et al.,* 2010). Layers with low dissolved oxygen concentrations can be used by zooplankton as a refuge to avoid predation, but it is unlikely that these organisms can feed efficiently in these layers (Ekau *et al.,* 2010). In contrast, some studies have suggested that zooplankton can feed on methane oxidizing bacteria (MOB) during their access to the oxic-anoxic zone (metalimnion) and anoxic hypolimnion via vertical migration. This could contribute to low $\delta^{13}C$ signatures in some zooplankton (Jones *et al*., 1999; Jones and Grey, 2011). However, in this thesis the $\delta^{13}C$ signatures of *Lovenula* sp. ranged between -22 ‰ and -22.2 ‰ in Lake Sonachi and for rotifers they ranged from -20.9 ‰ to -24.7 ‰. In Lake Bogoria the $\delta^{13}C$ signature of *Moina* sp. was approximately -23 ‰. These values do not reflect the low values of MOB, which typically range from -60 ‰ to -80 ‰ (Rudd and

Taylor, 1980). However, the dataset in the present study does not include samples of potential food items (e.g. bacteria, algae and POM) from different depths. These would have been useful to assess directly these interpretations. In general, the surface water layer is the most favourable habitat for zooplankton feeding because it is typically rich in food and oxygen (Bayly,1986; Ringelberg, 1999) which might encourage zooplankton in saline lakes to feed predominantly in the epilimnion. This suggests that vertical migration may have played a relatively minor role in affecting the stable isotope data collected here.

In Lake Sonachi (Chapter 3), the stable isotope analysis suggested that colonies of the cyanobacterium *Microcystis* sp. were not an important food item for the calanoid *Lovenula* sp. Similarly, in Lake Bogoria (Chapter 4), the results suggested that the filamentous alga *Arthrospira sp.* was not a significant dietary item for the cladoceran *Moina* sp. Instead, *Lovenula* sp. and *Moina* sp. appeared to preferentially utilise the pico-alga *Synechococcus* sp. and the nano-alga *Cyclotella* sp., respectively. Colonial and filamentous Cyanobacteria may interfere with the feeding mechanisms of zooplankton and hence decrease food ingestion (Lynch, 1980). Wlison *et al*. (2006) suggest that both the morphology and toxicity of some cyanobacterial taxa can reduce their consumption. In addition, compounds produced by some cyanobacteria taxa (e.g. cyanotoxins) can be toxic to other organisms and to humans (O'Neil *et al*., 2012). Cyanobacterial toxins may even have contributed to some lesser flamingo mortality in African saline lakes (Krienitz *et al*., 2005). Reduction in the utilisation of colonial, filamentous and toxic Cyanobacteria by zooplankton is considered to be an important biotic factor in promoting harmful cyanobacterial blooms (Perga *et al*., 2013), and a contribution to an overall accumulation of photosynthate in the water column. This can influence ecosystem function via, for example, decreased dissolved oxygen concentration (anoxia or hypoxia) because the accumulated photosynthate imposes a biochemical oxygen demand. This might increase fish mortality in those lakes which contain them (Paerl and Otten, 2013).

The results presented in this thesis based on stable isotope analysis differ from several other studies employing gut content analysis (e.g. Work *et al*., 2003). In the shallow Lake Okeechobee (USA), Work *et al*. (2003) found that the calanoid *Diaptomus dorsalis* and the cladoceran *Daphnia* sp. fed principally on colonial and filamentous forms of Cyanobacteria. On the basis of laboratory studies, Lampert (1987) suggested that relatively large Cladocera with body length of 1.75 mm are more efficient than calanoids in consuming *Synechococcus*. However, the results presented here do not support these

findings. The relatively large calanoid *Lovenula* sp. (average length 1.6 mm) in Lake Sonachi was shown to primarily feed on picoplanktonic alga *Synechococcus* sp. This may reflect differences between assimilation and ingestion. Stable isotope analysis is more useful than classic methods such as gut content analysis and laboratory observations of zooplankton feeding behaviour, because it reflects information about which food items are actually assimilated rather than ingested (Fry and Arnold, 1982; Makoto and Tsutomu, 1984; Kling *et al*., 1992). In addition, stable isotope analysis can detect food sources which are difficult to identify by gut content analysis and are, hence, much more suitable for planktonic studies (Grey *et al*., 2001). The data presented in this thesis suggested that the size and morphology of Cyanobacteria may not reduce their utilisation by zooplankton. For example, rotifers in Lake Bogoria (Chapter 4) appeared to significantly feed on filamentous *Arthrospira* sp. in both sampling seasons.

The tendency of rotifers to principally feed on filamentous Cyanobacteria (e.g. *Arthrospira* sp.) rather than on diatoms or POM implies that rotifers may be competitors for lesser flamingo (which predominantly consume *Arthrospira*). Many studies (e.g. Simmons, 1996; Simmons, 2000; Childress *et al*. 2008) have reported declines of flamingo populations in Africa in the last twenty years. Such declines may be due to the degradation and or loss of habitat (Krienitz and Kotut, 2010); changes in phytoplankton quality and quantity (Krienitz *et al.,* 2010; Kaggwa *et al.,* 2013; Krienitz *et al.,* 2016); bacterial infections (Sileo *et al*., 1979; Krienitz *et al.,* 2005); the effects of algal toxins (Krienitz *et al.,* 2003; Metcalf *et al.,* 2013); the effects of pollutants, such as heavy metals and pesticides (Greichus *et al*., 1978; Kairu, 1996) or the impact of cyanophages (Amer *et al*., 2018). They could also be due to competition effects (e.g. from zooplankton). Vareschi and Jacobs (1985) found that *Arthrospira* was probably an important dietary item for rotifers in Lake Nakuru (Kenya), but they were unable to quantify the relative size of this contribution in comparison with other food sources, such as algae and detritus. The results also suggested that the cladoceran *Moina* sp. principally consumed *Cyclotella* sp., or perhaps *Cyclotella*-derived carbon via the microbial loop (the return of carbon to higher trophic levels by incorporation into bacterial biomass, followed by subsequent consumption of the bacteria by higher organisms). *Arthrospira* sp. made a minor contribution to the diet of *Moina* sp., implying that *Moina* sp. is not a significant competitor for the lesser flamingo in Lake Bogoria. It has been suggested that the lesser flamingo may feed on alternative food items including zooplankton (Robinson, 2015).

However, the results presented here suggest that neither *Moina* sp. nor rotifers make a significant contribution to the diet of lesser flamingos; in the case of *Moina* this may be due to their large size. Instead, the isotopic signature of the flamingo feather which was analysed reflected a food source at the base of the food web, as expected (e.g. *Arthrospira*). The non-significant trophic interaction between rotifers and flamingos cannot be explained solely by their low density. Rotifers may have evolved mechanisms to avoid predation by lesser flamingo; for example, vertical migration deeper in the water column (Ohman, 1988; Gliwicz, 1986; Boeing *et al*., 2006; Garcia *et al*., 2007).

It is known that *Daphnia* sp. can migrate to deeper water to avoid predation by visually feeding fish (Ringelberg, 1991). Rotifers can also vertically migrate downwards to 2 m (Thorp and Covich, 2009). Furthermore, these organisms can migrate away from the shore to the pelagic zone (Preissler, 1980). In previous studies in Lake Baringo, rotifers, Cladocera and Copepoda have shown a diel vertical migration downwards by up to 4 m (Omondi *et al*., 2014 b). This migration may be controlled by feeding strategies, avoidance of visually feeding predators and light. Such vertical and horizontal migrations may, therefore, have minimised direct trophic interactions between zooplankton and lesser flamingo in Lake Bogoria.

Many factors have been suggested to explain the reasons behind fluctuations in the density of *Arthrospira* including changes in salinity and water level, nutrient concentrations and the prevalence of cyanophages (i.e. viruses that infect cyanobacteria) causing a reduced density of *Arthrospira* sp. (e.g. Melack, 1979; Melack, 1988; Schagerl and Oduor, 2008 Krienitz *et al*., 2013; Harper *et al.*, 2016; Krienitz *et al*., 2016). However, the potential role of zooplankton in controlling *Arthrospira* abundance and consequently altering food availability for lesser flamingos may have been previously underestimated. The extent to which *Arthrospira* grazing by rotifers can affect food availability for flamingos will depend on the size of the rotifer population compared to the density of *Arthrospira*, the average feeding rate of rotifers and their ability to avoid predation. It will also depend on the filtering rate of all feeding flamingos. According to Gosselain *et al*. (1998) high rotifer densities (more than 1000 indiv. L^{-1}) in the River Meuse in Belgium was partly responsible for the decline in total algal biomass. Similarly, in Lake Bogoria, the density of rotifers in the dry season was relatively high (over of 1000 indiv. L^{-1}). The *Arthrospira* densities in the present study in Lake Bogoria ranged between 2,060 coil ml^{-1} and 5,220 coil ml^{-1} (i.e. between 2 and 5×10^{6} coil L^{-1}). This range

is towards the low-end of the range in densities reported by Harper *et al*. (2003) in this lake (i.e. between 3,375 coil ml^{-1} in 2000 and 20,826 coil ml^{-1} in 2003).

