COMPARATIVE ASSESSMENT OF FEEDING AND REPRODUCTIVE ECOLOGY OF *OREOCHROMIS LEUCOSTICTUS* (PISCES: CICHLIDAE) AND *CYPRINUS CARPIO* (PISCES: CYPRINIDAE) IN LAKE NAIVASHA, KENYA

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EGERTON UNIVERSITY

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DECLARATION AND RECOMMENDATION

DECLARATION

This thesis is my original work and has not, wholly or in part, been presented for examination in any university

James Last Keyombe Atalitsa

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RECOMMENDATION

This thesis is the candidate's original work and has been prepared with our guidance and assistance. It is submitted with our approval as the University Supervisors

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DEDICATION

This work is dedicated to my wife, Vyone, and son Garvin. You are and will always be my source of strength.

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ABSTRACT

Lake Naivasha fishery is economically important to the communities living around the lake and nationally. The communities derive economic benefits directly and indirectly through fish sales and utilization of fish for food as a source of protein. The fishery is primarily based on exotic species, supported by six main species, namely; Blue spotted tilapia (*Oreochromis leucostictus*), Nile tilapia (*Oreochromis niloticus*), Red-bellied tilapia (*Tilapia zilli*), Largemouth bass (*Micropterus salmoides*), Common carp (*Cyprinus carpio*) and African sharp tooth catfish (*Clarias gariepinus*). Among the commercial fisheries, *O. leucostictus* is the most desired but less abundant compared to *C. carpio*, the most abundant fish in the lake. *O. leucostictus* was introduced into the lake in 1956 from Lake Victoria and quickly established itself while *C. carpio* was accidentally introduced in 1997. However, since the introduction of *C. carpio*, the populations of *O. leucostictus* have been on the decline due to reasons that are not yet well understood. The aim of this study was to assess the feeding and reproductive ecology of *O. leucostictus* and *C. carpio* in Lake Naivasha. Fish samples were collected monthly using gill nets (35 mm to 70 mm mesh size) between July and December 2013. Stomach contents of all the sampled fish were analysed using point method to determine the type of food items consumed. Detritus contributed 50% of the diet of *O. leucostictus* and 63% of the diet of *C. carpio*. The second most dominant food item for both *O. leucostictus* and *C. carpio* was algae contributing 35% and 30% respectively. This study demonstrates that both *O. leucostictus* and *C. carpio* in Lake Naivasha are predominantly detritus feeders. The ratio of males to females of *O. leucostictus* and *C. carpio* was tested using the Chi-square test. The ratio was 1.51:1 and 1.28:1 respectively. There was no significant difference between the sex ratios ($P > 0.05$) in the two species. There was suppressed fecundity in *O. leucostictus* probably caused by destruction of the spawning grounds through rooting and digging action of *C. carpio*. Length-weight relationships for males and females of both fish species showed that all the samples had negative allometric growth with the allometric coefficient value (b) being <3. A comparison of the two fish species showed *C. carpio* had a health condition factor of 1.51 while *O. leucostictus* had 1.32, indicating good healthy conditions. Therefore, it can be concluded that the feeding and reproductive habits of *C. carpio* has disrupted the natural environmental conditions of Lake Naivasha causing a decline in the numbers of *O. leucostictus* through alteration of its feeding and reproductive strategies.

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CHAPTER ONE

1.0 INTRODUCTION

1.1 Background information

Pioneer studies in Lake Naivasha in 1922 recorded only one native species of fish present, the endemic *Aplocheilichthys antinorii* (Vinc.). The documented records of the species was in 1962 (Elder *et al.,* 1971).The blue-spotted tilapia *Oreochromis leucostictus* (Trewavas, 1933) was first introduced, unintentionally, into the lake in 1956 from Lake Victoria Basin (Siddiqui, 1977). It is the most abundant tilapiine fish species in the lake (Oyugi *et al.,* 2011). Reasons for its successful establishment after introduction have not been exhaustively studied. However, Oyugi *et al*., (2012) attributes this to its feeding and reproductive strategies. It is a successful omnivore and offers strong parental (both parents involved) care through brooding (Oyugi *et al.,* 2011). Other tilapiine species introduced in 1950s were *Tilapia zillii* (Gervais), *Oreochromis niloticus* (Lin.1758) and *Oreochromis spirulus niger* (Gunther) (Hickley *et al.*, 2008). Both *O. spirulus niger* and *O. niloticus* did not establish viable populations in the new environment and disappeared by 1971 (Muchiri and Hickley, 1991). However, there was a hybrid produced between *O. leucostictus* and *O.spirulus niger* (Gunther) which became abundant in the early 1960s but due to back crossing with *O. leucostictus,* it disappeared by 1972 (Hickley *et al.*, 2008)**.** The purpose for the introduction of *O. spirulus niger* was to provide a forage fish for the American largemouth bass, *Micropterus salmoides.* The species *O. leucostictus* and *T. zillii* formed an important fishery in the Lake (Muchiri and Hickley, 1991), with both species being commercially exploited using gill nets by fishermen. Presently, they have been replaced from the commercial fishery by the invasive common carp, *Cyprinus carpio* (Oyugi *et al.,* 2011). In 2010, a large stock of *O. niloticus* was reintroduced into the lake to boost the tilapiine fisheries, and the population seems to be stabilizing reasonably fast (Oyugi *et al.*, 2011).

The common carp which currently accounts for over 90% of the commercial fishery in the lake (Oyugi *et al*., 2011) was accidentally introduced in the year 1997 from a fish farm in the catchment of River Gilgil (Hickley *et al.*, 2008). Among the commercially important fish species of the lake, *O. leucostictus* is the most desired by the local community for consumption. This is because it has fewer bones in its flesh compared to *C. carpio* and is perceived to be tastier (Ojuok *et al.,* 2007). However, its population has been on the decrease particularly after the invasion by the *C. carpio* in the Lake (Hickley *et al.*, 2008). The *C. carpio* probably interfered with the *O. leucostictus* breeding grounds through increasing turbidity of the water when feeding, and this could have reduced *O. leucostictus* spawning areas (Hickley *et al.*, 2008).

Ecologically, *O. leucostictus* can survive a wide range of pH, resists low levels of dissolved oxygen and feeds on a variety of food items (Njiru *et al.*, 2004; Oyugi *et al.*, 2012). In Lake Naivasha, some aspects of *O. leucostictus* was initially studied in the early 1970s. During this period, the lake was described as having clear waters and an extensive papyrus fringe with dense growth of submerged macrophytes within lagoons and low allochthonous nutrient input (Siddiqui, 1977). Water level fluctuations in the lake was primarily dependent on catchment rainfall (Becht and Harper, 2002). However, increased water abstraction from the catchment, changes in allodiversity and substantial increases in human population density have resulted in almost total loss of lagoons, and macrophytes and some of the fringe papyrus. At present, the lake has high water turbidity as a result of frequent algal blooms caused by increased eutrophication (Kitaka *et al.,* 2002). These changes in the environmental characteristics of Lake Naivasha may partly have contributed to the changes on the population of *O. leucostictus* (Njiru *et al.*, 2004).

Knowledge of the feeding and reproductive ecology of fishes coupled with their life history is essential for predicting population stability and/or fluctuations in the ecosystem. Information on reproduction can also be used to design fisheries management measures such as closed fishing areas or seasons. Such knowledge is particularly important for fish species like *O. leucostictus,* because they dependend on shallow, nearshore areas for reproduction. A number of studies have been done on *O. leucostictus* in Lake Naivasha but most were on their parasites and the effects of chemical pollution from surrounding horticulture farms on them (Aloo, 1995; Campbell *et al.*, 2003). Although some aspects of feeding and reproductive ecology of tilapiine species have been previously studied in Lake Naivasha and other Kenyan lakes (Muchiri *et al.*, 1990; Njiru *et al.*, 2004; Oyugi *et al.*, 2011; Oyugi *et al.*, 2012), no comparison of *C. carpio* and *O. leucostictus* has been done.

Interactions between fish species and between fish and planktonic organisms are frequently revealed through dietary studies. Gut content analysis which provides evidence of whether the invading population has increased pressure on prey items or increased competition for resources (Britton *et al.*, 2007), is also lacking in this lake. Similarly, common carp has had various impacts in Lake Naivasha ecosystem since its introduction (Oyugi *et al.*, 2011). However, knowledge of the effects of its interaction with *O. leucostictus* is limited. Therefore, the aim of this study was to compare the feeding and reproductive ecology of *O. leucostictus* and *C. carpio* in Lake Naivasha. The information generated would facilitate informed decision making processes for effective management of the fisheries resources in Lake Naivasha.

1.2 Statement of the problem

The most abundant tilapiine fish species in Lake Naivasha is *O. leucostictus*. It is also the second most important in terms of fisheries productivity in the lake. In addition, it is the most desired table fish in the lake. However, its population has been on a decline especially after the accidental introduction of *C. carpio*. On the other hand, *C. carpio* established itself quickly and is now a major component of the lake's commercial fishery. No sufficient study has compared the interactions of the two fish species in the lake and the effects they have on each other's existence. Lack of such information directly hinders the processes of policy making for suitable fisheries management. This study will compare the feeding, length- weight relationships, body condition factor and reproductive ecology of *C. carpio* and *O. leucostictus* in Lake Naivasha.

1.3 Objectives

1.3.1 General objective

To assess the feeding and reproductive ecology of *O. leucostictus* and *C. carpio* in Lake Naivasha.

1.3.2 Specific Objectives

i. To determine the diet and feeding habits of *O. leucostictus* and *C. carpio* in Lake Naivasha.
ii. To determine the sex ratios and reproductive potential of *O. leucostictus* and *C. carpio* in Lake Naivasha.
iii. To compare the length- weight relationships and fish health condition factors between male and female *O. leucostictus* and *C. carpio* in Lake Naivasha.

1.3.3 Hypotheses

i. There is no significant difference in the diet and feeding habits between *O. leucostictus* and *C. carpio* in Lake Naivasha.

ii. There are no significant differences in the sex ratios and fecundity between *O. leucostictus* and *C. carpio* in Lake Naivasha.
iii. The length-weight relationships and condition factors are not significantly different between the male and female fish of *O. leucostictus* and *C. carpio* in Lake Naivasha.

1.4 Justification

Lake Naivasha fishery is economically important to the communities living around the lake and nationally. Apart from the economic benefit through direct sales of the fish to the local market, fish also act as an important health item as food, being a source of protein to the people. It is for this reason that fisheries have been integrated into national policies related to poverty reduction and rural development as envisaged in the National Vision 2030. The most abundant tilapiine (*O. leucostictus*) is second in terms of fisheries productivity to *C. carpio*. However, there has been a consistent decline in its commercial landings especially after the accidental introduction of *C. carpio* in 1997. Therefore it is important to make comparative assessment of feeding and reproductive ecology of *O. leucostictus* and *C. carpio* as this may explain the interactions of the two fish species in terms of the feeding niches and reproductive requirements. Such interactions could have led to the decline in the abundance of *O. leucostictus* through competition. Ultimately, this study aims at establishing whether the two fish species share or compete for any of their ecological requirements, and how this impacts on their productivity.

CHAPTER TWO

2.0 LITERATURE REVIEW

2.1 Fish species in Lake Naivasha

There have been fish introductions in Lake Naivasha, for various reasons, since 1925 (Muchiri and Hickley, 1991). For example, the introduction of *Oreochromis spirulus niger* (Gunther) was to provide a forage fish for the American largemouth bass, *Micropterus salmoides* (Lacepede), which was later introduced at the suggestion of the U.S. President Franklin Roosevelt who believed that sport fishing in East Africa needed improvement (Robbins and MacCrimmon, 1974). A second cichlid, *Tilapia zillii* was introduced in 1956 from Lake Victoria Basin to establish a population for later commercial exploitation. The consignment of *T. zilli* also contained some *O. leucostictus* and both species became well established. A summary of these and subsequent fish species introduce into Lake Naivasha is given in Table 1.

