Linkages between Saline Lakes and their Riparian zone over climate change

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Statement of Originality

I certify that this thesis and the research presented with it are the product of my own work. During the Fieldwork campaigns I had multiple assistance from Undergraduate and Msc students, members of the local community, and a combined field excursion with members of the University of Southampton. I acknowledge the input of the above when relevant. The guidance I received from my supervisors is acknowledged in a section dedicated to this purpose. Other authors work is cited and the references listed at the end of the thesis. All other opinions and views given are my own.

Abstract

Research on resource transfer across ecosystem boundaries (i.e. allochthonous material; a subsidy) has been recognised since the 1920s and recognition of allochthonous inputs has been a part of food web theory since its inception. Nonetheless, only in recent decades have subsidies between ecosystems become a feature of large scale food web studies. Measures of subsidy links are usually restricted to studies on either marine or freshwater, the latter being the focus of most attention. In a recent meta-analysis of cross ecosystem boundary subsidies, two thirds of the 32 data sets used focused on freshwater ecosystems and one third on marine; none involved saline lakes. As a percentage of total global water volume saline lakes are almost equal to that of freshwater, yet there is a paucity of research carried out on linkage between saline lakes and their catchments. Two typical characteristics of saline lakes suggest that linkage between the aquatic and the terrestrial ecosystem is important. The first is that the communities in the aquatic ecosystem are generally made up of fewer actors of specialised species that occur in high abundances. The second is that saline lakes are usually found in arid landscapes which are depauperate in terrestrial production. It is well understood that specialised species with narrow niche widths will have a negative response to environmental change. In arid lake systems salinity is likely to be a function of lake volume, which is affected by the balance between evaporation and precipitation. Arid regions, particularly around the tropics, are susceptible to intensive perturbation caused by climate change. Very few studies on cross-ecosystem subsidies highlight the risk of perturbation to the stability of links in the light of climate change.

  This project aims to further our knowledge of resource subsidy between saline lakes and their arid catchment over climate change, which can be split into three main objectives.

1.   To use stable isotope analysis to investigate the relative strength and temporal patterns of aquatic subsidy to terrestrial consumers caused by the probable strongest link, the emerging chironomids. It is predicted that the strength of subsidy will change, following a lag, to any patterns of emergence that may exist through the chironomid life cycle. Therefore, temporal fluxes in the adult chironomid emergence rates and seasonal changes will be reflected in the isotopic signatures of consumers.

2.   The extent to which the aquatic subsidy impacts into Lake Bogoria will be measured and weather that impact expands and retracts in response to the cyclical behaviour of the chironomids. Bayesian mixing models and metrics will be employed, beyond the traditional ratio methods, to give further insight into landscape subsidy dynamics.

3.   Past salinity will be inferred through a transfer model created from the diversity of sub-fossilised chironomid head capsules in lake sediment extracted through coring methods. The density of sub-fossilised head capsules linked to the changes in salinity will be compared to contemporary larval densities. Contemporary larval densities will be measures across different salinity regimes provided by the three partially split lake basins and during different water levels as a result of seasonal changes to precipitation.

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Introduction and background literature review

Project Introduction

"Lake Bogoria, an empty wilderness occupied only by flamingos when I mapped it, is now more accessible and provides a unique open-air laboratory for such researches, but like all the Rift Valley lakes, is unique, sui generis*."*

Joseph McCall, 2010

The importance of research on resource transfer across ecosystem boundaries (i.e. allochthonous inputs; a subsidy) has been recognised since the 1920s and allochthonous inputs have been a part of food web theory since its inception. Nonetheless, only in recent decades have subsidies between ecosystems become a focus of larger scale food web studies. Measures of subsidies have typically been restricted to studies of either marine or freshwater ecosystems, whereas linkage between saline lakes and their riparian zone has been largely overlooked. Saline lakes are still perceived as being of less value, in terms of ecosystem goods and services, than other ecosystems. However, although saline lakes usually contain rather 'simple' communities, they are very productive and in addition they are typically found in arid landscapes where the terrestrial ecosystem is depauperate. Thus, such lakes provide an oasis in terms of food resources which the terrestrial ecosystem can exploit - provided there is a vector of transfer.

My aim is to further our knowledge of resource subsidy between saline lakes and their relatively arid riparian zone and consider such linkage with respect to climate change. I have three main objectives:

1) To investigate the relative strength of aquatic subsidy to terrestrial consumers, spatially and seasonally.
2) To investigate the short-term changes in relative strength of aquatic subsidy to terrestrial consumers, over seasons.
3) To infer historical conditions using a salinity transfer function applied to the chironomid larval assemblages found in the lake sediment palaeorecords.

Aquatic-terrestrial links

Cross-Ecosystem Resource Transfer

The transfer of resources such as nutrients, detritus and prey is ubiquitous at the landscape level. These movements can have strong influences on ecosystem dynamics including population, consumer-resource, food webs, and trophic interactions. Fluxes of energy result in direct and indirect increases in both primary and secondary production, and at a landscape scale connectivity varies considerably along a continuum starting at almost total isolation to strong mixing. The flow rate between ecosystems is affected by a number of factors (e.g. habitat geometry and area; similarity of, distance between, and relative productivity of interacting habitats; boundary permeability; and organism mobility (Polis et al., 1997). Seasonality and diurnal temporal functions also cause fluxes in subsidy strength.

Ecosystem linkage exists where any allochthonous input occurs between one system and another, and is likely to occur wherever there is an aquatic – terrestrial boundary. Water-land linkage is well known to humans and is well illustrated by the (originally) agricultural settlement of humans around the large flood flats of rivers such as The Thames and The Mississippi – and of course, the Ancient Egyptian civilisation depended completely on the annual floods of the Nile. Amazonian floods cover an area of 70,000 km^2 of the adjacent rain forest (Polis et al., 1997). There are systematic differences between aquatic and terrestrial ecosystems including energy flow and biomass partitioning between producers and herbivores, detritus and decomposers, and at higher trophic levels. The lack of structural tissues in aquatic primary producers mean they have faster growth rates and are more nutritious then in terrestrial ecosystems (Shurin et al., 2006). Resource pulses also behave differently in terrestrial and aquatic systems, moving through the aquatic ecosystem faster due to high growth rates and life history but longer lasting in terrestrial ecosystems because of greater generation times and life expectancy as well as reduced top down effects in terrestrial verses aquatic systems (Nowlin et al., 2008). Winds can transfer arthropods over a great area, supporting 'habitat islands' of consumers in barren landscapes such as deserts, mountain tops, snowfields, and volcanic islands (Polis et al., 1997). These differences in energy flow mean that a productive saline lake in an otherwise depauperate landscape offers an 'oasis' of energy to be exploited by the juxtaposed ecosystem.

Basic food web components such as nutrients and basal resources in the form of detritus and consumers all cross-ecosystem boundaries. The three main vectors that move material from terrestrial systems to aquatic are detritus from leaf and litter fall, dissolved organic matter (DOM) and particulate organic matter (POM) from soil run off, and detritus, POM and DOM from

floods. Flooding and wind can transport organic material in quantities up to 4.5 times as great as *in situ* productivity creating "edge effects", such as higher density and diversity in environs of the water than the in the wider landscape. There are also other important subsidies such as land-land coupling. The Amazon rainforest depends greatly on the 13 million tons of phosphorus annually blown 5000 km in the dust from the African deserts. Large herbivore and bird migrations will distribute organic material on a landscape scale (Polis et al., 1997), in addition, the migrating species then become prey and so are a subsidy in themselves. Wind carried and ontogenetic habitat switching (e.g. the emergence of adult insects from aquatic larvae) can add to ecosystem subsidy, while local behaviour patterns also contribute to energy transfer when birds and mammals defecate into lakes (Brinkhurst and Walsh, 1967; Grey and Harper, 2002). Reciprocal flows of invertebrate prey link riparian zones with streams and rivers. In such links emergence of adult insects can contribute 25-100% of the energy (or carbon) subsidy to riparian consumers, such as birds, bats, lizards, amphibians, insects and other arthropods. Emergences of adult insects are classed as ontogenetic habitat switch. Typically, interactions between consumers and allochthonous inputs are donor controlled and occur when the resource population is spatially partitioned into sub populations (e.g. adults and larvae) which occupy different ecosystem space, of which only one is available to consumers (Polis et al., 1997). In the case of emerging adult insects, the recipient (e.g. areal predators) can only exploit the resource after the donor has shifted ontogenetically and enters the exploitable space. There is some recycling from the avian community that is exploiting the emerging insects. This type of subsidy can be crucial to terrestrial predators affecting abundance, territoriality, feeding behaviour, and reproductive success (Baxter et al., 2005b; Polis et al., 1997).
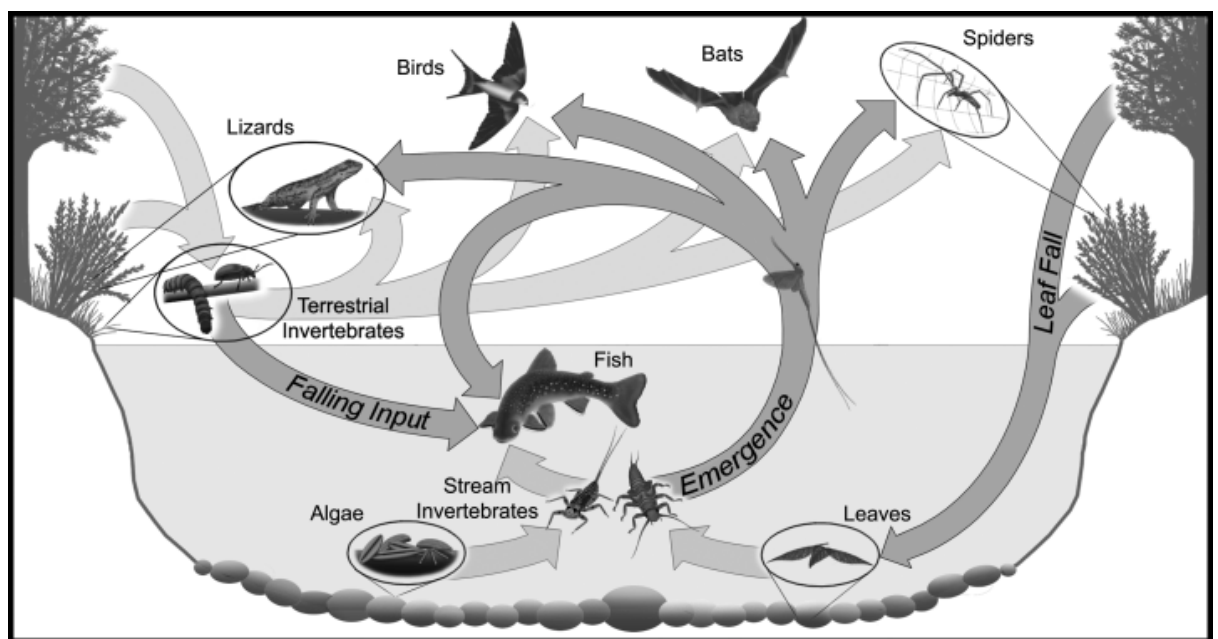
Figure 1.1 – A diagram to showing complex reciprocal subsidies across ecosystem boundaries (Baxter et al., 2005a).

Nutrient input from oceans and lakes can be a key "bottom up" factor in intertidal and shore line food webs. In oceans, trophically distinct fish feed in biomass "hotspots". The most biomass-rich community on Earth, the floor of the La Jolla submarine canyon, is entirely supported by allochthonous detritus: 15–300 m mats of detrital surfgrass and kelp are converted into >1 kg/m^3 of benthic crustaceans (up to 3×10^6 individuals/m^3) which the fish feed on (Vetter, 1994). Algal wrack and carrion has been recognised as a water to land subsidy along coasts and are considered very important inputs in places like the Gulf Islands, British Columbia, Canada (Polis and Hurd, 1996). Marine inputs of algal wracks can account for 3 to 24 times higher abundance of insects, spiders, scorpions, and vertebrates then inland areas.

Ecosystem linkage can also provide a relatively stable carbon source because the consumers cannot depress the renewal rate of imported prey: they cannot over exploit their food resources and therefore the dynamics of donor controlled interactions are stabilised (Polis et al., 1997). Physical and biotic transfers across ecosystems increase energy (C) and nutrients (N and P), typically resulting in a numerical response by the consumers through increases in primary productivity, detrital and prey availability (Polis et al., 1997). Flows of detritus generally result in bottom-up effects increasing consumers within the recipient food web (Polis et al., 1997). Knock-on effects, including numerical responses by consumers, can depress *in situ* production e.g. leaf fall produces large numbers of grazers that depress *in-situ* algae. Top down effects occur when subsidized consumers increase in density which effects local resources.

Aquatic-Terrestrial Ecotone

The ecotone between aquatic and terrestrial systems can have complex links, and which can display periodicity. Howard-Williams and Lenton (1975) discuss how a littoral zone swamp in a saline lake can have large effects on the functioning of the aquatic ecosystem by providing long-term and short-term nutrient exchange. The effect of littoral zone swamps and marshes can be observed in freshwaters as well, such as the papyrus fringe of Lake Naivasha, Kenya. A wide variety of taxa are shown to use energy subsidies across the aquatic-terrestrial interface, from invertebrates (Bastow et al., 2002) to vertebrates (Bump et al., 2009). Pygmy grasshoppers, prey for terrestrial vertebrates, increase in biomass over the summer months by grazing on exposed algal mats as river levels recede (Bastow et al. 2002). An important subsidy to riparian communities is the contribution of emergent adult insects to both vertebrate and invertebrate terrestrial predators (Figure 1.1). Burdon and Harding (2008) found a positive correlation between stream-insect biomass and both riparian arachnid biomass and web density. They observed a similar correlation between distance from the shoreline and decline in web-building spiders with stream-insect biomass as a strong covariant. Similar results have been found from freshwater lakes. Jonsson and Wardle (2009) found a similar response among web-building

spiders on the lake shores of 30 islands in the freshwater Lakes Hornavan and Uddjaur, Sweden. They had a higher density on small islands, presumed to be mediated by the perimeter-to-area ratio, and had a positive relationship to aquatic biomass. The potential strength of subsidy is high: it is reported that as much as 1200 - 2500 kg of chironomids ha^{-1}/year^{-1} are received by land adjacent to lakes in Iceland which contributes to a substantial amount of nutrient to the terrestrial environment (Gratton et al., 2008).

Few studies have tested for a response in the terrestrial community to cyclical patterns of emergence of aquatic insects. Generally, chironomid emergence in the tropics or other thermally stable environments is continuous; however, there can be some seasonal variability and lunar periodicity. Observations at Lake George, Uganda show clear lunar periodicity with the greatest chironomid abundance occurring during the first quarter of the lunar month and the least in the third, with similar patterns reported in Jinja, Uganda (Armitage, 1995). Vast emergences of chironomids have also been reported in Lake Bangweulu, Zambia, during the full moon, with reduced emergence during the rest of the lunar month (Fryer, 1959). The strength of emergence is related to productivity gradients and changes within the lake which may ultimately be controlled by climate change (Ballinger and Lake, 2006). No one has yet characterised the strength and pattern of subsidies via cross boundary transfer for saline environments or what might happen under climate change.

Effects of climate and local hydrology on saline lakes and their dependent biota

Changes in climate and local hydrology can have large effects on saline lakes and their biota, and lakes have been gained and lost through anthropogenic interference: Salada Chiprana, Spain's only permanent hypersaline lake, was formed due to long-term irrigation dating from the XVth century (Valero-garcés et al., 2000). This type of transition is still occurring and at a faster rate today. The rapid increase in size of Lake Beseka, Ethiopia over the last 40 years has transformed it from an extremely saline water body to nearly freshwater due to human influence causing increased water levels and subsequent expansion. In contrast the recent drastic decline in Lake Abiyata, Ethiopia has coincided with an increase in salinity (Alemayehu et al., 2006). Lake Mar Chiquita, the largest lake in Argentina, undergoes strong inter-annual changes in water level, which in general are inversely correlated with salinity. In this system, water level variation leads to salinity ranges between 24.8 – 360.3 g/L^{-1}, which has significant effect on the biota present during different salinity regimes. Over time, salinity has acted as a barrier to the invasion of Argentine silverside fish (*Basilichthys bonariensis*) which died when coming in contact with the hypersaline conditions but increases in water level now allow it to colonise periodically. Chilean

Flamingo (*Phoenicopterus chilensis*) populations increase and breeding success is raised during extremely high salinity levels. The lake wide community diversity of feeding strategies reduces, but the abundances of predators dependent upon dipteran larvae remain high (Reati et al., 1996). This type of biological response is predicted across saline lake ecosystems that have a few specialised dominant species. With rises in water level and drops in salinity, however, productivity would be predicted to drop, particularly in environments that have endured stability for a considerable period.

Stable isotopes in ecology

Holling (1992) proposes that a small set of plants, animals, and abiotic processes control the structure of ecosystems across scales of time and space. These key players create dominant temporal processes which entrain other ecosystem frequencies. Stable isotope analysis is an effective way to explore such structure and function. Lake Bogoria's simplicity, structure and unique primary producers makes it a good site for investigations using stable isotopes.

Stable isotope analysis (SIA) exploits the fractionation caused by the bias of metabolic reactions toward lighter isotopes of atoms within consumed molecules. Thus, stable isotopes provide a natural way to directly follow and trace details of element cycling (Fry, 2006). The use of stable isotopes is widespread and includes investigating global element cycling, past climate conditions, hydrothermal vent systems, tracing rock sources, food webs, palaeodiets, effects of waste spillage, ecosystem cycling and linkage between ecosystems such as allochthonous inputs (Lajtha and Michener, 1994; Grey and Harper, 2002; Grey, et al., 2004). $\delta^{13}C$ and $\delta^{15}N$ are typically used in ecology but the use of δD, $\delta^{18}O$, and $\delta^{34}S$ is increasing. Fractionation occurs at different rates for different elements: carbon fractionates at ~1‰ whereas nitrogen fractionates at ~3‰, although these can also vary in accordance to differences in diet, tissue sampled, and method of sample preparation. Carbon is thus a good indicator of food source, and nitrogen can be used to delineate trophic level. The primary variation found in stable isotopes is due to differing fractionation rates associated to different photosynthetic pathways. C3 plants including fruits, vegetables, shrubs and grasses from temperate regions or shaded habitats have a low $\delta^{13}C$ values averaging -26.5 ‰. C4 plants, primarily made up of dry adapted grasses including millet, savannah grasses, and maize, have a higher isotopic value averaging at -12.5 ‰. CAM (Crassulacean acid metabolism) plants including xerophytes, epiphytes and some cyanobacteria species, sit between C3 and C4 isotopic values but lean more toward the C4 values (Somerville et al., 2012). The ratios of $\delta^{13}C$ and $\delta^{15}N$ of a sampled consumer in comparison to

$\delta^{13}C$ and $\delta^{15}N$ natural abundances (or an isotopic "base-line") within the food web is how a food web is "mapped out" and presented in a standardised isotopic $^{15}N/^{13}C$ bi-plot (Grey, 2006). SIA is frequently applied to studies of resource partitioning/energy flux across aquatic and terrestrial ecosystem boundaries (Bastow et al., 2002; Gratton et al., 2008; Grey et al., 2001).

Past environmental indicators and chironomid head capsules

The use of biotic fossil records for quantitative palaeoenvironmental reconstructions is well-established (Birks et al 2012). These methods are currently incorporating powerful models to explore the ecological impacts of climate change (Jeffers et al., 2011). The use of fossil records to map potential threats to and likely future developments of ecosystem dynamics and biodiversity is growing. In this project we aim to reconstruct the past salinity of Lake Bogoria's three basins and explore the effects of salinity change on the importance of aquatic-terrestrial subsidies.

Natural climate archives, such as lake sediment cores, can be exploited to infer past climatic variation via transfer function from proxies such as chironomid larval head capsules. Chironomids lend themselves to being good proxies for a number of reasons; they are ubiquitous, occurring in high concentrations in inland saline waters, abundant, mobile as adults, stenotopic and respond rapidly to environmental changes, have a short life span, as well as species-rich: 399 genera and 4147 species have been described worldwide. Their life cycle consists of 4 stages (egg, larva, pupa and adult) of which the chitinous head capsules of the 3rd and 4th instar aquatic larvae are usually well preserved in lake sediments (Brooks et al., 1997; Chen et al., 2009a). This project will adopt the use of the salinity inference model developed by Verschuren and Eggermont (Eggermont et al., 2006; Verschuren et al., 2000). Chironomids respond in a step like threshold manner to a salinity gradient; (1) Stenotopic freshwater taxa never found above 1000 µS/cm, (2) Eurytopic freshwater taxa, limited to waters below 3000 µS/cm, (3) Salt-tolerant freshwater taxa, most common in freshwater lakes but tolerating up to ~5000–6000 µS/cm, (4) Halophilic taxa typical of meso- to polysaline soda lakes (conductivities of ~10,000–40,000 µS/cm) and also occasionally present in both freshwater and hypersaline lakes, and (5) Obligate halobiont taxa such as *Tanytarsus minutipalpus* and *Tanytarsus near barbitarsis*, dominant in hypersaline lakes with conductivities up to ~68,400 µS/cm such as Lake Bogoria. The step like response and the prediction error of the inference model of around ~3000 µS/cm, raises issues with the power of the model (Eggermont et al. 2006). Regardless, the extensive background information and data available combined with the relative speed by which

chironomids can be processed makes them the first proxy choice over others such as, diatom-based transfer functions.

Project objectives and overarching hypotheses

Saline lakes are typically found in arid landscapes where the adjacent terrestrial ecosystem or riparian zone is depauperate. Saline aquatic environments typically support low species richness but if there is an abundance of nutrients, such as at Lake Bogoria, which is fed by nutrient-rich hot springs, specialist species can occur in large numbers. This gives a productive system, with relatively fewer actors, which contrasts with the riparian zone and surrounding catchment. Provided a vector for the aquatic-terrestrial linkage is present, the link is likely to be strong in subsidy but, as explained in the next paragraph, weak in resilience and the effects of climate change are disproportionate. Recent research has focussed on the extent and ecological significance of trophic linkages across ecosystem boundaries (Gratton et al., 2008; Grey et al., 2001; McCauley et al., 2015; Milligan and Humphries, 2010), but to date no research has looked into climate effects on such linkages.

The strength of subsidy at Lake Bogoria is largely due to the contrast between the in-lake productivity and the surrounding depauperate riparian zone. With an increase in humidity or precipitation there is likely to be an increase in terrestrial productivity, marked by changes in vegetation. This may mean a reduction in the relative strength of subsidy despite an increase in overall biomass exportation. Alternatively, in-lake ecological complexity could rise with fewer emerging organisms exploiting the allochthonous resources or a drop in in-lake productivity resulting in a reduction of biomass exportation. Changes in vegetation at micro, local and landscape scales have occurred in East Africa and it is important to link subsidy with terrestrial production in order to gauge the relative strength of subsidy (Gillson, 2004).

The usual mechanisms for aquatic nutrient pathways are absent in Lake Bogoria, as there are no large consumers, such as fish. Therefore, flamingos bring nutrients into the lake and recycle nutrients while present at the lake. In addition, their foraging method (churning up the benthos) will help infuse nutrients from the benthos back into the pelagic zone. The turbidity of the lake makes almost all of the benthos aphotic which means that pelagic-benthic coupling is also the main source of energy for the chironomids through pelagic detrital fallout. The dominant phytoplankton species, a cyanobacterium, *Arthrospira fusiformis* moves in the lake water column during the daylight hours (see fig 2.3). However, a proportion of the biomass gets

bleached and forms a scum (Tebbs, 2014). Detritus falls therefore, include flamingo faeces and some dead phytoplankton and phytoplankton migrating from the surface. In addition to flamingo foraging, afternoon winds make this the upper water column well mixed and nutrients are turned over into the pelagic zone and become available for *A. fusiformis*. There may also be inputs from other bird species. Harper et al (2003) estimate local swallow, swift and house martin populations to be as large as the flamingos, and there are a variety of birds exploiting the chironomids through a range of behaviours: Grebe, duck dive and pick at pelagic drifting chironomids, teal float and take pupae on the surface, and many stilts and other wading birds feed in the shallow littoral water. All these birds produce guano, which is a very rich fertiliser. That guano produced while foraging will enhance the lake's nutrient status, which will be significant for *A. fusiformis* production while that guano produced while roosting will also be important for terrestrial fertilising (Kolb et al., 2010). There are also natural and anthropogenic inputs of nutrients through a small river at the south of the Lake.