Autochthonous carbon sources were clearly the main dietary items for zooplankton for all the lakes studied here. This finding is consistent with suggestions by Grey *et al.* (2000) and Carpenter *et al.* (2005) that phytoplankton become more important for zooplankton than allochthonous carbon sources as lakes become more productive. For example, Calanoids (*Lovenula* sp.) in Lake Sonachi and rotifers and Cladocera (*Moina* sp.) in Lake Bogoria predominantly utilised autochthonous carbon (*Synechococcus* sp., *Arthrospira* and *Cyclotella* sp., respectively). Mitrovic and Baldwin (2016) suggested that the importance of terrestrial organic matter increases in aquatic systems that have reduced light penetration, which limits photosynthesis. In Chapter 5 of the thesis, the isotopic results and analysis of C/N ratios of the food webs of Lakes Baringo and Naivasha suggest that the pelagic zooplankton in turbid Lake Baringo and less turbid Lake Naivasha were both largely dependent on autochthonous carbon. This may be due to the low density of terrestrial vegetation and low soil organic matter levels in the Lake Baringo catchment. About 90% of Lake Baringo's catchment has been degraded, due to natural instability and intensive human activities (e.g. deforestation, grazing and land clearance for human settlements: Johansson and Svensson, 2002; Hickley *et al.*, 2004; Wasonga *et al*., 2011; Omondi *et al*., 2017). Thus, although suspended solids inputs into Lake Baringo were high (from soil erosion), the organic matter content of this material was low. The high inorganic turbidity levels may have negatively affected feeding of zooplankton and, hence, fish production, which may also explain lower fish catches in Lake Baringo than in Lake Naivasha (Hickley *et al*., 2004). The present study stressed the need for better management of soil resources in the catchments of Lakes Baringo and Naivasha which could lead to a reduction in sediment load into these lakes and consequently a potential increase in the production of phytoplankton, zooplankton and, ultimately, fish in these lakes.

Many studies have shown that the relative importance of allochthonous and autochthonous carbon to zooplankton can change seasonally. However, most of these studies were conducted in temperate and subarctic lakes (Grey *et al*., 2001; Rautio *et al*., 2011; Berggren *et al*., 2015). They suggest that zooplankton often rely on autochthonous carbon in summer but may need to access allochthonous carbon more in winter, forming an important link between terrestrial habitats and aquatic consumers. In tropical regions,

lakes exist in an ‘‘endless summer’’ (Kilham and Kilham, 1990) and are often characterised by high and continuous autochthonous primary production (e.g. phytoplankton). This may minimise the general importance of allochthonous carbon to tropical zooplankton. Wilkinson *et al*. (2013) found that allochthonous carbon is often more important in small (e.g.<100 km^2) lakes than in larger ones in Michigan, (USA). However, this conclusion was not supported by the findings from the small lakes studied here (Lakes Sonachi and Bogoria). Allochthonous carbon resources often have lower nutritional value than autochthonous resources (e.g. phytoplankton). For example, they are often poorer in essential fatty acids than most phytoplankton (Brett *et al.*, 2012). The fatty acids DHA and EPA (Weers and Gulati, 1997) are crucial for the growth of zooplankton and fish (Reitan *et al*., 1997; Brett *et al*., 1997; Sargent *et al*., 1999; Ferrão-Filho *et al*., 2003). Moreover, some allochthonous carbon resources are resistant to digestion by aquatic consumers, due to high cellulose and lignin contents (Brett *et al*, 2009). Finally, algae typically have lower C:P ratios relative to terrestrial resources (Kelly *et al*., 2014). Phosphorus is essential for the synthesis of nucleic acids and for energy storage as ATP (Ferrão-Filho *et al*., 2003).

6.3 CONCLUSIONS

This was the first study to examine trophic interactions of different zooplankton taxa (Calanoida, Cyclopoida, Cladocera and Rotifera) in different seasons in saline and freshwater lakes in East Africa using stable isotope analysis. It extends our knowledge about the role of zooplankton in processing different dietary items in tropical lake ecosystems and it supports the idea of potential competition between zooplankton and the lesser flamingo in saline lakes.

The data presented here suggest that the consumption of small algal items (e.g. *Synechococcus* sp.) by the relatively large calanoid *Lovenula* sp. and their apparent avoidance of *Microcystis* sp. colonies may increase *Microcystis* sp. biomass and accumulation of their products in Lake Sonachi. This may make Lake Sonachi unfavourable for organisms such as the lesser flamingo, which are sensitive to the mucilaginous structure and potentially toxic products of *Microcystis* sp.

The results from Lake Bogoria showed that both rotifers and lesser flamingos consume *Arthrospira*. This suggests that these organisms are in competition. The densities for

Arthrospira in both the dry and wet seasons in this study were at the low end of the range of densities reported by Harper *et al*. (2003) in this lake, further suggesting that rotifers may influence food availability for flamingos (depending on their population size and the density of *Arthrospira*). Seasonality in the occurrences of the cladoceran *Moina* sp. and the diatom *Cyclotella* sp. were also observed in Lake Bogoria. These may have been caused by an increase in lake level and a decrease in surface salinity in the wet season. Such seasonal changes in planktonic food web structure in this lake are unlikely to have been beneficial for flamingos as they are shown here not to be utilising these plankton.

Zooplankton play a central role in transferring resources to higher trophic levels. Although, zooplankton are clearly consumed by fish in Lakes Naivasha and Baringo, they did not appear to be important food items for flamingos in Lake Bogoria. Different zooplankton taxa have evolved different antipredator strategies such as vertical migration and increasing body size (Ohman, 1988; Gliwicz, 1986; Boeing *et al*., 2006; Garcia *et al*., 2007). Both strategies may have played a role here: lesser flamingos feed only in the top 5 cm of water and reject particles larger than about 800 μm using their lamellae (Vareschi, 1978; Robinson, 2015).

Although, there is a strong physical connection between Lake Baringo and its surrounding catchment (large catchment: lake ratio and a high particulate input from extensive soil erosion), zooplankton in this lake were still largely dependent on autochthonous resources. This was also found in the other lakes studied in which the carbon of different zooplankton taxa (Calanoida, Cyclopoida, Cladocera and Rotifera) was largely autochthonous, in both seasons. These findings differ from those reported for many temperate and arctic lakes, which often show seasonal changes in the relative importance of allochthonous and autochthonous carbon for zooplankton. This lack of seasonality for tropical zooplankton may due to high year-round algal production in tropical lakes (Lewis, 1996; Lewis, 2000). The results presented in this thesis also provide strong evidence that the quantity of available food resources for zooplankton in tropical lakes is not only the factor controlling these organisms. Other significant factors include the size and morphology of prey items and zooplankton feeding responses to food items (i.e. feeding preferences of zooplankton for some food items to almost complete avoidance of other items).

6.4 FUTURE PERSPECTIVES

Paleolimnological data have shown that the lakes of the East African Rift valley have experienced large climatic and hydrological changes over past millennia (Vincens *et al*., 1986; Chalié and Gasse, 2002), which have influenced their ecological composition (Verschuren *et al*., 1999; Verschuren *et al*., 2000; Sanders, 2016). It is possible, therefore, that future climate change may cause significant ecological shifts. Under most climate change scenarios, the East African Rift Valley is predicted to get wetter (De Wit and Stankiewicz, 2006; Thomson *et al.*, 2018). This could mean an increase in the frequency of physical and biological connections between (otherwise separate) freshwater and saline lakes (e.g. during flooding events which reduce the distances between these lakes). For example, the distance between Lake Bogoria (saline) and Lake Baringo (freshwater) is only 24 km. These lakes have very different physiochemical conditions and biological communities, which could change (at least temporarily) if connection rates between these waterbodies increased. For example, saline lakes could become diluted more frequently. Under this predicted climate change scenario, specialised organisms such as flamingos, which depend on a limited number of planktonic food items, may be more vulnerable to climatic perturbations and thus face even more pressures than they do today. The mixing of saline and freshwater lakes may also allow the transfer of planktivorous fish and zooplankton between these systems. The successful establishment of freshwater organisms in saline lakes could place them in competition with flamingos for specialised phyoplanktonic items. The food webs of Lake Bogoria and Lake Sonachi, for example, are currently characterised by relatively few actors, but more frequent freshening could add new trophic levels, which could consequently reduce their overall efficiency. Several studies (e.g. Berglund *et al*., 2007; Dickman *et al*., 2008) have shown that the efficiency of food webs based on algal production can decrease with an incease in trophic levels.

Increased land degradation and loss of vegetation have occurred in many parts of East Africa (Kiage *et al.*, 2007). This may also contribute to an increase in the probability of flooding in this region in the future and to an increased input of allochthonous materials into the Rift Valley lakes. These materials often have low organic matter contents and may result in a reduction of phytoplankton and zooplankton production and, ultimately, other aquatic organisms that depend on them. This could, therefore, lead to a decrease in the overall turnover rate of the pelagic food web, which could be interpreted as a

reduction in function. Of course, such changes would also depend on the nutrient inputs to these lakes which also limit their productivity.

Other future scenarios suggest that some freshwater lakes in East Africa (e.g. Lakes Naivasha and Baringo) could face a reduction in size and depth due to increased water demands (e.g. for irrigation and domestic supply). High rates of soil erosion also promote sedimentation which could reduce basin volume (Becht and Harper, 2002; Odada *et al*., 2006). In this case, lakes would become shallower and more turbid (Harper and Mavuti, 2004). Such conditions are likely to have negative impacts on zooplankton feeding and production, which ultimately will be reflected in their fish production. A similar scenario (e.g. an increase in salinity levels and a decrease in volume) could also occur in many saline lakes under this alternative counterfactual (Williams, 2002). Changes in salinity levels due to changes in lake levels would play an important role in changing plankton community in these lakes (Vareschi *et al*., 1981; Melack, 1988; present study) in favour of organisms with a tolerance for high osmolarities.

Under the future scenarios for temperate regions, lakes are expected to experience longer cyanobacterial blooms which may become similar to eutrophic tropical lakes (Ger *et al*., 2016). Thus, the knowledge gained from the research described in this thesis may also help us to understand future trophic interactions between zooplankton and Cyanobacteria in temperate lakes.

6.5 FUTURE WORK

Several knowledge gaps remain about the composition and function of tropical lakes in general and about East African lakes in particular. For example, future work could look at the extent of vertical and horizonal migration of zooplankton (rotifers and Cladocera) in response to diurnal cycles in light and to predatory pressures. The diel migration of zooplankton can shape trophic interactions in lake food webs, but we know relatively little about them.

In this thesis, a relatively narrow range of analytical tools were employed to investigate food web interactions (predominantly taxonomic identification, stable isotope analysis and C/N ratios). Future work could apply other tools such as fatty acid analysis and compilations of carbon budgets as supplementary techniques which would make the analysis more powerful (Cloern *et al.*, 2002).

There is also a need to assess trophic interactions between components of aquatic food webs across a wider range of tropical lakes, which differ in ecological conditions, in order to deepen our general understanding about the role of zooplankton.