Despite these introductions, the fishery was still underperforming at the time, so there were proposals that more species should be introduced into the Lake (Muchiri *et. al.,* 1994). Based on prospective feeding guilds and the actual food web, Muchiri *et al.* (1994) identified four areas in terms of food and space with respect to the potential for stocking additional species of fish. The most convincing case was that of a bottom feeder, given that the benthic oligochaetes and chironomid larvae were under- utilized (Mavuti, 1990; Raburu *et al.,* 2002). One species of the *Mormyrus* genus was proposed as the suitable candidate for introduction (Mavuti, 1990). It was suggested that, if the concept of new introductions became acceptable, only African fish species should be considered as potential candidate. However, before this could be implemented, *Cyprinus carpio* accidentally introduced in 1997/1998 (Hickley *et al.,* 2004). *C. carpio* is native to Asia but can now be found on every continent except Antarctica (Edwards and Twomey, 1982). The carp escaped from a fish farm in the headwaters of River Gilgil, Lake Naivasha's second main inflow, and into which carp fingerlings had been stocked (Hickley *et al.,* 2004). The presence of the carp in the Lake was first recorded in March 2001, when the fishery was closed, and a fish eagle (*Haliaetus vocifer* (Gaudin) caught and landed a large carp approximately 680 mm in length (Hickley *et al.,* 2004).

Table 1: Summary of the observed change in the fish community in Lake Naivasha (1925 to 2010).

	Species	Date and success of fish introduction
1	*Aplocheilichthys* sp. "Naivasha"	Endemic. Probably extinct; last reported in 1962. Previously listed as *A. antinorii* (Vinci Guerra)
2	*Oreochromis spirulus niger* (Gunther)	Introduced in 1925. Disappeared by 1971.
3	*Micropterus salmoides* (La Cepède)	Introduced in 1929, re-introduced in 1951. Present today.
4	*Tilapia zillii* (Gervais)	Introduced in 1956. Present today.
5	*Oreochromis leucostictus* (Trewevas)	Introduced unintentionally in 1956 with *T. zillii*. Present today.
6	*O. leucostictus* x *O.s. niger* hybrid	Abundant in the early 1960s; due to back crossing with *O. leucostictus* disappeared by 1972.
7	*Oreochromis niloticus L.*	Introduced in 1967. Disappeared by 1971. Has been reintroduced in 2010
8	*Gambusia* sp. and *Poecilia* sp.	Introduced but dates unknown. Absent since 1977.
9	*Poecilia reticulata* Peters	Introduced; date unknown. Recorded since 1982. Present today.
10	*Oncorhyncus mykiss* (Walbaum)	Introduced into the River Malewa, dates unknown. Caught in the lake on rare occasions.
11	*Barbus paludinosus* Peters	Invaded from inflowing rivers (introduced into rivers?). Recorded since 1982. Present today.
12	*Cyprinus carpio L.*	Introduced by escape from a fish farm on the inflow river. First recorded in 2001. Present today.
13	*Clarias mossambicus*	Introduced in 2010, present to date

(Source: Hickley *et al.*, 2008; Oyugi *et al.*, 2012)

During the period 1st-15th March 2002, soon after the fishery was re-opened, 37 carps approximately 220 mm mean total length and 0.4 kg mean total weight were caught in the gill nets by fishermen (Oyugi *et al.*, 2012) confirming the presence of the fish in the lake. By the end of the year 2002, 1055 carps had been caught and their average weight indicated an increasing trend to a mean of 2.25 kg (Hickley *et. al.*, 2004). By 2004, there was a marked increase in the contribution of *C. carpio* to commercial catches and the species comprised 93.7% of the total catch by weightin 2006 (Ojuok *et al.*, 2007). Although the mean weight of landed carps was approximately 1.5 kg, some individuals exceeded 8 kg. Around the same period, *O. leucostictus* consistently declined in commercial catches (Table 2).

Table 2: Fish catches in Lake Naivasha from 2005 to 2008.

	Weight in Metric Tonnes (MT)			
Fish species	**2005**	**2006**	**2007**	**2008**
M. salmoides	9	1	0.06	0.03
O. leucostictus	0	0	0.09	0.06
C. carpio	90	95	100	120
T. zillii	0	0.02	0	0.01
Total	**99**	**96.021**	**100.154**	**120.1**

(Source: Ministry of Fisheries Development, Naivasha Station)

2.2 Habitat preference for *O. leucostictus* and *C. carpio*

Oreochromis leucostictus is a freshwater fish species in the Cichlidae family of the order Perciformes (perch-likes). It is a tropical species that prefers to live in shallow, warm waters. *O. leucostictus* tolerate low levels of dissolved oxygen, and feeds on a wide variety of food items (Trewevas, 1933). The temperatures suitable for their survival in natural habitats are between 11°C and 42°C. However, the preferred temperature range is between 25 and 28 °C (Trewavas, 1933). On the other hand, *C. carpio* usually dominates habitats because of their long life spans and large body size (Bonneau, 1999). They are the largest of the *Cyprinidae* (minnow) family and can weigh well over 9 kg and span to more than 60 cm total length (TL). They are extremely tolerant to a wide range of environmental conditions including extremely low dissolved oxygen and are found in every part of the water (Edwards and Twomey, 1982). However, they prefer shallow, warm, well vegetated lakes with mud and silt substrate. They are also tolerant to turbid waters. They gulp surface air when dissolved oxygen levels are less than 0.5 mg l^{-1} and can also be tolerant to brackish waters (Edwards and Twomey, 1982).

Domination of a lake ecosystem by *C. carpio* has many effects. They uproot aquatic macrophytes when feeding (Edwards and Twomey, 1982) thereby suspending bottom sediments and nutrients. This limits the amount of light penetration and affects submerged macrophyte growth. In addition, they reduce zooplankton and macroinvertebrate populations through predation and by eliminating macrophytes that provide cover. Consequently, phytoplankton populations increase due to increased release of nutrients and reduced predation by zooplankton

(Edwards and Twomey, 1982). Thus, other aquatic lives are adversely affected by the loss of zooplankton and the microinvertebrate food sources. Also, the loss of aquatic macrophytes which provide cover for larval and juvenile fish and substrate for eggs and invertebrates (Kahl, 1991). A summary of critical habitat requirements for *C. carpio* and *O. leucostictus* is shown in table 3.

Table 3: Critical optimum habitat requirements for *C. carpio* and *O. leucostictus*

	Optimal requirement (Range)	
Parameters	***C. carpio***	***O. leucostictus***
Dissolved Oxygen (mg/l)	5.0 -8.0	6.0 -8.0
Temperature (°C)	20.0 – 30.0	25.0 -28.0
pH	6.0 - 7.5	6.8 - 7.5

(Source: Edwards and Twomey, 1982)

2.3 Feeding ecology of *O. leucostictus* and *C. carpio*

O. leucostictus is mainly a phytoplankton feeder but can shift to omnivory feeding on periphyton, aquatic plants, small invertebrates, benthic fauna, detritus and biofilms associated with detritus (Oyugi *et al.*, 2012). It can filter-feed by entrapping suspended particles, including phytoplankton and bacteria, on a mucous film in the buccal cavity. However, its main source of nutrition is obtained by grazing on periphyton mats (Trewavas, 1933). Observations made in lakes and rivers where tilapiines occur also show that the species includes algae and higher plant material in its diet (Balirwa, 1998). It tends to feed on bottom deposits derived from the planktonic rain and other sources, and gains nutritive value from organic particles and other organisms, which cover their surfaces (Moriarty and Moriarty, 1973). *C. carpio* on the other hand, is omnivorous, with a high dependency on benthic organisms such as water insects, insect larvae, worms and mollusks. Additionally, it also consumes stalks, leaves and seeds of aquatic and terrestrial plants (Morgan, 1988). It is sometimes considered an opportunistic feeder mainly due to its ability to utilize any available food source (Edwards and Twomey, 1982). Rahman *et al.* (2006), found that when plankton and benthic macroinvertebrates were available, common carp ignored the plankton and strongly selected the benthic macroinvertebrates (which made up 76% of the total gut content by volume) and weakly selected zooplankton. These results suggested that common carp preferred benthic macroinvertebrate to zooplankton when they occur together.

This preference for benthic macroinvertebrates most probably influences the bottom grazing of the carp. It indicates that the feeding niche of common carp is largely benthic when only plankton and benthic macroinvertebrates are available in the system (Parkos *et al.*, 2003). Regardless of where the fish lives, it exhibits either shoaling or scattering during grazing but this varies among habitats and food resources (Morgan, 1988). The relationship between grazing and scattering time indicates that common carp prefers grazing individually (Morgan, 1988). Being a benthic feeder, common carp typically makes the water turbid, which has negative effects on the local fish communities and vegetation which prefer clear water (Oyugi *et al.*, 2012). In recent years, the fish community structure and ecosystem dynamics of Lake Naivasha have changed (Oyugi *et al.*, 2012). Other studies (Morgan, 1988) have found that fish usually change their diet with changes in environmental conditions, fish size and the prevailing season of the year.

2.3.1 Ontogenic shift in diet

Different sizes of *O. leucostictus* feed on different types of food items. For instance, smaller *O. leucostictus* of less than 5 cm tend to feed mostly on the zooplankton, which is not a major food item of fish larger than 10 cm (Muchiri, 1990). Muciri (1990) found insects to be a major source of food to these larger sized fish compared to those of less than 5 cm. However, juvenile fish, algae and other plant material were consistently important to all size groups of *O. leucostictus* (Trewevas, 1933). Many fish shift to less profitable foods when preferred food sources become depleted (Balcombe *et al.*, 2005), which can affect foraging, swimming and other social behaviours. This concept is also true for *C. carpio* that was observed to increase its preference for zooplankton in the absence of benthic macroinvertebrates (Balcombe *et al.*, 2005). In natural habitats, carp fries feed mainly on zooplankton and phytoplankton. The juveniles and adults are omnivorous and feed on worms, insect larvae, plant seeds and algae (Oyugi *et al.*, 2012). This feeding of fish on a specific type of food reduces the competition among fish of different sizes. Therefore feeding on a particular diet ensures that each size class of fish has its own trophic niche within the aquatic system.

2.4 Sex Ratio, Spawning and Fecundity

Sex ratio is the ratio of males to females in a population. It is usually expressed as the percentage of females in every population. The primary sex ratio is the ratio at the time of conception, secondary sex ratio is the ratio at time of birth, and tertiary sex ratio is the ratio of mature fish (Kjesbu *et al.*, 1991). In this study, only tertiary sex ratio will be considered.

Sex ratio is important in determining population viability. It is also an important factor in determining the balance of the males and females in the habitat. Sexual maturity of *O. leucostictus* in ponds as well as in the wild is reached at an age of 5-6 months. Spawning begins when the water temperature reaches 24°C (Njiru *et al.*, 2006). The breeding process starts when the male establishes a territory, digs a spawning nest and guards his territory. The ripe female spawns in the nest, and immediately after fertilization of the eggs by the male, they are collected into her mouth and she moves off. The female incubates the eggs in her mouth and broods the fry after hatching until the yolk-sac is absorbed. Incubation and brooding are accomplished in 1 to 2 weeks, depending on temperature (Njiru *et al.*, 2006). After fry are released, they may swim back into her mouth if danger threatens.

Fecundity is proportional to the body weight of the female. For example a 100 g female will produce about 100 eggs per spawn, while a female weighing 600-1000 g can produce 1000 to 1500 eggs (Njiru *et al.*, 2006). The male remains in his territory, guarding the nest, and is able to fertilize eggs from a succession of females. If there is no cold period, during which spawning is suppressed, the female may spawn continuously. Being a maternal mouth brooder, the number of eggs per spawn is small in comparison with most other fishes. While the female is brooding, she eats little or nothing. *O. leucostictus* can live longer than 10 years and reach a weight exceeding 5 kg (Oyugi *et al.*, 2012).

