BIOLOGY OF THE AFRICAN LUNGFISH Protopterus aethiopicus HECKEL 1851, AND SOME ASPECTS OF ITS FISHERY IN LAKE BARINGO, KENYA

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Biology of the African lungfish Protopterus aethiopicus Heckel 1851,

and some aspects of its fishery in Lake Baringo, Kenya.

By

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B.Sc. (Hons), M.Sc.



A thesis submitted to the School of Graduate Studies

in partial fulfilment of the requirements for the Degree of Doctor of Philosophy

Department of Biology

Memorial University of Newfoundland

October 2003

St. John's

Newfoundland

Canada

Abstract

The introduction of the marbled lungfish (*Protopterus aethiopicus*) into Lake Baringo created a new fishery. This study describes the life history characteristics and movements of this population, and provides baseline biological information for more rational exploitation and management of its fishery. Biological data were obtained from fishery landings, while movement and space use were studied using ultrasonic telemetry.

Biological data indicate Lake Baringo lungfish grow allometrically, individual growth in length was about 14.5 cm year⁻¹. Males mature later than females, but are less abundant in open waters, likely because they spend more time in inshore spawning areas. Spawning occurs year-round, probably related to the lack of a predictable rainy season in Lake Baringo. Internal differentiation of the digestive tract was apparent contrary to previous reports. Their diet in Lake Baringo is primarily piscivorous.

Ultrasonic telemetry showed lungfish are not sluggish, but rather make nonrandom daily movements (likely in search of prey) in the open waters and were active at night as well as in the day. Their movements consisted of: 1) shorter daily movements over several weeks or months, followed by 2) a series of successive longer daily movements over a few days, and there was evidence of navigational ability. Sonically tagged lungfish ranged widely but tended to avoid shallow inshore waters where crocodiles are abundant. However, some had home ranges of varying size $(5.8 - 19.8 \text{ km}^2)$ and which were occupied for 2 - 4.5 months. Ultrasonic-tagged fish were always relocated in the lake, however, one radio-tagged lungfish was caught in a swamp Biology of the African lungfish Protopterus aethiopicus Heckel 1851,

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Radio telemetry results suggested that *P. aethiopicus* are not obligate air breathers. Aerial respiration is necessary, however, during stress situations and this probably explains the death of most lungfish caught on long-lines. Attaching hooks to long leaders will allow hooked fish to access the surface and increase live lungfish landings, which earn more income. Maintenance of a viable lungfish fishery in Lake Baringo depends on protection and conservation of shallow inshore riparian areas and control of illegal fishing practices.

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Dedication

To my wife, my children, and my kin in the Greater Family of my father, the Late Mzee Mwathethe Bugo (aka Mtwenzi Bugoh) of Gede-Kizingo village.

This is for the many moments of sadness and joy in your individual and collective lives, that I could not physically be part of during the course of this study.

And

To the memory of my elder stepbrother, the Late Alfred Kazungu Mwatete (aka *Tsawe* BiKache), for his "big love" to all members of our father's family. *This is my tribute for his instrumental role in ensuring that we, all his stepsiblings, got a primary education and for encouraging each one of us to pursue formal education to the limit of our capabilities. It got me this far.*

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Chapter 1 Introduction

Knowledge of the biology and ecology of fish species is important to understanding the dynamics of their populations. For commercially exploited fish populations, such information is invaluable in guiding formulation of policies for rational exploitation and management (Ogutu-Ohwayo 1990, Molsa et al. 1999, Welcomme 2001). Lake Baringo has a history of commercial fishing that dates back to 1956 when a Mr. D. Roberts set up a fishing camp (Kampi Ya Samaki) on the western shores of the lake (DFO 1996). This fishing was conducted by gillnetting and primarily targeted the Baringo tilapia (Orechromis niloticus baringoensis Trewavas), although other indigenous species like the African catfish (Clarias gariepinus Burchell) and a cyprinid (Barbus gregorii Boulenger) were also caught. The smaller cyprinid (Labeo cylindricus Peters) was caught in small (1.5 inch) mesh bottom set gillnets (Ssentongo 1974). Fishing in Lake Baringo is carried out both by members of the local communities (II Chamus, Pokot and Tugen) and by immigrant fishermen of the Luo community from Nyanza province along the shores of Lake Victoria (DFO 1996). Available data indicates that annual fish production averaged above 500 metric tons in the late 1960's (Ssentongo 1995, Muchiri 1997). The highest annual catch was 717 metric tons landed in 1970 but catches subsequently declined to a low of 58 metric tons in 1972. Muchiri (1997) described the annual fluctuations in fish production in Kenya's three Rift Valley lake fisheries and showed that they closely corresponded with changes in water levels for both Lake Naivasha and Lake Turkana. Although catches in Lake Baringo showed similar fluctuations, lack of a comprehensive data set on water level changes could not allow demonstration of a similar relationship.