Physiochemical and biological characteristics in lakes vary over time. Furthermore, the inputs of allochthonous resources into lakes and the productivity of phytoplankton often show seasonal changes. Many shallow tropical lakes were previously assumed to be relatively static but are now known to have seasonality, mainly driven by differences in rainfall and wind characteristics in the dry and wet seasons (Schagerl and Oduor, 2003; Schagerl and Oduor, 2008). Seasonal and erratic interannual fluctuations in water inputs via rivers and rainfall can affect lake chemistries and physical conditions and ultimately their biota (Mavuti, 1990; Talling, 2001; Schagerl and Oduor, 2008; Ndebele-Murisa *et al*., 2010). The extent to which a two 'snap-shot' sampling approach such as that conducted here was able to capture these seasonal effects in all four lakes is currently uncertain. Future work with more frequent intra-annual sampling over several should attempt to ascertain the extent to which such snap-shot sampling strategies are representative of lake ecosystem composition and function in general.

Finally, given the existing anthropogenic pressures on many of these lake systems and the likely addition of climate change pressures, combined with human population growth and resource demand increases in future, it is important to think about how these lakes could be better managed. Future work is needed to investigate how human impacts could be reduced.

APPENDICES

Appendix 2.1 The average values of physical and chemical parameters of surface water at stations 1 and 3 in comparison with the values of central station in Lake Bogoria in December 2016.

Variables	Station 1	Station 2 (central station)	Station 3	Average values at stations 1 and 3
Depth (m)	15.2	14.3	14.8	15
pH	10.1	10.0	10.0	10
Surface dissolved oxygen (DO) mg L^{-1}	5.4	3.6	4.0	4.7
Surface water conductivity µS cm^{-1}	39225	38329	38331	38778
Surface water temperature °C	26.8	25.9	26.1	26.45
Secchi depth cm	37	47	47	42

Appendix 2.2 The average values of physical and chemical parameters of surface water at stations 1 and 3 in comparison with the values of central station in Lake Bogoria in March 2018.

Variables	Station 1	Station 2 (central station)	Station 3	Average values at stations 1 and 3
Depth (m)	12	11	11	11.3
pH	9.9	10	10	9.9
Surface dissolved oxygen (DO) mg L^{-1}	42.4	21	6.2	24.3
Surface water conductivity µS cm^{-1}	42260	42030	41950	42105
Surface water temperature °C	29.5	26.7	24.8	27.1
Secchi depth cm	15	15	15	15

Appendix 2.3 The average values of physical and chemical parameters of surface water at stations 1, 2, 4 and 5 in comparison with the values of central station in Lake Baringo in December 2016.

Variables	Sta. 1	Sta.2	Sta. 3 (central station)	Sta. 4	Sta. 5	Average values at stations 1,2, 4 and 5
Depth (m)	9.8	11	9.15	9.2	9.2	9.8
pH	8.7	8.7	8.7	8.7	8.7	8.7
Surface dissolved oxygen (DO) mg L^{-1}	6.7	6.9	7.1	7.2	7.2	7
Surface water conductivity µS cm^{-1}	475	476	479	477	478	476.5
Surface water temperature °C	25.4	25.5	27.7	27.1	26.1	26
Secchi depth cm	52	44	46	52	33	45.2

Appendix 2.4 The average values of physical and chemical parameters of surface water at stations 1, 2, 4 and 5 in comparison with the values of central station in Lake Baringo in March 2018.

Variables	Sta. 1	Sta.2	Sta. 3 (central station)	Sta. 4	Sta. 5	Average values at stations 1,2, 4 and 5
Depth (m)	8.2	8.7	8.2	8.5	8	8.3
pH	8.7	8.6	8.7	8.5	8.6	8.6
Surface dissolved oxygen (DO) mg L^{-1}	7.5	8.7	8.4	8.8	9.1	8.5
Surface water conductivity µS cm^{-1}	540	541	543	543	550	543.5
Surface water temperature °C	25.6	25.9	27	27.4	29	26.9
Secchi depth cm	70	70	50	30	25	48.7

Appendix 2.5 The average values of physical and chemical parameters of surface water at stations 1, 2, 4 and 5 in comparison with the values of central station in Lake Naivasha in November 2016.

Variables	Sta. 1	Sta.2	Sta. 3 (central station)	Sta. 4	Sta. 5	Average values at stations 1,2, 4 and 5
Depth (m)	5.7	6	6.4	6.9	7.2	6.4
pH	8.4	8.4	8.5	8.5	8.5	8.4
Surface dissolved oxygen (DO) mg L^{-1}	6.2	6.4	7.1	7.1	7	6.6
Surface water conductivity µS cm^{-1}	263	263	263	262	262	262.5
Surface water temperature °C	20.5	20.4	20.2	20.1	20.1	20.2
Secchi depth cm	50	60	73	85	79	68.5

Appendix 2.6 The average values of physical and chemical parameters of surface water at stations 1, 2, 4 and 5 in comparison with the values of central station in Lake Naivasha in March 2018.

Variables	Sta. 1	Sta.2	Sta. 3 (Central station)	Sta. 4	Sta. 5	Average values at stations 1,2, 4 and 5
Depth (m)	4.3	4.5	5	5	5.8	4.9
pH	8.8	8.6	8.8	8.6	8.5	8.6
Surface dissolved oxygen (DO) mg L^{-1}	7.8	8.0	8.8	9.6	9.8	8.8
Surface water conductivity µS cm^{-1}	334	332	331	331	331	332
Surface water temperature °C	21.6	21.9	21.7	23.6	23.5	22.6
Secchi depth cm	50	40	50	43	40	43.2

Appendix 2.7 Plankton composition at the three pelagic stations of Lake Bogoria in December 2016.

Group	Station 1	Station 2 (central station)	Station 3
Zooplankton	*Moina* sp. *Brachionus* sp. *Lecane* sp.	*Moina* sp. *Brachionus* sp. *Hexarthra* sp.	*Moina* sp. *Brachionus sp.* *Hexarthra* sp.
Phytoplankton	*Cyclotella* sp. *Arthrospira* sp.	*Cyclotella* sp. *Arthrospira* sp.	*Cyclotella* sp. *Arthrospira* sp.

Appendix 2.8 Plankton composition at the three pelagic stations of Lake Bogoria in March 2018.

Group	Station 1	Station 2 (central station)	Station 3
Zooplankton	*Brachionus* sp.	*Brachionus* sp. *Synchaeta* sp.	*Brachionus* sp. *Synchaeta* sp.
Phytoplankton	*Arthrospira* sp.	*Arthrospira* sp.	*Arthrospira* sp.

Appendix 2.9 Plankton composition at the five pelagic stations of Lake Baringo in December 2016.

Group	Station 1	Station 2	Station 3 (Central station)	Station 4	Station 5
Zooplankton	*Moina* sp. *Diaphanosoma* sp. *Ceriodaphnia* sp. *Macrothrix* sp. *Chydorus* sp. *Thermocyclops* sp. *Brachionus* sp.	*Moina* sp. *Diaphanosoma* sp. *Ceriodaphnia* sp. *Thermocyclops* sp. *Brachionus* sp.	*Moina* sp. *Diaphanosoma* sp. *Ceriodaphnia* sp. *Macrothrix* sp. *Daphnia* sp. *Thermocyclops* sp. *Cyclops* sp.	*Moina* sp. *Diaphanosoma* sp. *Ceriodaphnia* sp. *Macrothrix* sp. *Thermocyclops* sp. *Pseudodiaptomus* sp.	*Moina* sp. *Diaphanosoma* sp. *Ceriodaphnia* sp. *Macrothrix* sp. *Thermocyclops* sp. *Synchaeta* sp.
Dominant Phytoplankton	*Aulacosiera* sp., *Closterium* sp. *Microcystis*	*Aulacosiera* sp., *Closterium* sp. *Microcystis*	*Aulacosiera* sp., *Closterium* sp. *Microcystis*	*Aulacosiera* sp., *Closterium* sp. *Microcystis*	*Aulacosiera* sp., *Closterium* sp. *Microcystis*

Appendix 2.10 Plankton composition at the five pelagic stations of Lake Baringo in March 2018.

Group	Station 1	Station 2	Station 3 (Central station)	Station 4	Station 5
Zooplankton	*Moina* sp. *Daphnia* sp. *Cyclops* sp.	*Moina* sp. *Diaphanosoma* sp. *Daphnia* sp. *Cyclops* sp.	*Moina* sp. *Diaphanosoma* sp. *Cyclops* sp. *Mesocyclops* sp.	*Moina* sp. *Diaphanosoma* sp. *Cyclops* sp.	*Moina* sp. *Diaphanosoma* sp. *Cyclops* sp.
Dominant Phytoplankton	*Aulacosiera* sp., *Closterium* sp. *Microcystis*	*Aulacosiera* sp., *Closterium* sp. *Microcystis*	*Aulacosiera* sp., *Closterium* sp. *Microcystis*	*Aulacosiera* sp., *Closterium* sp. *Microcystis*	*Aulacosiera* sp., *Closterium* sp. *Microcystis*

Appendix 2.11 Plankton composition at the five pelagic stations of Lake Naivasha in November 2016.

Group	Station 1	Station 2	Sta. 3 (Central station)	Station 4	Station 5
Zooplankton	*Diaphanosoma* sp. *Mesocyclops* sp. *Thermocyclops* sp. *Asplanchna* sp. *Brachionus* sp.	*Diaphanosoma* sp. *Chydorus* sp. *Mesocyclops* sp. *Thermocyclops* sp. *Asplanchna* sp. *Brachionus* sp. *Trichocera* sp.	*Diaphanosoma* sp. *Ceriodaphnia* sp. *Mesocyclops* sp. *Thermocyclops* sp. *Asplanchna* sp. *Lecane sp.*	*Diaphanosoma* sp. *Chydorus* sp. *Mesocyclops* sp. *Thermocyclops* sp. *Asplanchna* sp. *Lecane sp. Keratella* sp	*Diaphanosoma* sp. *Alonella* sp. *Mesocyclops* sp. *Thermocyclops* sp. *Asplanchna* sp.
Dominant Phytoplankton	*Aulacosiera* sp.	*Aulacosiera* sp.	*Aulacosiera* sp.	*Aulacosiera* sp.	*Aulacosiera* sp.