C. carpio is a highly prolific breeder; they crowd into shallow bays to spawn unlike *O. leucostictus*. Carps spawn over a prolonged period of time (Oyugi *et al.*, 2012). They do not build nests hence exposing their eggs and fry, thus regarded as *r*-strategists. Eggs are deposited on flooded vegetation in areas with water depth of less than 1.8 m (Oyugi *et al.*, 2012). Their eggs are tolerant to fluctuating levels of dissolved oxygen and can even tolerate levels as low as 1.2 mg l^{-1}. Eggs hatch in 10 to 20 days and grow rapidly, reaching lengths of 20 cm or more in the first year (Peteri, 2006). Adult carps have no natural predators so they have low mortality rates making them comprise the majority of fish mass in a water body (Oyugi *et al.*, 2012). Spawning of the carp population starts when the water reaches 17-18^{o}C. Females release 100-230 g of eggs per 1 kg body weight. Eggs are laid on submersed aquatic plants and after contact with water; they become adhesive and swell 3-4 times in volume (Peteri, 2006). Embryonic development takes 60-70 days. Hatched fry stick to substrate and live on yolk supplies.

Three days after hatching, the posterior part of the swim bladder develops, the larvae start to swim and consume external food of 150 –180 µm size (Peteri, 2006). Table 4 describes sexual maturity of the two fish species.

Table 4: Maturity stages of ovaries in *O. leucostictus* and *C. carpio*.

Maturity stage	*O. leucostictus*	*C. carpio*
I	Sex cannot be differentiated	Immature, gonad tissue developing
II	Small ovary, tube like. Eggs not visible	Gonad non-vascularised
III	Ovary larger, occupies 1/3 of body cavity. Eggs visible as yellow granules	Eggs/milt visible
IV	Ovary dull grey. Occupies ½ of body cavity. Eggs visible as yellow granules	Mature, vascularised but not running
V	Ovary large. Greenish in colour. Occupies almost entire body cavity Golden green eggs extruded on applying pressure to abdomen	Running ripe
VI	Red wrinkled ovary	Spent

(Source: Witte and Van Densen, 1995; Bonneau, 1999; Donkers, 2004)

2.5 Fish Condition factor

The condition factor is an index reflecting interactions between biotic and abiotic factors in the physiological condition of fish. It shows the population's welfare during the various stages of the life cycle (Blackwell *et al.*, 2000). The analysis of fish condition factor has become a standard practice in the management of fish populations, as a measure of both individual and cohort (e.g., age or size group) fitness or well-being (Blackwell *et al.*, 2000). Condition factor has been generically described as the well-being or robustness of an individual fish (Blackwell *et al.*, 2000) and has typically been estimated by comparing individual fish weight of a given length to a standardized weight. Condition factor has also been estimated by directly measuring physiological parameters related to the energy stores such as tissue lipid content and reproductive status (Fechhelm *et al.*, 1995). Measurements of condition factor are generally intended to act as indicators of tissue energy reserves, with the expectation that a fish in relatively good condition should demonstrate higher growth rates, greater reproductive potential and higher survival rates than one with a lower condition factor, given comparable environmental conditions (Cone, 1989). As a result, numerous studies have investigated the relationship between fish condition factor and parameters such as population structure, growth, fecundity, life history adaptations, environmental conditions or management actions such as stocking (Blackwell *et al.,* 2000). Fish condition may be used to characterize components of the environment in which the fish exists (e.g., habitat, prey availability, competition). Measures of fish condition are of value to fisheries managers who must assess population status, impacts of management actions, and anthropogenic influences on the resource they are managing (Brown and Austin, 1996).

The condition factor usually increases when sexual maturation approaches (Brown and Austin, 1996). Values of condition indices vary among individuals, and may vary annually within individuals. Changes in environmental factors, such as temperature, may affect condition factor by influencing fish behaviour and metabolism, as well as food availability. In extreme cases, low condition can induce reproductive failure and lead to skipped spawning seasons (Livingston *et al.,* 1997)

2.6 Length-Weight Relationship

The length-weight relationship (LWR) is a useful tool in fishery assessment, which helps in predicting weight from length required in yield assessment (Garcia *et al*., 1998), and in the calculation of biomass (Martin-Smith, 1996). In sampling programs, it is usually easier to measure length only while weight cannot be measured simply. The LWR of a particular species allows the inter-conversion of these parameters. Also, morphometric comparisons can be made between species and populations (King, 1996). Furthermore, the LWR allows fish condition to be estimated. The relationship between the length (L) and weight (W) of a fish is usually expressed by the equation $W = aL^b$. Where a is the intercept and b is the allometry coefficient. Values of the exponent b provide information on fish growth. When $b = 3$, increase in weight is isometric. When the value of b is other than 3, weight increase is allometric (positive if $b > 3$, negative if $b < 3$). This is a useful tool that provides important information concerning the structure and function of fish populations (Anderson and Neumann, 1996). According to Gerritsen *et al*. (2003), the variations in ‘b’ values between males and females may depend on various factors such as number of specimens examined, and the sampling season.

However the change of *b* values may also depend primarily on the shape and fatness of the species as well as physical, chemical and biological factors such as temperature, salinity, food, sex and stage of maturity (Sparre and Venema, 1998; Sarkar *et al.*, 2013).

CHAPTER THREE

3.0 MATERIALS AND METHODS

3.1 Study site

Lake Naivasha is a shallow freshwater body, situated in the eastern arm of the Great Rift Valley in Kenya (0^o 46'6.70"S and 36^o 21'2.32"E). It lies at an altitude of about 1890 m above the sea level. The lake covers a surface area varying between 120 Km^2 and 160 Km^2 depending on the dry and wet seasons, respectively (Harper and Mavuti, 2004). The lake's mean depth varies between 4 m and 6 m (Hickley *et al.*, 2008). It lies in an endorheic basin but its freshness is mainly maintained by the inflows from the catchment area, biogeochemical sedimentation and the underground seepage. Lake Naivasha is a complex basin consisting of four lakes that include Oloidien, Crescent Lake, main Lake Naivasha and Sonachi,. Rivers Malewa and Gilgil are the most important feeders of the lake (Figure 1). Karati River flows into the lake intermittently. The lake is surrounded by a *Cyperus papyrus* swamp which covers an area of 64 km^2, but this can vary largely depending on rainfall intensity, livestock and prevailing wildlife populations in the riparian zone (Harper and Mavuti, 2004).

3.2 Sampling stations

The six sampling stations in both the main Lake Naivasha and Crescent Lake which were used in this study are indicated in Figure 1. These stations are Malewa (00^o43'49.9"S 036^o21'32.1"E), Korongo (00^o44'22.6"S 036^o19'28.9"E), Hippo Point (00^o47'14.0"S 036^o18'56.8"E), Mid Lake (00^o46'30.8"S 036^o20'49.9"E), Sher (00^o49'19.1"S 036^o21'49.4"E) and Crescent (00^o45'39.8"S 036^o24'31.2"E). Malewa and Korongo sampling stations are located approximately 100 m from the shore and characterized by floating mats of water hyacinth (*Eichhornia crassipes*), salvinia (*Salvinia molesta*) and papyrus (*Cyperus papyrus*) vegetation. They are characterized by muddy substrate, decayed plant materials and silt. The average depths of the stations are 3 m and 3.5 m respectively. Sher Bay and Crescent Lake are fairly sheltered from the wave action of the main lake and are characterized by calm waters occasionally invaded by the floating mats of *E. crassipes* and detached *C. papyrus* especially during strong winds at high water levels. The average depths in these stations are 2.5 m and 3 m respectively. The substrate is mainly silt and sand.

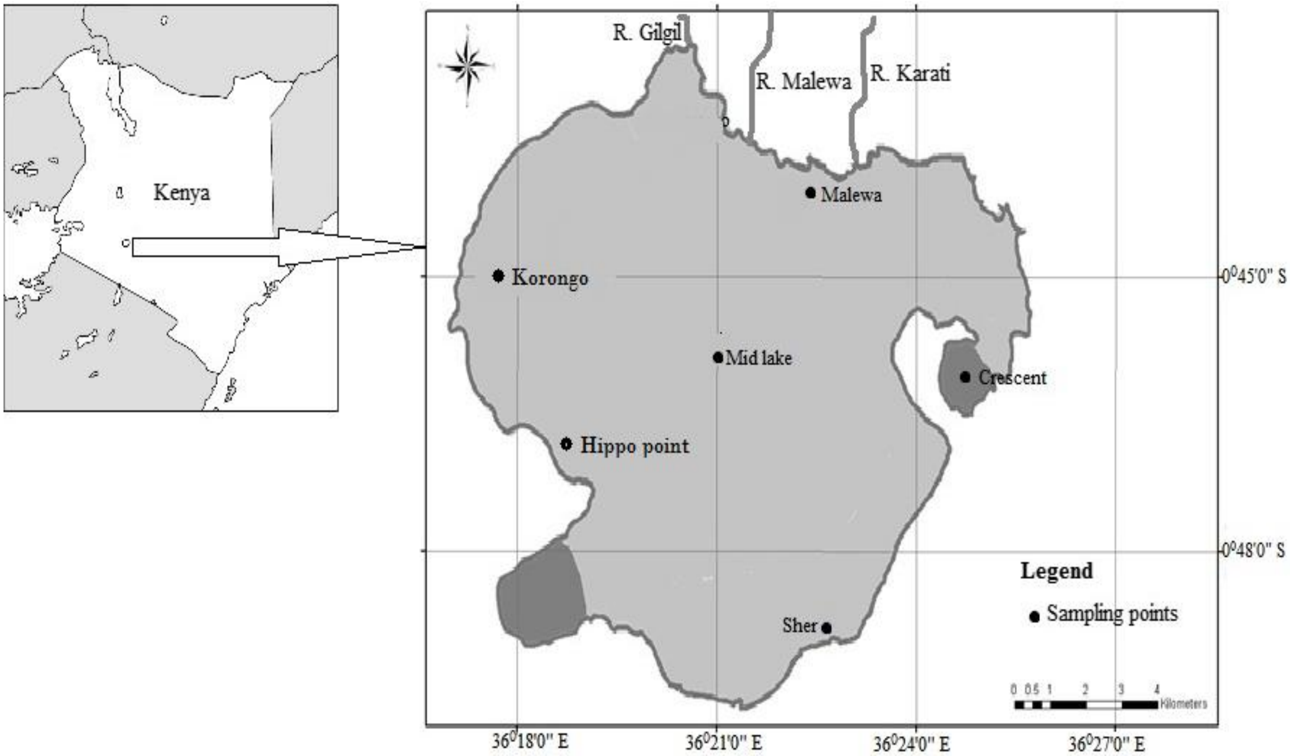


Figure 1: A map of Lake Naivasha showing the sampling stations during this study (modified from KMFRI, 2007)

3.3 Measurement of physico-chemical parameters

Temperature (ºC), dissolved oxygen (mg l^{-1}), pH and conductivity (µS cm^{-1}) were measured *in situ* using respective Hach multi-probe meter electrodes (HQ40d). Transparency of the lake water was determined using a black and white Secchi disk of 20 cm diameter. The disc was lowered until it just disappeared and then hauled until it just reappeared and the average of the two depths calculated. The physico-chemical parameters were measured at each sampling station before collection of the fish samples.

3.4 Collection of fish samples

Fish samples were collected monthly using gill nets (mesh size 35 mm, 40 mm, 50 mm, 60 mm and 70 mm) from the sampling stations (Malewa, Korongo, Hippo Point, Mid Lake, Sher and Crescent) between July and December 2013. The variations in mesh size of the nets allowed fish of different sizes to be caught. The nets were set at the first sampling station of the day at 0700 Hrs and hauled six hours later at 1300 Hrs. The nets were then set at 1330 Hrs and hauled at 1930 Hrs for the second station of the day. Two stations were sampled per day. Six hours was the adequate time to ensure enough fish for sampling were caught in the nets during the day.