According to the Baringo District Development Plan 1997-2001, the Lake Baringo fishery directly supports over 500 families (GOK 1997). Income generated from fishing varies with annual landings but is well over KSh. 3 million for most years (Kimakwa 2000). The tilapia is the most landed species by number but occasionally the introduced lungfish dominates landings by weight (De Vos *et al.* 1998). However, little is known about the biology and ecology of the fish species exploited in the Lake Baringo fishery. This study focused on the biology of the marbled African lungfish *Protopterus aethiopicus* Heckel 1851 (Plate 1.1) in Lake Baringo, a recent introduction that became naturalized and now has an established self-sustaining population that supports a commercial fishery.

Lungfish biology: a general review of the literature

Lungfishes derive their name from the possession of lungs, which enables them to obtain oxygen from air like other higher vertebrates (Thomson 1969, Helfman *et al.* 1997). As a group, lungfishes have a well-documented evolutionary history attributed to a good fossil record as they almost entirely evolved in freshwater habitats, which are more prone to stagnation and drying up, hence conducive to fossilization (Moyle and Cech 2004). Stratigraphical and palaoecological evidence shows lungfishes first arose in shallow marine habitats (Campbell and Barwick 1986) during the Devonian period (about 400 mya) but invaded freshwaters early in their evolutionary history and were dominant freshwater fishes on all continents throughout the Mesozoic era (Helfman *et al.* 1997). The fossil record



Plate 1.1 The marbled African lungfish Protopterus aethiopicus Heckel 1851

shows lungfishes became extinct during late Cretaceous in all but the Neotropical, Australian and African zoogeographical regions; which collectively have the six extant lungfish species (Moyle and Cech 2004). According to Helfman *et al.* (1997) the families and genera of extant lungfishes date back to the Cretaceous period in the Mesozoic.

Extant lungfish belong to Dipnoi, a universally recognized natural group, which dates back to the Lower Devonian (Cloutier and Ahlberg 1996). Since the first specimen of South American lungfish was caught in 1836, lungfishes have remained an evolutionary and biologically interesting and often controversial group of fishes. This has been related largely to their possible link to tetrapod evolution (Thomson 1969, Bruton 1998). The systematics literature is replete with reviews and revisions of lungfish position on the taxonomic hierarchy and hence their relationship with other fishes and tetrapods (see Conant 1986, Cloutier and Ahlberg 1996). However, it is generally held that in terms of extant organisms, the Dipnoi are the Recent sister-group of the Tetrapoda (Cloutier and Ahlberg 1996, Venkatesh et al. 2001). In his revised classification of fishes Nelson (1994) placed extant lungfishes in the infraclass Dipnoi, superorder Ceratodontimorpha. Together with the only known species of coelacanths (Family: Coelacanthidae) of the subclass two Coelacanthimorpha, they belong to the Class Sarcopterygii, a group of lobe-finned fishes with largely cartilaginous skeletons. Nelson (1994) classified the six living lungfish species into three genera and families: Protopterus (P. aethiopicus, P. amphibius, P. annectens, and P. dolloi, family; Protopteridae, African lungfishes); Lepidosiren (L. paradoxa, family; Lepidosirenidae, South American lungfish); and Neoceratodus (N. forsteri, family; Ceratodontidae, Australian lungfish).

Biologically, extant lungfishes are interesting because they possess both gills and lungs hence their ability to obtain respiratory oxygen from water and air (Thomson 1969). Other distinguishing characteristics include the possession of primitive fins, a largely cartilaginous skeleton, internal nares, platelike teeth, intestinal spiral valves and a heart structure very similar to that of amphibians (Nelson 1994). The Australian lungfish is considered most primitive (Kemp 1986, Helfman et al. 1997); however, this facultative air breather possesses a single dorsal lung that possibly functions more as a hydrostatic than a respiratory organ (Thompson 1969) much like some higher fishes. The South American and African lungfishes are more similar in morphology and physiology. For example, both have two ventral lungs and are obligate air breathers (Smith 1931, Greenwood 1986) obtaining about 90% of their oxygen uptake via the pulmonary route (Lenfant and Johansen 1968, Helfman et al. 1997). They can also aestivate and survive periods of drought by burrowing and remaining inactive in a cocoon (Smith 1931, Johnels and Svensson 1954, Greenwood 1986). Males of South American and African lungfish provide parental care; however, those of South America develop vascularized pelvic filaments when guarding the young, which is thought be an adaptation to aid in oxygenation of the young in the nest (Helfman et al. 1997, Bruton 1998). The larvae of both South American and African lungfishes possess external gills (Greenwood 1986).

A voluminous scientific literature exists on lungfishes. In an extensive bibliography, Conant (1986) listed a total of 2209 references to research work spanning more than 150 years. However, nearly all of the work is on morphology, phylogenetics and comparative physiology. Liem (1986) pointed out the paucity of information on the ecology of lungfishes and recommended that detailed field biology and ecological studies were needed, including habitat preference and utilization, population dynamics, spawning and reproductive strategies, and behavioural responses to stress. A survey of the literature on African lungfishes published over the last 20 years indicates that the situation has not changed and most studies still deal with such aspects as ultra-structure and function, biochemistry and endocrinology. Recent studies on the field biology of the African lungfishes have looked at some aspects of feeding of *Protopterus aethiopicus* (Pabari 1997) and *Protopterus annectens* (Otuogbai *et al.* 2001); and reproductive biology of *Protopterus aethiopicus* (Mosille and Mainoya 1988) with their findings largely corroborating those of earlier workers. Baer *et al.* (1992) reported on the growth for the slender African lungfish *Protopterus aethiopicus* population in Lake Victoria based largely on fishery catches. Clearly the knowledge gap noted above still largely exists.