When nutrient inputs increase plant (or cyanobacteria) productivity and quality a consequence is the elevated densities of herbivores and higher-level consumers (Polis et al., 1997). This works in a similar way to the upwelling found in oceans which result in algal blooms (Polis et al., 1997). As the extreme conditions of the aquatic habitat at Bogoria dictate that no higher consumers can survive to exploit the elevated numbers of chironomid larvae, they are free to exploit as much of the niche they can tolerate as possible. This means that almost all their energy is transferred to the terrestrial food web of the riparian zone via emerging adults with only a small amount being recycled back into the lake from the unsuccessful emergence and the dead adults that fall, over the lake.

One lake, Three Basins

There is a trade-off between collecting data from multiple saline lakes for short periods of time irrespective of season or to look at one lake for a more substantial length of time, in greater detail, and with a relatively high sample frequency. Nutrient fluxes between land and rivers have been shown to have greater uncertainty with lower sample frequency (Johnes, 2007). Chironomid life cycles can vary substantially, between and within species (as well as between sites), from 7 years in cold conditions to 12 days in the tropical pools of central Africa (Armitage, 1995; Butler, 1982; McLachlan and Cantrell, 1980). The time it takes to complete development depends on environmental conditions such as food availability, temperature, and photoperiod, and also genetically determined physiological conditions (Jackson and Sweeney, 1995). Food availability has effects on body size from cold environments to warm and the assumption is that aquatic insects develop quickly in the tropics, but there are complications as to the periodicity of such development (Jackson and Sweeney, 1995; Schütz and Füreder, 2018). Mating adult

chirnomids rely heavily on the biomass accumulated during larval stage and thus minimise adult life stage and emerge in mass (Tokeshi, 1995). The emergence of chironomid imagos have been recorded with monthly or more frequent periodicity, with links to the luna cycles in some cases, but stochastic emergent patterns in others sites and species (Armitage, 1995). Lake Bogoria is nutrient rich with abundant food and a warm, consistent temperature therefore it is likely that *T. minutipalpus* will develop quickly, with synchronous emergence over a short period of time, with unknown periodicity. In this project we chose to focus on one lake to get high frequency sampling over a length of time long enough to ensure that we capture at least one if not two peak emergences of the periodic resource flux – chironomids. To include another saline lake in with the same detail considering the logistic difficulties in the EARS is beyond the scope of this project.

Lake Bogoria is an ideal model because it has three basins. The saline lakes of the Kenyan Rift Valley fluctuate greatly in lake volume and alkalinity (Owino et al., 2001). It has been shown in a number of other saline lakes that basins within the same lake can have differing chemical regimes and gradients (see chapter two). Previous research at Lake Bogoria describes a gradient from north to south (McCall, 2010). I hypothesise that lake level is the main driver of salinity, but basin morphology also may affect the rates of salinity change, particularly if the basins become disconnected, and this may influence the strength of subsidy differentially in each basin. Shallow, pan-shaped basins, such as the northern basin of Lake Bogoria, may be affected disproportionally due to the rate of loss of benthic habitat, but the steeper and deeper southern basin may remain stratified. Due to the steeper topography and bathymetry in the southern basin the relative loss of benthic habitat as the lake level falls will be lower than in shallower flatter areas such as the northern basin. It is well understood that the gradients of subsidy between ecosystems allow predictions concerning how changes in one system affect biodiversity change in another (Hocking and Reynolds, 2011). Therefore, the different chemical regimes and basin morphology across the three basins at Lake Bogoria will be provide a useful preliminary study to examine how lake volume can drive lake chemistry which in turn can affect resource transfer from the lake to its ecotone.

Wet vs Dry seasons

The changes in temperature in tropical lakes are often minimum or absent and seasonality is driven by precipitation – the rainy and the dry seasons. Insect seasonality in the topics is complex but on average the activity seasons (timings of events such as emergence, growth, dispersal, and reproduction) of tropical insects increases with length with decreasing latitude towards the equator. However, this is a general rule and in fact evidence shows that insect seasonality is present and can vary from site to site and across species and although, large, nonseasonal

fluctuations in insect abundance do occur they are rare (Wolda, 1988). Furthermore, the assumption that tropical insects develop many times a year (are multivoltine) means that multivoltine species should produce more individuals, have greater secondary production, recover more rapidly from natural or anthropogenic disturbance, and track or exploit temporally variable resources effectively (Jackson and Sweeney, 1995). Chironomid population dynamics are heavily effected by environmental and substratum factors (Roy et al., 1980). In tropical endorheic lakes salinity is driven by precipitation and evaporation rates and ratios (Talling, 2001). Therefore, it is imperative that an important subsidy such as chironomids are studies in both the dry and the wet season as the species at Lake Bogoria are likely to be multivoltiner, and so will track environmental changes such as salinity because of its effect on them and the changes in the wet and dry seasons at Lake Bogoria (see chapter 2).

I hypothesise that the occurrence of detrital subsidies in the form of feathers shed by the large but nomadic population of flamingo and prey subsidies in the form of emerging chironomids differ in both quality and periodicity. The amount of allochthonous input will affect terrestrial community structure, both spatially and temporally. Despite the flamingos' itinerant nature which results in stochastic population numbers (Childress, Hughes, et al., 2007), the input of feathers into the terrestrial ecosystem is constant, with little variability on a temporal scale. Flamingos typically occur in populations order of magnitude greater than other water bird populations in the Kenyan rift valley lake system. Although they make up the bulk of the population of water birds in most alkaline lakes their population fluctuates greatly at all feeding locations apart from Lake Bogoria (Owino et al., 2001). However, mass die offs and fluctuations in flamingo populations at Lake Bogoria have been observed even during periods of stable *A. fusiformis* biomass (Tebbs et al., 2015). Nevertheless, die off also produce feather detritus along the swash and shore lines and long term data suggests over all more relatively stable populations of flamingos (Owino et al., 2001). This combined with the longevity of feathers in detritus (Becker et al., 2007) would agree with field observations that feather content is a more consistent food source then the periodic chironomid emergence. However, it is likely that this input has a long exploitation time as the feathers themselves require colonisation by microorganisms which start the breakdown of the resource and eventually make it available to the detritivorous terrestrial community. Comparatively, the emergence of chironomids has much more short-term temporal variability which will be reflected in the terrestrial community structure over time as many opportunistic predators will exploit the short but large resource pulse. Due to the contrast in production and biomass accumulation in the lake compared to its surrounding landscape it is likely that the transfer of chironomids as a prey subsidy results in an

increase of predator abundance beyond the carrying capacity of the surrounding terrestrial landscape.

As in all of the biotic factors influencing the link between aquatic and terrestrial ecosystems in and around Lake Bogoria, the chironimids are ultimately driven by lake water salinity. Therefore, to assess the changes in aquatic-terrestrial linkages in the context of climate change it is important to estimate past salinity regimes in lake. This project will investigate the ecological systems at Lake Bogoria using stable isotopes, and tie them into a past climate regimes by analysing the paleorecord using sub fossil chironomid head capsules.

Chapter Two: Lake Bogoria Site Description

An introduction to saline lakes

In this chapter I will outline our current knowledge of saline lake formation and ecology, to set the context for the studies described in this thesis. Saline lakes are important assets to the environment, wildlife, industry, and human health. They provide critical habitat for migrating birds, minerals for extractive industries, and recreational opportunities, all of which are economically important. They have considerable aesthetic, cultural, scientific, conservation and ecological values, but their importance is often overlooked. Here I discuss our knowledge of their formation, ecology, and the biotic and abiotic interactions contained within them, to better inform our understanding of food web ecology. I then describe the physical, chemical and ecological characteristics of my study site, Lake Bogoria, Kenya.

Perception of Saline Lakes

The contribution of saline lakes to global water volume is close to that of freshwater, 0.008 and 0.009% being freshwater and salt respectively. Yet despite being chemically and biologically fascinating they are not given equal consideration in research, largely because they are thought to be of less value compared to freshwater lakes in terms of ecosystem goods and services (Wetzel, 2001). Contributing to this perception is that almost all saline lakes are found in endorheic drainage areas, a landscape feature often located far from centres of population and study (Williams, 1981), and are often overlooked as sites for conservation (McCulloch et al., 2003). Regardless, saline lakes are widely distributed over the globe, and make up some of the world's largest inland water bodies. They occur on all continents and range in elevation between 0 and 5000 m a.s.l. Inland saline waters also play a major role in biogeochemical cycling and, inland surface waters are often undervalued for their role in the carbon cycle (Gitay et al., 2001). In these respects they are scarcely less important than freshwater lakes (Fischlin et al., 2007; Williams, 1981).

Freshwater bodies are considered of greater value to the public water supply, irrigation, and of most hydrological power generation (Arnell and Liu, 2001), but saline lakes also hold economic value. Deposited sediments and evaporative deposits have been exploited for at least 2000 years and today include borates, sodium carbonate, sodium sulphate, sodium chloride, certain types of clays, sodium sesquicarbonate, gypsum, magnesium sulphate, sodium sulphate, lithium, uranium and potassium chloride. It is expected that large uranium deposits will be found in playa lake basins but the most important due to the rise in industrial uses of silicates. The brines of saline lakes can also be economically important: the Dead Sea forms the basis of the

Israeli chemical industry and in 1981 the top 10 m of 1 Red Sea brine pool was valued at $2.5 billion. To date, only the mildest saline waters can be used for irrigation but if the salt tolerance of commercial plants is increased there is scope for expansion. Some forms of algae and cyanobacteria have been historically, and are still, utilised by communities local to the lakes as a food source (Williams, 1981), and now there is a large industry around *Spirulina* sold as a food supplement. *Artemia* and some other invertebrates are exploited for fish fry: 30 tons per annum of dry *Artemia* is used by aquaculturists, aquarists, and in research projects (Williams, 1981). Halophilic bacteria contribute to coloration and curing in the food industry, while microbes found in Lake Bogoria have provided 'wash out' agents for the textile industry, a controversial find (Barnett, 2004; Henrard, 2013; Williams, 1981). In 2006, saline inland waters contributed 41.7 Mt to global production and utilisation of fish from inland waters (FAO, 2009).

Despite these beneficial effects on ecosystems and for humanity, saline lakes and their flora and fauna have suffered from human exploitation. The Caspian and Aral Seas have been subjected to the intentional introduction and subsequent exploitation of fish species. The subsequent overfishing, habitat loss, and mismanagement has resulted in the reduction of up to 90% of some sturgeon species, particularly in the Caspian Sea (Gesner et al., 2010; UNEP-WCMC, 2010). In addition, many saline lakes are exploited for their introduced species. Almost the entire fauna of the Salton Sea is introduced, and the Saskatchewan has seen 30 species introduced, all of which are exploited for economic value (Williams, 1981). These inland waters are valuable for biodiversity, recreation, and aesthetics, which in the case of saline lakes, can be converted into economic value around industries such as fishing, hunting, swimming, boating, and walking.

Saline lakes are excellent experimental systems for studying limnology and could contribute to general ecological theory - their scientific value should not be underestimated (Williams, 1972; McCall, 2010). Many of the complexities found in freshwater systems, such as species diversity, habitat heterogeneity, and intricate trophic interactions are at a minimum in salt lakes. Therefore they provide a spectrum of localities from which to explore the macroscopic attributes of ecosystems (Hammer, 1986; Williams, 1972). Saline lakes have been traditionally understood as discrete closed systems (Hammer, 1986; Williams, 1972), although Williams (1972) goes on to state that interesting questions arise when thinking of the transfer of energy in lakes where birds such as flamingos feed, which hold an important role in cross ecosystem boundary resource transfer. Saline lakes are scientifically fascinating and provide close to ideal conditions for specialised primary producers and secondary consumers (Wetzel, 2001). In addition, the sensitivity of saline lakes to relatively small climatic changes makes them an informative study for palaeolimnologists (Williams, 1993).

Saline Lake ecology

General introduction

Saline lakes are common on every continent and are often the only surface waters found in dry climates. In many respects they are simple models of ecosystem structure and function (Walker, 1973). Hypersaline lakes have stimulated the interest of biologists for a long time because of their relatively simple biological composition (Hammer, 1986). The difficulties associated to researching complex ecosystems such as expense and time can be reduced in saline lakes due to their simplification. Williams (1972) also noted that within lake heterogeneity can be caused by their, typically, relative shallowness and the concomitant high turbulence. Although there are very large permanent lakes such as the Great Lakes of the USA, Lake Urmia in Turkey, Lake Balkhash in Russia, and Lake Eyre in Australia, nevertheless most saline lakes are shallow and many are ephemeral. This means that they are more exposed to wind action and mixing. Therefore, habitat homogeneity is more likely than in freshwater lakes. Generally, saline homogeneity extends to the lake substratum; they lack areas of defined macrophyte growth, and contain reduced chemical and biological stratification, either vertically or horizontally. Lastly, lakes as a whole are useful "sentinels of change". The palaeorecords archived in lake sediments sediments provide logs of past environmental change and an insight into the mechanisms and effects of climate change (Pienitz et al., 2004).

During the early examination and description of saline inland waters, comparisons to marine environments were commonplace. The comparison of biota with that of marine rather than fresh water flora and fauna persisted for some time (Hammer, 1986; Williams, 1981). Williams (1981) defines a saline inland water as any water body with a salinity greater than 3 ‰ although the author notes that this is relatively arbitrary and other researches such as Hammer (1986), have discussed that it could be lower in regards to the tolerances of freshwater biota. The salinity of 3 ‰ has now been widely adopted as standard because during early research it was hard to define a biotic standard with precision due to the variability of fauna – modern methods of using faunal tolerances have now become accurate at predicting salinity. More recently, Zheng (2001) proposed that saline lakes *sensu stricto* should be defined at > 3.5‰ and saline lakes *sensu lato* at ≥ 0.3‰ but this has not widely entered the literature.

Shallow lakes, basin morphology and salinity

The geological conditions necessary for a saline lake to exist are an evaporation rate greater then precipitation, an endorheic lake basin, and the availability of soluble salts (Hammer, 1986).

The chemical sequence of salinization is marked by the loss of biota, which results in colonisation by a few specialised species which may or may not occur in high abundances e.g. Lake Bogoria or Lake Abhé, Ethiopia (Talling and Lemoalle, 1998). Shallowness is a prominent feature of lakes in the tropical regions, of all shapes and size but generally of around ~ 5 m average depth. Thus shallowness and tropicality are strong drivers of the structure and function of physical aspects which regulate environmental drivers (table 2.1) (Talling, 2001).

Physical apsects		Environmental Regulation
Water input and output	Correlates with	Water level and salinity
Energy balance and distribution		Temprature density and startification
Wind driven water movments		Chemical and biological distributions

Table 2.1 – Physical aspects and their correlation with environmental regulation, after Talling (2001).

The three main mechanisms that control salinity are: (1) rock dominance; (2) atmospheric precipitation; and (3) evaporation-precipitation processes (Wetzel, 2001). Salinity is expressed by the sum total of cations and anions present, particularly of bicarbonates, carbonates, sulphates, and chlorides. In practical terms, salinity is the concentration of four major cations, Ca^{++}, Mg^{++}. Na^{++}, and K^+, and four major anions, HCO_3^-, CO_3^- ,SO_4^-, and Cl^-. Salinities should be expressed on a mass per mass basis, such as mass total ions per mass of solution (g/Kg^{-1}, mg/L^{-1} or meq/L^{-1}), which are temperature independent (Wetzel, 2001). As a consequence of the logistical issues associated with working in many saline lakes, however, conductivity is also sometimes used. Specific conductivity is the measurement of resistance of a solution to electric flow. While conductivity is temperature dependant and increases around 2% per °C, it is closely proportional to the concentrations of the major ions, and is positively correlated with the pH of mid-range bicarbonate waters. Ion concentrations fluctuate, within and between years, induced by changes in the hydrological budget and evaporation rates, which have biological consequences (Talling and Lemoalle, 1998). This study adopts conductivity as a measurement of salinity.

Because of their specific structure, high quantities of plant biomass are often associated with shallow lakes. In very shallow water bodies such as swamps, this vegetation influences water, particulate, and solute exchange between inflows, swamp, and open water. High light attenuation from suspended silts or phytoplankton biomass can mean that even in shallow lakes the photosynthetic zone can be can be considerably less than the average depth. Diurnal patterns in thermal stratification can interact with chemical changes in the water and also with the biota (particularly cyanobacteria). Shallow lakes are not known for stability over longer

timescales. Year to year changes are observed in a wider range of shallow lakes. These hydrological changes have large effects on community composition and tropical lakes of altitude have seen multiple introductions of subtropical and temperate species. Shallow lakes often experience seasons but equatorial shallow lakes are often closer to an aseasonal state depending on local conditions and altitude (Talling, 2001).

Saline lakes can have interchanges with local water bodies, channels, and between basins. The world's largest saline lake, the Caspian Sea, which constitutes 40% of the world continental surface water, is a very interesting example because of its longitudinal zonation of salinity depth and climate. These factors separate the water body to produce three basins that are less similar to each other than some individual lakes (Dumont, 1998). Lake George in Uganda shares a channel with the, slightly downstream, Lake Edward which acts as a buffer to physical aspects such as the hydrology regime and chemistry (Talling, 1992). In Devils Lake, North Dakota, the water level is in a constant flux of either increase of decrease which can spill into its sister lake, Stump Lake and in very large water increasing into the nearby Sheyenne River affecting the physio-chemical aspects of all three water bodies (Wiche et al., 2000).

At greater than 3 g L^{-1} salinity, an inverse correlation between salinity and biodiversity is observed - with increasing absolute salinity, species richness and diversity decrease in a threshold sequence. Between 3 and 20 g L^{-1} (hyposaline), most taxa present are also found in freshwater. Between 20 and 50 g L^{-1} (mesosaline), the community comprises mostly of taxa restricted to inland waters of moderate salinity and halotolerant freshwater taxa are much less abundant. At salinities between 50 and 350 g L^{-1} (hypersaline) the biota is almost entirely restricted to highly saline water. These thresholds show that although salinity undoubtedly plays a role in determining the structure of biological communities, there are many other factors responsible (Williams, 1998). The medium of saline waters adds a further dimension of chemical stratification and basins within a lake can vary as a result which has been shown in the Caspian Sea (Dumont, 1998) and is noted also to occur at Lake Bogoria (McCall, 2010). In most saline lakes, very few species occur, usually no macrophyte or fish species: between 10-100 ‰ salinity fish and macrophyte diversity is greatly reduced. However, although species richness decreases, abundance rarely does (Hammer, 1986). The specialised species that persist do so in high abundances and can be important to the surrounding terrestrial ecosystem. The production they experience from the aquatic environment is likely to subsidise the terrestrial via cross ecosystem boundary transfer.

Decreased vertebrate and macrophyte species richness contribute to the simplification of trophic structure in these lakes. Primary production is restricted to periphytic and planktonic algae and cyanobacteria and can be very high. In very shallow lakes, such as Lake Elementeita,

Kenya, a lowering in water level and the respective rise in salinity can cause abrupt reductions in phytoplankton populations and increases in the rich diatom flora. Evaporation can also lead to the loss of zooplankton such as copepods in Lake Elementeita (Talling and Lemoalle, 1998). Secondary production can also be substantial, particularly in the grazing food web, reflecting the high primary production (e.g. Lake Weroerap see's 650 kg / ha^{-1} / month^{-1} wet weight of *Tanytarsus barbitarsus* (Diptera; Paterson, per. comm. in Williams, 1972)). In part, this may be attributed to high ecological efficiencies of energy transfer. With respect to benthic standing crop, 4 of the 5 lakes with the greatest species richness in North America are saline. Zooplankton crops have a correlation with salinity (Williams, 1972). Despite interest in allochthonous contributions of energy into salt lakes and the reciprocal interaction with the surrounding ecosystem, utilisation of these 'natural mesocosms' to study such interactions has been neglected. Energy flow between salt lakes, the riparian zone and their catchment is likely to be substantial, with many falling into the anemotrophic category (Williams, 1972).

Hypersaline ecosystem models

Hammer (1986) lists a few simple models of hypersaline lakes, including interactions between lakes and their catchment as well as within-lake interactions. Stephens and Gillespie developed two models for the southern basin of the Great Salt Lake, USA. The main energy input is photosynthetic, with phytoplankton as the main producers, gaining nutrients (organic and inorganic) from river inflows. Only two major consumers exist, *Artemia* (brine shrimps) and *Ephydridae* (shore flies), the former feeding on benthic and pelagic autotrophs and the latter on detritus. Energy outflow is to birds feeding on *Artemia* and emerging *Ephydridae* and also via imagos of *Ephydridae* which are likely to perish on land, providing another energy export. This model does not consider losses through sedimentation which previous studies have highlighted as important. Post developed a model for the northern basin in 1977 and updated it in 1981 (Post, 1977, 1981). Although similar to the southern basin model, it also includes recycling of nutrients such as ammonia, from zooplankton to the phytoplankton they consume. Bacteria provide CO_2 in the form of carbonates and bicarbonates, and other gasses and nutrients are released from sediments. Post also includes a large organic pool which is likely to be prominent in saline lakes as the bacteria community is undoubtedly reduced. No loss of energy from the system is shown, but reduced levels of zooplankton are likely to mean lower export to birds from emergence. Autochthonous material from the southern basin and allochthonous material from the drainage basin are important. The earlier 1977 paper includes a model describing seasonal changes in the main components of his interaction model showing the annual dynamics of a saline lake in a temperate region. Parallels can be seen between the Great Salt Lake and Australia's Victorian saline lakes in Williams 1984 work. The basic groups are similar but Williams

puts more emphasis on allochthonous organic material and its utilization by invertebrates, thus phytoplankton is a less significant supply of energy. Again fewer invertebrates means less export to birds, which are not included in the model (Hammer, 1986).

Concluding remarks

There are economic, cultural, aesthetic, recreational, scientific, educational, and economic reasons why aquatic systems should be conserved – all of which add value and saline lakes are of no exception. For example, Lake Mono with its exposed tufa columns is classified as an area of outstanding beauty and Lakes Nakuru, Bogoria, and the Etosha Pan with their flamingo populations have drawn tourists to observe these graceful and beautiful birds. As discrete system, saline lakes are interesting to a range of scientific disciplines including ecologists, physiologists, evolutionary biologists, and geologists. Due to their sensitivity to perturbation and the knock-on effects to biota they are ideal for palaeolimnological studies. Not only is it important to understand how these systems respond to climate change in order to protect them, their response to perturbations can help us predict the effects of future climate change. Research into saline lakes has reduced over recent decades, but saline lakes still have a prominent role in the scientific literature with Zheng (2001) calling for the term salinology to be adopted.

Lake Bogoria: physical characteristics, chemistry, and biology.