Immediately after retrieving the nets, each fish caught was weighed in grams using an electronic weighing scale (Digitron T745) (to the nearest 0.1 grams). The total length of each fish was measured to the nearest centimeter using a measuring board. The sampled fish were then eviscerated and their sex determined according to Witte and Van Densen (1995) as outlined in Table 4. In the laboratory, fish stomachs were removed, fullness index determined using the modified method of Hyslop (1980), and preserved in labeled plastic vials with 5% formalin for further analysis.

3.5 Sample Analyses

3.5.1 Gut Contents

In the laboratory, the stomach contents were analysed using a modified point method according to Hynes (1950) as reviewed by Hyslop (1980). Fullness of each stomach was estimated then contents emptied into a petridish. The different food items were identified and sorted into categories. Benthic macroinvertebrates and plant materials were identified and counting was done through a binocular (X50) microscope. The smaller components such as algae and zooplankton were counted using an inverted compound microscope at x200 and x400 magnification after dilution to 100 ml. Each food item was assigned a number of points proportional to the estimated contribution. The phytoplankton and zooplankton obtained in the gut were identified using keys by Lizeth (2001) and Jung (2004).

3.5.2 Length-Weight Relationship and Fish Condition Factor

Length and weight of individual fish were measured and recorded. The total length (TL) in cm from snout to the end of the caudal fin of each fish was measured using a meter rule. Weight of each fish was measured using the Digitron T745 weighing balance. The length-weight relationship was calculated using the formula by Wooton (1990):

$$W = aTL^b$$

Where W is the total body weight of fish in grams, TL is the total length in centimeters, *a*, the intercept and *b* the slope of the regression line.

Condition factor (K) was estimated following Le Cren (1951):

$$K = \frac{W}{L^b}$$

Where K is the condition factor, W is the total body weight of fish in grams, L the total length in centimeters and *b* is the regression slope.

3.5.3 Sex Ratio

Sex ratio was determined for only those fish whose gonads were identifiable as male and female. Maturity status was assigned as stage I–VI according to Witte and Van Densen (1995) as summarized in Table 4. Fish in maturity stages I, II, III were considered immature, while those in stages IV-VI were considered mature.

3.5.4 Fecundity

Fecundity was estimated from total counts of ova in the ovaries of female fish in the most advanced stages of development (Stage IV-VI) (Table 4). In the laboratory, ovary samples preserved in 5% formalin were first weighed individually. They were then dissected in a petri dish. *C. carpio* usually has high fecundity; therefore, sub sampling of the ovaries had to be done. This was achieved by halving one of the two ovaries of each mature fish. Physical counting of the ova in the halved ovary was done and extrapolated four times to represent the two ovaries. *O. leucostictus* did not have high fecundity so all the ova for each mature fish were physically counted. A dissecting microscope was used in cases where ova were too small.

3.6 Data Analyses

Data on gut contents was tested for normality and homogeneity of variance using MS Excel 2010 then by Statistica. The differences in the contribution of each food item were tested using Quadratic fit. The relationship between fecundity and fish length-weight were determined by linear regression technique. The best predictive equation was computed as a logarithm transformation of the equation $F = a X^b = \text{Log } F = \text{Log } a + b \text{ Log } X$. The sex ratio, expressed as male: female, was analyzed for the whole lake with the use of chi-square test. Descriptive and inferential data analysis was conducted using MS Excel 2010. In all the analyses, 95% level of significance was used as the critical point for rejection of the null hypotheses.

CHAPTER FOUR

4.0 RESULTS

4.1 Physico-chemical parameters

Mean values of physico-chemical parameters obtained from all the sampling stations are indicated in table 5. Mid lake had the deepest waters at 7.9 ± 0.01 m while the shallowest mean depth was at Sher with 2.7 ± 0.06 m. The water was clearest at Korongo with a mean Secchi depth of 52.0 ± 9.5 cm while the most turbid area was Hippo point with a mean Secchi depth of 40.3 ± 7.8 cm. One way ANOVA (F= 11.84, P <0.005) showed a significant difference in the secchi depth values among the sites.

Table 5: Mean values of physico-chemical parameters in Lake Naivasha during the sampling period (July to December 2013).

Sampling site	Depth (m)	Secchi (cm)	Temperature (ºC)	Conductivity (µS cm^{-1})	DO (mg l^{-1})	pH
Crescent	3.1 ± 0.09	50.3 ± 6.2	22.2 ± 0.49	257.8 ± 0.87	7.5 ± 0.26	8.1
Korongo	3.6 ± 0.17	52.0 ± 9.5	21.9 ± 0.34	258.2 ± 1.17	7.9 ± 0.21	8.5
Hippo point	4.7 ± 0.17	40.3 ± 7.8	22.1 ± 0.50	257.3 ± 0.92	7.4 ± 0.20	8.3
Malewa	3.7 ± 0.25	41.2 ± 6.5	22.3 ± 0.32	257.5 ± 0.50	8.2 ± 0.30	8.3
Mid lake	7.9 ± 0.08	45.7 ± 2.1	22.4 ± 0.39	258.2 ± 0.54	7.8 ± 0.36	8.6
Sher	2.7 ± 0.06	47.3 ± 8.5	22.5 ± 0.35	259.0 ± 1.03	7.6 ± 0.32	8.6

One way ANOVA showed no significant differences in the values of temperature among the sampling stations (F= 2.53, P > 0.005) with the lowest value being 21.9 ± 0.34 ºC and highest being 22.5 ± 0.35 ºC at Korongo and Sher sampling stations respectively. Conductivity was stable ranging between 257.3 ± 0.92 and 259 ± 1.03 µS cm^{-1} at Hippo point and Sher stations respectively (Table 5). The results showed no significant difference in the conductivity values (One way ANOVA; F=10.13, P > 0.005)

Crescent lake sampling station had the lowest pH level at 8.1. The highest level was at Sher and Mid lake at 8.6. Korongo, Hippo point and Malewa sampling stations had pH values of 8.5, 8.3 and 8.3 respectively. There were no significant differences in pH among the sites (One way ANOVA; F= 2.54, P > 0.005). Dissolved oxygen (DO) levels were lowest at Hippo point Malewa station at 7.4 ± 0.20 mg l^{-1}. The highest was at Malewa which had 8.2 ± 0.30 mg l^{-1}.

One way ANOVA showed no significant differences in the DO levels among the sampling stations (F= 10.80, P <0.005). The values of temperature, conductivity, dissolved oxygen and pH obtained in this study, are within the ranges necessary for normal growth and reproduction of both *C. carpio* and *O. leucostictus* (Oyugi *et al.*, 2012).

4.2 Diet and Feeding Habits

4.2.1 Contribution of food items in fish diet

During the period of July to December 2013 the gut contents of 153 *O. leucostictus* and 162 *C. carpio* were analysed. Detritus, algae and zooplankton were the most abundant food types in the guts of the two fish species, with fish of all sizes including the dietary items in their diet (Fig. 2). Detritus contributed the highest proportion in the diet of both *O. leucostictus* and *C. carpio* in all the sampling stations. Despite *O. leucostictus* and *C. carpio* having diversified their feeding habit to include mainly detritus and phytoplankton, higher plant materials still contributed significant portion of food items consumed by the fish in Lake Naivasha.

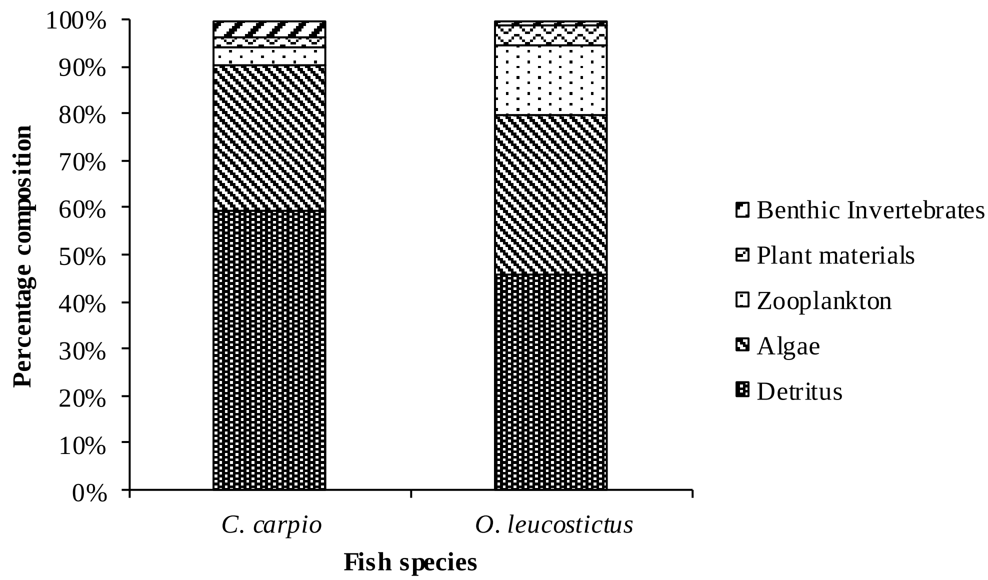


Figure 2: Dietary composition of *C. carpio* and *O. leucostictus* in Lake Naivasha from July to December 2013.

4.2.2 Spatial variation in diet composition

There was minimal spatial variation in the composition of the food items consumed by both *C. carpio* and *O. leucostictus* in Lake Naivasha. Detritus dominated *C. carpio* diet in both the inshore (Crescent, Korongo, Malewa, Sher, Hippo point) and offshore (Mid lake) sampling stations (Fig. 3). The lowest composition of detritus was at Korongo and the highest at Sher sampling stations at 61% and 75% respectively. The other important food items in the guts of *C. carpio* were zooplankton, benthic invertebrates and plant materials.

Zooplankton abundance ranged from 1- 8% in all the sampling stations. Zooplankton in the guts of *C. carpio* at Crescent, Korongo and Malewa sampling stations constituted 8%, 4% and 3% respectively. Carps from Mid lake, Sher and Hippo point sampling stations had 2%, 1% and 2% of zooplankton as their gut contents (Fig. 3). A chi-square test detected no significant differences between the food items ingested by *C. carpio* in all the sampling stations.

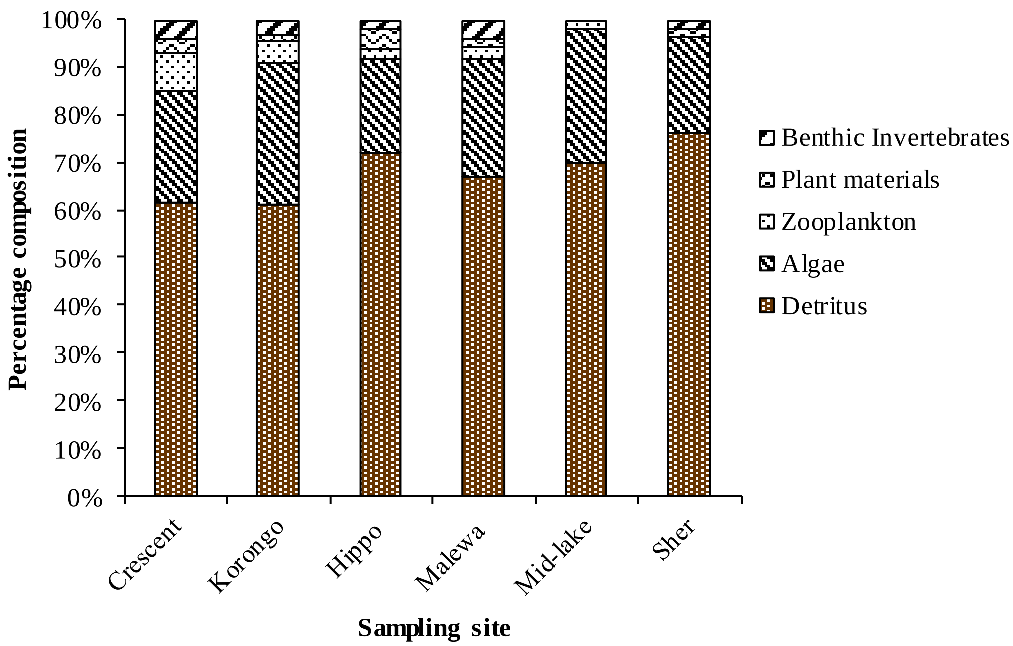


Figure 3: Food composition in the guts of *C. carpio* at different sampling stations in Lake Naivasha from July to December 2013.