Appendix 2.12 Plankton composition at the five pelagic stations of Lake Naivasha in March 2018.

Group	Station 1	Station 2	Sta. 3 (Central station)	Station 4	Station 5
Zooplankton	*Diaphanosoma* sp. *Cyclops* sp. *Mesocyclops* sp. *Brachionus* sp.	*Diaphanosoma* sp. *Cyclops* sp. *Mesocyclops* sp. *Brachionus* sp.	*Diaphanosoma* sp. *Cyclops* sp. *Thermocyclops* sp. *Euchinus* sp. *Brachionus* sp.	*Diaphanosoma* sp. *Cyclops* sp. *Brachionus* sp.	*Diaphanosoma* sp. *Cyclops* sp. *Brachionus* sp.
Dominant Phytoplankton	*Aulacosiera* sp.	*Aulacosiera* sp.	*Aulacosiera* sp.	*Aulacosiera* sp.	*Aulacosiera* sp.

Appendix 2.13 T-test to test the difference between $\delta^{13}C$ signatures of non-acidified and acidified samples of calanoid *Lovenula* sp. in Lake Sonachi in November 2016.

Column B	$\delta^{13}C$ signature of non-acidified calanoid *Lovenula* sp. in November 2016
vs.	vs.
Column A	$\delta^{13}C$ signature of acidified calanoid *Lovenula* sp. in November 2016
Unpaired t test	
P value	0.4149
P value summary	ns
Significantly different (P < 0.05)?	No
One- or two-tailed P value?	Two-tailed
t, df	t=0.9086 df=4
How big is the difference?	
Mean ± SEM of column A	-22.23 ± 0.4414, n=3
Mean ± SEM of column B	-21.8 ± 0.1631, n=3
Difference between means	0.4276 ± 0.4706
95% confidence interval	-0.8789 to 1.734
R squared (eta squared)	0.1711
F test to compare variances	
F, DFn, Dfd	7.322, 2, 2
P value	0.2403
P value summary	ns
Significantly different (P < 0.05)?	No

Appendix 2.14 T-test to test the difference between $\delta^{15}N$ signatures of non-acidified and acidified samples of calanoid *Lovenula* sp. in Lake Sonachi in November 2016.

Column B	$\delta^{15}N$ signature of non-acidified calanoid *Lovenula* sp. in November 2016
vs.	vs.
Column A	$\delta^{15}N$ signature of acidified calanoid *Lovenula* sp. in November 2016
Unpaired t test	
P value	0.0217
P value summary	*
Significantly different (P < 0.05)?	Yes
One- or two-tailed P value?	Two-tailed
t, df	t=3.652 df=4
How big is the difference?	
Mean ± SEM of column A	5.588 ± 0.2096, n=3
Mean ± SEM of column B	6.813 ± 0.2618, n=3
Difference between means	1.225 ± 0.3353
95% confidence interval	0.2937 to 2.156
R squared (eta squared)	0.7693
F test to compare variances	
F, DFn, Dfd	1.56, 2, 2
P value	0.7814
P value summary	ns
Significantly different (P < 0.05)?	No

Appendix 2.15 T-test to test the difference between $\delta^{13}C$ signatures of non-acidified and acidified samples of cladoceran *Moina* sp. in Lake Bogoria in December 2016.

Column B	$\delta^{13}C$ signature of non-acidified cladoceran Moina sp. in December 2016
vs.	vs.
Column A	$\delta^{13}C$ signature of Acidified cladoceran Moina sp. in December 2016
Unpaired t test	
P value	0.0050
P value summary	**
Significantly different (P < 0.05)?	Yes
One- or two-tailed P value?	Two-tailed
t, df	t=5.591 df=4
How big is the difference?	
Mean ± SEM of column A	-24.05 ± 0.1198, n=3
Mean ± SEM of column B	-23.01 ± 0.1428, n=3
Difference between means	1.042 ± 0.1864
95% confidence interval	0.5244 to 1.559
R squared (eta squared)	0.8865
F test to compare variances	
F, DFn, Dfd	1.42, 2, 2
P value	0.8264
P value summary	ns
Significantly different (P < 0.05)?	No

Appendix 2.16 T-test to test the difference between $\delta^{15}N$ signatures of non-acidified and acidified samples of cladoceran *Moina* sp. in Lake Bogoria in December 2016.

Column B	$\delta^{15}N$ signature of non-acidified cladoceran *Moina* sp. in December 2016
vs.	vs.
Column A	$\delta^{15}N$ signature of acidified cladoceran *Moina* sp. in December 2016
Unpaired t test	
P value	0.0203
P value summary	*
Significantly different (P < 0.05)?	Yes
One- or two-tailed P value?	Two-tailed
t, df	t=3.728 df=4
How big is the difference?	
Mean ± SEM of column A	6.692 ± 0.1743, n=3
Mean ± SEM of column B	7.392 ± 0.06998, n=3
Difference between means	0.7001 ± 0.1878
95% confidence interval	0.1786 to 1.221
R squared (eta squared)	0.7765
F test to compare variances	
F, DFn, Dfd	6.202, 2, 2
P value	0.2777
P value summary	ns
Significantly different (P < 0.05)?	No

Appendix 2.17 T-test to test the difference between $\delta^{13}C$ signatures of non-acidified and acidified samples of POM 0.7-25 µm in Lake Sonachi in November 2016.

Column B	$\delta^{13}C$ signature of acidified POM 0.7-25 µm
	In Lake Sonachi
vs.	vs.
Column A	$\delta^{13}C$ signature of non-acidified POM 0.7-25 µm
	in Lake Sonachi
Unpaired t test	
P value	0.0130
P value summary	*
Significantly different (P < 0.05)?	Yes
One- or two-tailed P value?	Two-tailed
t, df	t=4.268 df=4
How big is the difference?	
Mean ± SEM of column A	-20.72 ± 0.1989, n=3
Mean ± SEM of column B	-22.71 ± 0.422, n=3
Difference between means	-1.991 ± 0.4666
95% confidence interval	-3.287 to -0.696
R squared (eta squared)	0.82
F test to compare variances	
F, DFn, Dfd	4.501, 2, 2
P value	0.3636
P value summary	ns
Significantly different (P < 0.05)?	No

Appendix 2.18 T-test to test the difference between $\delta^{13}C$ signatures of non-acidified and acidified samples of POM 0.7-2 µm in Lake Sonachi in March 2018.

Column B	$\delta^{13}C$ signature of acidified POM 0.7-2 µm In Lake Sonachi
vs.	vs.
Column A	$\delta^{13}C$ signature of nonacidified POM 0.7-2 µm In Lake Sonachi
Unpaired t test	
P value	<0.0001
P value summary	****
Significantly different (P < 0.05)?	Yes
One- or two-tailed P value?	Two-tailed
t, df	t=24.05 df=4
How big is the difference?	
Mean ± SEM of column A	-12.26 ± 0.3031, n=3
Mean ± SEM of column B	-21.87 ± 0.2602, n=3
Difference between means	-9.606 ± 0.3995
95% confidence interval	-10.72 to -8.497
R squared (eta squared)	0.9931
F test to compare variances	
F, DFn, Dfd	1.356, 2, 2
P value	0.8489
P value summary	ns
Significantly different (P < 0.05)?	No

Appendix 2.19 T-test to test the difference between $\delta^{13}C$ signatures of non-acidified and acidified samples of POM 0.7-25 µm in Lake Bogoria in December 2016.

Column B	$\delta^{13}C$ signature of acidified POM 0.7-25 µm in Lake Bogoria
vs.	vs.
Column A	$\delta^{13}C$ signature of nonacidified POM 0.7-25 µm in Lake Bogoria
Unpaired t test	
P value	<0.0001
P value summary	****
Significantly different (P < 0.05)?	Yes
One- or two-tailed P value?	Two-tailed
t, df	t=51.19 df=4
How big is the difference?	
Mean ± SEM of column A	-13.16 ± 0.0714, n=3
Mean ± SEM of column B	-24.62 ± 0.2122, n=3
Difference between means	-11.46 ± 0.2239
95% confidence interval	-12.08 to -10.84
R squared (eta squared)	0.9985
F test to compare variances	
F, DFn, Dfd	8.831, 2, 2
P value	0.2034
P value summary	ns
Significantly different (P < 0.05)?	No

Appendix 2.20 T-test to test the difference between $\delta^{13}C$ signatures of non-acidified and acidified samples of POM 0.7-2 µm in Lake Bogoria in March 2018.

Column B	$\delta^{13}C$ signature of nonacidified POM 0.7-2 µm in Lake Bogoria
vs.	vs.
Column A	$\delta^{13}C$ signature of acidified POM 0.7-2 µm in Lake Bogoria
Unpaired t test	
P value	<0.0001
P value summary	****
Significantly different (P < 0.05)?	Yes
One- or two-tailed P value?	Two-tailed
t, df	t=43.67 df=4
How big is the difference?	
Mean ± SEM of column A	-22.17 ± 0.1136, n=3
Mean ± SEM of column B	-12.38 ± 0.1934, n=3
Difference between means	9.794 ± 0.2243
95% confidence interval	9.171 to 10.42
R squared (eta squared)	0.9979
F test to compare variances	
F, DFn, Dfd	2.901, 2, 2
P value	0.5127
P value summary	ns
Significantly different (P < 0.05)?	No

Appendix 2.21 T-test to test the difference between $\delta^{13}C$ signatures of non-acidified and acidified samples of POM 2-20 µm in Lake Bogoria in March 2018.