Introduction

Lake Bogoria is situated in the East African Rift Valley System (EARS), approximately 25 Km north of the equator in Kenya (Figure 2.1). It is a hyper-saline lake reaching ~40 ‰ (conductivity > 64 mS cm^{-1}). It has three basins that have different physical characteristics, which in turn have different chemical and biological characteristics. The harsh conditions in and surrounding Lake Bogoria attract communities of specialist organisms, which not only explains the low species richness but also accounts for a food web structure with few trophic levels. These specialist organisms, coupled with the simplicity of the Lake Bogoria ecosystem means that environmental shifts that change its structure and function can easily be monitored. Furthermore, it is likely to show low ecological resilience and little buffering capacity against the changes predicted under a variety of climate change scenarios. There are at least two vectors of subsidy: a bi-monthly pulse of emerging chironomids; and a continuous supply of flamingo feathers. Lake Bogoria shows evidence of water volume fluctuations in the past in the form of two stromatolite belts at 999 m (dated at 4140 ± 60 BP) and 995 m a.s.l (3880 ± 60 and 3750 ± 180 BP). It is possible

that the levels were higher during the mid to early Holocene (Vincens et al., 1986). To the north of Bogoria are the Loboi silts, an outcrop of up to 20 m of fluvial to lacustrine silts of Holocene age which has a maximum elevation of 975 m a.s.l. The Marigat-Loboi plain consists of a complex of channels. It is possible that Bogoria and the larger freshwater Lake Baringo either merged or had some hydrological exchange during the Holocene.
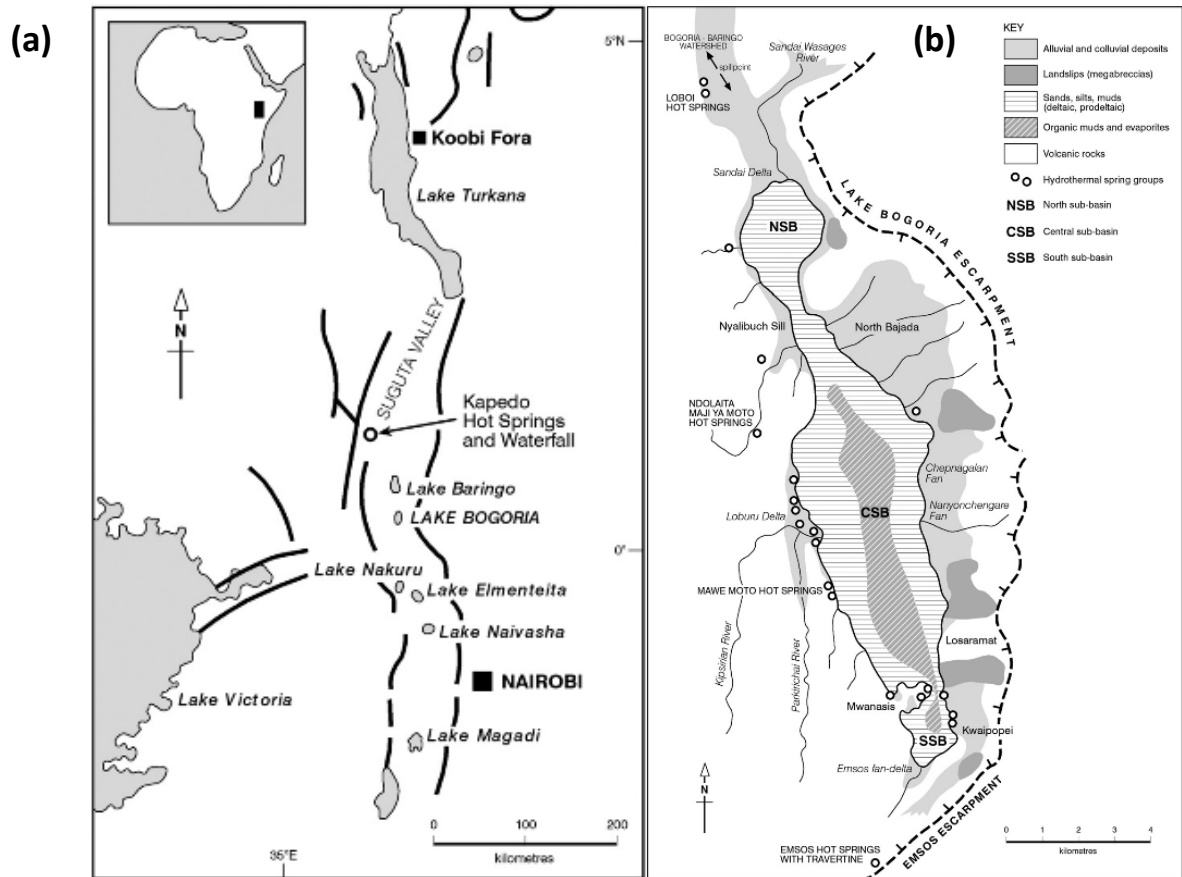
Figure 2.1 – (a) Lake Bogoria's location in the Kenyan region of the East African Rift Valley. (b) The lake and its three basins including inlets, hot springs and sills (McCall, 2010).

Lake Bogoria National Reserve

Lake Bogoria is not an ancient lake and the Baringo-Bogoria basin sits in the subsided zone of a 30,000 year old half-graben created by the East African Rift. Lake Baringo is a larger freshwater lake to the north of Lake Bogoria. It was made a National Reserve in 1973 and designated a Ramsar site in 2001, and is famed for its hot springs, fumaroles and geysers. It is a refuge for flocks reaching 1 million strong of the nomadic lesser flamingo, a major consumer of east African saline alkaline lake primary production (Tebbs et al., 2013). Similar numbers of migrating swallows, swifts, and house martins use the lake as a stop off and it is home to several rare birds, such as the black necked-grebe and the cape teal (Harper et al., 2003). Many of these birds are supported completely or partially by aquatic subsidies when they are present. Despite being situated in an arid landscape with an otherwise depauperate terrestrial ecosystem, the lake

catchment also supports a rich diversity of reptiles, amphibians and mammals such as the Greater Kudu (rare in Kenya) which may indirectly benefit from the aquatic subsidies (Hobara et al., 2001; Polis et al., 1997).

Physical Characteristics of the lake

Lake Bogoria is an endorheic hypersaline lake, situated 990 m a.s.l in the southern part of the Baringo-Bogoria basin (at 0° 16' N and 0° 36' E). The climate is semi-arid and experiences ~700 mm precipitation per year and ~2500 mm evapotranspiration per year (Ashley et al., 2004). It is approximately 17 km long by 3.5 km wide and is divided into three sub basins by the Nyalibuch and Mwanasis sills (Tiercelin et al., 1987). The basins have differing physical attributes such as depth, basin topography, bathymetry, and inlet type, volume, and chemistry. The Sandai-Wasages River enters the lake in the northern basin and dominates the freshwater input whereas the Parkirichai River, which enters the central basin and the Emsos River, which enters the southern, are reported to be ephemeral, flowing after heavy rains (Harper et al., 2003; Owen, 2004). However, it should be noted that during data collection for this project, both the 2011 and 2012 dry seasons saw the Emsos River in continuous flow. In addition, there are ~200 hot springs, geysers, and fumaroles, the majority of which cluster around the Luburu Delta and Mari Moto, both in the central basin, but there are also a few hot spots in the southern basin. The wetter conditions during data collection could be attributed to a strong La Niña event in 2010 / 2011 leading into a weak a La Niña in 2011 / 2012: these are known to increase the precipitation in the EARS region (Anyamba et al., 2002).

This project defines the wet and dry season after Ashely et al., 2004 (figure 2.2). In the 25 year precipitation record there are two dry seasons depicted, a relatively long period from December through to February and a short one month period over September. There are also two monsoon seasons, one during April and a second during October and November. Despite their being a second monsoon season, greater precipitation rates are observed during the four months preceding the short September dry season, immediately following the precipitation peak in the April monsoon season (Ashley et al., 2004). Therefore, in the context of sampling stable isotopic signatures, affected by seasonal environmental change, the best period to pick up season signals is at the end of the longer dry season over February and into March and the best wet season signals will be picked up after the monsoon peak but further into the consistently wet season where the longevity of water input into Lake Bogoria will be at its greatest. It must be noted that the yearly average of evaporation/evapotranspiration greatly exceeds that of the precipitation (by over 3 times, above) and other then where water can pool during the moosnoon season, the terrestrial landscape around Lake Bogoria remains arid throughout the year. The greatest effects of the wet season is in the lake itself.
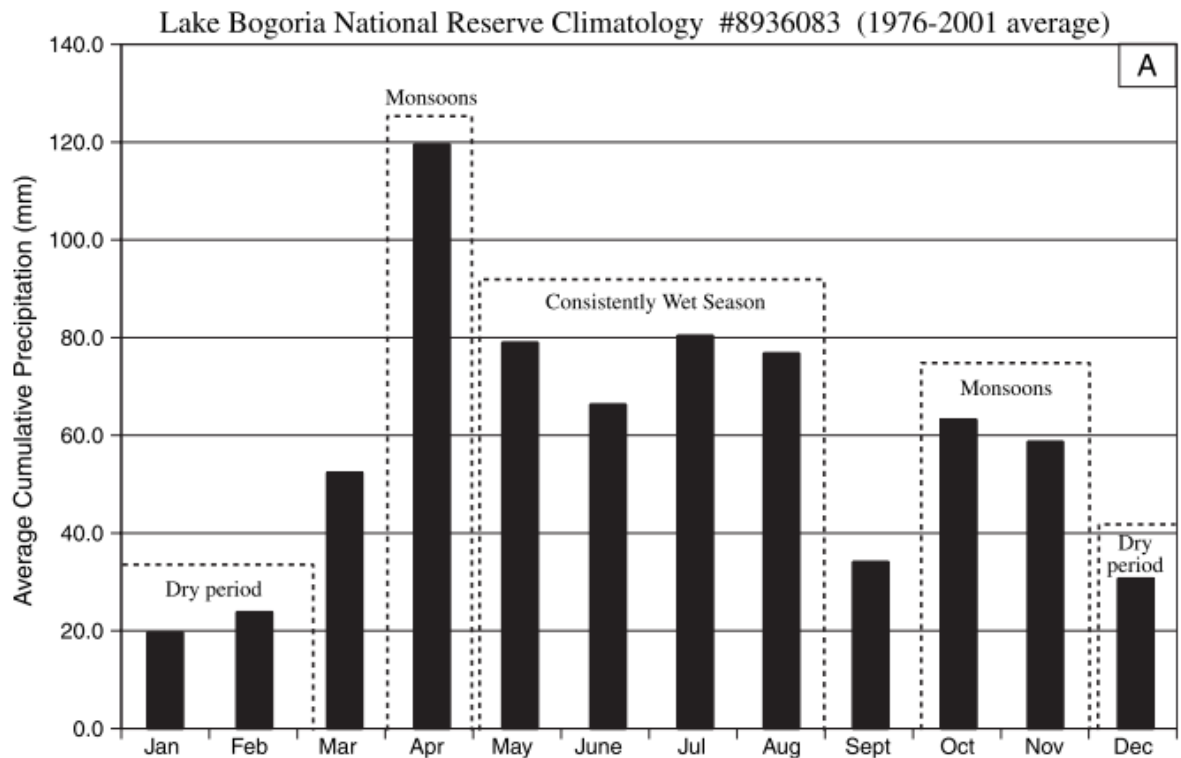
Figure 2.2 – Average rainfall patterns over a 25-year period of the Lake Bogoria National Reserve. The figure depicts a longer dry season from December to February and a short dry season over September. With two monsoon seasons and a consistent wet season (Ashley et al., 2004).

Tables 2.2 and 2.3 describe some of the physical characteristics of Lake Bogoria as a whole, and the physical differences between the basins from observations and Hickely et al's (2003) study on the bathymetry of the lake.

Parameter	Unit	Value
Maximum length	Km	17.25
Maximum width	Km	3.75
Mean width	Km	1.68
Maximum depth	M	10.2
Mean depth	M	5.68
Shoreline length	km	44
Lake area	km^2	28.95
Volume	m^3 x 10^6	164.4

Table 2.2 – Physical parameters of Lake Bogoria.

Basin	Avg Depth	Basin shape	Catchment shape	Inflows
North	5.9 m	Pan shaped	low topography	1 Freshwater river
Central	10.2 m	Long with an undulating bathymetry	Changing topography, Escarpment on both sides at points	1 Freshwater river, the Loburu Delta
South	8.4 m	Bowl shaped	Steep crater like	2 rivers / streams & hot springs

Table 2.3 – Physical parameters of Lake Bogoria three basins.

Lake Chemistry

There are numerous and diverse wetlands around the lake particularly over fault lines. The hot springs are fed by two geothermal aquifers, one shallow with a temperature of 100 °C and a deeper aquifer at 170 °C. They mainly discharge sodium bicarbonate, carbonate soda, and silicon dioxide rich water into the lake but also add Mg^{+2}, F, Li, K, and Cl (Cioni et al., 1992; Renaut and Jones, 1997). The constant input of dissolved solids into the lake combined with weathering processes of the neogene volcanic rock, forming the basins and local topography and the high evaporation rates result in 70-100 g/L^{-1} TDS and a pH of ~10.5 (Cioni et al., 1992; Jirsa et al., 2012; Renaut et al., 1998). At the water surface the hot springs range in both salinity and temperature (38 °C – 100 °C), but in general have a lower conductivity than the lake water (table 2.4).

Parameter	Lake	Hot Springs
pH	10 - 10.5	9
Conductivity (μS cm^{-1})	67200	6410
Salinity (‰)	45.6	3.5
Alkalinity (meq l^{-1})	1020	78
Total N (mg l^{-1})	1.4	<0.5
Total P (mg l^{-1})	5.4	0.019

Table 2.4 Differences in the chemical parameters of Lake Bogoria and its hot springs (Cioni et al., 1992; Krienitz et al., 2003).

McCall (2010) reported salinity increases southwards away from the main Sandai-Wasages River input. However, my data suggests that this feature is seasonally dependent and during the dry season more homogeneity between basins can be observed than during the wet season (table 2.5). I found no statistically significant difference in the chemistry of the lake between the wet and dry season despite heavy rainfall and water inflow from Sandai-Wasages River during the wet season (table 2.6). The Northern basin had higher salinity concentrations during the dry season compared to the other two basins but lower than the other two basins in the wet season. The salinity of the Northern basin during the dry season may be explained to the high wind speeds in the afternoon which aid in mixing the lake and could increase salt transfer from the deposits around the basin left as the lake volume reduces from the previous wet season to the

dry. The salinity gradient observed in the wet season not only agrees with McCall's observations but also fits with the general saline ecology described above.

Basin	Conductivity (μS cm^{-1})		Salinity (‰)		Temperature (°C)	
Season	Dry	Wet	Dry	Wet	Dry	Wet
North	52.6 ± 1.4	45.9 ± 2.9	33.6 ± 0.8	28.5 ± 1.6	25.9 ± 1.3	26.6 ± 1.9
Central	51.4 ± 3.3	51.6 ± 1.9	33.4 ± 0.9	31.1 ± 0.6	25.5 ± 3.2	30.1 ± 1.5
South	52.1 ± 2.3	52.4 ± 3.0	33.5 ± 1.0	32.2 ± 2.1	25.5 ± 3.4	28.3 ± 1.0

Table 2.5: Mean SD conductivity, salinity, and temperature during the wet and dry season for each basin. (See page 42 for methods)

Season	Variable	χ^2	df	p-value
Wet	Con	27	2	< 0
	Sal	13.12	2	< 0
	Temp	33.41	2	< 0
Dry	Con	0.41	2	0.81
	Sal	6.17	2	0.05
	Temp	0.54	2	0.76

Table 2.6 - Kruskal-Wallis rank sum test comparing the chemical differences between the wet and dry seasons (see page 42 for methods)

Lake Bogoria Ecology

Introduction

In addition to its extreme salinity, Lake Bogoria is naturally eutrophic because of the nutrient flux from the hot springs and nutrient recycling from the flamingos. The extreme environment supports specialist halophiles, resulting in low species richness, agreeing with general saline lake ecology as described by Hammer (1986). High concentrations of nutrients support an abundance of primary producing cyanobacteria, which are in turn are able to support an abundance of consumers, mainly flamingos and chironomids. These consumers create the aquatic-terrestrial link, which is likely to create a strong subsidy to the recipient terrestrial community. Laboratory experiments have shown that phytoplanktonic based food webs with few trophic levels are more efficient, and that the expected perturbations of climate change are predicted to be detrimental to food web efficiency (Berglund et al., 2007).

The Aquatic System

Cyanobacteria

Lake Bogoria has very high microbial productivity leading to the deposits of sapropelic muds below the chemo line (Renaut and Tiercelin, 1994). The microbial community in Lake Bogoria shows a high level of diversity and endemism around the clusters of hot springs where water temperatures and salinities vary. The pelagic zone, on the other hand, is colonised by a few

species of *Arthrospira* and *Anabaenopsis* – of which the *Arthrospira* is also detected in the hot springs and sediments indicating its key role as a primary producer (Dadheech et al., 2013). By far the most common pelagic species is *Arthrospira fusiformis* which occurs in great abundance.

At Lake Bogoria the vertical differences in the water column of microbial biomass are large, with the biomass in the top 5 cm being 20 times greater than the biomass in the upper 25 cm (Harper et al., 2003). Whether actively moving as a strategy to prevent damage or passively driven by photosynthesis as described in some *Arthrospira* spp. (Ma and Gao 2009), cyanobacteria are known to vertically migrate during the daylight hours in response to changing photosynthetic active radiation (PAR) or ultraviolet radiation (UVR). Figure 2.3 shows the diurnal migration of *A. fusiformis* during the wet season at Lake Bogoria. A. fusiformis appears to rise to the surface water of the lake during the morning hours, dropping in the water column during the hottest hours of the day to rise again for the afternoon light. The morning upward migration is more abrupt and is the peak of density at the surface. During periods of calm wind (in the morning at Lake Bogoria) the organisms rising to the surface form a dense surface scum or a subsurface layer a few centimetres thick due to the reduction in water mixing. PAR and UVR can kill the off the scum which results in these major die offs (Tebbs et al., 2013).
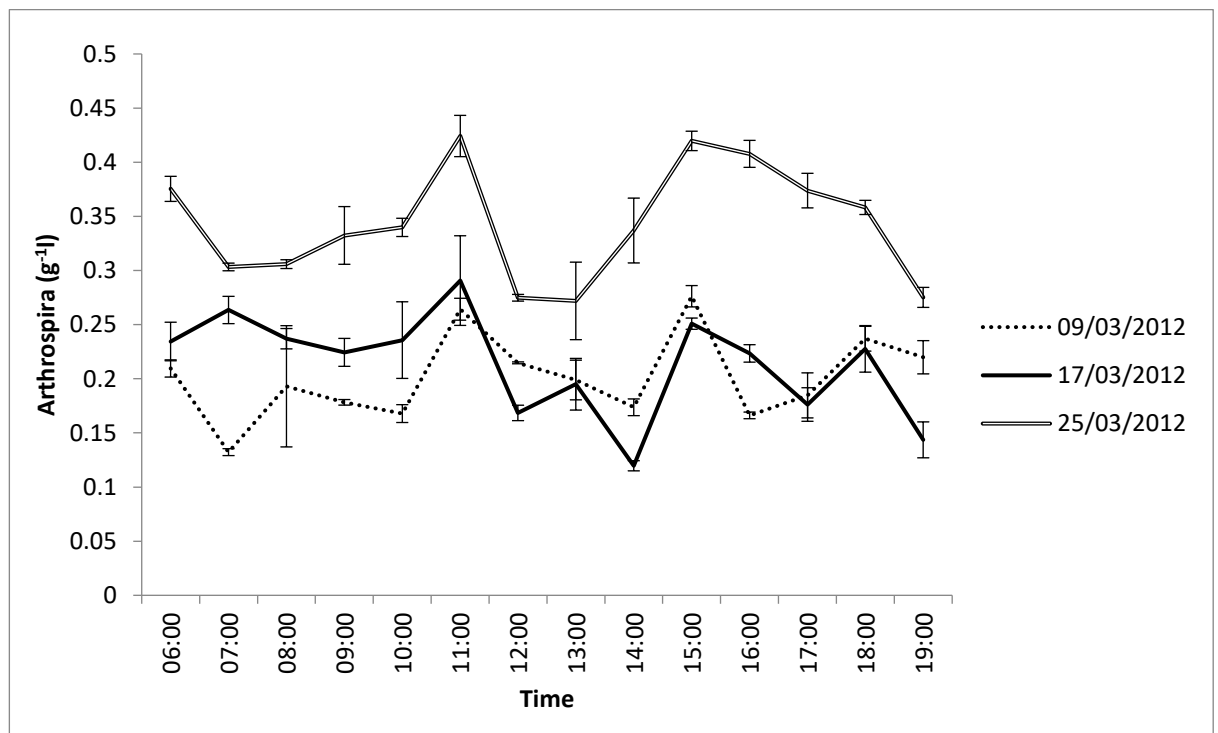
Figure 2.3 – *Arthrospira fusiformus* diurnal migration patterns in the central basin across three different dates during the dry season.

A collection of studies spanning almost 40 years show instability in the phytoplankton populations of African soda lakes (Krienitz and Kotut, 2010; Oduor and Schagerl, 2007b, 2007a; Tuite, 2000; Vareschi, 1978). Shallow lakes situated in arid regions experience fluctuations in

their variables which are linked to climatic changes and in particular rainfall (Talling, 2001). Nonetheless, the key factors affecting productivity fluctuations and changes in community structure are not well understood (Melack, 1988). Fluctuations and changes in nutrient concentrations (nitrogen, nitrate-N and phosphorus), light supply, and water level, among others contribute to the dynamics of primary producers in the rift valley soda lakes (Melack, 1988; Oduor and Schagerl, 2007b). In addition, in response to evaporative concentration, salinity is cited as a main driving force to changes in the microbiological community. The greatest specific growth rates for *Arthrospira* are observed at low salinities, 13g/L^{-1} but, quantum yield (Φ%) is greatest in salinities ranging from 33 to 51 g/L^{-1} (Kebede, 1997).

At low salinities, *Arthrospira* is unlikely to exist as unialgal populations typical of Lake Bogoria. The complexity of the community is likely to affect the overall biomass and resource utilization (Neill, 1975), which may contribute to the lower wet weight biomass recorded in Lake Nakuru and Lake Elmenteita, which both have lower salinities (Ballot et al., 2004). When water levels are high, other phytoplankton species are present, as water chemistry accounts for 44% of the variance in community composition (Schagerl and Oduor, 2008). Therefore, climate change effects on precipitation, evaporation, and hydrology are likely to have effects on primary production in salt lakes (Talling, 2001).

Primary Consumers (aquatic – terrestrial subsidies)

There are two main consumers of primary production in Lake Bogoria, the lesser flamingo (*Phoeniconaias minor*) and the chironomid species *Tanytarsus minutipalpus*. In addition to these two consumers, the greater flamingo also grazes on Lake Bogoria but in much lower numbers than the lesser flamingo and several other invertebrate species colonise the littoral, profundal, and ephemeral shore pools during the wet season.

The unpredictable variation in phytoplankton biomass and in particular the contribution of *A. fusiformis* to total biomass has mixed knock-on effects on the dominant primary consumers and donor community. The relationship between the abundance of chironomid species and the biomass of their prey is complex and species specific. The abundance of many chironomid species is positively correlated with primary production, but others show negative or independent responses (Dermott et al., 1977; Specziár and Vörös, 2001), and functional responses to food availability over long periods are not indicated (Goldfinch and Carman, 2000). These difficulties in understanding the relationship between productivity and consumer abundance are further compounded by changes in environment, like water volume and the synergistic reduction in salinity and nutrients. In addition, as the salinity decreases, making the

environment less extreme, it is likely that other organisms will migrate into the area and colonise which can change community structure and can reduce the abundance and distribution of chironomids (Cuker, 1983; Hargeby et al., 1994). Despite this, many articles cite chironomid secondary production as not only sufficient but important for supporting populations of consumers at higher trophic levels (Anderson et al., 2012). During periods of low biomass of *Arthrospira*, flamingos occur in numbers below 100,000 (Krienitz and Kotut, 2010). The change in primary producer species composition that coincided with a reduction in salinity in 2008 changed the microbial community to one of lower quantity and quality with higher toxicity which resulted in a flamingo die off (Krienitz and Kotut, 2010).

Tanytarsus minutipalpus

Although Harper et al (2003) placed it in the *Paratendipes* genus, more recent work from Eggermont and Verschuren have identified the species inhabiting Lake Bogoria as *Tanytarsus minutipalpus*. This was first described by Ekrem and Harrison (1999) who collected *T. minutipalpus* from lakes ranging from 19,000 to 40,000 μS/cm. However later studies have found that their true salinity tolerance is between ~10,000 μS/cm and ~68,400 μS/cm with an optimum of 35,479.7 μS/cm (Eggermont et al., 2006). As an obligate halobiont species, it is adapted to the extreme conditions in the soda lakes of the Rift valley and is found in most poly- to hypersaline lakes in Kenya and Ethiopia. It is the only species present at Lake Bogoria and other Rift Valley saline lakes (Eggermont and Verschuren, 2004b; Ekrem and Harrison, 1999). *T. minutipalpus* is one of 6 halobiont chironomid species found in East Africa, of which only three have tolerances greater than 5000 μS/cm, the others being *Tanytarsus* near *barbitarsis*, *Paratendipes* type Naivasha, *Pentaneurini* indet. type Naivasha, *Kiefferulus disparilis*, *Microchironomus deribae*. The latter two have tolerances greater than 5000 μS/cm and *Tanytarsus* near *barbitarsis* replaces *T. minutipalpus* further west in the saline lakes of western Uganda (Eggermont and Verschuren, 2004b; Verschuren et al., 2004). *T. minutipalpus* emergences account for the presence of over 50 bird species (Harper et al., 2003).

Flamingos

"Flamingo skins, flesh and eggs have long been trade items around the shores of the Mediterranean, and the ancient Phoenicians traded flamingo tongues which, according to the Roman Pliny, were a delicacy 'without which no Roman banquet was complete'." (Williams, 1993)

Both the greater flamingo (*Phoenicopterus roseus*) and the lesser flamingo (*Phoeniconaias minor*) forage at Lake Bogoria and are characteristic birds of alkaline-saline lakes and the pans of Africa and India. The lesser flamingo accounts for more than 90% of the total flamingo

population and will be the focus of this description. The East African Rift Valley is home to the largest population of lesser flamingos of 1.5 - 2.5 million, where single flocks of several hundred birds are regularly seen. The greatest densities are observed in Kenya, with a population in excess of one and a half million, and Tanzania, with approximately 600,000 birds (Childress, et al., 2007). Flamingos are a non-migratory itinerant species, which respond to changes in local environmental conditions by moving among wetlands, thus depending on a network of 15 Lakes in the East African Rift valley (Childress, et al., 2007; Krienitz and Kotut, 2010). Flamingo flights can exceed 400km and average ~100 km and length of stay at one of the 15 lakes between Lake Logipi, Kenya and Bahi Swamp, Tanzania varies considerably, from less than a day to over 150 days but averaging at ~14.5 days (Childress, et al., 2007; Tebbs et al., 2015). Although they have the capability of traveling between southern and eastern populations, genetic studies have shown restricted interchange (Zaccara et al., 2008). Compared to other water birds, flamingos show the highest variation of individual numbers at Kenyan lakes studied (Owino et al. 2001).