The important food items of *O. leucostictus* in all sampling stations was detritus at Sher (52%) followed by algae at Hippo point (35%) and zooplankton at Mid lake (24%). Benthic macroinvertebrates and higher plant materials constituted insignificant proportions of *O. leucostictus* food each at 4%. Chi-square test detected no significant differences between the food items ingested by *O. leucostictus* in all the sampling stations ($P < 0.005$).No significant spatial variation was detected between the other food items. Further analyses revealed that detritus was the most important food item for *O. leucostictus* in all the sampling stations.

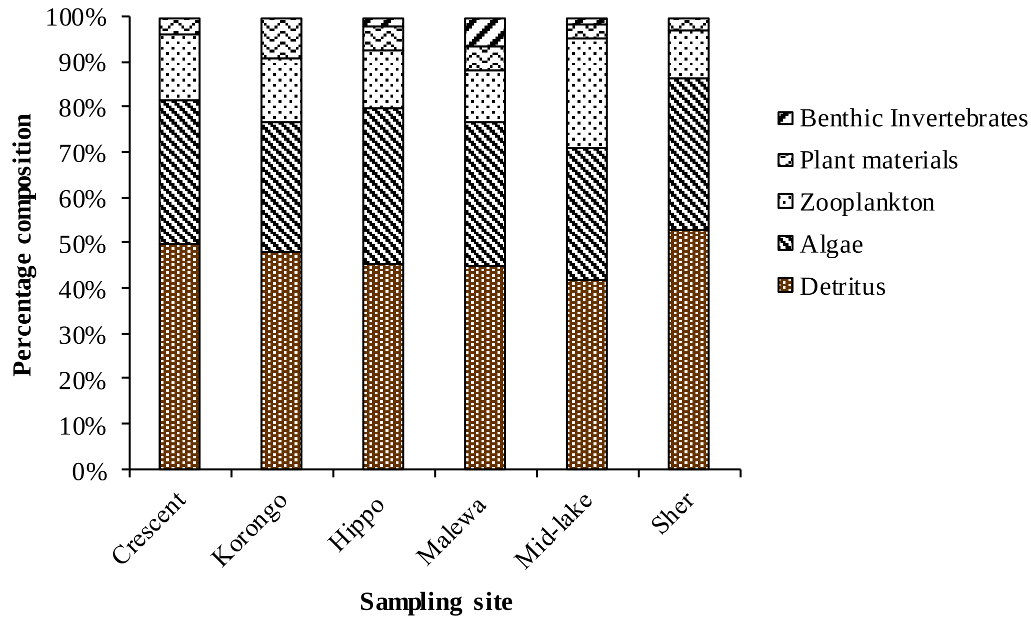


Figure 4: Items contributing to the gut contents of *O. leucostictus* at different sampling stations in Lake Naivasha from July to December 2013.

4.3 Morphometrics

4.3.1 Length-weight relationships

A total of 315 fish were measured. Total length of *C. carpio* ranged from 22.3 to 58.6 cm and their weight from 250 to 1995 g while *O. leucostictus* ranged from 19.5 to 27.9 cm in total length and 115 to 900 g in total weight. The total length - total weight relationships were separately evaluated for all individuals and grouped by sex (females and males). The length-weight relationship slopes were typically below the values of 3 for fish growth in general to be assumed to be isometric (Fig. 5 and 6).

Results from this study showed that all samples of *O. leucostictus* and *C. carpio* from all sampling stations had regression slopes with values of $b < 3$. However, *C. carpio* had higher a and b values compared to *O. leucostictus* (Fig. 5).

Figure 5 (a) shows the length-weight relationship of both male and female *O. leucostictus* combined. The regression slope, b, was 1.093, which is lower than the allometry coefficient value of 3. This indicates that the fish had negative allometric growth.

When sexes were seperated, male (Fig. 5b) and female (Fig. 5c) *O. leucostictus* had different allometry coefficient values of 1.152 and 0.922 for male and femalerespectively. These values indicated that both male and female *O. leucostictus* had negative allometric growth.

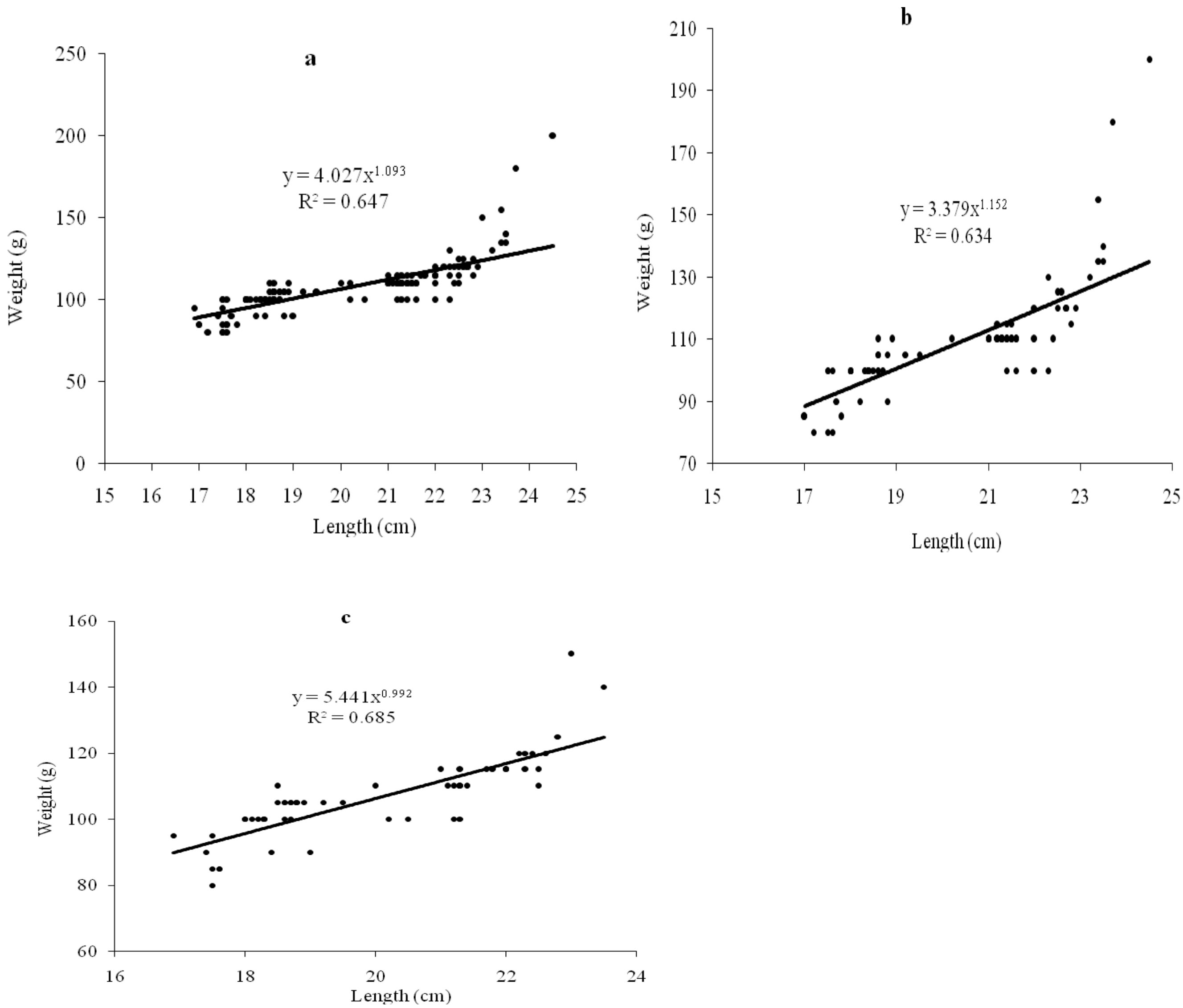


Figure 5: L – W relationship of (a) both sexes, (b) male and (c) female *O. leucostictus* in Lake Naivasha.

A combination of both male and female (Fig. 6a) fish of *C. carpio* had a *b* value of 2.565 which was less than 3, also showing negative allometric growth in this fish species. Males (Fig. 6b) in *C. carpio* had *b* value of 2.597 and females (Fig. 6c) had *b* value of 2.484 indicating that both male and female *C. carpio* had negative allometric growth.

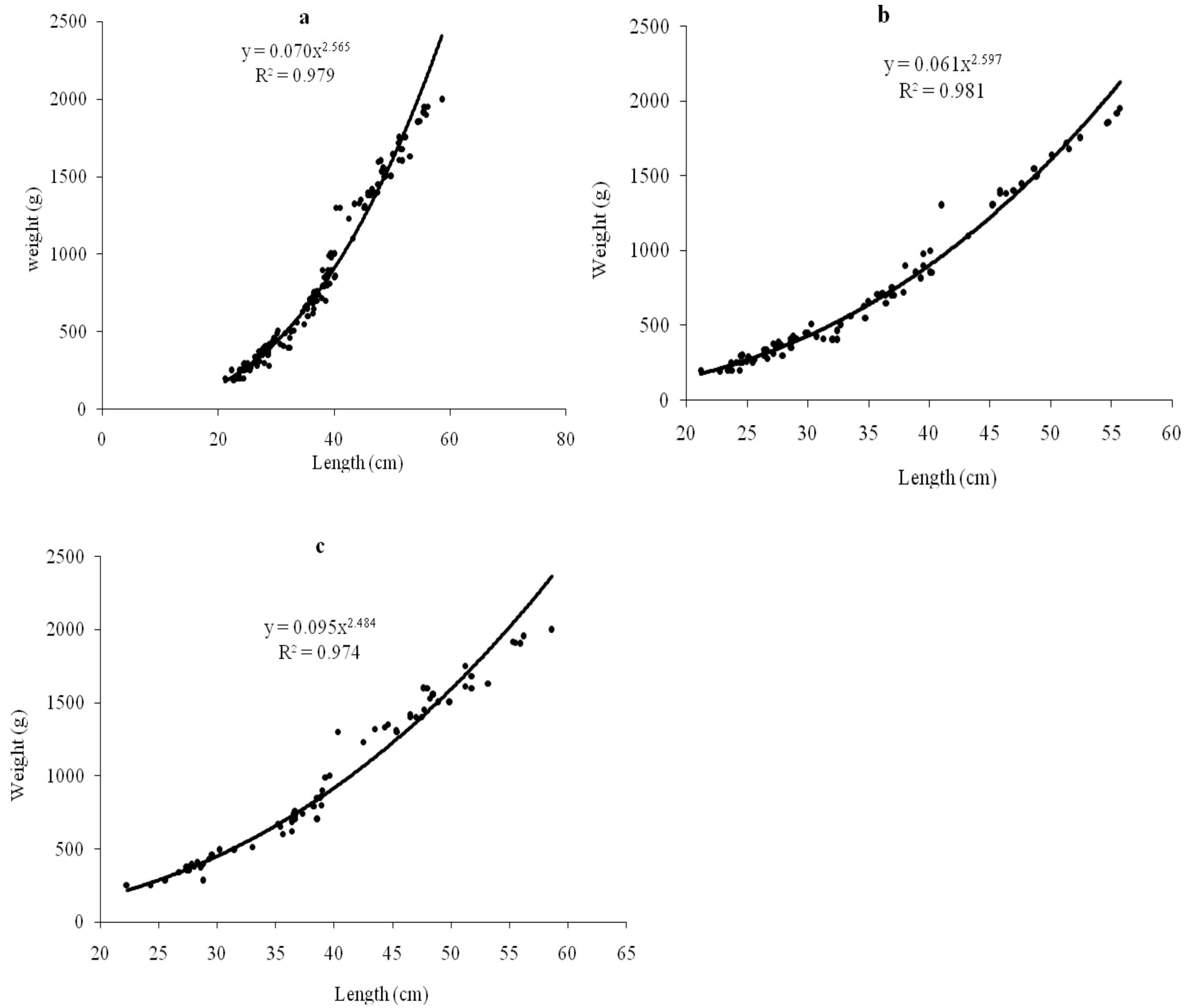


Figure 6: L – W relationship of (a) both sexes, (b) male and (c) female *C. carpio* in Lake Naivasha.