Column B	$\delta^{13}C$ signature of acidified POM 2-20 µm in Lake Bogoria
vs.	vs.
Column A	$\delta^{13}C$ signature of nonacidified POM 2-20 µm in Lake Bogoria
Unpaired t test	
P value	0.0003
P value summary	***
Significantly different (P < 0.05)?	Yes
One- or two-tailed P value?	Two-tailed
t, df	t=12.18 df=4
How big is the difference?	
Mean ± SEM of column A	-10.82 ± 0.1723, n=3
Mean ± SEM of column B	-22.6 ± 0.9518, n=3
Difference between means	-11.78 ± 0.9672
95% confidence interval	-14.47 to -9.097
R squared (eta squared)	0.9738
F test to compare variances	
F, DFn, Dfd	30.5, 2, 2
P value	0.0635
P value summary	ns
Significantly different (P < 0.05)?	No

Appendix 2.22 T-test to test the difference between $\delta^{13}C$ signatures of non-acidified and acidified samples of POM 20-48 µm in Lake Bogoria in March 2018.

Column B	$\delta^{13}C$ signature of acidified POM 20-48 µm in Lake Bogoria
vs.	vs.
Column A	$\delta^{13}C$ signature of nonacidified POM 20-48 µm in Lake Bogoria
Unpaired t test	
P value	0.0967
P value summary	ns
Significantly different (P < 0.05)?	No
One- or two-tailed P value?	Two-tailed
t, df	t=2.161 df=4
How big is the difference?	
Mean ± SEM of column A	-19.51 ± 0.4444, n=3
Mean ± SEM of column B	-20.49 ± 0.08634, n=3
Difference between means	-0.9785 ± 0.4527
95% confidence interval	-2.235 to 0.2784
R squared (eta squared)	0.5387
F test to compare variances	
F, DFn, Dfd	26.49, 2, 2
P value	0.0727
P value summary	ns
Significantly different (P < 0.05)?	No

Appendix 2.23 T-test to test the difference between $\delta^{13}C$ signatures of non-acidified and acidified samples of POM 0.7-25 µm in Lake Baringo in December 2016.

Column B	$\delta^{13}C$ signature of acidified POM 0.7-25 µm in Lake Baringo
vs.	vs.
Column A	$\delta^{13}C$ signature of nonacidified POM 0.7-25 µm in Lake Baringo
Unpaired t test	
P value	0.1001
P value summary	ns
Significantly different (P < 0.05)?	No
One- or two-tailed P value?	Two-tailed
t, df	t=2.131 df=4
How big is the difference?	
Mean ± SEM of column A	-27.48 ± 0.268, n=3
Mean ± SEM of column B	-26.26 ± 0.5045, n=3
Difference between means	1.217 ± 0.5713
95% confidence interval	-0.3688 to 2.804
R squared (eta squared)	0.5317
F test to compare variances	
F, DFn, Dfd	3.544, 2, 2
P value	0.4402
P value summary	ns
Significantly different (P < 0.05)?	No

Appendix 2.24 T-test to test the difference between $\delta^{13}C$ signatures of non-acidified and acidified samples of POM 48 µm < POM in Lake Baringo in March 2018.

Column B	$\delta^{13}C$ signature of acidified 48 µm < POM in Lake Baringo in March 2018
vs.	vs.
Column A	$\delta^{13}C$ signature of nonacidified 48 µm < POM in Lake Baringo in March 2018
Unpaired t test	
P value	0.0229
P value summary	*
Significantly different (P < 0.05)?	Yes
One- or two-tailed P value?	Two-tailed
t, df	t=3.594 df=4
How big is the difference?	
Mean ± SEM of column A	-29.32 ± 0.6099, n=3
Mean ± SEM of column B	-26.81 ± 0.3368, n=3
Difference between means	2.504 ± 0.6967
95% confidence interval	0.5696 to 4.439
R squared (eta squared)	0.7635
F test to compare variances	
F, DFn, Dfd	3.279, 2, 2
P value	0.4674
P value summary	ns
Significantly different (P < 0.05)?	No

Appendix 2.25 T-test to test the difference between $\delta^{13}C$ signatures of non-acidified and acidified samples of POM 0.7-25 µm in Lake Naivasha in November 2016.

Column B	$\delta^{13}C$ signature of acidified POM 0.7-25 µm in Lake Naivasha
vs.	vs.
Column A	$\delta^{13}C$ signature of nonacidified POM 0.7-25 µm in Lake Naivasha
Unpaired t test	
P value	0.7163
P value summary	ns
Significantly different (P < 0.05)?	No
One- or two-tailed P value?	Two-tailed
t, df	t=0.3902 df=4
How big is the difference?	
Mean ± SEM of column A	-24.03 ± 0.1466, n=3
Mean ± SEM of column B	-24.1 ± 0.117, n=3
Difference between means	-0.0732 ± 0.1876
95% confidence interval	-0.5941 to 0.4477
R squared (eta squared)	0.03667
F test to compare variances	
F, DFn, Dfd	1.569, 2, 2
P value	0.7784
P value summary	ns
Significantly different (P < 0.05)?	No

Appendix 2.26 T-test to test the difference between $\delta^{13}C$ signatures of non-acidified and acidified samples of POM 2-20 µm in Lake Naivasha in March 2018.

Column B	$\delta^{13}C$ signature of acidified POM 2-20 µm in Lake Naivasha
vs.	vs.
Column A	$\delta^{13}C$ signature of nonacidified POM 2-20 µm in Lake Naivasha
Unpaired t test	
P value	<0.0001
P value summary	****
Significantly different (P < 0.05)?	Yes
One- or two-tailed P value?	Two-tailed
t, df	t=19.02 df=4
How big is the difference?	
Mean ± SEM of column A	-11.58 ± 0.2214, n=3
Mean ± SEM of column B	-21.89 ± 0.4947, n=3
Difference between means	-10.31 ± 0.542
95% confidence interval	-11.81 to -8.804
R squared (eta squared)	0.9891
F test to compare variances	
F, DFn, Dfd	4.991, 2, 2
P value	0.3338
P value summary	ns
Significantly different (P < 0.05)?	No

Appendix 2.27 T-test to test the difference between $\delta^{13}C$ signatures of non-acidified and acidified samples of POM 20-48 µm in Lake Naivasha in March 2018.

Column B	$\delta^{13}C$ signature of acidified POM 20-48 µm in Lake Naivasha
vs.	vs.
Column A	$\delta^{13}C$ signature of nonacidified POM 20-48 µm in Lake Naivasha
Unpaired t test	
P value	0.0008
P value summary	***
Significantly different (P < 0.05)?	Yes
One- or two-tailed P value?	Two-tailed
t, df	t=9.019 df=4
How big is the difference?	
Mean ± SEM of column A	-19.65 ± 0.1353, n=3
Mean ± SEM of column B	-21.6 ± 0.1688, n=3
Difference between means	-1.951 ± 0.2163
95% confidence interval	-2.551 to -1.35
R squared (eta squared)	0.9531
F test to compare variances	
F, DFn, Dfd	1.555, 2, 2
P value	0.7827
P value summary	ns
Significantly different (P < 0.05)?	No

Appendix 3.1 Depth profiles of some variables at the central station of Lake Sonachi in November 2016.

Depth (m)	T (°C)	DO (mg/ $L^{-1)}$	conductivity µS cm^{-1}	pH
Surface	21	11.8	8028	9.7
1	20.7	9.8	8015	9.7
1.5	20.0	0.6	7977	9.6
2	19.8	0.3	7962	9.6
3	19.8	0.1	7962	9.6
4	20.3	0.1	9115	9.5
5	20.7	0.1	15440	9.5

Appendix 3.2 Depth profiles of some variables at the central station of Lake Sonachi in March 2018.

Depth (m)	T (°C)	DO (mg/ $L^{-1)}$	conductivity µS cm^{-1}	pH
Surface	23.7	8.5	11270	9.7
1	23.2	8.2	11270	9.7
2	21.6	0.7	11200	9.7
3	21	0.4	11150	9.7
4	20.8	0.2	15300	9.5

Appendix 3.3 The isotopic values of $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) for major components of the pelagic food web and from several types of terrestrial carbon sources at Lake Sonachi for the two sampling campaigns. M=mean, SD= standard deviation, n=number of measured samples.

	November 2016		**March 2018**	
Sample type	M $\delta^{13}C$ ‰ (S.D.,n.)	M $\delta^{15}N$‰ (S.D.,n.)	M $\delta^{13}C$‰ (S.D.,n.)	M $\delta^{15}N$‰ (S.D.,n.)
Zooplankton				
Non-acidified *Lovenula* sp.	-22.0 (0.5,4)	6.6 (0.5,4)	-21.1(0.1,3)	9.6 (0.03,3)
Acidified *Lovenula* sp.	-22.2 (0.7,3)	5.5 (0.3,3)		
Phytoplankton				
Colonies of *Microcystis* sp.	-16.5 (1.0,3)	-2.4 (0.2,1)		
Fractions of particulate organic matter				
0.7-25 μm (acidified for carbon only) (mainly *Synechococcus* sp.)	-22.7 (0.7,3)	-0.6 (1.4,3)		
0.7-25 μm (nonacidified)	-20.7 (0.3,3)			
0.7-2 μm (acidified for carbon only) (mainly *Synechococcus* sp.)			-21.8 (0.4,3)	2.5 (0.1,1)
0.7-2 μm (nonacidified)			-12.2 (0.5,3)	
2-20 μm (acidified for carbon only) (mainly *Synechococcus* sp.)			-22.5 (0.1,1)	3.6 (0.1,1)
2-20 μm (nonacidified)			-21.1 (0.6,3)	
20-48 μm (acidified for carbon only)			-23.9 (0.1,1)	4.0 (0.1,1)
20-48 μm (nonacidified)			-23.1 (1.1,3)	
DOM	-17.1 (0.1,3)	4.5 (0.3,3)		
Soil	-25.1 (1.2,3)	5.9 (0.1,3)		
Sediments	-13.8 (0.2,3)	6.2 (0.1,3)		
Vegetation				
Terrestrial plant leaves				
Vernonina sp.	-26.6 (0.01,3)	6.1 (0.1,3)		
Cyperus sp.	-12.9 (0.02,3)	-4.2 (0.2,3)		

Appendix 4.1 Depth profile of dissolved oxygen (mg/ L^{-1}) at stations (1, 2 and 3) of Lake Bogoria in December 2016.