Flamingos are highly specialised to a diet of micro cyanobacteria and benthic diatoms. At Lake Bogoria, *A. fusiformis* contributes the bulk of their food intake (Krienitz and Kotut, 2010). Flamingo distribution around the East African soda lakes is linked to the quality and quantity of food available. Two patterns have been observed, clumped and distributed. The population becomes clumped when there is enough food at one or more lakes to support the entirety of the lesser flamingo population and during breeding. During periods of low *A. fusiformis* biomass the flamingos switch to the more reliable but less dense food source, benthic diatoms, and the population becomes dispersed. Although the productivity of diatoms is $1 - 2$ orders of magnitude lower than *A. fusiformis*, as a resource they are more predictable and widely available (Tuite, 2000). *A. fusiformis* is known to form slicks which the flamingos avoid as it clogs their filter (Vareschi, 1978). In an experiment with caged lesser flamingos at Lake Nakuru, Vareschi (1978) established that an adult bird is able to filter ~30 L of lake water and to ingest 5.6 g dry mass (DM) of *A. fusiformis* per hour, which equals to $70 \, g/d^{-1}$ DM. The whole flamingo population of ~1 million birds therefore extracts $~60 \, t/d^{-1}$ of food algal DM, representing 50%–94% of the daily primary production of the lake.

Although it is the most numerous species of flamingo, the lesser flamingo is considered "Near Threatened" (IUCN, 2015), due to loss and or the degradation of its specialised habitat (Krienitz and Kotut, 2010). There have been declines of, 21% for East African populations and 27% in South African populations (Simmons, 2000). Breeding is confined to five sites, of which Lake Natron is the only breeding site where East African flocks have had breeding success in the past 45 years, as seasonal floods between November and February provide isolation from predators (Childress, et al., 2007; Childress, et al., 2007). The toxins produced by cyanobacteria at the hot

springs are thought to contribute to flamingo deaths as the birds drink and groom here because of the lower salinities (Krienitz et al., 2003). Considering the lack of breeding sites, adaptation to a specialised environment, fluctuating and unpredictable food source, and anthropogenic encroachment of their habitat, good understanding and conservation of saline lakes are important for high profile birds such as these (McCulloch et al., 2003).

Terrestrial system and beyond

Figure 2.4 is a schematic showing the groups of actors involved in the transfer of energy between the lake and the riparian zone at Lake Bogoria. The recipient community can be divided into to two, the predatory and the detritivorous recipient guilds. The important components of the predatory guild are web building spiders, non-web building spiders, tiger beetles, and scorpions. The detritovorous guild is mainly made up of *Quadrideres* spp and Ants.
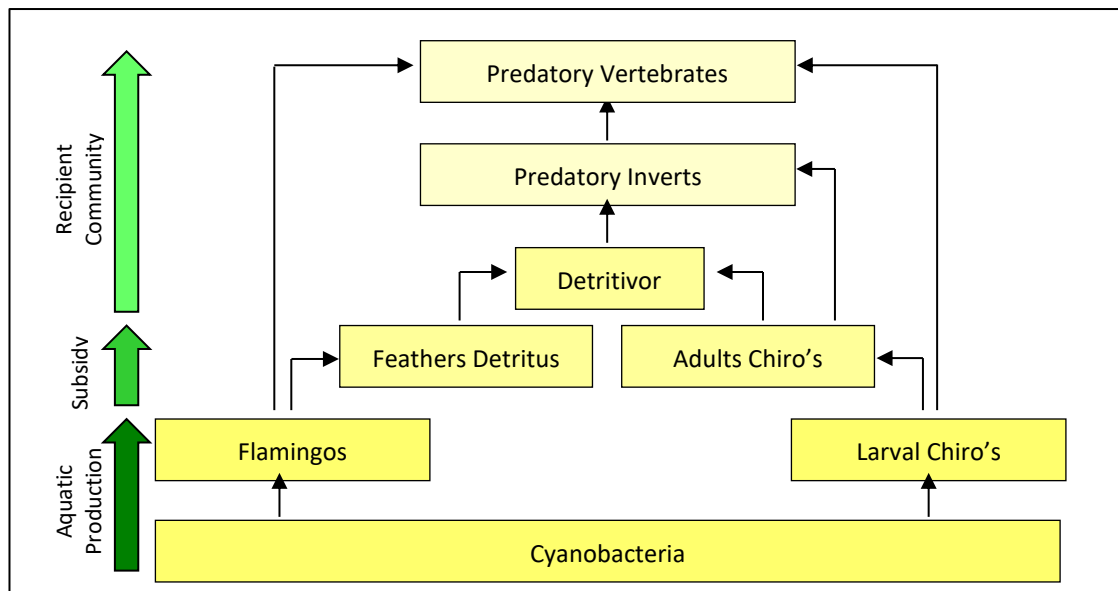
Figure 2.4 – Schematic of the important components of the two systems under investigation and how they are linked.

Aquatic subsidies continue to feed into the higher trophic levels. As well as foraging for invertebrates along the shore of the lake, baboons were captured on film by the BBC, in both The Life of Mammals and Earthflight, hunting flamingos. I have observed African fish eagles, marabou stalks, and tawny eagles hunting and scavenging on the lesser flamingo (e.g. figure 2.5). Although they are present in the reserve, hyenas are thought to scavenge but not hunt flamingos as they do at Lake Oleidon and Lake Nakuru.

Figure 2.5 – African fish eagle feeding on a flamingo carcass after a successful hunt.

Baboons regularly forage for arthropods which feed on the emerging chironomids and predators such as the serval cat feed on birds which prey on emerging chironomids.

Concluding remarks

Saline lakes are undervalued and understudied but because their ecosystems usually contain fewer actors they are useful sites for scientific inquiry and provide a valuable "natural lab". Lake Bogoria is one of a small network of soda lakes that harbour high abundances of *A. fusiformis* and play a vital role in sustaining the population of Lesser Flamingos - a near threatened species (Childress et al 2007, Tuite 2000, IUCN 2012), and abundant populations of the chironomid *T. minutipalpus*. *A. fusiformis* plays a key roll as a 'wasp-waist' species in this food web, patricianly along come of the links i.e. the flamingos to higher predator's link. *A. fusiformis* therefore allows for short and efficient resources transfer links within this landscape food web (Padovani et al 2012). Ecological efficiencies do not determine trophic structure; rather, they are its product (Hairston and Hairston, 2015). Links between ecosystems at a regional scale are likely to be changed by differences in community composition and diversity (Chapin III et al., 1997; Peterjohn et al., 1984), and in Lake Bogoria the differing basin morphologies mean that the chemistry and biology behave differently. This is likely to have an effect on the relative strength of subsidy between basins and seasons. By looking at the palaeorecord using lake sediments, past changes in salinity can be inferred and compared to contemporary ecology to assess how linkage between saline lakes and their riparian zone will be affected by climate change.

Chapter Three: Aquatic to terrestrial subsidies in a saline lake – arid environment.

Introduction

Emergence of adult insects constitutes a substantial export of aquatic energy to a recipient terrestrial community and may account for 25% to 100% of some terrestrial population's diet (Baxter et al., 2005b). Stable isotope ratios have proved a valuable tool for studying resource transfer across ecosystem boundaries and contribution of allochthonous material into consumer diets. Such links are well documented for freshwater and marine habitats but linkage between saline lakes and their riparian zone has been largely overlooked (Jones and Grey, 2001; Grey and Harper, 2002; Grey and Jackson, 2012; McCauley et al., 2015).

Saline lakes are ideal study systems to investigate aquatic-terrestrial linkages because food webs in the extreme aquatic environment and arid surrounding landscape, although complex, often have less actors and can be construed as 'simple' (Hammer, 1986; Williams, 1981). In addition, tropical saline lakes are recognised as among the most productive water bodies in the world, and have great potential to supply resources to the surrounding depauperate landscape (Talling et al., 1973).

Lake Bogoria is naturally eutrophic and lies in the semi-arid region of the Kenyan Rift Valley (Harper et al., 2003; Tebbs et al., 2013). The contrast between the two ecosystems at Lake Bogoria provides a "natural mesocosm" (Williams et al., 1990) for addressing questions related to cross-ecosystem subsidies. Lake Bogoria's basin has a unique shape, divided into three parts by projections of sediments around hot springs forming 'sils' (McCall, 2010). The shape of a lake affects the physical, chemical and biological properties of the ecosystem, and in Lake Bogoria, basins have been found that are less similar to the main water body then individual lakes (Dumont, 1998; Johansson et al., 2007). Lake Bogoria's three basins vary in morphometry, catchment relief, inputs, and chemistry (Harper et al., 2003; Hickley et al., 2003; McCall, 2010).

Shallowness affects the environmental regulation and functioning of tropical lakes and seasonal periodicity on the magnitude of water input is dependent on inter-tropical convergence zone (Talling, 2001). Therefore, basin morphology and seasonal hydrological variation will have combined effects on chemical regulation. Temporal changes in chemistry affects phytoplankton communities in different lakes (Schagerl and Oduor, 2008) and primary producers are known to have an effect on subsidies between ecosystems (Polis et al., 1997). Thus, each of the basins in

Lake Bogoria will function differently and between basin functioning will vary with season, potentially altering aquatic-terrestrial subsidies.

There are two main aquatic-terrestrial food web links in the lake; a high quality but temporally variable emergence of chironomids, dominated by a single species (*Tanytarsus minutipalpus*), and a temporally constant supply of shed feathers from a population reaching into the millions of lesser flamingos (*Phoeniconaias minor*). Both of these consumers rely on cyanobacteria in the lake as their primary food resource. It is hypothesised that stable Isotope Analysis (SIA) can be used to differentiate between the carbon and nitrogen isotopic signatures of the aquatic primary producers (cyanobacteria) and the terrestrial basal resources (C3 and C4 plants), and thus be used to trace contributions of aquatic energy to the terrestrial ecosystem. Furthermore, I hypothesis that the two vectors of subsidy between the ecosystems will vary across basin and season and that this will be recorded in the stable isotopes of the recipient community. Using SIA, I measure the subsidy strength of both aquatic-terrestrial vectors across space (basins) and time (seasons).

Methods

Sampling

Samples were collected and data recorded for the duration of ~7 weeks in the dry (09/02/12 – 31/03/12) and wet (10/07/12 – 27/08/12) seasons of 2012. Conductivity, salinity and temperature were taken every 2 days using a Camlab conductivity / TDS / salinity meter (model CW/6220). The meter was programmed to adjust salinity and conductivity for temperature because the measurements for each basin were taken at slightly different times of the day and both air and water temperature could increase very quickly in the mornings.

Organisms required for SIA were collected every four days. All components of the recipient terrestrial community were collected with 0-5 m from the swash line. Scorpions, non web-building spiders, predatory beetles, detritivorous beetles, and ants were all hand collected by searching their typical refugia. Web building spiders where collected using a sweep net. Between 3 and 6 individuals were combined as a single sample for stable isotope analysis and sample size for each population in each season is given in Table 3.1

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Basel resources, link vectors and consumers	Dry season	Wet season	Dry season			Wet season		
			North	Central	South	North	Central	South
Ants	11	97	3	4	4	3	91	3
Phytoplankton	103	99	34	38	31	36	35	28
C3 plants	17	35	7	5	5	13	12	10
C4 plants	21	26	6	10	5	9	9	8
Chironomids	140	138	37	56	47	38	65	35
Feather detritus	15	10	6	6	3	2	2	1
Non-web building Spiders	108	178	38	34	36	37	105	36
Detritivorous beetles	100	100	34	35	31	38	31	31
Scorpion	102	106	34	37	31	35	36	35
Shore flies	109	102	19	24	66	32	1	36
Predatory beetles	107	93	32	38	37	35	31	27
Termites	9	6	3	4	2	2	2	2
We building spiders	138	206	37	52	49	44	119	43

Table 3.1 – Sample sizes for each food web and link component for each season and for each basin with in the season.

Flotsam and jetsam were collected from along the swash line, from which, flamingo feathers were picked. The most recent growth of C3 and C4 plants where collected from a wide range of species at the beginning, middle and end of 8-week sample period, including grasses, scrubs, trees and climbing species. At least three individual plants were pooled together of each of the species represented for SIA. *A. fusiformis* was collected using a phytoplankton net (53 μm) dragged through the littoral zone for 2.10 m every 4 days.

Emerging adult chironomids were collected using 0.045m^2 submerged emergence traps. A total of 15 traps were set every 2 days, 5 in each of the basins and in the large central basin the traps were split across three sites. The height of trap above sediment surface was randomised (35.42 cm ± 3.73, mean ± SD) and the traps were moved twice over the sample period to accommodate for rising/falling lake level.

Stable isotope analysis

Samples were dried to a constant weight at 60 °C. and then homogenised to a fine and uniform powder in an agate mortar and pestle. The arthropods and feather detritus were weighed to between 0.5 and 0.6 mg, *A. fusiformis* between 0.8 and 1.0 mg, and terrestrial plant materiel between 0.9 and 1.2 mg. Homogenised *A. fusiformis* and the feather detritus were treated with an acidification "rinse method" using HCL following Brodie et al., (2011). Chironomid samples were not acidified as during the picking process they were subject to a sequence of rinses.

$^{13}C{:}^{12}C$ and $^{15}N{:}^{14}N$ ratio's are expressed using conventional notations (δ) relative to international standards (C- Pee Dee Belemnite, N to atmospheric nitrogen). Samples were placed in 6 x 4mm tin cups and combusted in an elemental analyser (Flash EA, 1112 series; Thermo-Finnigan)

coupled to a continuous-flow isotope ratio mass spectrometry (Finnigan MAT DeltaPlus; Thermo- Finnigan) and recorded using Isodat NT version 2.0 (Ings et al., 2010).

Analysis

Analysis of variance (ANOVA) was used to test for significant differences between the carbon and nitrogen values of resources populations (phytoplankton and terrestrial plants) using the statistical programme R (R Core Development Team, 2008). The resources differed significantly in carbon values (dry season, $F_{2,51}$ = 192.2, p-value < 0.01; wet season, $F_{2,157}$ = 2008, p-value < 0.01) and therefore stable isotopes can confidently be used to trace aquatic resource subsidies to the terrestrial ecosystem. ANOVA's were also used to test for significant differences in terrestrial predator diet (i.e. carbon and nitrogen values) between basins and seasons.

SIAR in the statistical package R (Parnell et al., 2008; R Development Core Team, 2008) was then used to calculate metrics of trophic structure outlined by Layman et al. (2008) and Jackson et al. (2011). I calculated standard ellipse areas (SEA) and total area (TA) as a measure of trophic niche for of the entire terrestrial community, and for each separate consumer population. A large niche reflects a greater variation in diet. I also calculated carbon range (CR) and nitrogen range (NR) as further metrics of diet variability related to resource range and trophic level, respectively.

Bayesian mixing models which incorporate variability in resource (diet), trophic enrichment factors, and consumer isotope values (Jackson et al., 2011) were used to estimate the contribution of each resource to the diet of each terrestrial population. Fractionation factors between resource and consumer were assumed to be 2.2 ± 0.30 ‰ for δ^{15}N and 0.5 ± 0.19 ‰ for δ^{13}C; these values are derived from freshwater consumers in a meta-analysis by McCutchan Jr et al., (2003). Since I used resources two trophic levels below the consumers, the values were doubled for the analysis (see Figure 3.1 to recap the schematic from the site description).
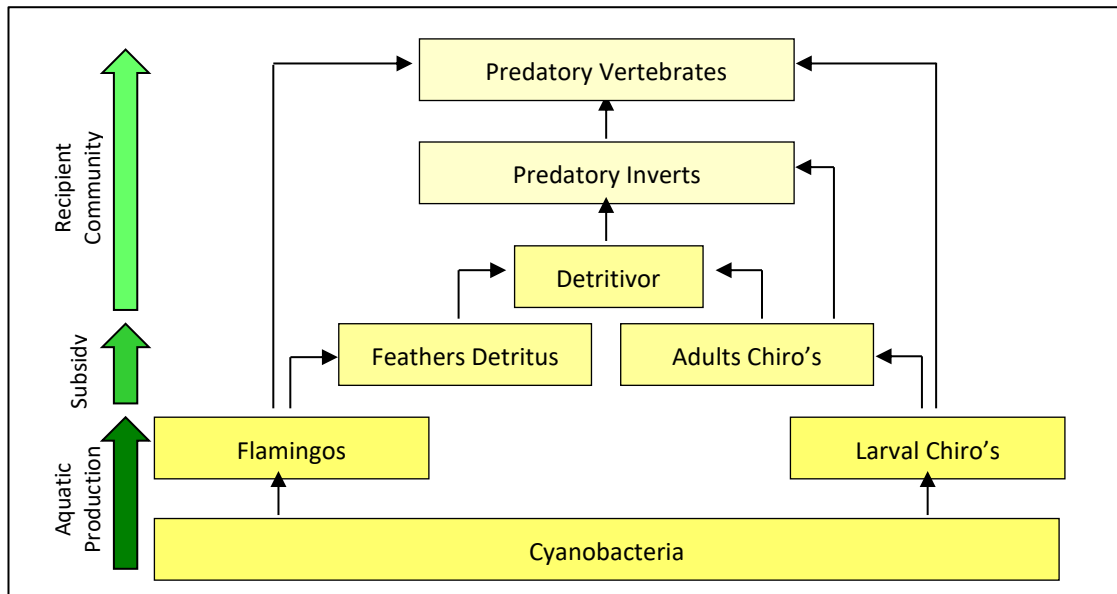
Figure 3.1 – Schematic of the important components of the two systems under investigation and how they are linked.

Results

Seasonal variation in aquatic-terrestrial subsidy

A. fusiformis, which dominated the phytoplankton community, was isotopically distinct from common terrestrial C3 and C4 plants (see Methods). Between the dry and wet seasons, C3 and C4 plants shift from δ^{15}N 1.90 to δ^{15}N 4.47 and δ^{15}N 3.37 to δ^{15}N 4.41, respectively. The aquatic basal resource, phytoplankton, had a mean δ^{15}N shifts from 4.48‰ to 2.92‰. Stable isotope ratios of emerged chironomids closely reflect those of the phytoplankton in the dry season (Figure 3.2a), but less so in the wet season (Figure 3.2b). Step wise enrichment of mean δ^{15}N and δ^{13}C of consumers from basal resources through to higher consumers are observed; the values are similar to predicted values (Table 3.2).

The niche (measured as SEA) and nitrogen range of phytoplankton was larger during the dry season (Figure 3.2c). Nitrogen range of phytoplankton halved (10.55 to 4.28 ‰) and SEA declined by an order of magnitude (8.15 to 0.83‰^{2}) in the wet season (Figure 3.2d). This is reflected in relative reductions of SEA and δ^{15}N range in chironomids, which consume the phytoplankton. The mean δ^{15}N range of feather detritus declines from 8.20 to 4.60‰ and the SEA value falls from 6.22 to 2.55‰ in the wet season, however, the δ^{13}C range increases from 3.98 to 5.06‰. The reduction in nitrogen range in phytoplankton and feather detritus along with an increase in carbon range in feather detritus is mirrored by the associated changes in shore

flies; 7.61‰ to 0.89‰ and 3.06 to 6.34‰, respectively. However, in the recipient terrestrial community there is greater isotopic variation in the wet season; every metric increases other than carbon range (Table 3.3).

Dry Season (a)				
Interacting organisms	$\delta^{13}C$		$\delta^{15}N$	
	Observed	Expected	Observed	Expected
Arthro - Chiro	0.99	0.5	1.42	2.2
Chiro - WB	0.4	0.5	2.12	2.2
WB - SCOR	1.04	0.5	2.83	2.2

Wet Season (b)				
Interacting organisms	$\delta^{13}C$		$\delta^{15}N$	
	Observed	Expected	Observed	Expected
Arthro - Chiro	1.35	0.5	2.45	2.2
Chiro - WB	0.07	0.5	1.61	2.2
WB - NW	0.6	0.5	2.5	2.2

Table 3.2 – Examples of dry (a) and wet (b) season stepwise changes similarities to the predictions after McCutchan et al., (2003).

Season	SEA	SEAc	TA	$\delta^{15}N$ range	$\delta^{13}C$ range
Dry	5.17	5.18	39.51	6.18	10.57
Wet	5.36	5.37	51.44	7.82	10.39

Table 3.3 – Recipient community isotopic response to seasonal changes using Layman's metrics.

All members of the recipient community show a significant difference in $\delta^{15}N$ between season suggesting seasonal diet variation, but only ants and predatory beetles have significant differences in $\delta^{13}C$ (Table 3.4). There is a general pattern of lower nitrogen values (and therefore lower trophic level) in the recipient terrestrial consumers in the wet season (Figure 3.2, e and f). Scorpions had reductions in all isotopic metrics in the wet season. Web building spiders saw a small reduction in SEA and nitrogen range but increases in TA and carbon range. Non-web building spiders show a reduction in $\delta^{13}C$ range. However, all other metrics for recipient assemblages show a larger isotopic niche in the wet season. The largest change is observed by ants which show a large shift towards the aquatic derived resources in the wet season. During the dry season, discreet isotopic niches are observed between the predatory and detritivorous beetles as well as between the web building and non-web building spiders. The SEA beetle niches overlap to a value of 0.71 (0 = no overlap, 1 = complete overlap) in the wet season and, although the spiders SEA does not overlap, there is greater overlap in total area in the wet season compared to the dry.

Recipient	$\delta^{13}C$			$\delta^{15}N$		
	N	F value	p-value	N	F value	p-value
Ants	106	41.51	0	106	26.15	0
Non- web building spiders	284	0.03	0.86	284	109.15	0
Detritivorous beetles	198	0.57	0.45	198	63.93	0
Scorpions	206	2.22	0.14	206	100.51	0
Predatory beetles	198	43.61	0	198	18.66	0
Web building spiders	342	3.2	0.07	342	104.76	0

Table 3.4 – ANOVA test results comparing $\delta^{13}C$ and $\delta^{15}N$ isotope values between seasons.

Dry Season

Consumers	C3		C4		Phytoplankton	
Ants	4.1	0.0 - 10.8	79.2	57.4 - 96.9	16.7	0.0 - 38.3
Scorpions	0.7	0.0 - 2.0	30.3	24.8 - 35.7	68.9	63.1 - 74.9
Non- web building spiders	0.7	0.0 - 1.9	33.4	28.6 - 38.3	65.9	60.6 - 71.1
Web building spiders	20.0	15.5 - 24 .5	32.1	28.0 - 36.2	47.9	39.6 - 56.1
Predatory beetles	0.3	0.0 - 0.0	25.4	23.4 - 27.4	74.3	72.1 - 76.4
Detritivorous beetles	0.8	0.0 - 2.1	61.3	55.8 - 66.8	37.9	31.9 - 43.7

Wet Season

Consumers	C3		C4		Phytoplankton	
Ants	8.0	0.0 - 16 - 7	18.4	10.7 - 26.2	73.6	57.7 - 88.2
Scorpions	44.4	42.4 - 46.6	54.8	52.7 - 56.8	0.8	0.0 - 2.3
Non- web building spiders	40.1	36.9 - 42.8	57.2	54.5 - 59.5	2.7	0.0 - 7.3
Web building spiders	0.5	0.0 - 1.3	12.7	11.0 - 14.4	86.8	84.6 - 88.9
Predatory beetles	40.0	38.3 - 41.6	59.0	57.4 - 60.5	1.0	0.0 - 2.7
Detritivorous beetles	27.7	23.1 - 31.8	69.2	65.1 - 73.0	3.1	0.0 - 8.8

Table 3.5 – Mixing models comparing $\delta^{13}C$ contribution to diet between seasons. Values are given as estimated mean percentage of resource to diet, with confidence intervals in subscript.