4.3.2 Condition factors

All the fish samples collected had condition factor values > 1. Between the two fish species, *C. carpio* had a condition factor of 1.51 while *O. leucostictus* had 1.32. The females of *C. carpio* had a K value of 1.53 while female *O. leucostictus* had 1.35. Similarly, male *C. carpio* had K value of 1.52 while males of *O. leucostictus* had a value of 1.33 (Fig. 7).

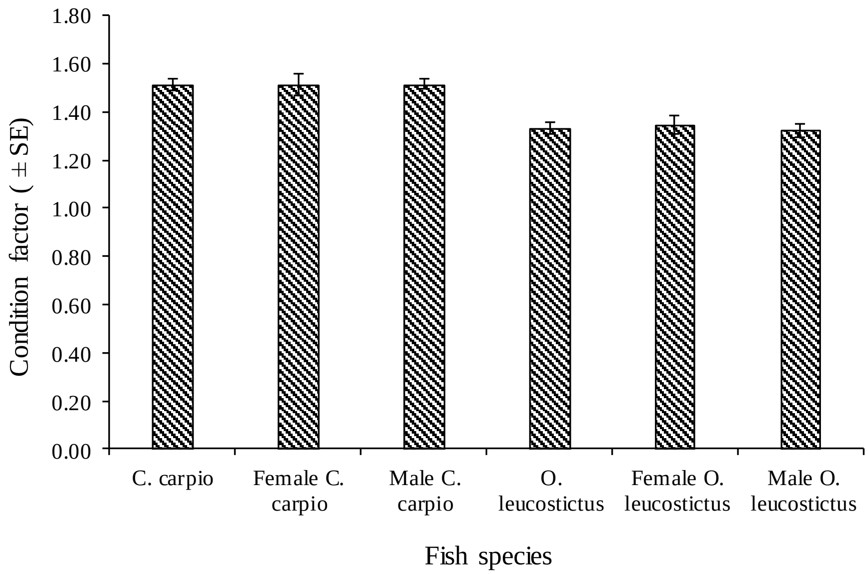


Figure 7: Variations in condition factors of *O. leucostictus* and *C. carpio* in Lake Naivasha during this study.

4.4 Reproduction

4.4.1 Sex ratios and maturity stages

A total of 315 fish were measured in this study, out of which 153 were *O. leucostictus* and 162 *C. carpio*. Of the 153 specimen, 92 were males and 61 were females giving an overall sex-ratio (males/females) of 1.51:1. *C. carpio* had 91 males and 71 females with a sex-ratio of 1.28:1. Figure 8 shows the classification of *C. carpio* based on their total lengths. The least dominant *C. carpio* were males in size class 21-25 cm while the most dominant were females in class 26-30 cm TL (Fig. 8). Males were dominant between 21-35 cm TL and 51-55 cm TL size classes while females were dominant in classes 36-40 cm, 46-50 cm and 56-70 cm TL. There was equal proportion of male and female *C. carpio* in 41-45 cm TL class (Fig. 8).

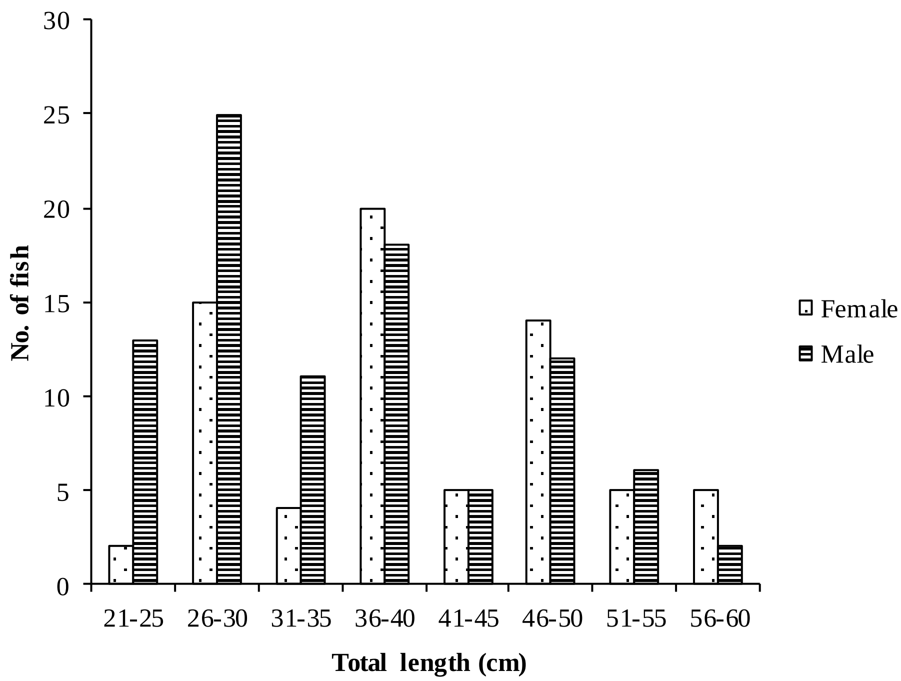


Figure 8: Sex classification of *C. carpio* in different size classes in Lake Naivasha during the study.

Maturity stages of *C. carpio* were classified seperately (Fig. 9 a and b). The lowest abundance of males was in class the 56-60 cm TL having 2 fish (M5) while the highest was class 26-30 cm TL with 25 fish at 3 different maturity stages (M2, M3 and M4). The maturity stage with the most males in a single class was stage 3 in the 26-30 cm TL size class. Male maturity stage VI had no representative in the samples collected.

Female *C. carpio* were least represented in maturity stage 2 in class 21-25 cm TL having 2 fish. The 36-40 cm TL size class had 20 representatives making it the class with the most female fish. Unlike the males, female *C. carpio* had representatives in stage VI, all occuring in 56-60 cm TL class.

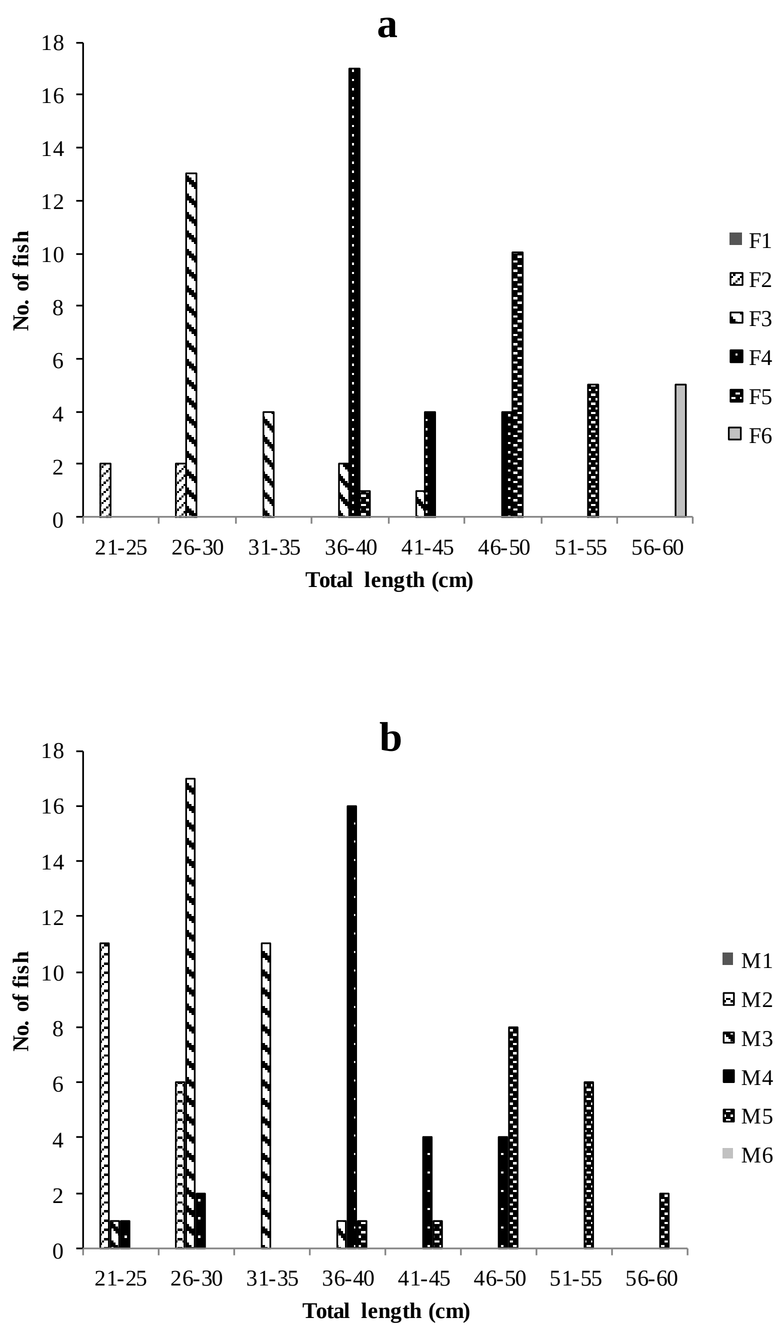


Figure 9: Total number of (a) female and (b) male C. *carpio* into different maturity stages in Lake Naivasha from July to December 2013.

From a total population of 153 *O. leucostictus*, 60% were males and 40% female. The 17-19 cm and 21-23 cm TL size classes contained most of the fish species. The 25-27 cm TL size class had only two male fish (Fig. 10).

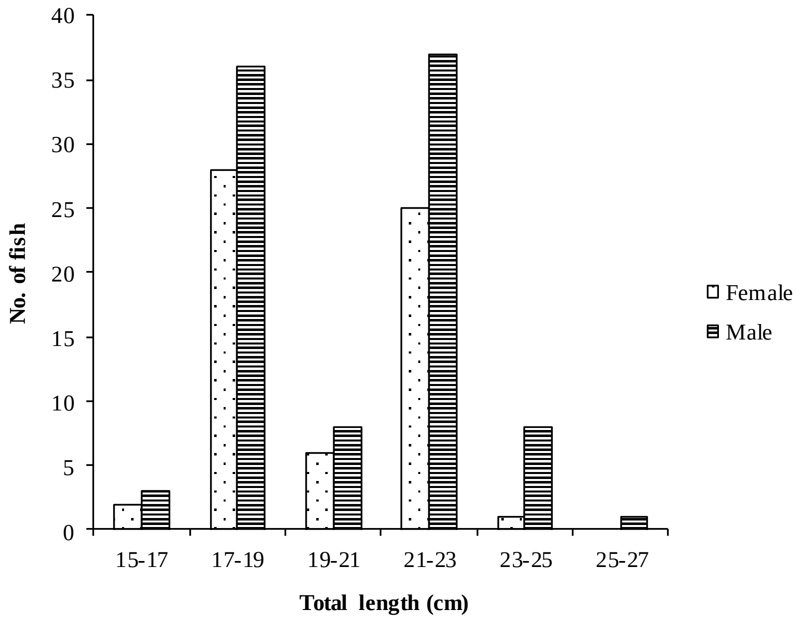
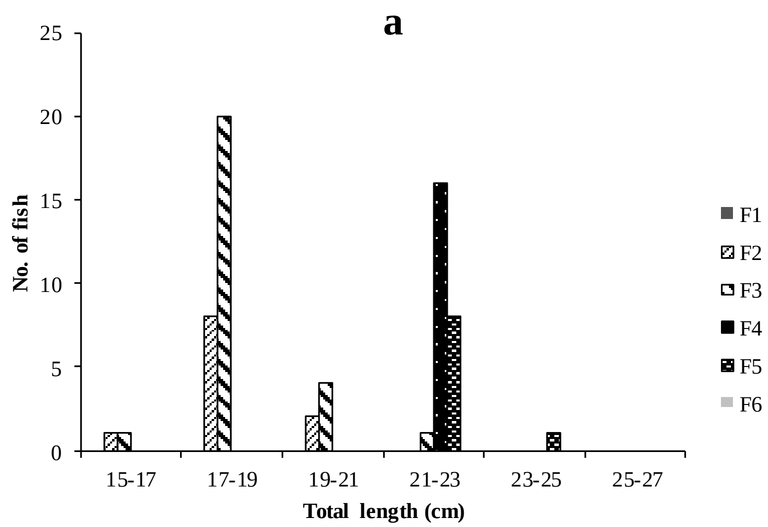


Figure 10: Sex classification of *O. leucostictus* into different size classes in Lake Naivasha from July to December 2013.