Depth (m)	Station 1	Station 2	Station 3
Surface	5.4	3.6	4
1	5.1	2.5	2.4
2	4.8	1	1.1
3	0.2	0.7	1
4	0.2	0.3	0.9
5	0.1	0.1	0.6
6	N/A	N/A	N/A
7	N/A	0.1	N/A
8	0.1	0.1	N/A
9	N/A	0.1	0.1
10	0.1	0.1	0.1
11	0.1	0.1	0.1
12	N/A	0.1	0.1
13	0	0.1	0.1
14	0	0.1	0.1

Appendix 4.2 Depth profile of pH at stations (1, 2 and 3) of Lake Bogoria in December 2016.

Depth (m)	Station 1	Station 2	Station t3
Surface	10.1	10	10
1	10	10	10
2	10	10	10
3	10	10	10
4	10	10	10
5	10	10	10
6	N/A	N/A	N/A
7	N/A	N/A	N/A
8	10	10	N/A
9	N/A	10	10
10	10	10	N/A
11	N/A	10	N/A
12	9.9	10	10
13	9.9	9.9	10
14	9.9	9.9	10

Appendix 4.3 Depth profile of conductivity µS cm^{-1} at stations (1, 2 and 3) of Lake Bogoria in December 2016.

Depth (m)	Station 1	Station 2	Station t3
Surface	39225	38331	38329
1	38026	38324	38355
2	38050	38427	38406
3	38208	38434	38388
4	38331	38397	38402
5	38385	38447	38407
6	N/A	N/A	N/A
7	N/A	N/A	N/A
8	38372	38461	N/A
9	N/A	38477	38381
10	38450	38485	N/A
11	43250	38560	N/A
12	61515	38572	60486
13	63137	42916	62962
14	63997	43022	62705

Appendix 4.4 Depth profile of temperature (°C) at stations (1, 2 and 3) of Lake Bogoria in December 2016.

Depth (m)	Station 1	Station 2	Station 3
Surface	26.8	25.9	26.1
1	26.8	25.8	25.8
2	26.8	25.8	25.6
3	26.3	25.7	25.6
4	26.2	25.7	25.6
5	26.1	25.7	25.5
6	25.9	25.6	25.5
7	25.8	25.6	25.5
8	25.7	25.5	25.4
9	25.7	25.5	25.4
10	25.7	25.5	25.4
11	26.6	25.9	26
12	29.9	28	26.2
13	29.4	28.6	26.2
14	29.1	28.6	26.2

Appendix 4.5 Depth profile of dissolved oxygen (mg/ L^{-1}) at stations (1, 2 and 3) of Lake Bogoria in March 2018.

Depth (m)	Station 1	Station 2	Station 3
Surface	42.4	21	6.2
1	0.9	4.6	5.9
2	0.4	1	4.6
3	0.3	0.6	4.5
4	0.2	0.4	3
5	0.2	0.4	2.8
6	0.2	0.5	3
7	0.1	0.3	2.6
8	0.1	0.2	1.6
9	0.1	0.1	0.8
10	0.1	0.1	0.5
11	0.1	0.1	0.2
12	0.1		

Appendix 4.6 Depth profile of pH at stations (1, 2 and 3) of Lake Bogoria in in March 2018.

Depth (m)	Station 1	Station 2	Station 3
Surface	9.9	10	10
1	9.9	9.9	10
2	9.9	10	10
3	9.9	10	10
4	9.9	10	10
5	10	10	10
6	10	10	10
7	10	10	10
8	10	10	10
9	10	10	10
10	10	10	10
11	10	10	10
12	10		

Appendix 4.7 Depth profile of conductivity µS cm^{-1} at stations (1, 2 and 3) of Lake Bogoria in March 2018.

Depth (m)	Station 1	Station 2	Station 3
Surface	42260	42030	41950
1	42100	41970	41960
2	42080	42010	41960
3	42020	42010	41930
4	42030	42000	41940
5	42030	42000	41910
6	42020	42000	41890
7	42020	42000	41860
8	42020	42000	41860
9	42020	42000	41830
10	42020	42000	41920
11	42010	41960	41920
12	42100		

Appendix 4.8 Depth profile of temperature (°C) at stations (1, 2 and 3) of Lake Bogoria in March 2018.

Depth (m)	Station 1	Station 2	Station 3
Surface	29.5	26.7	24.8
1	25	25.1	24.7
2	24.8	24.8	24.6
3	24.8	24.7	24.6
4	24.8	24.7	24.5
5	24.8	24.7	24.4
6	24.8	24.6	24.3
7	24.7	24.5	24.3
8	24.7	24.5	24.2
9	24.7	24.5	24.1
10	24.6	24.5	24
11	24.6	24.5	23.9
12	24.5		

Appendix 4.9 The isotopic values of $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) for major components of the pelagic food web and from several types of terrestrial and benthic carbon sources at Lake Bogoria for the two sampling campaigns. M=mean, SD= standard deviation, n=number of measured samples.

	December 2016		**March 2018**	
Sample type	M $\delta^{13}C$ ‰ (S.D.,n.)	M $\delta^{15}N$‰ (S.D.,n.)	M $\delta^{13}C$‰ (S.D.,n.)	M $\delta^{15}N$‰ (S.D.,n.)
Zooplankton				
Non-acidified Pelagic *Moina* sp.	-23.0 (0.2,3)	7.3 (0.1,3)		
Acidified pelagic *Moina* sp.	-24.0 (0.2,3)	6.6 (0.3,3)		
Pelagic Rotifers	-20.9 (0.1,3)		-24.7 (1.8,3)	6.8 (1.4,3)
Phytoplankton				
Arthrospira sp.	-21.3 (0.1,3)	1.0 (1.2,5)	-24.9 (0.5,3)	2.1 (0.2,3)
Cyclotella sp.	-23.6 (0.3,1)	1.6 (0.8,1)		
Birds				
Lesser flamingo	-19.8 (0.08,3)	4.6 (0.2,3)		
Fractions of particulate organic matter				
0.7-25 µm (acidified for carbon only)	-24.6 (0.3,3)	6.6 (0.2,3)		
0.7-25 µm (nonacidified)	-13.1 (0.1,3)			
0.7-2 µm (acidified for carbon only)			-22.1 (0.1,3)	6.1 (0.1,1)
0.7-2 µm (nonacidified)			-12.3 (0.3,3)	
2-20 µm (acidified for carbon only)			-22.5 (1.6,3)	5.7 (0.1,1)
2-20 µm (nonacidified)			-10.8 (0.2,3)	
20-48 µm (acidified for carbon only)			-19.5 (0.7,3)	2.7 (0.1,1)
20-48 µm (nonacidified)			-20.4 (0.1,3)	
DOM	-20.0 (0.08,3)	-1.2 (0.9,3)		
Soil	-23.7 (0.6,3)	8.1 (0.1,3)		
Sediments	-23.5 (0.2,3)	6.7 (0.4,3)		
Vegetation				
Terrestrial plant leaves				
Balanites sp.	-25.3 (0.03,3)	8.2 (0.1,3)		
Salvadora persica	-27.3 (0.02,3)	13.3 (0.08,3)		

Appendix 5.1 Depth profile of dissolved oxygen (mg/ L^{-1}) at stations (1, 2, 3, 4 and 5) of Lake Naivasha in November 2016.

Depth (m)	Station 1	Station 2	Station 3	Station 4	Station 5
Surface	6.2	6.4	7.1	7.1	7.0
1	6.4	6.4	6.9	6.9	6.9
2	6.4	6.3	6.9	6.8	6.7
3	6.3	6.3	6.7	6.8	6.5
4	6.3	6.3	6.7	6.8	6.4
5	6.2	6.3	6.7	6.7	6.4
6			6.7	6.6	6.4
7					6.3

Appendix 5.2 Depth profile of pH at stations (1, 2, 3, 4 and 5) of Lake Naivasha in November 2016.

Depth (m)	Station 1	Station 2	Station 3	Station 4	Station 5
Surface	8.4	8.4	8.5	8.5	8.5
1	8.4	8.3	8.5	8.5	8.5
2	8.3	8.3	8.5	8.5	8.5
3	8.3	8.3	8.5	8.5	8.5
4	8.3	8.3	8.5	8.5	8.5
5	8.3	8.3	8.5	8.5	8.4
6			8.5	8.4	8.4
7					8

Appendix 5.3 Depth profile of conductivity µS cm^{-1} at stations (1, 2, 3, 4 and 5) of Lake Naivasha in November 2016.

Depth (m)	Station 1	Station 2	Station 3	Station 4	Station 5
Surface	240	263	263	262	262
1	241	263	263	262	262
2	241	264	263	262	262
3	241	264	263	262	262
4	241	264	263	262	262
5	241	264	263	262	262
6			263	262	262
7					262

Appendix 5.4 Depth profile of temperature (°C) at stations (1, 2, 3, 4 and 5) of Lake Naivasha in November 2016.

Depth (m)	Station 1	Station 2	Station 3	Station 4	Station 5
Surface	20.5	20.4	20.2	20.1	20.1
1	20.5	20.4	20.2	20.1	20.1
2	20.5	20.4	20.2	20.1	20.1
3	20.5	20.4	20.2	20.1	20.1
4	20.5	20.4	20.2	20.1	20.1
5	20.5	20.4	N/A	20.1	20.1
6				20.1	20.1
7					20.1

Appendix 5.5 Depth profile of dissolved oxygen (mg/ L^{-1}) at stations (1, 2, 3, 4 and 5) of Lake Naivasha in March 2018.

Depth (m)	Station 1	Station 2	Station 3	Station 4	Station 5
Surface	7.8	8	8.8	9.6	9.8
1	7.4	7.5	8.9	10.3	10
2	7.2	6.6	7.6	8.3	8.1
3	7	6.4	7.2	7.1	7.7
4	6.8	6.2	7.3	7.2	7.2
5			7.3	7	6.8

Appendix 5.6 Depth profile of pH at stations (1, 2, 3, 4 and 5) of Lake Naivasha in March 2018.