Dry Season

The mixing models demonstrated a general trend of consumers to include more resources associated with C3 plants in their diet in the wet season compared to the dry. However, web-building spiders are the only consumers to incorporate a significant percentage of C3-derived carbon in the dry season, but switch to the highest contribution of aquatic carbon of any group during the wet season (Table 3.5). Ants shift from a predominantly C4 plant-derived carbon source in the dry season to phytoplankton-derived carbon in the wet season. Scorpions, non-web building spiders and predatory beetles are estimated to have between 66 and 75% aquatically derived carbon in the dry season, but have extremely low contributions in the wet (Table 3.5). Predatory and detritivorous beetles also shift towards a lower aquatic derived carbon diet, with the predatory beetles reducing from 74% to an approximate 40 – 60% split

Lake - Dry Season (a)

Lake - Wet Season (b)

C3 C3 plants	ARTHRO - Phytoplankton
C4 C4 plants	CHIRO - Chironomids
SF Shore flies	SCOR - Scorpions

TB :datory beetles	NW - Non-web building spiders
Q :ritivorous beetles	WB - Web building spiders
FD :ther detritus	TER - Termites
	ANT - Ants

Lake - Dry Season Subsidy (c)

Lake - Wet Season Subsidy (d)

● Shore fly	● Feathers detritus
● Chironomids	● Phytoplankton
● Recipient community	

● Shore fly	● Feathers detritus
● Chironomids	● Phytoplankton
● Recipient community	

Lake - Dry Season Recipient Community (e)

Lake - Wet Season Recipient Community (f)

● Ants	● Scorpions
● Predatory beetles	● Non-webbuilding spiders
● Detritivorous beetles	● Webbuilding Spiders

● Ants	● Scorpions
● Predatory beetles	● Non-webbuilding spiders
● Detritivorous beetles	● Webbuilding Spiders

Figure 3.2 – Stable isotope bi-plots for the entire lake during the dry (a) season and the wet (b) season. The SEA showing isotopic niches for the basal resources, vectors, and recipient community.

between C3 and C4 plant-derived carbon in the wet. Detritivorous beetles shift from 38% aquatic carbon contribution to an approximate 30 – 70 % diet between the dry and wet seasons (Table 3.5).

Variation in aquatic-terrestrial link between basins

In both the wet and the dry seasons, ants are the only recipient that did not show resource separation across the basins (Table 3.4). All other assemblages have a significant difference of $\delta^{13}C$ between basins.

Both ants and scorpions have a smaller $\delta^{13}C$ range and larger $\delta^{15}N$ range in the northern basin, compared to the southern basin. Whereas the scorpions shift in isotopic space to a more ^{13}C-depleated mean value, ants shift to a more ^{13}C-enritched diet (Figure 3.3). In addition, the ants mean $\delta^{15}N$ reduces from north to south. Isotopic space shifts from greater $\delta^{13}C$ variation to greater $\delta^{15}N$ variation from north to south, and also shift to greater $\delta^{13}C$ depletion from north to south

$\delta^{13}C$

Recipient	Dry Season			Wet Season		
	N	F value	p-value	N	F value	p-value
Ants	8	3.95	0.06	94	0.22	0.8
Non-web building spiders	105	11.09	0	175	13.16	0
Detritivorous beetles	97	15.41	0	97	27.8	0
Scorpions	99	16.32	0	103	9.83	0
Predatory beetles	104	7.26	0	90	17.58	0
Web building spiders	135	28.39	0	203	16.41	0

Table 3.6 – ANOVA test results comparing $\delta^{13}C$ isotope values between basins for each season.

$\delta^{15}N$

Recipient	Dry Season			Wet Season		
	N	F value	p-value	N	F value	p-value
Ants	8	1.22	0.35	94	0.31	0.73
Non-web building spiders	105	3.88	0.02	175	8.48	0
Detritivorous beetles	97	8.75	0	97	34.74	0
Scorpions	99	1.48	0.23	103	2.61	0.08
Predatory beetles	104	3.84	0.02	90	9.15	0
Web building spiders	135	4.19	0.02	203	2.32	0.1

Table 3.7 – ANOVA test results comparing $\delta^{15}N$ isotope values between basins for each season.

Dry Season

North

Consumers	C3		C4		Phytoplankton	
Ants	17.0	0 - 44.2	49.2	11 - 87.5	33.7	0 - 66
Scorpions	2.1	0 - 6.2	50.3	41.2 - 59.6	47.6	36.2 - 58.6
Non- web building spiders	1.5	0.0 - 4.4	26.3	19.6 - 32.9	72.1	63.9 - 80.1
Web building spiders	19.5	12.5 - 26.9	21.6	15.9 - 28.5	58.8	45.3 - 25.8
Predatory beetles	1.0	0 - 2.7	29.6	25.3 - 33.9	69.4	64.1 - 74.5
Detritivorous beetles	2.2	0 - 6.4	82.5	77.2 - 88	15.3	5.9 - 22.8

Central

Consumers	C3		C4		Phytoplankton	
Ants	9.6	0 - 26.5	61.5	29.6 - 89.9	28.9	0 - 56.5
Scorpions	2.0	0 - 5.9	25.1	16.2 - 34.1	72.8	61.8 - 83.8
Non- web building spiders	2.4	0 - 6.8	49.4	40.4 - 58.3	48.2	36.4 - 59.2
Web building spiders	16.5	7.5 - 25.6	27.5	19.6 - 35.2	56.0	39.4 - 72.6
Predatory beetles	0.6	0 - 1.8	21.8	19.5 - 24.2	77.5	74.5 - 80.3
Detritivorous beetles	2.1	0 - 6.1	51.8	45.3 - 58.4	46.1	36.6 - 54.5

South

Consumers	C3		C4		Phytoplankton	
Ants	21.6	0 - 48.1	52.1	18 - 85	26.3	0 - 53.3
Scorpions	2.2	0 - 6.5	21.5	13.1 - 30	76.3	64.7 - 87.1
Non- web building spiders	2.1	0 - 6	30.1	21.3 - 38.8	67.8	56.8 - 78.5
Web building spiders	25.2	18.8 - 31.6	45.6	39.9 - 51.3	29.2	17.8 - 40.9
Predatory beetles	1.0	0 - 2.8	27.3	23.2 - 31.2	71.7	66.7 - 76.7
Detritivorous beetles	2.3	0 - 6.6	53.7	40.6 - 67.2	44.0	28.8 - 59.1

Table 3.8 – Recipient consumer mixing models across basins for the dry season.

Wet Season

North

Consumers	C3		C4		Phytoplankton	
Ants	31.2	2.4 - 55.2	34.6	5.9 - 58.5	34.2	0.5 - 64.9
Scorpions	42.1	37.1 - 46.7	55.1	50.6 - 59.2	2.8	0 - 8.3
Non- web building spiders	32.6	26.8 - 37.8	62.8	57.9 - 67.4	4.7	0 - 12.1
Web building spiders	1.3	0 - 3.7	15.5	11.3 - 19.6	83.2	77.3 - 88.4
Predatory beetles	35.2	32.2 - 37.8	62.9	60.4 - 65.4	1.9	0 - 5.3
Detritivorous beetles	20.0	16 - 23.9	77.9	74.2 - 81.4	2.1	0 - 6

Central

Consumers	C3		C4		Phytoplankton	
Ants	7.8	0 - 16.7	18.5	10.8 - 26.8	73.7	57.4 - 88.4
Scorpions	48.7	44.8 - 52.5	49.0	45.5 - 52.4	2.3	0 - 6.7
Non- web building spiders	39.5	33.1 - 45.4	51.4	46.3 - 56.1	9.1	0 - 19
Web building spiders	0.9	0 - 2.6	9.8	9.8 - 12.1	89.3	85.7 - 92.4
Predatory beetles	40.1	35.6 - 44.1	54.3	50.6 - 57.7	5.6	0 - 12.4
Detritivorous beetles	24.2	19.9 - 27.8	72.8	69.4 - 76	2.9	0 - 8.6

South

Consumers	C3		C4		Phytoplankton	
Ants	31.9	2.7 - 55.7	27.6	1.9 - 49.1	40.5	2.6 - 78.3
Scorpions	39.8	36.6 - 42.9	58.6	55.6 - 61.5	1.6	0 - 4.7
Non- web building spiders	36.2	29.8 - 40.9	58.5	53.5 - 62.4	5.4	0 - 15.5
Web building spiders	1.7	0 - 4.8	20.6	17 - 24.4	77.7	71.4 - 82.9
Predatory beetles	41.7	38.2 - 44.7	55.9	52.9 - 58.6	2.4	0 - 7.1
Detritivorous beetles	16.4	1.1 - 30.5	36.8	24.2 - 49	46.9	23.7 - 71.7

Table 3.9 – Recipient consumer mixing models across basins for the wet season.
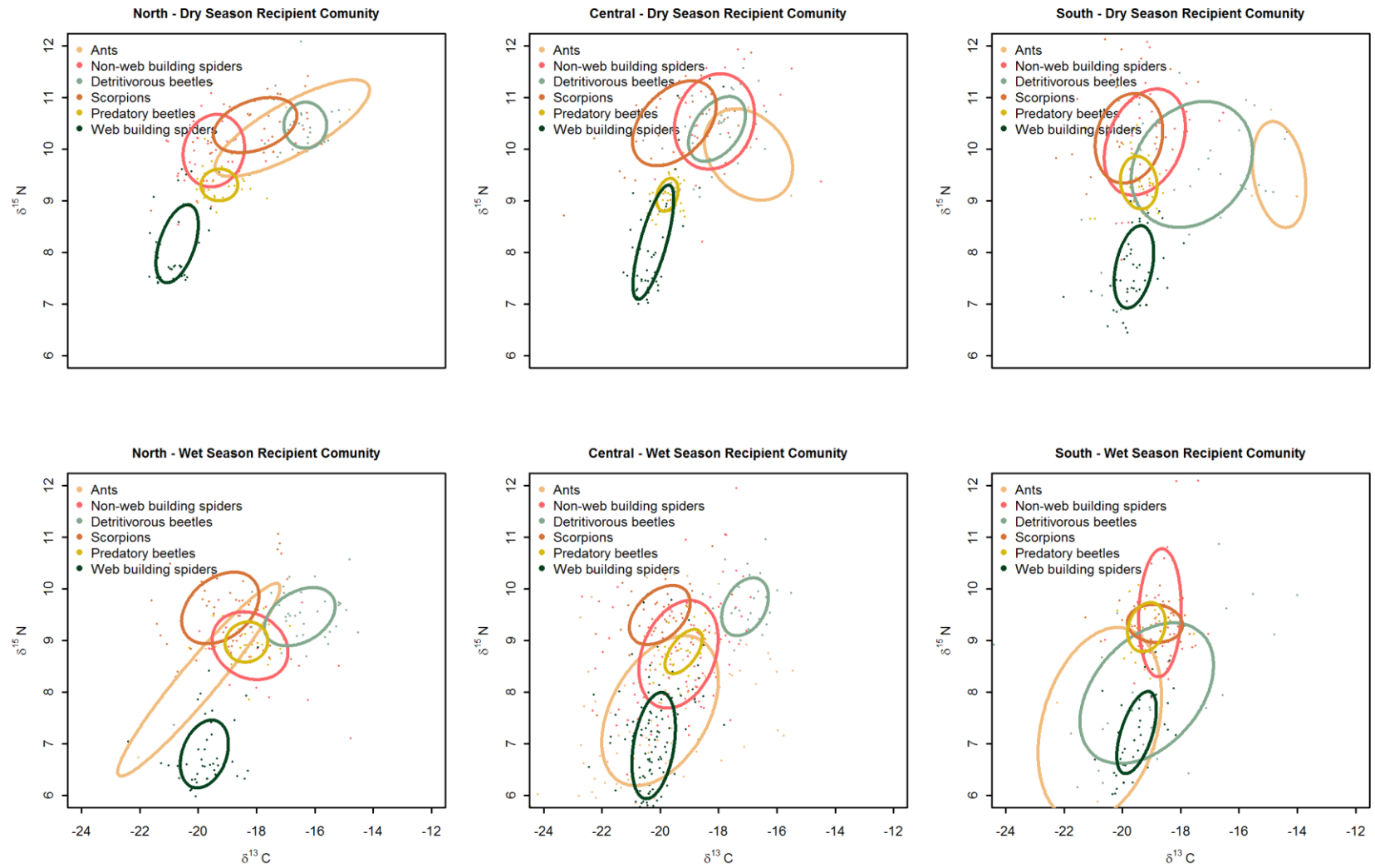
Figure 3.3 – SEA isotopic niches for each assemblage of the recipient community, across basins for each season.

Discussion and conclusion

The diet of terrestrial consumers around Lake Bogoria varied between seasons and basins. I was able to demonstrate these differences because of significant variation in aquatic and terrestrial resource carbon values. Stable isotope analysis, therefore, provided a valuable tool to address my hypothesis.

Isotopic differences between seasons and basins

Phytoplankton isotopic variability declined in the wet season despite an increase in density. This could be due to less build-up of scum and increased lake mixing creating a more homogenised aquatic environment. Chironomid niche variation follows that of its resource, the phytoplankton, and narrows during the wet season. However, this pattern does not continue to higher trophic levels. Instead there is greater isotopic variation in the wet season in the recipient terrestrial community, and every metric increases other than carbon range (Table 3.3). This suggests increased trophic variation but a general reliance on aquatically derived carbon in both seasons. This could be the result of the terrestrial ecosystem's availability of basal resources expanding isotopically during the wet season, and therefore the terrestrial consumers have a more varied diet including both aquatic and terrestrial resources. In contrast, in the dry season the terrestrial community is forced to rely on aquatic resources alone, as terrestrial ecosystems become unproductive.

The shore flies δ^{15}N is closely associated to that of the phytoplankton but its δ^{13}C is more associated to the flamingo detritus. Niche overlap with the chironomids could indicate resource competition, and as the phytoplankton niche decreases in size that competition may become intensified. The combined effects of phytoplankton δ^{15}N reduction and feather detritus δ^{13}C range increase reflected in the shore flies isotopic niche may suggest that they recycle feather detritus nutrients during the wet season to avoid competition with the chironomids for the phytoplankton.

Only ants and predatory beetles have significant differences in δ^{13}C between seasons but all terrestrial consumers have significant differences in δ^{15}N (Table 3.4). The trend among terrestrial consumers to have lower nitrogen values, and therefore lower trophic levels, in the wet season may reflect a shift towards terrestrial resources which are isotopically lower down the food web.

In contrast to other consumers, scorpions had reduced niche metrics in the wet season, suggesting that their niche became more specialised, however, the mixing models shows a shift from aquatic derived carbon to terrestrial derived carbon. Conversely, web building spiders, the only organism to have significant contribution of C3 δ^{13}C in its dry season diet, obtains > 85% of its diet from aquatic sources in the wet season. This is probably due to an increase in abundance of flying midges from the lake in the wet season (Table 3.10); the aquatic subsidy availability increased with aquatic derived carbon apart from in the north basin. Despite a reduction in the chironomid emergence in the northern basin, the spiders continue to acquire carbon primarily from the aquatic ecosystem (Table 3.8). The wind blows from south to north at Lake Bogoria and *T. minutipalpus* swarm over relatively large distances which means that there is likely to be cross basin transfer. Therefore, this is the type of response we would expect from a species "specialised" in harvesting the airborne aquatic vectors.

Season	North	Central	South
Dry	5.34	15.99	1.01
Wet	1.29	22.21	8.92

Table 3.10 – Chironomid emergence (ind m$^{2 -1}$/d^{-2}) between seasons and across basins.

The statistically significant changes in the isotopic niches observed means that the organisms observed in this study are likely to be generalists rather than specialists but continue to obtain carbon via an aquatic route irrespective of season.

The robustness of using SIA to identify subsidy at Lake Bogoria

The phytoplankton community, dominated by *A. fusiformis*, had a distinct carbon isotope ratio, likely due to a combination of the photosynthetic systems that cyanobacterium can utilise, particularly in the presence of bicarbonates, and the uptake of 'old carbon' which enter the lake from geological thermal aquifers (Farquhar et al., 1989; Guy et al., 1993). However, the phytoplankton is positioned equidistant between the C3 and C4 plants δ^{13}C signals. Therefore, if the terrestrial community was feeding on a mixture of C3 and C4 derived primary producers the results of SIA could be inherently flawed. This is unlikely because in 2011 (February – March) during a reconnaissance trip, 45 groups of organisms and resources were collected and preliminary isotopic analysis showed very little reliance on C3 or C4 derived carbon, and those organisms that did show reliance did not occur in great enough numbers to be practically collected (Sanders et al*.,* unpublished data). Further to this, patterns in mixing models were similar between seasons, despite the δ^{15}N enrichment of terrestrial plant resources and δ^{15}N depletion of phytoplankton between seasons. Thus, we can conclude that aquatic resources are substantial drivers of community structure and trophic functions in the lake.

Plant nitrogen composition is controlled by the isotope ratios of external resources and internal physiological mechanisms which change during growing seasons and can be affected by environmental conditions (Farquhar et al., 1989; Evans, 2001). Cyanobacteria, including those of the *Arthrospira* genus, contribute substantially to nitrogen fixation and low $\delta^{15}N$ has been reported in tropical oceans as a result of nitrogen fixation (Capone et al., 1997; Montoya et al., 2002; Wu et al., 2005). Phytoplankton density was substantially greater during the wet season (Table 3.11). Some change in $\delta^{15}N$ was to be expected and the enrichment C3 and C4 $\delta^{15}N$ and the depletion observed in the phytoplankton could be attributed to mechanisms outlined above. These two changes may have synergistically contributed to the increase in $\delta^{15}N$ range of the recipient community as some shift focus to a terrestrial or aquatic carbon source.

Season	North	Central	South
Dry	0.19	0.17	0.20
Wet	0.75	1.14	1.50

Table 3.11 – Phytoplankton density (g/L^{-1}) for each basin and both seasons.

Chironomids go through metamorphosis between feeding on phytoplankton and being assimilated by terrestrial consumers. Metamorphosis causes a significant difference in $\delta^{13}C$ ($F_{1,63}$ = 4.496, p-value = 0.03) but not in $\delta^{15}N$ ($F_{1,63}$ = 0.876, p-value = 0.35), thus a correction should be made during statistical analysis.

Summary

Here, I used SIA to show that terrestrial consumer diet in a linked saline lake-arid ecosystem varies between the wet and dry season. In the dry season, consumers rely heavily on the productive lake for their energy. Whereas in the wet season the terrestrial environment becomes more productive – resulting in increased resource availability and diet variation. With accelerating rates of global climate change there are more chances of extreme events, such as droughts and floods. Here, I have shown that these changes in rainfall could have significant implications for food webs by changing species diet, and therefore interactions with one another. By accepting the paradigm that ecosystems should be studied at open landscape scale, ecosystem dynamics can be explored in the context of climate change and the changes that are to be expected to occur between interlinking ecosystems as they respond to environmental change.

Chapter Four: Temporal response of recipient arthropods to prey availability

Introduction

Cross-ecosystem transfer of resources, organisms, and energy (i.e. ecosystem subsidies) can have complex effects on the trophic interactions in the recipient food web (Polis et al., 1997). The use of stable isotope ratios to quantify the impact of ecosystem subsidies on communities has grown considerably in recent decades (Finlay and Kendall, 2007; Phillips et al., 2014). However, few studies have quantified the extent to which such linkages between aquatic to terrestrial ecosystems extend into the wider landscape. Ignoring allochthonous inputs to recipient communities inhibits understanding of ecosystem dynamics, and there is a need to adopt the idea that ecosystems are "open" to fully appreciate food webs at a landscape scale.

Both the quality and quantity of ecosystem subsidy needs to be considered when identifying mechanisms that govern food web dynamics (Marcarelli et al., 2011). Quality and quantity of subsidy can change in space and time, for instance between seasons (Baxter, Fausch and Saunders, 2005; Ives et al., 2008) and the majority of stable isotope studies looking at temporal changes in subsidy focus on seasonal dynamics (Vizzini and Mazzola, 2003; Grey, Kelly, et al., 2004; Willson et al., 2010; Popa-Lisseanu et al., 2015). In Chapter 3, I quantified seasonal variation in aquatic subsidies to terrestrial consumers in Lake Bogoria. However, emerging aquatic insects, an important subsidy to terrestrial systems, can also have large within season fluctuations, particularly in the tropics where emergences have been linked to lunar cycles (Fryer, 1959; Oliver, 1971; Hare and Carter, 1986; Armitage, 1995; Huang and Cheng, 2011; Kaiser et al., 2011). Other resources are more temporally stable but are of lower quality.

Stable isotopes are a useful tool for mapping food webs in $\delta^{13}C$ and $\delta^{15}N$ isotopic space. Organisms have a unique isotopic signature as a result of the isotope ratios of consumed resources and fractionation during metabolic reaction, where heavier isotopes are fractionated out and organisms become lighter isotope enriched (Grey, 2006; Fry, 2006; Farquhar et al., 1989). Different tissues have different metabolic dynamics and as a result $\delta^{13}C$ and $\delta^{15}N$ can vary within an organism (Gratton and Forbes, 2006; Nardoto et al., 2006; Revelles et al., 2007). It is unlikely that the whole organism will be in isotopic equilibrium with its resource as a combination of differences in tissue metabolic turn over, and digestion.

Lake Bogoria is situated in an arid landscape with a depauperate terrestrial ecosystem but the lake is eutrophic and provides a donor "oasis" of resources to the recipient terrestrial community. Thus, it is important to look at how far into the landscape lake subsidies influence

the terrestrial ecosystem. A recent meta-analysis found that emerging insects from streams can still be traced as a subsidy in the terrestrial food web more than 500m away (Muehlbauer et al., 2014). Therefore, this study, measures how far from the lake shore the aquatic derived $\delta^{13}C$ can be recorded into the riparian zone and explores within season changes in the strength of aquatic to terrestrial resource subsidy. I use an abundant and relatively stable aquatic-terrestrial resource, feather detritus (from the presence of a large population of the lesser flamingo, *Phoeniconaias minor*) and compare to a higher quality but periodical or fluctuating pulse of emerging chironomid *Tanytarsus minutipalpas* at Lake Bogoria. A supporting laboratory experiment is used to compare the measurement of isotopic lag during a diet shift.

Hypotheses

1) There will be a reduction in aquatically derived carbon with distance from the lake swash line.

2) The reduction in aquatic resource with distance from lake will vary between Invertebrates of differing feeding methods.

3) Aquatically derived carbon through a feather detrital pathway will remain steady within season.

4) Pulses of chironomid emergence will be reflected in a dietary switch from aquatic to terrestrial derived carbon sources. Such dietary switches will be traced in lag of fluxes in prey availability.

5) The inclusion of metabolically inert tissue in insect samples for stable isotope analysis will record longer lag times than if those materials are kept to a minimum.

Methods

Laboratory experiment

Consumer and resource will not be in isotopic equilibrium because of the time it takes to handle, digest and lay down tissue – the reactions that fractionate isotopes and make them a useful tool for studying food webs. It is important to take this into account when studying isotopic response to fluctuations of prey availability in nature. Not only will there be a time lag, but different tissues will also metabolise at different rates. To support the natural study of dietary shifts, laboratory experiments were set up to measure the difference in carbon and nitrogen isotope sensitivity to dietary shifts when tissues of differing metabolic reactiveness are included or excluded. I used adult meal worms, *Tenebrio moliteor,* as a model species and analysed them including metabolically inert elytra and with the elytra removed. Elytra is the heavy protective tissue usually associated to the modified protective forewing cases found in Coleoptera.

I hypothesis that the inclusion of elytra will desensitise SIA to the speed and magnitude of dietary shifts in consumer beetles because elytra will have slower turnover rates than soft tissue.

Three dietary treatments were administered in a temperature (26° C) and humidity-controlled room. Five replicates were carried out of the three treatments, C3 plant only, C4 plant only, and a C3 – C4 diet swap. Wheat bran was used as the C3 diet source, while maize and maize gluten meal were the C4 sources. The control diet was a mixture of these C3 and C4 plants with some fruit sources such as apple to match the diet used by the suppliers. Fifteen individuals were placed in fifteen mesh covered plastic containers (n = 225). The experiment ran for 4 weeks (typical *T. molitor* adult phase is 5 weeks) and each week two individuals were removed for isotope analysis. Samples were dried in an oven at 60° C for 42-hour period, one individual from each pair had its head and elytra removed before being prepared and analysed for SIA summarised below and described in full in Chapter 3. Two sample t-tests were then used to test for significant differences between diet treatments.

Sampling

Sampling was carried out for approximately 7 weeks during the wet and dry season (09/02/12 – 31/03/12 and 10/07/12 – 27/08/12, respectively) at Lake Bogoria, Kenya.

Cross ecosystem vectors

Flotsam and jetsam were collected from along the swash line, from which, flamingo feathers were picked. Emerging adult chironomids were collected every two days using $0.045m^2$ submerged emergence traps. A total of 15 traps were set every 2 days, 5 in each of the basins and in the large central basin the traps were split across three sites. The height of trap above sediment surface was randomised (35.42 cm ± 3.73, mean ± SD) and the traps were moved twice over the sample period to accommodate for rising lake level.