All male and female *O. leucostictus* (153 samples) were classified separately based on the level of maturity of their gonads (Fig. 11). Most males were in the maturity stage III while stage VI had the least representatives. There was no male fish in stage I. The highest percentage of the males was fish of total length between 17cm and 23 cm. The males of *O. leucostictus* were more evenly distributed across the classes than females. Majority of the *O. leucostictus* were in maturity stage III. It was followed by stage IV with 16 female fish. Female fish in the size class 17-19 cm TL were the most represented in the samples having 28 fish.



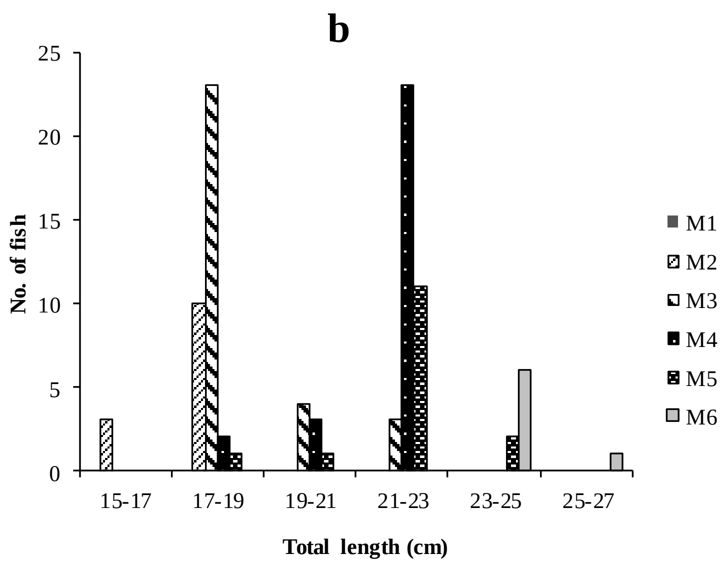
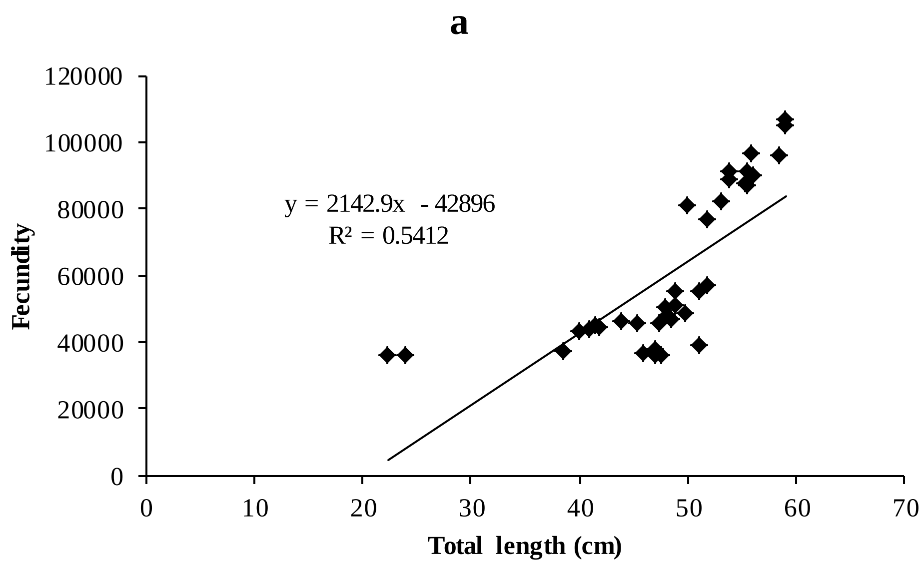


Figure 11: Total number of (a) female and (b) male *O. leucostictus* in different maturity stages in Lake Naivasha from July to December 2013.

4.4.2 Fecundity

A total of 50 gravid *O. leucostictus* ranging in size from 19.5 to 27.9 cm of total length and 115 – 900 g in weight, and 61 gravid *C. carpio* ranging from 22.3 to 58.6 cm total length and 250 – 1995 g weight were studied. Fecundity varied markedly between the two fish species.

All samples of *O. leucostictus* were in maturity stages IV and V while *C. carpio* had fish from maturity stage III to stage VI. Fecundity for *C. carpio* varied between 35,654 and 106,520 eggs per female for maturity stages III–VI. Fecundity of *O. leucostictus* was between 998 and 1974 eggs per female in maturity stages IV and V (Fig. 12 and 13). The heavier and longer fish tended to be more fecund than the less heavy and shorter fish. Fecundity in relation to total length and body weight for both fish species are shown in figures 12 and 13. The curves and lines were fitted by calculated regressions.



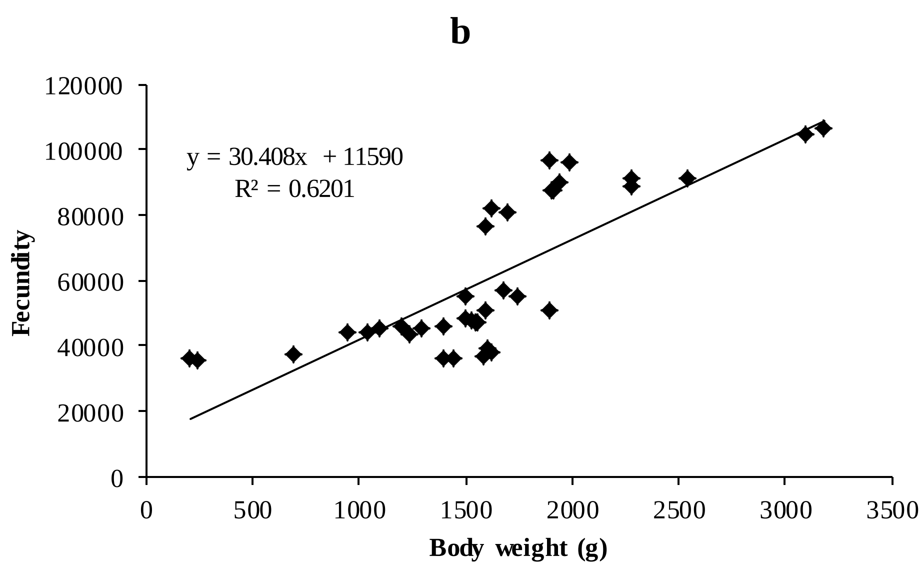
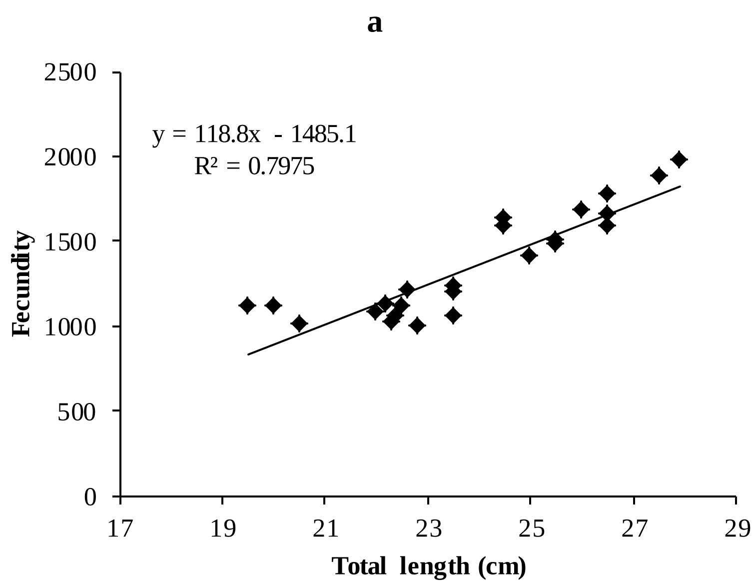


Figure 12: Relationship between (a) fecundity and total length and (b) fecundity and body weight of *C. carpio* females in Lake Naivasha from July to December 2013.



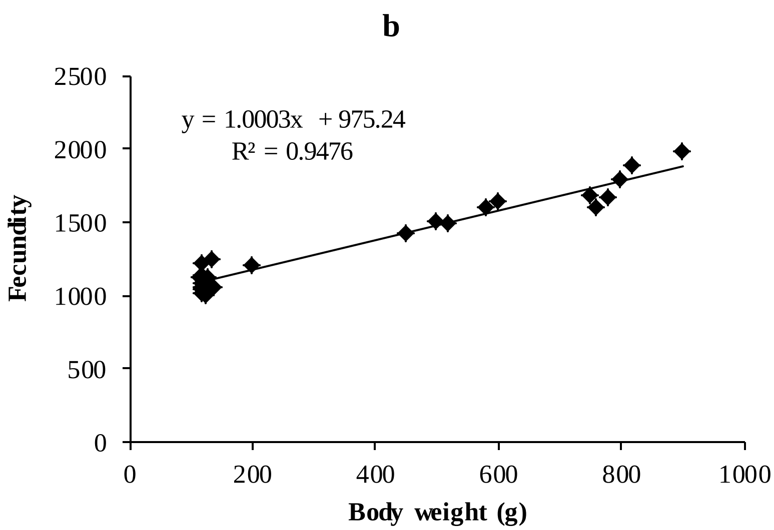


Figure 13: Relationship between (a) fecundity and total length and (b) fecundity and body weight of *O. leucostictus* females in Lake Naivasha from July to December 2013.

CHAPTER FIVE

5.0 DISCUSSION

5.1 Physico-chemical parameters

The physico-chemical parameters of Lake Naivasha have great influence on the feeding habits, reproduction and growth of fish in the lake (KMFRI, 2007: Oyugi *et al.*, 2014). The pH, depth and secchi depth measurements throughout the sampling period did not differ from previous measurements (KMFRI, 2007) and are also similar to measurements by Outa *et al.,* (2014). The high turbidity at Malewa station was likely influenced by the inflowing water from River Malewa which carries sediments to the lake. Another influence on the turbidity of Malewa sampling station could be the input from the decaying plant materials from the macrophytes in the area and non-point inflows from horticultural farms. This could also explain the higher conductivity and low oxygen values in these areas as decomposition consumes oxygen present in the water leading to low pH levels. There was no significant difference in the temperature values recorded and this could be attributed to the fact that the lake is small in size with a relatively shallow depth thus mixes easily (Ndung'u *et al.*, 2013).

5.2 Diet and feeding habits of *O. leucostictus* and *C. carpio*

The highest proportion of phytoplankton was consumed in the open waters compared to the areas closer to the shore. This could be due to the openness and lack of free floating macrophytes in these off shore sampling stations allowing for more light penetration hence more phytoplankton biomass compared to areas closer to the shore where macrophytes shade the water from direct sunlight hence inhibiting phytoplankton development.