Depth (m)	Station 1	Station 2	Station 3	Station 4	Station 5
Surface	8.8	8.6	8.8	8.6	8.5
1	8.6	8.6	8.8	8.1	8.5
2	8.6	8.6	8.6	8.0	8.2
3	8.6	8.5	8.7	7.9	8.1
4	8.6	8.5	8.6	7.9	8.0
5			8.5	7.9	8.0

Appendix 5.7 Depth profile of conductivity µS cm^{-1} at stations (1, 2, 3, 4 and 5) of Lake Naivasha in March 2018.

Depth (m)	Station 1	Station 2	Station 3	Station 4	Station 5
Surface	334	332	331	331	331
1	333	332	331	330	328
2	333	332	331	331	330
3	333	333	331	331	330
4	333	333	331	331	330
5			331	331	331

Appendix 5.8 Depth profile of temperature (°C) at stations (1, 2, 3, 4 and 5) of Lake Naivasha in March 2018.

Depth (m)	Station 1	Station 2	Station 3	Station 4	Station 5
Surface	21.6	21.9	21.7	23.6	23.5
1	21.5	21.7	21.6	21.6	21.1
2	21.5	21.5	21.1	20.9	20.8
3	21.5	21.5	21	20.9	20.7
4	21.5	21.4	21	20.8	20.7
5			21	20.7	20.7

Appendix 5.9 Depth profile of dissolved oxygen (mg/ L^{-1}) at stations (1, 2, 3, 4 and 5) of Lake Baringo in December 2016.

Depth (m)	Station 1	Station 2	Station 3	Station 4	Station 5
Surface	6.7	6.9	7.1	7.2	7.2
1	N/A	N/A	7.3	7.1	7.1
2	6.6	N/A	7.1	6.9	6.7
3	6.6	6.7	6.8	6.7	6.7
4	6.5	6.6	6.7	6.6	6.6
5	6.5	6.6	6.7	6.6	6.6
6	6.5	6.6	6.7	6.6	6.6
7	6.5	6.6	6.7	6.6	6.6
8	6.5	6.6	6.7	6.6	6.6
9	6.5	6.6	6.7	6.6	4.8
10		6.5			
11		6.3			

Appendix 5.10 Depth profile of pH at stations (1, 2, 3, 4 and 5) of Lake Baringo in December 2016.

Depth (m)	Station 1	Station 2	Station 3	Station 4	Station 5
Surface	8.7	8.7	8.7	8.7	8.7
1	N/A	N/A	8.7	8.7	8.7
2	N/A	N/A	8.7	8.7	8.7
3	8.7	8.7	8.7	8.7	8.7
4	8.7	8.7	8.7	8.7	8.7
5	8.7	8.7	8.7	8.7	8.7
6	8.7	8.7	8.7	8.7	8.7
7	8.7	8.7	8.7	8.7	8.7
8	8.7	8.7	8.7	8.7	8.6
9	8.7	8.7	8.6	8.7	8.5
10		8.6			
11		7.7			

Appendix 5.11 Depth profile of conductivity µS cm^{-1} at stations (1, 2, 3, 4 and 5) of Lake Baringo in December 2016.

Depth (m)	Station 1	Station 2	Station 3	Station 4	Station 5
Surface	475	476	479	477	478
1	N/A	N/A	476	476	478
2	475	N/A	476	476	478
3	475	476	476	476	478
4	475	476	476	476	478
5	475	476	476	476	478
6	475	476	476	476	478
7	475	476	476	476	478
8	475	476	476	476	478
9	475	476	476	475	475
10		476			
11		540			

Appendix 5.12 Depth profile of temperature (°C) at stations (1, 2, 3, 4 and 5) of Lake Baringo in December 2016.

Depth (m)	Station 1	Station 2	Station 3	Station 4	Station 5
Surface	25.4	25.5	27.7	27.1	26.1
1	N/A	N/A	25.8	25.6	25.8
2	25.4	N/A	25.3	25.2	25.5
3	25.4	25.3	25.2	25.2	25.4
4	25.4	25.3	25.2	25.2	25.4
5	25.4	25.3	25.2	25.2	25.4
6	25.4	25.3	25.2	25.2	25.4
7	25.4	25.3	25.2	25.2	25.4
8	25.4	25.3	25.2	25.2	25.4
9	25.4	25.3	25.2	25.2	25.4
10		25.3			
11		25.3			

Appendix 5.13 Depth profile of dissolved oxygen (mg/ L^{-1}) at stations (1, 2, 3, 4 and 5) of Lake Baringo in March 2018.

Depth (m)	Station 1	Station 2	Station 3	Station 4	Station 5
Surface	7.5	8.7	8.4	8.8	9.1
1	N/A	8.5	8.5	8.6	9.1
2	N/A	N/A	N/A	N/A	N/A
3	7.3	N/A	N/A	N/A	N/A
4	N/A	N/A	N/A	N/A	N/A
5	7.2	7.7	7.5	7.5	7.9
6	N/A	N/A	N/A	N/A	N/A
7	N/A	7.3	7.5	7.1	7.5
8	6.8	6.4	7.4	7	
8.2	5.4				

Appendix 5.14 Depth profile of pH at stations (1, 2, 3, 4 and 5) of Lake Baringo in March 2018.

Depth (m)	Station 1	Station 2	Station 3	Station 4	Station 5
Surface	8.7	8.6	8.7	8.5	8.6
1	N/A	8.5	8.7	8.6	8.7
2	N/A	N/A	N/A	N/A	N/A
3	8.7	N/A	N/A	N/A	N/A
4	N/A	N/A	N/A	N/A	N/A
5	8.7	8.4	8.6	8.3	8.5
6	N/A	N/A	N/A	N/A	N/A
7	N/A	8.4	8.5	8.3	8.2
8	8.7	8.3	8.5	8.3	
8.2	8.6				

Appendix 5.15 Depth profile of conductivity µS cm^{-1} at stations (1, 2, 3, 4 and 5) of Lake Baringo in March 2018.

Depth (m)	Station 1	Station 2	Station 3	Station 4	Station 5
Surface	540	541	543	543	550
1	N/A	541	541	541	541
2	N/A	N/A	N/A	N/A	N/A
3	541	N/A	N/A	N/A	N/A
4	N/A	N/A	N/A	N/A	N/A
5	541	540	540	541	544
6	N/A	N/A	N/A	N/A	N/A
7	N/A	540	540	541	543
8	541	540	540	541	
8.2	540				

Appendix 5.16 Depth profile of temperature (°C) at stations (1, 2, 3, 4 and 5) of Lake Baringo in March 2018.

Depth (m)	Station 1	Station 2	Station 3	Station 4	Station 5
Surface	25.6	25.9	27	27.4	29
1	N/A	25.5	25.5	25.7	27.8
2	N/A	N/A	N/A	N/A	N/A
3	25.6	N/A	N/A	N/A	N/A
4	N/A	N/A	N/A	N/A	N/A
5	25.6	25.5	25.2	25.2	25.6
6	N/A	N/A	N/A	N/A	N/A
7	N/A	25.4	25.2	25.2	25.5
8	25.4	25.1	25.2	25.2	
8.2	25.3				

Appendix 5.17 T-test to test the difference between phytoplankton density in Lake Naivasha and Lake Baringo in 2016.

Table Analyzed	Data 4
Column B	Density of phytoplankton L^{-1} in Lake Naivasha in November 2016
vs.	vs.
Column A	Density of phytoplankton L^{-1} in Lake Baringo in December 2016
Unpaired t test	
P value	<0.0001
P value summary	****
Significantly different (P < 0.05)?	Yes
One- or two-tailed P value?	Two-tailed
t, df	t=18.21 df=4
How big is the difference?	
Mean ± SEM of column A	29090 ± 9848, n=3
Mean ± SEM of column B	257166 ± 7739, n=3
Difference between means	228076 ± 12525
95% confidence interval	193302 to 262850
R squared (eta squared)	0.9881
F test to compare variances	
F, DFn, Dfd	1.619, 2, 2
P value	0.7636
P value summary	ns
Significantly different (P < 0.05)?	No

Appendix 5.18 T-test to test the difference between phytoplankton density in Lake Naivasha and Lake Baringo in March 2018.

Table Analyzed	Data 5
Column B	Density of phytoplankton L^{-1}in Lake Naivasha in March 2018
vs.	vs.
Column A	Density of phytoplankton L^{-1}in Lake Baringo in March 2018
Unpaired t test	
P value	0.0002
P value summary	***
Significantly different (P < 0.05)?	Yes
One- or two-tailed P value?	Two-tailed
t, df	t=13.54 df=4
How big is the difference?	
Mean ± SEM of column A	8693 ± 1476, n=3
Mean ± SEM of column B	63416 ± 3762, n=3
Difference between means	54722 ± 4041
95% confidence interval	43502 to 65943
R squared (eta squared)	0.9787
F test to compare variances	
F, DFn, Dfd	6.495, 2, 2
P value	0.2668
P value summary	ns
Significantly different (P < 0.05)?	No

Appendix 5.19 T-test to test the difference between Secchi depth (cm)in in Lake Naivasha and Lake Baringo in in the wet season.

Column B	Secchi depth (cm)in Lake Naivasha in 2016
vs.	vs.
Column A	Secchi depth in Lake Baringo in 2016
Unpaired t test	
P value	0.0108
P value summary	*
Significantly different (P < 0.05)?	Yes
One- or two-tailed P value?	Two-tailed
t, df	t=3.302 df=8
How big is the difference?	
Mean ± SEM of column A	45.4 ± 3.487, n=5
Mean ± SEM of column B	69.4 ± 6.377, n=5
Difference between means	24 ± 7.268
95% confidence interval	7.241 to 40.76
R squared (eta squared)	0.5768
F test to compare variances	
F, DFn, Dfd	3.344, 4, 4
P value	0.2692
P value summary	ns
Significantly different (P < 0.05)?	No

Appendix 5.20 T-test to test the difference between Secchi depth (cm) in in Lake Naivasha and Lake Baringo in in the dry season.