Transects

Three transects where cut into the acacia shrub perpendicular to the central basin during the wet season sample period. The arthropod community was sampled at 5 intervals every 50 m to a distance of 200 m from the lake swash line. Three samples of > 6 individuals of each specimen group were collected following the 4-day cycle described in chapter 3. Web building and non-web building spiders were collected to compare different predation methods, and ants were collected to represent generalist foraging. Please see Chapter 3 regarding the methods by which recipient consumers were collected.

Analysis

Stable isotope samples were dried, homogenised and treated following the procedures outlines in chapter 3. $^{13}C:^{12}C$ and $^{15}N:^{14}N$ ratios are expressed using conventional notations (δ) and measured relative to international standards during mass spectrometry and output analysis.

Analysis of variance (ANOVA) and linear regression were used to identify patterns in aquatic resource use across the landscape, and were followed up using Bayesian mixing models developed for SIA using the package SIAR in the statistical programme R (Parnell et al., 2008; R Development Core Team, 2008). Fractionation factors between resource and consumer were assumed to be 2.2 ± 0.30 ‰ for $δ^{15}N$ and 0.5 ± 0.19 ‰ for $δ^{13}C$; these values are derived from freshwater consumers in a meta-analysis after McCutchan et al., (2003).

Chironomid emergence was plotted against date and interpolated values were used for alternate days when the emergence was not monitored. Linear regression of the interpolated data was used to test for correlation between mean $δ^{13}C$ of recipients and emergent rates of chironomids from the lake. A stepwise lag time of 7 days was introduced to check for dietary response in the context of the *T. molitor* lab experiments.

Results

T. molitor experiments

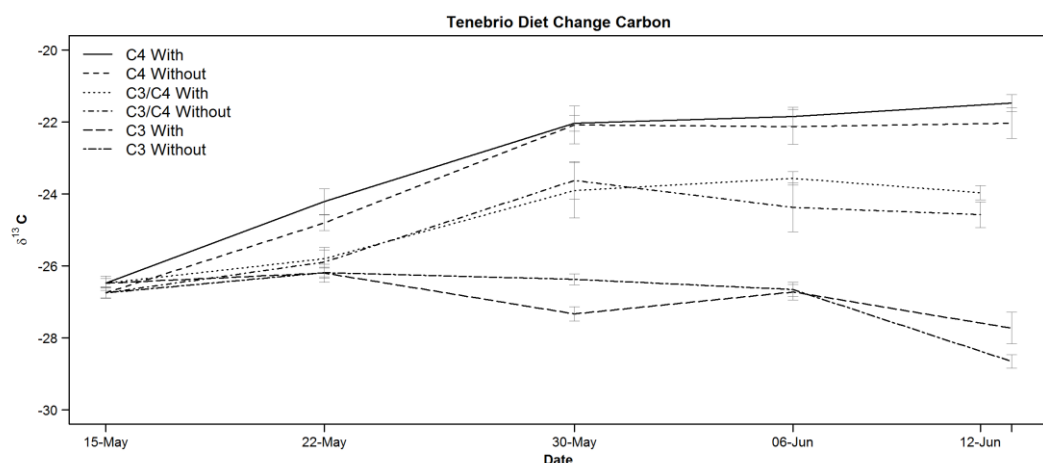Figure 4.1 – $δ^{13}C$ change in Tenebrio diet for the control group, C4 diet group, and C3 diet group, with and without elytra.

Figure 4.1 displays the pattern of isotopic drift during diet change of the three groups of *T. molitor*, with and without elytra. No significant difference was recorded between the *T. molitor* with elytra included in mass spectrometry and those without C3-C4 (t = 0.50, df = 37, p=0.622),

C4 (t = 0.55, df = 37, p=0.584), C3 (t = 0.33, df = 37, p=0.740). A significant difference in $\delta^{13}C$ was found across all diet treatments (One way ANOVA, $F_{2,117}$ = 32.25, p<0.001) and the C4 diet treatment was significantly different to both the C3 and C3-C4 treatments after a single week (t = 8.27, df = 30, p<0.001 and t = 2.80, df = 30, p=0.006). The control group was $\delta^{13}C$ depleted by the end of the experimental period. No significant difference was found in $\delta^{15}N$ in any of the above tests.

Chironomid emergence

Chironomid emergence varied seasonally and across basins. During the dry season, the fewest chironomids emerge from the southern basin and the greatest from the central basin (table 4.1). During the wet season, the fewest numbers emerged from the north basin and, again the most from the central basin (table 4.1). The central basin has the highest frequency oscillating between higher and lower emergent rates, but also has the greatest variation between traps. Comparing the central basin to the northern in the dry season and the southern in the wet season, it appears that the midges could be emerging on a weekly to fortnightly basis. The southern basin has a single and abrupt increase in emergent rates on the 24th of July but settles into relatively low emergent rates from that date onwards (Figure 4.2).

Season	Central	North	South
Dry	15.99	5.34	1.01
Wet	22.21	1.29	8.92

Table 4.1 – Chironomid emergence between seasons and across basins

There was no significant difference for emergence recorded for the whole lake between seasons ($F_{1,133}$ = 1.731, p-value=0.191) but seasonal differences between basins were significant for the north and south basins and not the central (table 4.2). Significant differences were observed between basins within season (table 4.3).

Basin	N	F value	p-value
North	43	11.51	0
Central	43	1.33	0.26
South	43	7.14	0.01

Table 4.2 – ANOVA's comparing seasonal differences of emerging chironomids between basins.

Seasons	N	F value	p-value
Wet	63	17.59	0
Dry	66	21.49	0

Table 4.3 – ANOVA's comparing chironomid emergence differences across basins within seasons.

Linier regression was used to test if the mean $\delta^{13}C$ of recipients respond to oscillations in the abundance of midges emerging from the lake. The *T. molitor* experiments report a significant difference after 7 days of diet change (regardless of the amount of metabolically inert tissue included) thus, each day for, 7 days, a lag was introduced to the regression analysis (table 4.4).

Any significant relationships are highlighted in bold; 17 out of 210 regressions were significant, with the greatest contributor being the least likely (according to my hypotheses) recipient to show a diet shift with changes in prey availability - the detritivorous beetles. However, up to 70% of the variation is explained during the dry season in the central basin with a lag of 3 days (R^2 = 0.70, p-value <0.01). Over all very little variation was explained using this method of analysis, mean R^2 was 0.13 with the maximum being attributed to the detritivorous beetles. No link between prey availability and aquatic-terrestrial diet shift can be observed in these results.
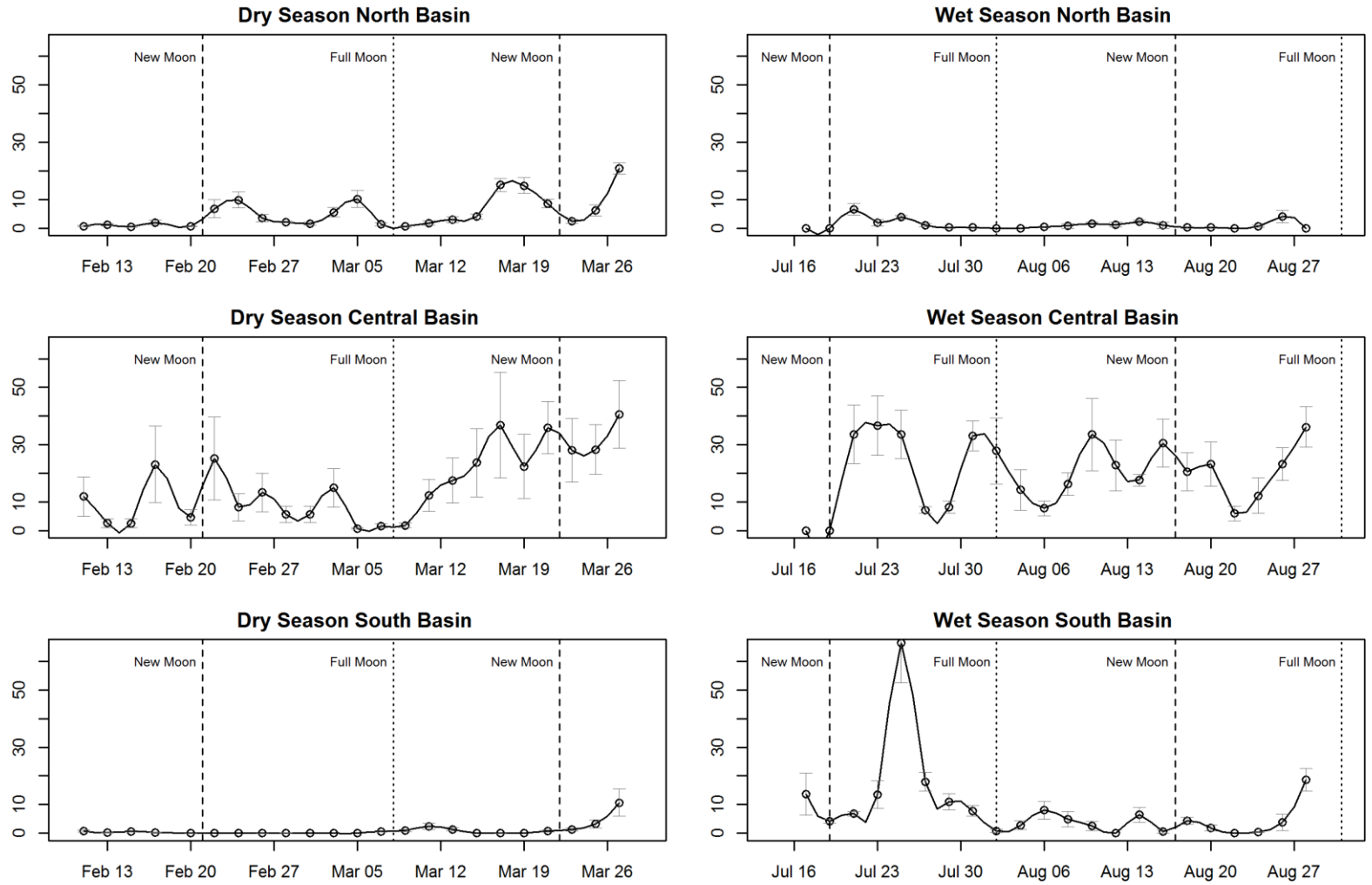
Figure 4.2 – Chironomid emergent plots across seasons and basins.

Season	Basin	Lag (Days)	Non-web building Spiders R²	p-value	Detritivorous beetles R²	p-value	Scorpion R²	p-value	Predatory beetles R²	p-value	Web building spiders R²	p-value
Dry	North	1	0.42	**0.03**	0.19	0.18	0.14	0.26	0.05	0.55	0.18	0.19
		2	0.24	0.15	0.02	0.74	0.24	0.15	0.15	0.31	0.15	0.26
		3	0.18	0.22	0.00	0.93	0.13	0.30	0.05	0.57	0.05	0.53
		4	0.08	0.43	0.01	0.76	0.00	0.97	0.01	0.79	0.00	0.90
		5	0.02	0.69	0.01	0.83	0.17	0.24	0.02	0.73	0.00	1.00
		6	0.00	0.88	0.02	0.72	0.07	0.49	0.04	0.63	0.00	0.95
		7	0.00	1.00	0.05	0.58	0.11	0.38	0.40	0.09	0.07	0.48
Wet	North	1	0.04	0.56	0.21	0.15	0.62	**0.00**	0.00	0.89	0.01	0.77
		2	0.04	0.60	0.05	0.53	0.02	0.72	0.02	0.70	0.06	0.50
		3	0.05	0.55	0.08	0.42	0.02	0.71	0.01	0.76	0.06	0.51
		4	0.03	0.65	0.13	0.31	0.02	0.68	0.01	0.84	0.11	0.36
		5	0.02	0.69	0.04	0.60	0.00	0.88	0.00	0.86	0.00	0.99
		6	0.18	0.25	0.14	0.31	0.40	0.07	0.00	0.87	0.32	0.11
		7	0.13	0.34	0.15	0.31	0.42	0.06	0.00	0.87	0.25	0.17
Dry	Central	1	0.30	0.10	0.54	**0.01**	0.09	0.36	0.03	0.57	0.24	0.10
		2	0.24	0.15	0.70	**0.00**	0.01	0.77	0.14	0.24	0.07	0.42
		3	0.00	0.94	0.66	**0.00**	0.00	0.87	0.36	0.05	0.00	0.97
		4	0.01	0.84	0.47	**0.03**	0.03	0.62	0.28	0.10	0.04	0.57
		5	0.01	0.79	0.48	**0.03**	0.14	0.25	0.29	0.09	0.14	0.25
		6	0.01	0.83	0.47	**0.03**	0.11	0.32	0.34	0.06	0.11	0.32
		7	0.56	**0.03**	0.26	0.16	0.03	0.62	0.50	**0.02**	0.01	0.78
Wet	Central	1	0.00	0.87	0.23	0.16	0.04	0.60	0.02	0.73	0.00	0.93
		2	0.13	0.28	0.24	0.15	0.02	0.67	0.01	0.75	0.02	0.69
		3	0.52	**0.02**	0.14	0.33	0.24	0.19	0.00	0.96	0.01	0.75
		4	0.63	**0.01**	0.08	0.46	0.32	0.11	0.02	0.75	0.01	0.78
		5	0.17	0.24	0.08	0.46	0.10	0.42	0.07	0.50	0.01	0.77
		6	0.05	0.56	0.57	**0.02**	0.04	0.60	0.04	0.61	0.00	0.97
		7	0.10	0.41	0.27	0.18	0.30	0.16	0.07	0.54	0.08	0.46
Dry	South	1	0.02	0.65	0.00	0.98	0.00	0.91	0.00	0.95	0.05	0.52
		2	0.00	0.95	0.05	0.53	0.01	0.73	0.00	0.85	0.05	0.51
		3	0.01	0.78	0.06	0.47	0.01	0.82	0.00	0.86	0.07	0.44
		4	0.00	0.93	0.29	0.11	0.15	0.28	0.07	0.46	0.11	0.36
		5	0.00	0.97	0.51	**0.02**	0.01	0.78	0.00	0.89	0.02	0.71
		6	0.00	0.99	0.57	**0.01**	0.00	0.87	0.09	0.40	0.00	0.87
		7	0.00	0.95	0.53	**0.02**	0.01	0.81	0.13	0.30	0.00	0.91
Wet	South	1	0.07	0.44	0.20	0.17	0.01	0.79	0.03	0.70	0.20	0.17
		2	0.04	0.55	0.15	0.23	0.03	0.61	0.01	0.79	0.13	0.29
		3	0.01	0.81	0.15	0.25	0.00	0.90	0.15	0.35	0.01	0.73
		4	0.02	0.74	0.16	0.25	0.25	0.14	0.03	0.71	0.21	0.18
		5	0.03	0.66	0.13	0.32	0.25	0.14	0.02	0.79	0.20	0.19
		6	0.00	0.95	0.21	0.18	0.43	**0.04**	0.06	0.61	0.27	0.13
		7	0.39	0.05	0.30	0.10	0.53	**0.02**	0.39	0.14	0.13	0.31

Table 4.4 – Linier regression, testing emergence with mean δ¹³C with a lag time of 7 days for each basin and season.

Aquatic resource impact into landscape

Significant differences in $\delta^{13}C$ were recorded between transects ($F_{2,291}$ = 20.21, p-value < 0.001) and distance from the swash line ($F_{2,292}$ = 44.94, p-value < 0.001). Meaning that there is significant variation parallel to the swash line as well as perpendicular to it. In addition, ANOVA analysis revealed significant differences between consumer groups at the basin and transect levels (table 4.5)

Level	N	F value	p-value
Basin	291	10.72	<0.001
1	140	5.21	<0.01
2	65	13.83	<0.001
3	80	7.87	<0.001

Table 4.5 – Significant differences between recipient groups at the basin level and at transect level.
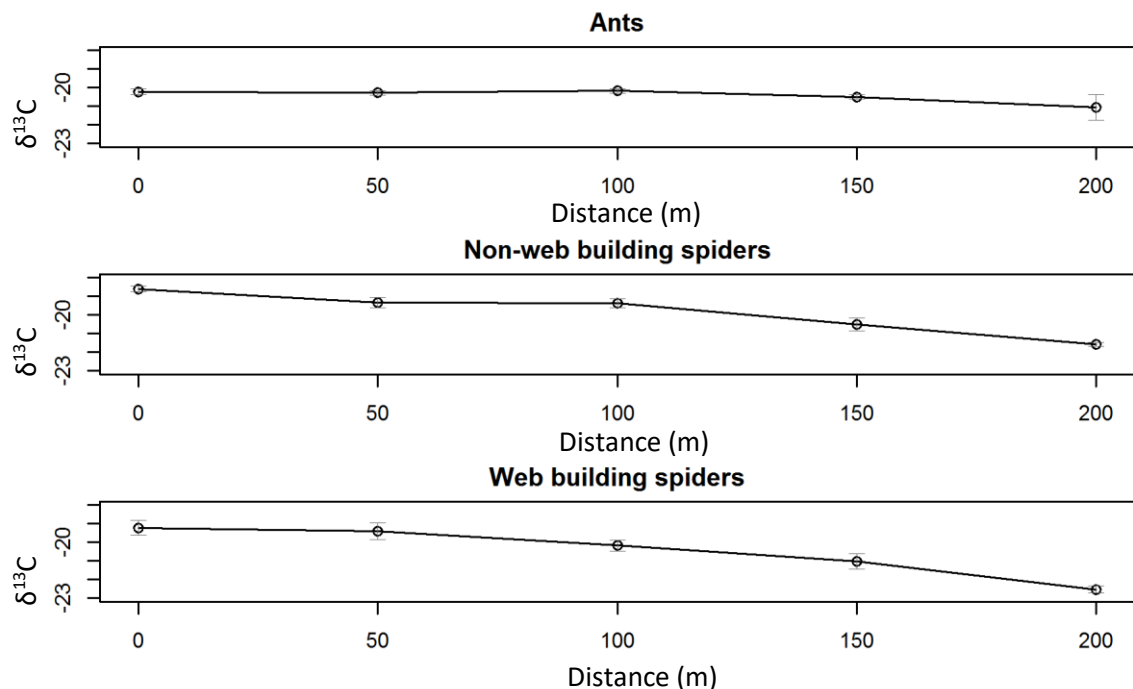
Figure 4.3 – Mean $\delta^{13}C$ with distance from the swash line.

Plotting the mean $\delta^{13}C$ against distance from the swash line suggest that all three consumer groups shift from an aquatic to a C4 carbon resource with distance (figure 4.3). Ants shift the least and web building spiders the most. The estimated contribution of aquatic carbon to the diets of consumers (estimated using mixing models) shows a similar pattern with distance from the swash line in ants, but not spiders (figure 4.4). Ants have a very high percentage of aquatic resources in their diet at the swash line which starts to decrease between 150 and 200 m from the lake. Both the web building and non-web building spiders have an increase in aquatic carbon contribution until around 100 to 150 m from the lake, at which point they both decline.
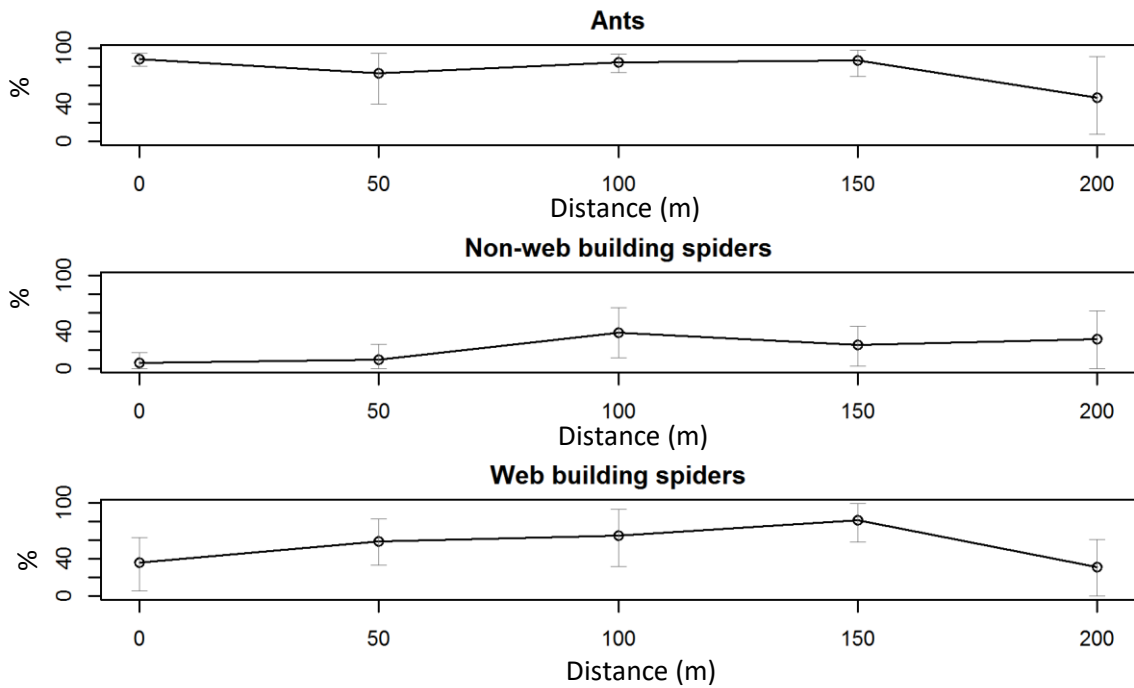
Figure 4.4 – Contribution (%) of aquatic carbon to consumer diets against distance from swash line.

Discussion

T. molitor experiments

The diet shift from the mixed C3-C4 to either a C3 or a C4 diet only was detectable in *T. molitor* within 7 days. In this study, no significant difference was found between samples that included elytra material and those that did not. On these results, we can conclude that the inclusion of metabolically inert tissue into SIA samples does not affect the methods sensitivity. In contrast Gratton and Forbes, (2006) reported that in an experiment with two predacious adult beetles the switch from a C3-based diet to a C4-based diet was observed faster in tissues such as body fat and reproductive tissues, than in wings and elytra where the change were observed more slowly. The main difference between the two experimental designs is that the different tissues were tested from the same individual by Gratton and Forbes, (2006), whereas in my experiment, different individuals were homogenised. In addition, their specimens were dissected while I concentrated on a more practical "in field" removal of easily accessible parts. Therefore, the beetles in my experiment had less distinct tissue types and a higher percentage of more inert tissue. This method should only be employed if the field species has been tested in the laboratory and if it is practical to dissect samples from the field in the quantities required for robust studies on nature. My findings under experimental conditions demonstrate that my field survey results are robust as long as a lag time of 7 days is included in the analyses to reflect isotopic turnover.

Chironomid emergence

Chirinomid emergence varied in time and space at Lake Bogoria but, unlike in other African lakes, the periodicity is unclear and cannot be linked to lunar cycles (Armitage, 1995). The smaller basins had periods of low emergence with little variation. This occurred in the northern basin during the wet season and in the southern basin during the dry season. In the southern basin, density of phytoplankton was very high and much of the surface has patched and streaks of thick *A. fusiformis* scum. The presence of cyanobacteria in such large quantities could have affected oxygen concentrations inhibiting chironomid growth and survival. The larger central basin appeared to have semi-regular pulsed of emergence on a weekly to bi-monthly cycle.

Emergence patterns of chironomids explain very little of isotopic variation in the recipient community, and no pattern was discovered to when a 7-day lag time was introduced to the regression. It stands to reason that in this warm productive tropical lake, where aquatic predation is minimal, cyclical emergence behaviour does not occur. Therefore, no dietary shift response was detected in the recipient terrestrial community. This may be because the midges emerge in sufficient numbers even at their minimum density, so that there is a background emergence to maintain the recipient community, or that the recipients go hungry when there is insufficient prey. As a reduction in prey occurs over short periods these fluctuations are not reflected in the recipient stable isotopes. However, instead a reduction in recipient community growth rate or abundance may occur as a result of low chironomid availability, while the active recipient species continue feeding on the insects that are available. If the first two possibilities are true, then the abundance of the recipient community is unchanged by short reductions in the availability of the prey and the terrestrial community can be considered stable in MacArthur's (1955) definition. Further to this, some of the stability observed in the recipient community could be attributed to a prey switch between the chironomids and something that shares a similar isotopic signature, e.g. the termites. This would indicate that, as MacArthur states, the stability of the recipient community is due to interactions between the species the community is composed of. This is unlikely as the termites are the only organism found to share a similar isotopic space as the chironomids, they do not occur in the same abundance as the chironomids, and they do not emerge as constantly. The species of termite found in the Baringo-Bogoria half-grabbon only have dispersal events during the rainy periods, and the data from both dry periods show little fluctuation in C and N isotopes across time. Therefore, it is likely that the lack of fluctuations observed in the recipient isotope data are unlikely to be something intrinsic to the species which compose the community. A way of testing whether the community is oscillating between "feast and famine" with chironomid emergence is by looking at the C to N ratio to establish if the recipients are surviving on reserves during periods of low emergence.