The higher percentages of higher plant materials recorded in the near shore areas (Korongo and Hippo point) than in the sites located in the open deeper areas of the lake (Sher Bay, Oserian and Crescent Island) could be due to the infestation and presence of water hyacinth and other macrophytes as compared to the open lake which only receives floating macrophytes occasionally especially during strong winds. There was no significant difference in the amount of detritus in the diet of both fish in all the sampling stations. However, slightly higher detritus amounts were recorded in the near shore areas. This could be attributed to the decaying of plant materials abundant at the littoral zone. Occasionally, the decayed plant materials and other sediments are usually carried to the deeper waters through lake mixing particularly by wind thus distributing the detritus throughout the lake. This could explain the almost equal contribution of detritus in all the sampling station within the lake.

An earlier study by Oyugi *et al.* (2012) found that *C. carpio* in Lake Naivasha had diversified its diet by feeding on plant materials (57%), detritus (12%) and fish remains (11%). A study of *O. leucostictus* in Lake Naivasha by Muchiri (1990) found detritus to be the principal component of their diet. Detritus is the most abundant food material available to fish in the lake and its importance has been previously noted by Malvestuto (1974) and Siddiqui (1977). Of the other dietary constituents, various algae, especially planktonic forms, were predominant.

5.3 Morphometrics

5.3.1 Length-weight relationship

Results of the length-weight relationship slopes did not obey cube law (Taylor *et al.*, 2011). The fish exhibited negative allometric growth, which is an indication that the condition of the sampled fish is not normal therefore irregular. The negative allometry in the length-weight relationship of fish in the whole lake is an indication that the population of the species in these zones had heterogeneous groups with body weights varying differently with the cube of total length. This (b<3) means that large fish had more elongated body shape and smaller fish were in better nutritional condition at the time of sampling (Garcia *et al.*, 1998). The inshore sampling stations are intensively fished and use of illegal methods, such as seine nets, was rampant during the study possibly leading to reduction in fish size. According to Tesch (1971), the slope is often nearly constant throughout the year or throughout a series of different environments for the same species. This study shows similar findings where the only differences in intercepts are noted between the fish species and not the habitats. The slope, therefore, offers a more objective method for analyzing growth and production in fishes.

In this study, the higher correlation coefficient (r) of LWR of *C. carpio* indicates that length increases with increasing weight. This observation corresponds to earlier study by Aera *et al.*, (2014) in Lake Naivasha which indicated that Length-weight relationships between males and females ($p < 0.05$) with 'r' values of 0.82 and 0.72 respectively.

The growth exponent ('b' values) of the length-weight relationship for the male fish indicated isometric growth and negative allometric growth for females. In contrast to the values obtained in this study, Britton *et al.* (2007) showed that *C. carpio* and *O. leucostictus* in Lake Naivasha had *b* values of 3.108 and 3.0583 respectively indicating isometric growth for the two fish species. The causal factors of the differences between this study and Britton *et al.*, (2007) possibly include the number of samples examined, sample size range and reproductive stages, and the waters experiencing different climatic and environmental variables. Fish caught in 2007 were of a larger size compared to those caught in this study.

According to Gerritsen *et al.* (2003), the variations in '*b*' values between males and females may depend on various factors such as number of specimen examined, and the sampling season. However, the change of *b* values may also depend primarily on the shape and fatness of the species as well as physical factors such as temperature, salinity, food and stage of maturity (Sparre and Venema, 1998; Sarkar *et al.*, 2013).

5.3.2 Condition factor

Fish body condition is known to vary seasonally depending on changes in gonadal development, food availability, and other environmental factors (Pope and Willis, 1996). Although both fish species had different K values, the results show they were in good condition with condition factor values above 1.

According to Le Cren (1951), values of the condition factor vary according to seasons and are influenced by environmental conditions. The favourable physico-chemical water parameters in Lake Naivasha may therefore have been a catalyst for the good condition factor of the two fish species.

The physico-chemical parameters of Lake Naivasha measured in this study were within the tolerable range for both *O. leucostictus* and *C. carpio* (Edwards and Twomey, 1982). In a study of *O. leucostictus* in Lake Naivasha, Siddiqui (1977) found all stages of gonad maturation all year round and did not observe any seasonal fluctuation in relative condition factor, which he attributed to a constant proportion of fish with gonads in different stages of development.

A study of *C. carpio* by Nathaniel *et al.* (1998) found that irrespective of the location of sampling in the Victoria reservoir (Uganda), the condition factor of gravid females was within the range 1.6 and 2.0. However, the average body condition of ripe females from the reservoir was better than those sampled from a fish pond. The results from this study are similar to the findings of Victoria reservoir in which the condition factor of *C. carpio* was 1.52.

5.4 Reproduction

5.4.1 Sex ratios

Both *O. leucostictus* and *C. carpio* in Lake Naivasha show a well-defined reproductive strategy, which has probably contributed to their success in the lake. Domination of males in the catch was possibly because of differential migration of the sexes (Lowe-McConnell, 1958; Rinne & Wanjala, 1982). The males of *O. leucostictus* establish nests in the shallow waters and tend to aggregate there during the spawning period, whilst ripe females visit the nests to spawn but disperse after doing so. Consequently, fishing in nesting areas, as is the case in Lake Naivasha, could result in the catch being biased towards males. This kind of observation is a frequent occurrence in the cichlid trawl fisheries on Lake Victoria (Njiru *et al.*, 2006).

In addition, male fish of *O. leucostictus* tend to be more territorial compared to female ones which make them more vulnerable to being caught in nets. Furthermore, the faster growth of males (Fryer and Iles, 1972) may mean that they achieve the size at which more of them are caught in the gill nets, causing selection of males against the smaller females. This argument is supported by findings from Ugandan waters of Lake Victoria where the male:female sex ratios in populations of tilapia caught by gillnets, which exhibit less selective sex discrimination, were close to 1:1 (Balirwa, 1998). After fertilization of eggs, the male *O. leucostictus* emigrated from spawning areas towards feeding grounds located in shallow parts of the lake. Meanwhile, the females move towards submerged vegetation and rocky areas for incubation of the eggs. During the incubation period, feeding and movement are minimized by the female fish making them unlikely to be caught during sampling hence the low numbers of females obtained during this study. Similar sex ratio results were obtained by Hailu (2013) in his investigation of the reproductive aspects of *C. carpio* in a tropical reservoir in Ethiopia.

A study on a tilapiine fish (*O. niloticus*), which is similar to *O. leucostictus* by Njiru *et al.*, (2006) indicated a male dominated population with sex ratio being significantly different from 1:1 in the Kenyan portion of Lake Victoria. Males were significantly more abundant than females except in the 20–25, 25–30, 35–40 cm TL size classes. The total numbers of males were significantly greater than females in all the stations sampled.

5.4.2 Fecundity

The spawning characteristics of fish vary in respect to their species and the ecological properties of the water system in which they live (Nikolsky, 1963). Irrespective of the location, the fecundity of *C. carpio* recorded in this study compares well with those recorded by Nathaniel *et al.* (1998) for different size classes of common carp in Victoria reservoir and a fish pond adjacent to the lake in Uganda. The maximum total length and weight of gravid females collected from the reservoir was 46.0 cm and 1990 g respectively, whereas those from the pond had a maximum length of 31.9 cm and a weight of 542.3 g. Gravid females from the reservoir had heavily yolked ova with a maximum fecundity of 240, 100 eggs whereas those from the pond had less energy rich pale yellow ova with a maximum fecundity of 65, 642. Irrespective of the location, the fecundity of females within the same length group fell within the same broad range, and compares well with that recorded by Jhingran and Pullin (1985).

In Lake Naivasha, the maximum number of eggs recorded for *C. carpio* was 106, 520. This is much lower compared to the fecundity from the Victoria reservoir number of 240, 100 eggs. In the reservoir, the main factor that influenced the availability of substrates is the wide fluctuation in water level which is not the case in Lake Naivasha. During high water level a large area around the reservoir is submerged for a sufficiently long period and the lush growth of grasses and macrophytes provide an ideal substrate for spawning. There are minimal submerged grasses and macrophytes in Lake Naivasha and as a result there is a reduced area of substrate for spawning by *C. carpio*. There are rarely frequent flooding seasons compared to Victoria reservoir.

C. carpio provide no parental care, and the high reproductive capacity tends to compensate for the mortality of eggs and young which are exposed to hazards of the environment. The development of gametes within the gonads of common carp is determined primarily by water temperature and food availability (FAO, 1985). To reproduce efficiently the female needs warm water above 17°C and food rich in protein (FAO, 1985). Field and experimental studies conducted on the fecundity of many different fish species reveal that changes in fecundity occur in response to food quality as well as quantity (Oyugi *et al*., 2012)

The entry of *C. carpio* into Lake Naivasha has also shown significant initial disruption on life-history traits particularly for *T. zillii* and *M. salmoides* (Oyugi *et al.*, 2012). For instance, *T. zillii* and *O. leucostictus* depend on submerged macrophyte areas for breeding, thus increase in turbidity leads to loss of such habitats (Britton *et al*., 2007). Since the entry of the carp into the lake in the late 1990s (Hickley *et al*., 2004) and its subsequent proliferation, the reproductive investment and consequent abundance of the tilapines has significantly declined (Oyugi *et al*, 2012). This invasive character of *C. carpio* leading to poor water quality is the main factor of the reduction of the fecundity of tilapiine as result of disruption of their nest building strategies.

CONCLUSIONS AND RECOMMENDATIONS

6.1 Conclusions

Based on the results of this study, it can be concluded that:

i. The habit of *C. carpio* of rooting or digging in the bottom has had a negative effect on the environmental condition of Lake Naivasha through increase in turbidity, decrease in oxygen and mobilization of nutrients to the water column from the benthos. This has in turn led to both *C. carpio* and *O. leucostictus* ingesting the suspended detritus as their main source of food with *C. carpio* outcompeting *O. leucostictus* due to its prolific nature and better adaptability to such conditions. Therefore, both fish species are detritus feeders.

ii. The faster growth of male *C. carpio* and *O. leucostictus* in the lake and their aggregative nature could have led to the sex ratio favouring more male than female fish. Rooting and digging action of *C. carpio* may have led to destruction of the spawning grounds of *O. leucostictus* and could have also indirectly led to a decrease in fecundity of *O. leucostictus*.

iii. The negative allometric growth observed in the length-weight relationship of *C. carpio* and *O. leucostictus* could be attributed to the relatively small body and sample sizes, and lower maturity stages of both fish species. However, the good condition factor of *C. carpio* in Lake Naivasha is an indication that the fish have better tissue energy reserves, greater reproductive potential and higher survival compared to *O. leucostictus* which have a lower condition factor.

It can therefore be concluded that the feeding and reproductive ecology of *C. carpio* has disrupted the natural environmental conditions of Lake Naivasha causing a decline in the numbers of *O. leucostictus* through alteration of its feeding and reproductive strategies.

6.2 Recommendations

Based on the conclusions made from this study, it can be recommended that:

i. Dietary studies need to be done on other fish species in Lake Naivasha to find out if there is change of diet as a result of the effects of the feeding habit of *C. carpio*. This will conclusively indicate if *C. carpio* had an influence on the diet of *O. leucostictus*.

ii. Results from this study also showed the mature reproducing females of *O. leucostictus* to be smaller in body size compared to the same fish from Lake Victoria and other natural water bodies. Therefore, it is necessary to carry out biochemical analysis on the soft tissues of *O. leucostictus* in Lake Naivasha to establish whether the fish population is under stress.

iii. For both fish species to co-exist in the lake and for fish consumers to derive benefits from both, fisheries stakeholders should consider restocking of *O. leucostictus* in Lake Naivasha to ensure constant supply of the fish.

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