Column B	Secchi depth in Lake Baringo in 2018
vs.	vs.
Column A	Secchi depth (cm)in Lake Naivasha in 2018
Unpaired t test	
P value	0.6656
P value summary	ns
Significantly different (P < 0.05)?	No
One- or two-tailed P value?	Two-tailed
t, df	t=0.4487 df=8
How big is the difference?	
Mean ± SEM of column A	44.6 ± 2.272, n=5
Mean ± SEM of column B	49 ± 9.539, n=5
Difference between means	4.4 ± 9.806
95% confidence interval	-18.21 to 27.01
R squared (eta squared)	0.02455
F test to compare variances	
F, DFn, Dfd	17.64, 4, 4
P value	0.0167
P value summary	*
Significantly different (P < 0.05)?	Yes

Appendix 5.21 T-test to test the difference between zooplankton density in Lake Naivasha and Lake Baringo in 2016.

Table Analyzed	Data 1
Column B	Zooplankton density in Lake Naivasha (individ. L^{-1}) in November2016
vs.	vs.
Column A	Zooplankton density in Lake Baringo (individ. L^{-1}) in December 2016
Unpaired t test	
P value	0.0142
P value summary	*
Significantly different (P < 0.05)?	Yes
One- or two-tailed P value?	Two-tailed
t, df	t=2.617 df=28
How big is the difference?	
Mean ± SEM of column A	0.3665 ± 0.1399, n=15
Mean ± SEM of column B	2.569 ± 0.8301, n=15
Difference between means	2.203 ± 0.8418
95% confidence interval	0.4784 to 3.927
R squared (eta squared)	0.1965
F test to compare variances	
F, DFn, Dfd	35.19, 14, 14
P value	<0.0001
P value summary	****
Significantly different (P < 0.05)?	Yes

Appendix 5.22 T-test to test the difference between zooplankton density in Lake Naivasha and Lake Baringo in 2018.

Table Analyzed	Data 2
Column B	Zooplankton density in Lake Naivasha (individ. L^{-1}) in March 2018
vs.	vs.
Column A	Zooplankton density in Lake Baringo (individ. L^{-1}) in March 2018
Unpaired t test	
P value	0.0368
P value summary	*
Significantly different (P < 0.05)?	Yes
One- or two-tailed P value?	Two-tailed
t, df	t=2.193 df=28
How big is the difference?	
Mean ± SEM of column A	5.578 ± 2.84, n=15
Mean ± SEM of column B	66.46 ± 27.61, n=15
Difference between means	60.88 ± 27.76
95% confidence interval	4.02 to 117.7
R squared (eta squared)	0.1466
F test to compare variances	
F, DFn, Dfd	94.51, 14, 14
P value	<0.0001
P value summary	****
Significantly different (P < 0.05)?	Yes

Appendix 5.23 The isotopic values of $\delta^{13}C$ and $\delta^{15}N$ for major components of the pelagic food web and from several types of terrestrial, littoral and benthic carbon sources for Lake Baringo for the two sampling campaigns. M=mean, SD= standard deviation, n=number of measured samples.

	December 2016		**March 2018**	
	M $\delta^{13}C$ ‰ (S.D.,n.)	M $\delta^{15}N$‰ (S.D.,n.)	M $\delta^{13}C$‰ (S.D.,n.)	M $\delta^{15}N$‰ (S.D.,n.)
Zooplankton				
Pelagic Cladocera (mixed)	-27.0 (0.1,3)	6.2 (0.7,3)	-27.2 (0.1,3)	4.7 (0.1,3)
Pelagic Cyclopoida (mixed)	-25.5 (0.5.3)	8.0 (0.4,3)	-26.5 (0.2,3)	7.1 (0.03,3)
Pelagic Cyclopoida (adult)	-25.6 (0.3,4)	7.7 (1.0,4)		
Pelagic copepodites	-25.2 (0.5,4)	6.1 (0.1,1)		
Pelagic nauplii	-25.2 (1.1,3)	7.6 (0.1,1)		
Phytoplankton	-27.4 (0.7,4)	2.2 (0.5,1)	-26.2 (1.0,2)	3.1 (0.1,2)
Fish				
Barbus	-26.7 (1.4,3)	12.0 (1.0,3)		
Oreochromis	-26.9 (2.2,3)	9.7 (1.0,3)		
Clarias	-25.4 (1.8,3)	11.0 (0.7,3)		
Heterobranchus	-25.8 (1.3,3)	11.3 (0.7,3)		
Fractions of particulate organic matter				
0.7-25 μm (acidified for carbon only)	-26.2 (0.8,3)	3.8 (0.5,3)		
0.7-25 μm (nonacidified)	-27.4 (0.4,3)			
2-20 μm (acidified for carbon only)			-27.3 (0.2,1)	4.3 (0.4,1)
2-20 μm (nonacidified)			-24.4 (0.9,3)	
20-48 μm (acidified for carbon only)			-26.0 (0.2,1)	3.5 (0.4,1)
20-48 μm (nonacidified)			-23.9 (0.7,3)	
48 μm < POM (acidified for carbon only)			-26.8 (0.5,3)	1.6 (0.4,1)
48 μm < POM (nonacidified)			-29.3 (1.0,3)	
Periphyton				
Periphytopn from *Eichhornia*	-26.2 (0.1,3)	5.6 (0.4,3)		
Sediments	-23.7 (0.1,3)	6.5 (1.5,3)		
DOM	-21.2 (0.2,3)	3.3 (0.5,3)		
Vegetation				
Terrestrial plant leaves				
Cyperus sp.	-12.9 (0.03,3)	9.7 (0.5,3)		
Sesbania sesban	-27.1 (0.4,6)	0.3 (0.2,6)		
Acacia tortilis	-27.7 (0.02,3)	3.4 (0.1,3)		
Aquatic plants				
Eichhornia crassipes	-28.3 (0.05,3)	5.9 (0.4,3)		

Appendix 5.24 The isotopic values of $\delta^{13}C$ and $\delta^{15}N$ for major components of the pelagic food web and from several types of terrestrial, littoral and benthic carbon sources for Lake Naivasha for the two sampling campaigns. M=mean, SD= standard deviation, n=number of measured samples.

	November 2016		**March 2018**	
	M $\delta^{13}C$ ‰ (S.D.,n.)	M $\delta^{15}N$‰ (S.D.,n.)	M $\delta^{13}C$‰ (S.D.,n.)	M $\delta^{15}N$‰ (S.D.,n.)
Zooplankton				
Pelagic Cladocera	-23.9 (0.3,3)	4.2 (0.5,3)	-17.2 (0.2,3)	5.4 (0.5,3)
Pelagic Cyclopoida	-23.8 (0.2,3)	4.4 (0.4,3)	-18.4 (0.6,3)	4.5 (0.3,3)
Phytoplankton	-24.1 (1.0,3)	1.0 (0.2,3)	-17.8 (2.5,3)	1.5 (0.4,3)
Fish				
Cyprinus	-23.3 (3.3,3)	8.3 (1.5,3)		
Small *Oreochromis*	-24.1 (0.9,3)	8.5 (3.5,3)		
Large *Oreochromis*	-23.8 (0.6,3)	6.9 (0.09,3)		
Clarias	-22.7 (1.8,3)	11.5 (1.1,3)		
Procambarus	-23.9 (1,2)	9.2 (1.8,3)		
Oligochaetes	-25.1 (0.2,3)	4.0 (0.3,3)		
Fractions of particulate organic matter				
0.7-25 μm (acidified for carbon only)	-24.1 (0.2,3)	3.4 (0.1,3)		
0.7-25 μm (nonacidified)	-24.0 (0.2,3)			
0.7-2 μm (acidified for carbon only)			-22.3 (0.9,2)	1.5 (0.4,1)
0.7-2 μm (nonacidified)			-18.3 (0.4,3)	
2-20 μm (acidified for carbon only)			-21.8 (0.8,3)	4.8 (0.8,3)
2-20 μm (nonacidified)			-11.5 (0.3,3)	
20-48 μm (acidified for carbon only)			-19.6 (0.2,3)	2.7 (0.1,3)
20-48 μm (nonacidified)			-21.5 (0.2,3)	
DOM	-18.2 (0.1,3)	0.6 (1.4,3)		
Periphyton				
Periphyton from *Eichhornia*	-26.4 (0.04,3)	3.3 (0.6,3)		
Periphyton from *Salvinia*	-25.2 (0.07,3)	5.6 (0.6,3)		
Soil				
Soil (Gilgil river)	-24.6 (0.3,3)	4.4 (0.3,3)		
Soil (Malewa river)	-24.7 (0.1,3)	5.1 (0.03,3)		
Sediments	-21.2 (0.1,3)	1.8 (0.2,3)		
Vegetation				
Terrestrial plant leaves				
Juncus sp. (Gilgil river)	-28.4 (0.08,3)	7.4 (0.3,3)		
Rhus sp. (Gilgil river)	-26.9 (0.02,3)	4.8 (0.4,3)		
Syzygium sp. (Gilgil river)	-25.7 (0.03,3)	4.4 (0.3,3)		
Senna didymobotrya (Gilgil river)	-29.1 (0.04,3)	6.6 (0.07,3)		
Senna sp. (Gilgil river)	-28.5 (0.03,3)	3.6 (0.2,3)		
Cyperus papyrus (Gilgil river)	-13.3 (0.01,3)	7.0 (0.5,3)		
Dombeya burgessiae (Malewa river)	-30.8 (0.05,3)	8.1 (0.3,3)		
Ficus sur (Malewa river)	-29.1 (0.04,3)	8.5 (0.1,3)		
Pennisetum purpureum	-13.6 (0.04,3)	6.3 (0.2,3)		
Cyperus dives	-10.5 (0.05,3)	4.2 (0.4,3)		
Aquatic plants				
Eichhornia crassipes	-26.6 (0.1,3)	7.2 (0.1,3)		
Salvinia molesta	-27.9 (0.05,3)	5.8 (0.1,3)		

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