This follows what MacArthur states, that there is a diverse predatory community exploiting a plentiful food source which is unlikely to be affected greatly by the predator population. Perhaps a better analogy of this should be that the midges are to the recipient community like the sun is to photosynthetic organisms, a constant and abundant resource to be relied upon but fluctuating, diurnally, day to day, and seasonally.

Aquatic resource impact into landscape

Although $\delta^{13}C$ showed promising results in attempting to measure aquatic impact at a landscape level, mixing models results did not agree with similar research (Ives et al., 2008; Muehlbauer et al., 2014). Chironomid swarming in land may account for the increase of aquatic carbon seen in spiders between 50 and 150 m from the lake. This study goes to show that the use of mixing models aids in the understanding of aquatic-terrestrial linkage at the landscape level.

Chapter Five: Sub-fossilised chironomid larval head capsules as a proxy for changes in lake water salinity

Introduction

Equatorial East African Lakes are recorded to have substantial fluctuations in water level over the past 20,000 years from the order of tens to hundreds of meters, despite relatively moderate changes in evaporation-precipitation ratios (Olaka et al., 2010). East Africa and the Rift Valley have complex landscape where lakes vary in altitude heights and have catchments of differing regional climate regimes. This heterogeneous landscape has shown regional differences in hydrological responses to large scale climate change (Gasse, 2000; Gasse, 2002; Verschuren, 1994, 2000). The Baringo-Bogoria basin has generally been arid since the little ice age but the climate has oscillated on the centennial- to decade-scale between wet and dry episodes (Kiage and Liu, 2009). Lake Bogoria shows sustained increases in lake level from 5 to 9 m. Some East African lakes during the early-mid Holocene show periods of higher water level, suggesting more humid periods and the fossil biota suggests lower salinity. At these altitudes there may have been some spill over of water to Lake Baringo to the north (Renaut et al., 1986; Vincens et al., 1986; McCall, 2010). There is much evidence to suggest a larger water mass on the geological time scale but could the lakes join during abrupt changes in regional hydrology (Richardson and Dussinger, 1987)?

Palaeoenvironmental data is fundamental to understanding climate change, which is of particular importance in areas such as East Africa where fluctuations have a substantial impact on water availability and chemistry (Bessems et al., 2008). Lake sediments can provide high quality continuous records of climate and other variables, making them excellent sensors of environmental change. Lake sediments archive both short- and long-term regional climate dynamics while incorporating anthropogenic influences and other environmental factors within their sediments. They provide records from across most latitudes and longitudes as well as from sea level to high altitudes. It is therefore important that the lake system under investigation is well understood, including site-specific response to climate change, changes in evaporation-precipitation ratios, lake water level changes, and knock on chemical and biological effects. Areas of tectonic activity make the interpretation of lake sediment data more complex, as responses to climate are also mediated by the hydrologic and the geomorphic setting of the basin (Olaka et al., 2010).

Morphological features affect almost every physical, chemical, and biological property of a lake. The shape of a lake regulates sedimentation, benthos dynamics, and suspended particulate matter concentrations (Johansson et al., 2007). Lake Bogoria has three distinct basins separated by the Nyalibuch and Mwanasis sills. Each basin has a different morphology, which in turn creates different chemical regimes (McCall, 2010). Thus, Lake Bogoria is unique in that we should expect the sediment record to differ in each one and each basin should give us different insights into past environmental conditions.

Sub-fossilised chironomid larval head capsules (HC) have been used as a robust quantitative indicator of climate-driven environmental change for some time (e.g. Brooks et al. 2012; Chen et al. 2009). Chironomid species are ubiquitous and they also respond relatively quickly to environmental change as a result of high mobility and dispersal rates. The East African chironomid assemblage is well recorded (Eggermont et al. 2006; Verschuren et al. 2004).

The bulk of palaeoenvironmental studies of East Africa focused on long term geological change (Livingstone, 1967; Vincens et al., 1986; Tiercelin et al., 1987; Taylor, 1990; F Gasse, 2000; Thompson et al., 2002; Vincens et al., 2003, 2005) and only recently have studies concentrated on higher resolution short term environmental change (Verschuren et al., 2000; Ashley et al., 2004; Owen, 2004). My study therefore provides a novel perspective on short term environmental change. Subfossilised chironomid larval head capsules and other observations from the cores of Lake Bogoria are used in this chapter to explore Lake Bogoria's biotic response to salinity changes due to lake water level fluctuations as a result of regional climate changes.

Environmental change can occur abruptly in East African Rift Lakes, particularly when there are changes to the hydrology in a basin which can be caused by tectonic/volcanic action (Verschuren, 1999; De Cort et al., 2013; Funiciello et al., 2003). This chapter will take not of terphra layers and past hydrological regimes and using satellite data on the topography of the Baringo-Borgoria basin suggest and overspill site.

Objectives

1. Chironomid HC will be used to reconstruct the past salinity of Lake Bogoria's three basins and HC abundance will be used as a proxy for subsidy strength.
2. To assess basin morphology effect on the speed and extent of seasonal and climatic perturbation to subsidies.

Methods

Fieldwork

A collaborative field excursion was undertaken in March 2011 between Queen Mary University of London, London Natural History Museum, and the University of Southampton to the Lake Bogoria region, Kenya. Because of the morphological differences between each basin (Table 5.1), long cores (> 1 m) were collected from the deepest part of each sub-basin of the lake using a Livingstone corer and additional shorter cores (<= 1 m) were extracted using a Uwitec gravity corer. 15 sediment-water interface samples were also collected throughout the lake (Figure 5.1). The deepest part of the basin was chosen as it is expected that greater water depth will provide a better representation of the chironomid assemblage.

Basin	Avg Depth	Basin shape	Catchment shape	Inflows
North	5.9 m	Pan shaped	low topography	1 Freshwater river
Central	10.2 m	Long with an undulating bathymetry	Changing topography, Escarpment on both sides at points	1 Freshwater river, the Loburu Delta
South	8.4 m	Bowl shaped	Steep crater like	2 rivers / streams & hot springs

Table 5.1: Morphological differences between each basin (Harper et al., 2003; Hickley et al., 2003; McCall, 2010)

Coring took place from a coring platform built on site and a dingy, and was carried out during the morning hours, while it was cooler and before the wind picks up in the afternoon. The cores were extruded into plastic guttering and wrapped in cling film for transport to the lab where they were sliced at 1 cm intervals during the evening when temperatures were cooler. All sediment samples were stored at -18 °C in the field lab for approximately one month and transported to the UK in a cold box. Three of the short cores were sent for ITRAX micro-XRF scanning at the National Oceanographic Centre (Table 5.2). The samples have been kept at 4 °C since transport before subsampling. The cores were correlated with lithological changes and loss-on-ignition analysis (LOI). Unconsolidated sediments at the water-sediment interface dictated at which depth below the sediment surface the piston cores could start, but the gravity corer was better equipped to deal with these sediments and so was used to collect sediments immediately below the water-sediment interface and provided an overlap in the northern and central basins. The unconsolidated sediments were up to 3 meters deep in the southern basin and so the piston core was collected at a depth of 300 cm below the sediment-water interface.
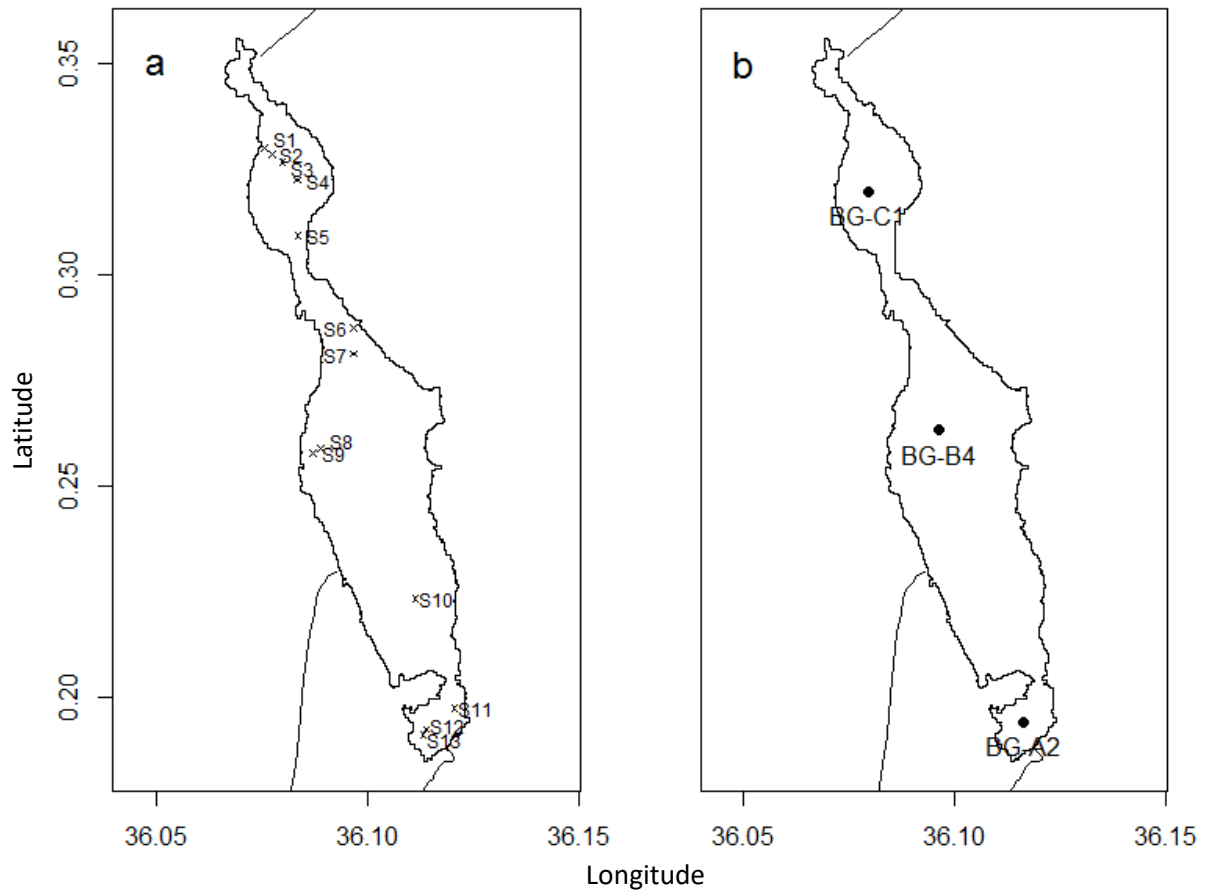
Figure 5.1 – Map showing Bogoria and the positions of where the sediment surface samples (a) and long cores (b) were extracted.

Basin	Core	Length (cm)	Depth (cm)	Use	Ash
South	BG-A2	48	~5 - 100	ITRAX	-
South	BG-A3	300	300 - 600	Head capsules	Yes
Central	BG-B4	330	10 - 340	Head capsules	No
Central	BG-B5	97	~50 -150	ITRAX	No
North	BG-C1	400	50 - 450	Head capsules	Yes
North	BG-C2	86	~330 - 410	ITRAX	Yes

Table 5.2: The 6 cores taken in association with this project, their depths, lengths and presence of tephra indicated

Loss on ignition (LOI)

LOI analysis following Heiri et al. (2001) was carried out on contiguous samples at 2 cm intervals. LOI at 550 °C as a percentage of dry weight was used as a proxy for organic content of sediments and used to assess where the most relevant depths to retrieve sub fossilised head capsules would be.

Head capsule picking, mounting and identification

During the early stages, kerosene flotation (Rolland and Larocque, 2007) and the universal method (Walker, 2001; Brooks et al., 2007) for sorting sediments and picking head capsules were

tested against each other. Despite kerosene flotation efficiencies of 83% ± 8.0 reported in the literature, the universal method was chosen as the more suitable method as the kerosene flotation method returned organic matter but very few head capsules. Head capsules were mounted in Euparal for identification following Eggermont and Verschuren (2004a; 2004b). A total of 20 sediment samples were picked for head capsule analysis between the depth of 18.5 cm and 196.5 cm. The most effort was centred on the part of the core where LOI values were highest as this potentially indicated a period of significant environmental change. Down core taxonomic diversity was calculated using Hill's (1973) N2 using PalaeoSig package in the statistical software R (R Development Core Team, 2008; Telford and Birks, 2011).

Radiocarbon dating and Tephrochronology

Radiocarbon dating was chosen as the most reliable method of obtaining dates from sediments from this lake. Dr. Ian Donohue of Trinity College, Dublin, attempted ^{210}Pb dating of bulk sediments of a short littoral core from Lake Bogoria without success because concentrations were below detectable levels (*pers. comm*). In addition, we expected sediments from this lake to exceed ^{210}Pb age detectability and radiocarbon dating has been successful in previous studies (Vincens et al. 1986; Renaut and Tiercelin 1993; Renaut and Tiercelin 1994). ^{14}C dating was attempted by sending bulk sediment samples and aquatic macrophyte samples to the Keck Carbon Cycle AMS Facility at University of California, Irvine. A number of tephra layer samples were sent to Tephrochronology & Quaternary Geochronology - School of Archaeology - University of Oxford for investigation.

Results

Radiocarbon dating and Tephrochronology

Previous attempts to radiocarbon date sediments from Lake Bogoria have been successful (Vincens et al. 1986; Renaut and Tiercelin 1993; Renaut and Tiercelin 1994). The bulk sediments we retrieved were not suitable because of the carbon reservoir effect from old carbonate inputs from the geothermal aquifers. Only a single reliable date was obtained (380 ± 15 YBP) from a plant macrofossil recovered from an organic rich laminate at a depth of 146.5 cm in the central basin. All other bulk sediment samples rejected because they appear to be contaminated with old carbon. As a result, no age model could be created (Table 5.3). Attempts to create a tephrochronology of the cores were unsuccessful. The glass fragments picked from the tephra

layers were not of high enough quality to be referenced with other East African tephra layers and tephrostratigraphical analysis was impossible.

Basin	Sample name	Depth (cm)	^{14}C age	±
South	1;S1-372;BGA-3/1; .040mgC	372.5	1775	45
South	2;S2-444;BGA-3/2; .24mgC	444.5	2855	20
Central	3;C1-044;BG-B4/1; .15mgC	44.5	2015	20
Central	4;C2-080;BG-B4/1;.21mgC	80.5	2535	20
Central	5;C3-120;BG-B4/2; .19mgC	120.5	1850	15
Central	**6;C4-146;BG-B4/2; plant**	**146.5**	**380**	**15**
Central	7;C5-158;BG-B4/2; .19mgC	158.5	1660	25
Central	8;C6-196;BG-B4/3; .17mgC	196.5	3495	25
North	9;N1-182;BG-C1/3; .11mgC	182.5	2320	25
North	10;N2-254;BG-C1/4; .10mgC	254.5	2405	25

Table 5.3: Results from the Keck Carbon Cycle AMS Facility at University of California, Irvine.

Correlation and core description

In the absence of an age depth model, LOI and the lithology was used to correlate the three cores, centring around the only reliable C^{14} date (Figure 5.2). The sharp increase in organic carbon at a depth of approximately 200 cm is dated to 380 ± 15 BP, approximately 1570 AD, which places it during the Little Ice Age. In each core an abrupt organic increase occurs immediately after evidence of tephra ash and where the core is marked by multi-coloured laminations ~190 – 215 cm. Both the northern and the southern cores display evidence of tephra ash reworked from the surrounding land, rather than being resuspended from the lake seidments (*) or deposited (†) with other material around this period. The northern basin has a second area of such laminations immediately after a tephra layer at a depth of 250 cm. Both the northern and southern basins display an overall trend of increasing organic carbon from a sharp drop after the abrupt increase, rising from 6.7 % (196 cm) to a maximum of 17.6 % (128 cm) and 4.6 % (184 cm) to 11.4 % (62 cm) respectively. Organic content is generally higher in the northern basin (mean = 10.14%) than the central (mean = 4.44 %) and southern (mean = 6.40 %) basins. The central basin displays less dynamic sediment processes with initial lithological observations being clearer. Both the rise and fall in organic carbon occurs within a defined area of multi-coloured laminations which were well conserved during core extrusion. Although there is an overall increase in the organic carbon toward the top of the sequence, the increase is not as great as the two smaller basins. In addition, both head capsule abundance per dry weight and diversity peak at the same depth as the organic carbon peak (208 cm). Head capsule abundance

follows a similar pattern to the bimodal shape of the organic curve between the depths of 190 and 215 cm. Recent sediments (< 190 cm) in all three cores consisted of extremely soft undefined muds intersected with periods of harder lightly laminated sediments. Older sediments (> 215 cm), deposited prior to the main tephra ashes, typically consist of harder muds and clays intersected by tephra deposits.
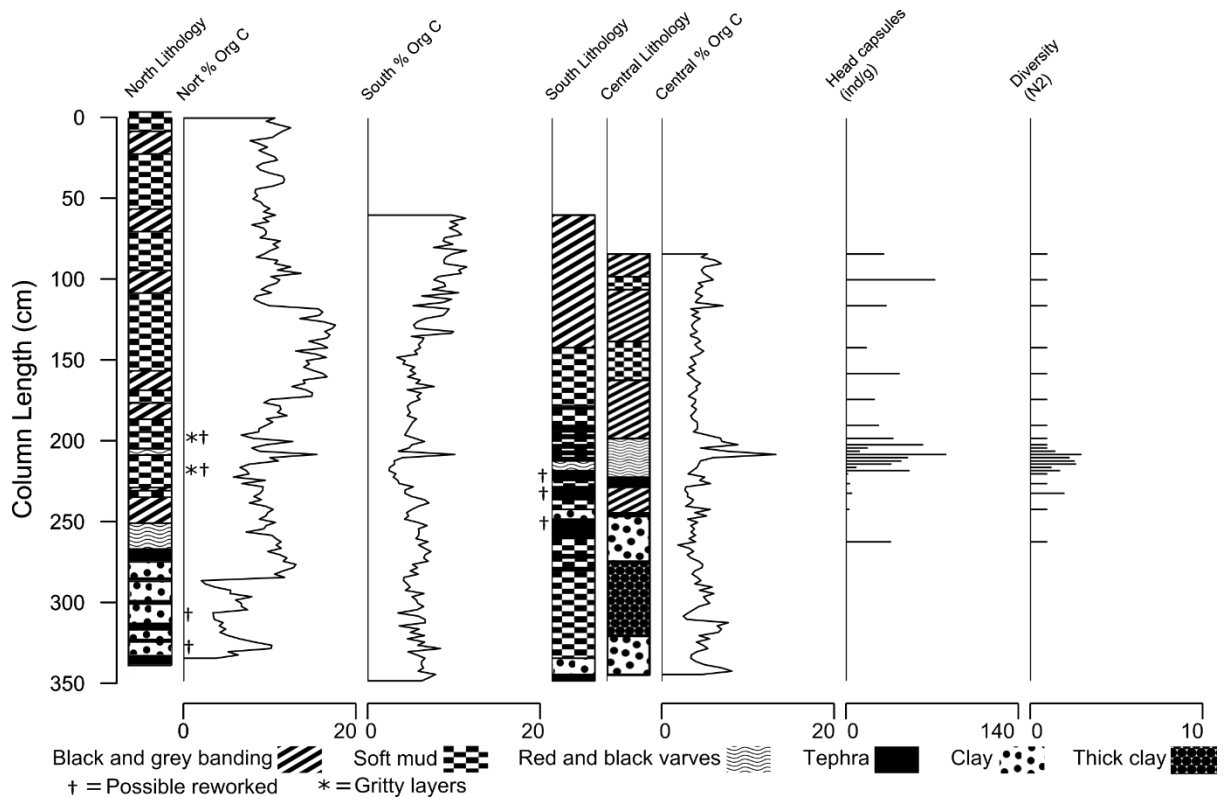

Figure 5.2: Percentage of down core organic carbon 'zeroed' to organic peak with lithology and head capsule abundance and diversity for the central basin.

Chironomid taxa and salinity

Figure 5.3 shows the differing chironomid taxa down core. In total 10 macroinvertebrate taxa have been identified from the central core (comprising chironomids, Ceratopogonidae, *Bosmina*, Trichoptera, and ostracods), the 6 chironomid taxa were identified to species or morphotype. The obligate halobiont chironomid *T. minutipalpus* (conductivity optima of 35479.7 μS/cm^{-1}) is dominant and is the only species to occur in deposits prior to and after the occurrence of high organic carbon marking the Little Ice Age. Coinciding with this increase are the occurrences of *Ablabesmyia* type Kayihara, *Parametriocnemus* type Tanganyika, *Paratendipes* type Naivasha, *Rheotanytarsus* near *ceratophyllid* and *Pentaneurini* indet. type Naivasha which all have significantly lower conductivity optima than *T. minutipalpus* (Table 5.4).

Chironomid Taxa	Conductivity optima μS/cm^{-1}
Ablabesmyia type Kayihara	629.3
Parametriocnemus type Tanganyika	471.0
Paratendipes type *Naivasha*	327.9
Rheotanytarsus near *ceratophylli*	395.9
Tanytarsus minutipalpus	35479.7
Pentaneurini indet. type Naivasha	793.5

Table 5.4: Present chironomid taxa and their corresponding conductivity optima (Eggermont and Verschuren, 2004a, 2004b).

There is a significant correlation between the organic carbon and head capsule abundance, Pearson's product-moment correlation t = 2.8558, df = 20, p-value = 0.00977. There is also a correlation between the diversity and head capsule abundance (t = 1.9118, df = 20, p-value = 0.07034) even when only samples picked from the Little Ice Age period are tested (t = 2.9867, df = 5, p-value = 0.03056). However, there are periods where diversity is high but abundance is not. During the Little Ice Age, *T. minutipalpus* disappears abruptly (152 cm), there is a small period when no head capsules were found (i.e. within the Tephra). *Ablabesmyia* type Kayihara and *Paratendipes* type *Naivasha* are the first of the new taxa to appear in the sequence following the LOI increase. *Pentaneurini* indet. type Naivasha (second highest conductivity optima) quickly dominates the Little Ice Age assemblage and *Rheotanytarsus* near *ceratophylli* is the last in the sequence while *T. minutpalpus* starts to reappear (132 cm). It is notable that *Ablabesmyia* type Kayihara does appear in the sequence prior to the tephra layer
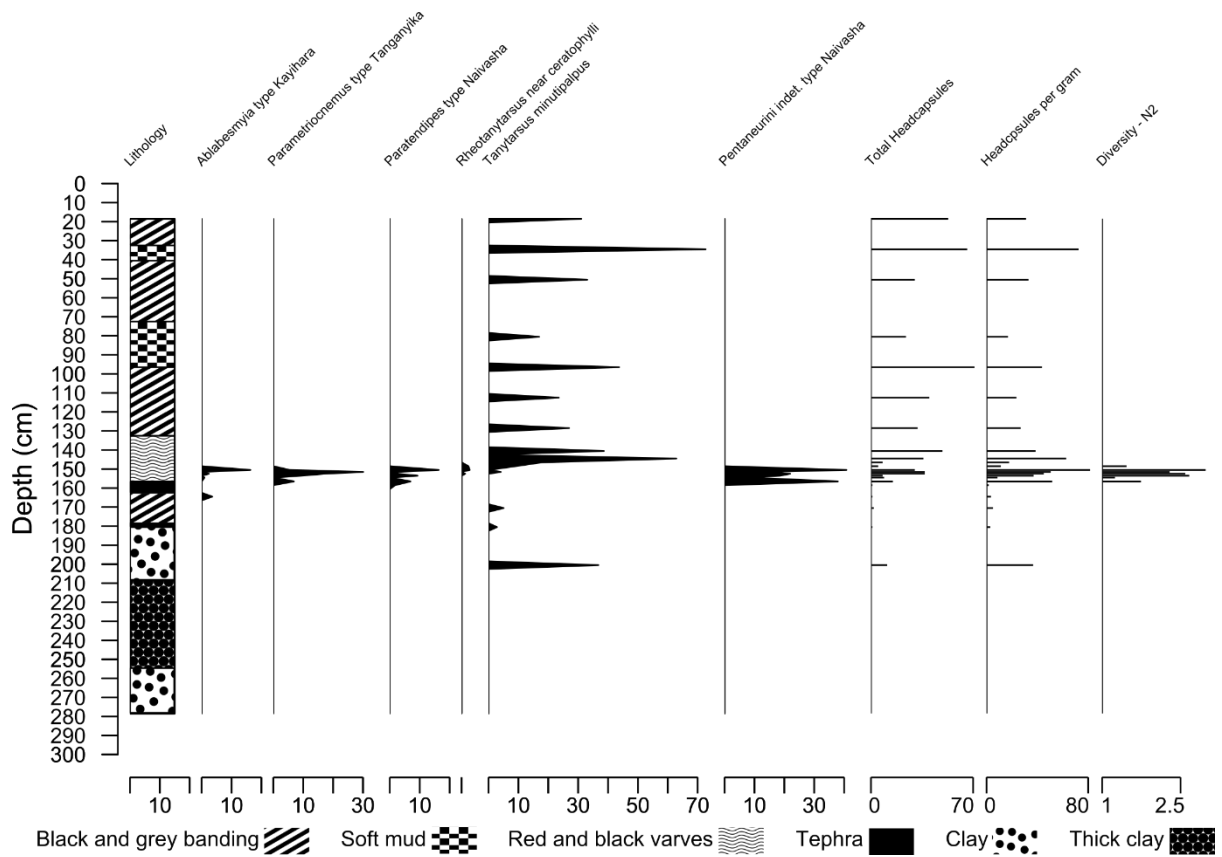
Figure 5.3: Central Basin increase in chironomid larval HC abundance (per gram) and diversity (N2)

Discussion and Conclusion

Radiocarbon dating and Tephrochronology

[14]C dating of Bogoria sediments has been successful in the past, most recently by De Cort et al. (2013), who used the ^{137}Cs of 1964 to calculate a modern-day old-carbon age offset of 3980 ^{14}C years. This approach could not be used in combination with our data as the data contains dates as young as 1660 BP and our ^{14}C dates were non-linear. The errors in our results could be accounted for by low carbon content, some of which was measured at weights lower than 1%. Either, LOI was based on the loss of bound water and inaccurate or most of the carbon was labile and lost during the acid-base-acid treatment. As our LOI data shares similar amounts as De Cort et al., (2013) I would expect the main issue is the treatment of the samples and lack of ^{14}C charcoal / [137]Cs samples. Unsupported levels of ^{210}Pb and ^{137}Cs have been reported too erratic and untrustworthily low at Lake Bogoria because of the regional semi-arid climate which limits atmospheric deposition (Dr. Ian Donohue, 2010, pers. comm., De Cort et al., 2013). However, Ward (2014) was successful in dating the short cores we collected and got similar accumulation rates from both ^{210}Pb and ^{137}Cs, averaging at 0.54 cm/yr^{-1}, a slightly greater rate than that

estimated by De Cort et al., (2013). The important abrupt change seen in our sediment sequence is observed by De Cort et al., (2013) for a similar time period. They state that between the Using our date, we can calculate an accumulation rate of 1.38 cm/yr^{-1}.

Correlation and core description

Lake Bogoria is noted to have an undulating bathymetry (Hickley et al., 2003). Due to the naturally high trophic state of Lake Bogoria, there is a layer of extremely soft deposits at the sediment-water interface, particularly prevalent in the south basin. Ward (2014) reports high organic-matter content in the most recent deposits which could reflect incomplete diagenesis of decaying Cyanobacteria (Verschuren et al., 2004). The unconsolidated sediments combined with the undulating lake bed not only created difficulties in detecting the water-surface interface but sediments were too soft to be collected using the Livingstone corer, which accounts for the different starting depths of each core (Table 5.1). Similar percentages of organic content have been observed in other Rift Valley lakes, e.g. Lake Baringo (Bessems et al., 2008). If LOI is used as a proxy for trophic condition (Inda et al., 2006), the steady organic increases observed in the southern basin may suggest an increase in trophic condition to its current state as the basin with the greatest in-lake production. There are obviously great differences in the deposition rates and dynamics between the basins which are reflected in the cores. In order to successfully collect deposits in the southern basin Verschuren (2000) developed a wedge shaped freeze corer utilising solid CO_2. I was unable to collect the unconsolidated sediments in the upper layer of the lake deposits. As a result, my sequence is in complete and the data could be missing some of the lithology and LOI which could be used to correlate with the sequences obtained from the other basins. Basin specific dynamics may have affected the northern basins sediment sequence. Shallower, pan shaped basins are typically exposed to greater mixing and more exaggerated effects during drought or periods of low lake level as a result of the large surface area to water volume reduction (Johansson et al., 2007). This could lead to a greater amount of sediment disturbance during deposition and the presence of hiatuses, even at the deepest points of the lake basin. However, the Sandai-Wasages River is a substantial input to this basin and a fan of sediment expanding across the majority of the basin can be observed in the mornings before the wind increases. Deposition into Lake Bogoria from the River Sandai-Wasages has increased in recent years due to regional population growth and the associated, simplification of river channel, riparian vegetation, and over grazing in the northern basins catchment (Harper et al., 2003; Childress, Nagy, et al., 2007; Kiage and Liu, 2009). Allochthonous deposition could be relatively greater in the basin particularly in recent years.

In all three basins, the LOI peak is closely associated to the presence of tephra ash in the sequence, which is a continuous deposit or more widely dispersed in the core giving evidence of reworking from the surrounding land. The East African Rift is geologically active and the Gregory rift, on which the Baringo-Bogoria basin is situated, has experienced a sequence of historical volcanic eruptions, generally on the millions of years to tens of thousands of years ago scale rather than the hundreds (Pyle, 1999; Hautot et al., 2000). There are several confirmed volcanic eruptions in Kenya and the surrounding region around 380 ± 15 BP which could have effected Baringo-Bogoria catchment hydrology temporarily until the volcanic deposits have been eroded and the hydrology had returned to a structure more similar to pre eruption (Pierson and Major, 2014; Venzke, n.d.).

Chironomid taxa and salinity

Recent work at Bogoria looking at the effects of lake level drop describe evapoconcentration resulting in short term rises in salinity from 20‰ to 63‰, TDS and other parameter increases coinciding with a clear change in DOC and depletion of dissolved Fe (Jirsa et al., 2012). Increasing salinity is likely to shock the ecosystem and increase the extremity of the environment so biota are likely to respond negatively. The low abundance of *T. minutipalpus* head capsules through most of the sequence, apart from the period of high LOI values, could be a reflection of the harsh environmental conditions. Nevertheless, the presence of *T. minutipalpus* as the only chironomid species in most of the sediment sequence, other than at the point of high organic carbon, suggests that Bogoria has maintained a similar salinity regime as contemporary levels, as *T. minutipalpus* has a salinity optimum of 35,479.7 $\mu S/cm^{-1}$ (Eggermont et al., 2006).

Ablabesmyia occurred at very low densities immediately prior to the tephra deposits. The presence of *Ablabesmyia* at this point could be the first sign of change but its presence below the tephra depth may be a result of weathered sediments reworked from the surrounding land. Not as much is known of the ecology of the Afrotropical species of *Ablabesmyia* but it is generally a cosmopolitan genus, occupying a range of water chemistries and temperatures and are typically obligate predators. *Rheotanytarsus*, is often associated with running water rather than of lakes (Brooks, et al 2007). Afrotropical species collected by Kyerematen and Sæther (2000) were from river, streams and water falls, but the morphotype found here has been identified in Lake Tanganyika, Lake Chad, Lake Edward and in 10 lakes in Kenya and Uganda (Eggermont and Verschuren, 2003b). *Parametriocnemus* has been found in both fresh and saline waters in East Africa, and Eggermont and Verschuren (2003a) posit the possibility that it may group more than one species each with differing ecological niche's, and this species has also been associated to running water (Brooks et al., 2007). Pentaneurini has been found in both fresh and saline lakes

again suggesting more than one species group (Eggermont and Verschuren, 2003b) but the morphotype of Paratendipes, usually morphologically indistinguishable, probably represents a distinct species and has also been found in Lake Bagusa, Uganda (Eggermont and Verschuren 2003a). *T. minutipalpus* is described in greater detail in the site description chapter but it has been found widley in afrotropic saline waters and has never been found in waters with conductivity values below 10,000 μS/cm^{-1} (Eggermont and Verschuren 2003a). Eggermont and Verschuren 2003a) found *T. minutipalpus* in most poly- to hypersaline lakes in Kenya and Ethiopia, but not in similar habitat in Uganda where it appears to be replaced by a different morphotype. Results suggest salinity fell to 300-800 uS, based on the optima of the chironbmid taxa present.

Baringo-Bogoria 'spill-over'

McCall (2010) is one of the first people to have done a survey of the Baringo-Bogoria basin and in his 2010 synopsis of Lake Bogoria he states the possibility of a spillage from Lake Bogoria into Lake Baringo following the Sandai-Wasages River north and escaping through the Loboi Hot Springs which maintain the Loboi Marsh (Driese et al., 2004). No detailed maps describe the topography or relief in this part of rural Kenya. To investigate if water transfer between these lakes could occur at Loboi Springs and explain an abrupt change in salinity I downloaded elevation data from ASTER (Advanced Spaceborne Thermal Emission and Reflection Radiometer). ASTER is a high resolution imaging instrument aboard NASA's flagship satellite of NASA's earth Observing System (EOS) and tasked with producing detailed maps of the earth's surface including elevation (USGS, and Japan ASTER Program, 2006). Figure 5.4 has four maps displaying possible water coverage at incremental increases of 5 meters at a time from Lake Baringo's water level. According to this data, it would take an increase in water level greater than 15 m for spill-over to occur. This is greater than evidence of high waters from ~3750 and ~3880 years BP, and water level increases nearer those experienced in the Pleistocene (Vincens et al., 1986; Olaka et al., 2010). It is worth nothing that the satellite data for this area is not a priority and therefore is not at the top end of ASTRA's data quality, errors as large as 15 m can be observed at individual 30 m or 90 m areas. These data contain many thousands of measurements.

  The Little Ice Age (LIA) falls between 1300 and 1850 AD but considering the accumulation rates cited above and the abruptness of the lowering in salinity it is unlikely that the period covered by the core includes the whole of the LIA. High resolution climate-proxy records concur that during the Medieval Warm Period and the Little Ice Age, East Africa witnessed a succession of century-scale climate shifts. But there are regional differences in the equatorial climate

response to the Little Ice Age. Records from Lake Victoria, Lake Milawi, and vegetation changes from Ethiopia indicate that the region was significantly drier between AD 1400 and 1850 but records from Lake Tukana and Lake Tanganika infer wetter conditions from AD 1250 to 1600 (Verschuren, 2001).

So do you think the LOI peak may be a result of short term increase in freshwater input such as increase intensity of rainfall? Can you sium yup here? But in conclusions you say you think it is because of the tephra altering the hydrology.
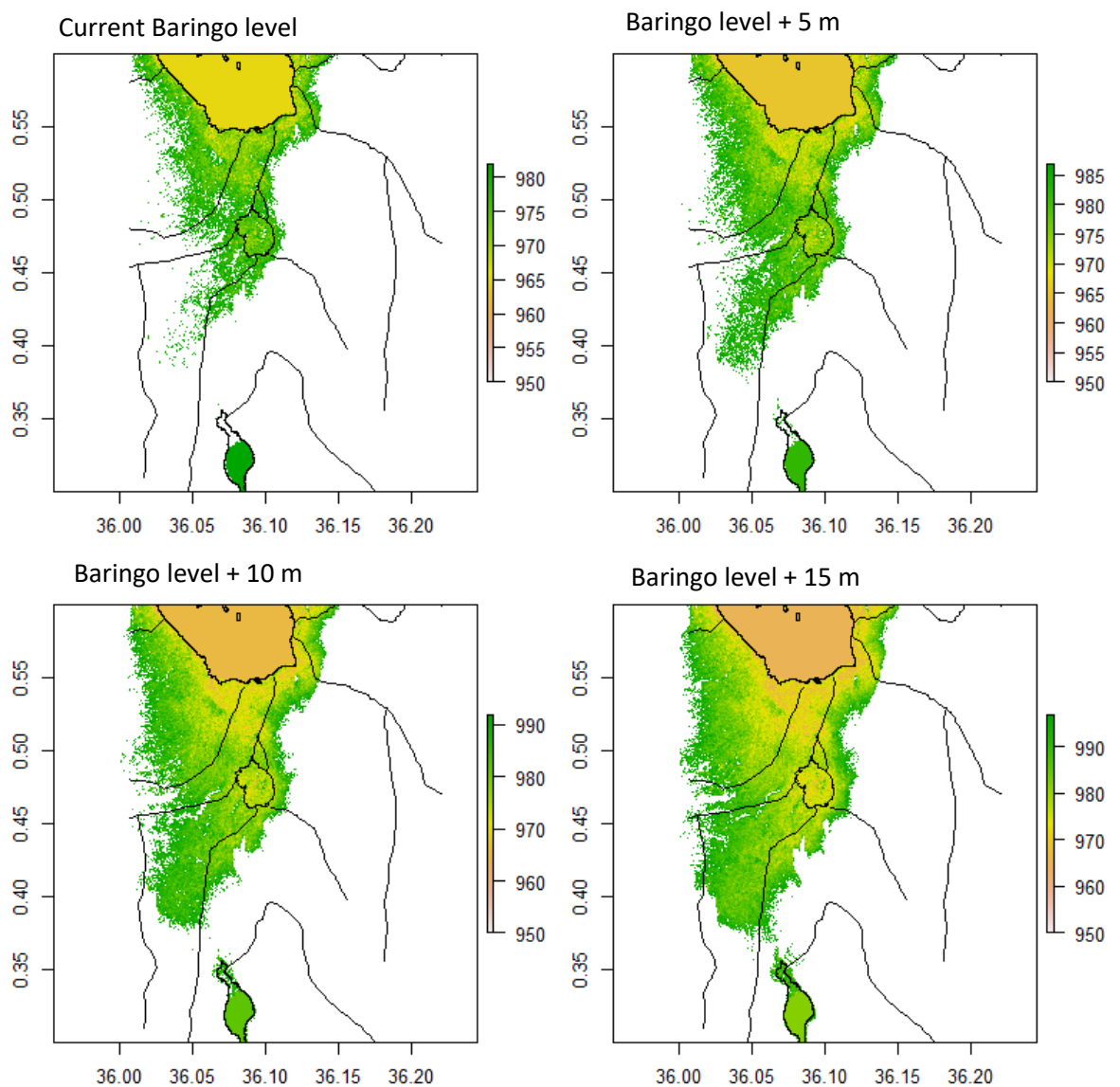

Figure 5.4 maps displaying the water coverage and elevation increase required for spillage to occur between Lake Bogoria and Lake Baringo.

Concluding remarks

From the evidence, we can conclude three possibilities for the abrupt increase in organic carbon deposits, and the inferred associated reduction in salinity. Firstly, as with other lakes in the East African Rift area, water level was fluctuating and a sudden increase over a short period of time, increased organic input into deposited sediments and reduced lake salinity opening up the habitat to be colonised by chironomid species with lower salinity tolerances. Secondly, as a result of local volcanic activity the hydrology in the catchment was drastically changed for a short period of time. This would account for the evidence of reworked tephra ash from the surrounding land and the presence of *Parametriocnemus* and *Rheotanytarsus*, two species known to occur in running water and which could have been deposited from lake inputs rather than from in the lake. Thirdly, the water level increase could have surpassed the narrow high point of land separating Lake Bogoria from the large freshwater Lake Baringo. There are several marshes between the two lakes and in 1992 a new lake appeared, Lake 92 between the two lakes and hydrologically linked to Lake Baringo. Lake Naivasha experienced high levels of organic carbon around a similar time frame but it was the result of a lowering of the lake level to the point that plant macrofossils increased due to the lake entering a marshy phase (Verschuren, 2001). I find this unlikely though as if a similar occurrence happened at lake Bogoria, salinities would increase so much that most flora would find it difficult to survive and thick mineral deposits would accompany such a phase. In light of the number of chironomid morphotypes associated with running water and their local to tephra deposits, known to affect catchment hydrology, it is likely that these species were introduced via an input change approximately 380 ± 15 years BP. However, Lake Bogoria has a fascinating history, in which the sediment record in each of its basins records in ways and other mechanisms should not be discounted. Better, and more expansive study of the Bogoria lake sediments is likely to resolve questions about past climate in East Africa.

Chapter Six: Project Discussion

Originality

This study used stable isotope analysis to look at cross-ecosystem boundary resource transfer in the context of climatic and seasonal environmental change. Studies on ecosystem subsidies rarely consider them in the context of environmental change, so this is a novel area of study (Bastow et al., 2002; Gratton et al., 2008; Grey et al., 2001). I used quantitative metrics derived from stable isotopes to examine the seasonal food web differences between the three bodies of water at Lake Bogoria. Previous work has focused on resource transfer over relatively short periods of time and rarely between seasons. The different environmental conditions between basins and seasons permit me to gain insights into how food webs and resource subsidies might alter in the future with ongoing climate change.

In the study I also provide some indication of how the abrupt environmental change marked in the paleorecord by a sudden increase in chironomid diversity and organic matter can occur at Lake Bogoria. The paleorecord shows a biotic change that follow an abrupt chemical change. The paleolimnilogical work in this thesis clearly shows an abrupt change in the hydrology of the lake in the past. This could be attributed to volcanic occurrences marked by a tepha layer immediately before the change, or to lake level rise at both Bogoria and Lake Baringo, resulting in an overspill of freshwater to Lake Bogoria.

Critique

N=1, I only used one lake. While I have outlined in the previous chapters why a focus on one lake with three semi-distinct basins has merit, the project would have been strengthened by the inclusion of lakes that had greater salinity differences then Lake Bogoria does between basins in the wet season. Williams (1981) lists the three points as of fundamental biological importance in saline lakes, 1) the great difference in salinity and composition between one water and another, 2) the enormous seasonal changes in salinity which can range from almost freshwater to saturation depending on the evaporation:precipitation ratios between seasons, and 3) the tendency to desiccate during dry seasons. While Bogoria shows seasonality and has not desiccated historically (but has in the last 1,300 years) The seasonal variation could have been greater at other lakes, and the differences in chemical regime would also be important.

Although ~49 samples for $\delta^{13}C$ and $\delta^{15}N$ should be sufficient for tropical invertebrates, trophic fractionation in the tropics can be complex and an inclusion of a bioassay to test for enrichment

in *T. minutipalpus* may have been prudent (de Carvalho et al., 2015). Further to this, variability of C-N stable isotopes within all organic-matter pools is high. Despite *A. fusiformis* being the predominant primary producer, disentangling their "central" stable isotopic signature from the C3 and C4 terrestrial plant signatures may have been more complicated than previously thought. Using an isotope-based approach may have been more powerful if used when complemented by other tools, such as molecular biomarkers, bioassays, direct measures of production, and compilations of organic-matter budgets (Cloern et al., 2002). Future work should also involve population estimates alongside stable isotope analysis to determine if the relative availability of chironomids is reflected in the abundance of the recipient community. or if the recipient community went into feast and famine with chironomid emergence patterns.

Ideally, I would have liked to expand the climatic context of ecosystem subsidies. To test the hypothesis that an increase or decrease in salinity may ultimately see a reduction in strength of subsidy, I should have linked my salinity reconstruction to dated regional precipitation and lake level fluctuations (Tierney et al. 2013; Verschuren et al. 2009). However, with very few core sections that showed diversity it is questionable whether this would have worked or not.

Overarching Conclusions

Salinity at Lake Bogoria is driven by lake volume and will affect the subsidy from the aquatic to the terrestrial ecosystem. When salinity decreases the in-lake environment can support a more diverse assemblage of invertebrates. In most cases, when species diversity increases, biomass and productivity decreases (Johnson et al., 1996). The alternative, when lake volume decreases and salinity increases (creating a harsher environment), results in fewer species able to tolerate the in-lake conditions, and it may even exceed that of the tolerance levels of *T. minutipalpus*. This might be the reason for the low head capsule abundance was observed immediately prior to the LOI peak. Which, could indicate a period of low chironomid subsidy coinciding with a drier climate. This period or a drier climate is observed in other research of the same period (De Cort et al., 2013) Therefore, Bogoria has at least two likely outcomes in the light of future climate change:

1. volume ⬆ salinity ⬇ complexity ⬆ strength of subsidy ⬇
2. volume ⬇ salinity ⬆ productivity ⬇ strength of subsidy ⬇

At low salinities, *A. fusiformis* is unlikely to exist as unialgal populations typical of Lake Bogoria. The complexity of the community is likely to affect the overall biomass and resource utilization (Neill, 1975). At the primary consumer level, lower salinities and differing microbial make up is

likely to make the lake less attractive to the large populations of flamingos which recycle nutrients. Laboratory experiments show that phytoplanktonic based food webs with few trophic levels are more efficient, and that the expected perturbations of climate change are predicted to be detrimental to food web efficiency (Berglund et al., 2007). Therefore, in a system like Lake Bogoria where there fewer actors in a productive environment, climate change may cause perturbations in food web efficiency.

I hypothesised that the predatory recipient temporal isotopic signal is likely to follow that of the strength of the subsidy provided by chironomid emergence periodicity. In contrast, the recipient detritivore community's temporal isotopic signature is likely to be more stable since they are sustained by the consistent flamingo feather matrix along the swash line. However, I found that this was not true. Instead, perhaps an analogy of chironomid availability could be that the midges are to the recipient community like the sun is to photosynthetic organisms, a constant and abundant resource to be relied upon which fluctuates, diurnally, day to day, and seasonally. As the detritivorous beetles are the only organism's which had a significant relationship with chironomid emergence, this suggests that they include fallen adult chironomids in their diet.

At longer time scales, climate change, and tectonic or volcanic activity can affect catchment hydrology, which in turn may cause abrupt changes in lake chemistry. Lakes in the East African Rift System have seen large fluctuations, at geological, millennial and century times scales (Verschuren et al., 2000; Olaka et al., 2010), and smaller but significant fluctuations at decadal scales in recent history (Hickley et al., 2004). This includes large water level rises resulting in several lakes combining into a single large water body, to complete lake desiccation (De Cort et al., 2013; Kiage and Liu, 2009). In Chapter three of the thesis I hypothesised that Lake Bogoria and its basins will have experienced these types of fluctuations because of its proximity to Lake Baringo (and the possibility of an overspill site near Loboi marsh), and its three basins possibly being divided by the two sills during low lake level periods. Recent research has confirmed that over the last 1,300 years Lake Bogoria is likely to have experienced such fluctuations, with higher water levels estimated at a similar time scale to my own estimations. Furthermore, the authors predict a spill over at a similar area to the predictions I made from Landsat data (De Cort et al., 2018). The hind cast De Cort et al. (2018) makes is likely to have strong effects on subsidy between basins, and have caused abrupt changes in lake chemistry during high standing overspill events with freshwater Lake Bogoria.

Implications

Current climate models predicting precipitation, air temperature, and drainage surface water are complex and the outcomes of such models can vary dramatically depending on the model used, data input, and outcome interpretations. Nonetheless, the predominant view is that East Africa will get wetter and warmer. Hulme et al*.,* (2001) predicts modest wetting trends over East Africa, reflecting the greater wetting zone across equatorial Africa with rainfall increasing by 5 to 30% in some models, but decreasing by 5 to 10% in other scenarios. In the most extreme scenario, rainfall may increase by up to 50 to 100% over parts of East Africa. Wit, et al., (2005) predicts enough increases in surface water drainage to accompany such increases in precipitation to potentially change the water regime to a wet climate. Mean soil moisture, number of extremely wet seasons and run off are also likely to increase (Bates et al., 2008). If general themes from the climate models are to occur then a wetter and warmer Baringo-Bogoria basin could develop once again into a single larger body of water. However, if regional microclimates force temperatures up without the corresponding precipitation increase, a reduction in lake level is likely to occur. Both scenarios will have substantial effects on the linkage of Lake Bogoria to its riparian ecotone. And knock on effects to broader systems, both natural and anthropogenic. It is worth noting at this stage that small increases in lake level result in an overall increase in chironomid emergence which is observed in two out of the three basins in Lake Bogoria (figure 6.1), larger fluctuations in lake level would likely have more complex effects on subsidy.

Season	Central	North	South
Dry	15.99	5.34	1.01
Wet	22.21	1.29	8.92

Table 6.1 – Chironomid emergence between seasons and across basins

Williams (2002), states that by 2025 most natural saline lakes will have undergone some adverse change including decreasing in size, increases in salinity, and the appearance of unnatural saline bodies in certain areas and longer dry periods for ephemeral water bodies. Recent, short term flooding, of EARS lakes have caused devastating impacts to both natural processes and community lively hoods. Affecting the ecology of the riparian zone has had impacts on biodiversity, wildlife, tourism infrastructure and the settlements around the lakes (Obando et al., 2016). Riparian degradation has been reported in several of the EARS lakes leading to the collapse of fisheries in some freshwater lakes (Hickley et al., 2004). Considering the climatic

hindcasts, climate model predictions, saline lake management and current flooding episodes, the hydrological regime at Lake Bogoria is likely to undergo significant change in the future. Lake Bogoria is a national reserve and as such enjoys some protection and management but an understanding of how that change will affect Lake Bogoria's riparian zone is more important than ever.

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