Natural distribution of the marbled African lungfish

The marbled African lungfish is restricted to the African continent, where together with its three congeners, it is endemic (Roberts 1975). The species is more common in the central and east African region (Greenwood 1986) where it is widely distributed in the Nile system, and several rivers and lakes in the Great Lakes region including Lakes Malawi and Tanganyika. Greenwood (1986) noted that the four African lungfish species seem to have widespread and often overlapping distribution in freshwater bodies in the western, central, southern and eastern parts of Africa. Their preferred habitats include swampy vegetated areas of lakes and major river systems, which are often prone to drying up during periods of extensive drought. In Kenya, the natural distribution of the marbled lungfish seems to be centred around the Lake Victoria drainage basin or watershed, where it is common in swamps, streams and satellite lakes.

Although the marbled lungfish tends to be associated with shallow swampy inshore water habitats, it is also known to occur in offshore open waters of lakes. The marbled lungfish is considered to be a demersal species (Curry-Lindahl 1956, Greenwood 1986). In Lake Victoria, Kudhogania and Cordone (1974) classified the marbled lungfish among the oligobathic species, with depth zone limits of 50 – 59 m, although they were most commonly caught at depths between 0 and 20 m. Okedi (1971) reported that lungfish in Lake Victoria were readily caught in waters 0 - 30 m deep but became rare in waters deeper than 50 m. He noted that the species' absence in deeper waters was probably related to "its breathing requirements, which necessitate surfacing regularly to breathe atmospheric air". Perhaps because of their air breathing ability, the marbled lungfish occur in diverse aquatic habitats of variable depths, dissolved oxygen, salinity and temperature regimes (Smith 1931, Greenwood 1986, Goudswaard et al. 2002). For example, temperatures in its natural habitats are generally high ranging from 27 - 37 °C but it can withstand higher temperatures of over 40 °C in shallow pools and during aestivation (Smith 1931).

Witte and van Densen (1995) noted that the marbled lungfish is distinguished from the other African lungfish species by its large flattened head. According to Greenwood (1986), *P. aethiopicus* attain the largest size of all extant lungfishes; mature males can attain
a maximum size of about 2 m. Individuals of the species have a sub-cylindrical elongate body that ends in a pointed diphycercal tail (Bruton 1998).

Like other lungfish species, most research undertaken on P. aethiopicus has focused on morphological, biochemical, genetic, and evolutionary aspects. Relatively little information is available on the species biology and ecology. Greenwood (1986) noted that a possible reason for the paucity of ecological studies could be the inhospitable conditions of its natural habitats. Corbet (1961) and Pabari (1997) reported on aspects of the species feeding ecology in Lake Victoria and concluded that the species was largely muscivorous, but Curry-Lindahl (1956) had earlier reported a largely piscivorous diet for lungfish caught by fishermen in Lake Edward. Witte and van Densen (1995) noted that in its natural environments the marbled lungfish appears to be among the top fish predators. Greenwood (1958) described its breeding biology, including nesting behaviour and early development of young based on field observations of nesting males in shallow inshore waters of the northern part of Lake Victoria, while Okedi (1971) reported largely on its fecundity. Much later, Mosille and Mainoya (1988) reported findings on its reproductive biology in the Mwanza Gulf region of Lake Victoria that largely corroborated those of Greenwood (1958) and Okedi (1971). Mosille and Mainoya (1988), however, also found males matured earlier than females and suggested that the lungfish population in the southern part of Lake Victoria was different from that in northern part of the same lake, where the females matured earlier (Greenwood 1958, Okedi 1971). Information on the reproductive biology of the marbled lungfish in Lake Victoria indicates that the species is a seasonal spawner, breeding in nests in marginal swampy vegetation, with peak spawning activity coinciding with the onset of the long rains. Clearly the available data on the field biology of the marbled lungfish are based on its natural populations in Lakes Victoria and Edward, all part of the Nile River system (Roberts 1975), with little known about its populations in other water bodies where it is known to occur naturally.

The lungfish in Lake Baringo: its introduction and development of its fishery

There was no early record of lungfish in Lake Baringo. The earliest survey of fish fauna of Lake Baringo recorded four species: tilapia (*Tilapia nilotica* L. 1852), African catfish (*Clarias mossambicus* Peters 1852), and two cyprinids (*Barbus gregorii* Boulenger 1902, and *Labeo cylindricus* Peters 1852) (Worthington and Ricardo 1936). Much later Mann (1974) reported two more species: *Barbus lineomaculatus* and *Aplocheilichthys* sp. in his taxonomic notes on the fish fauna of the Baringo area. Mountain ranges and hills on the western side of the eastern arm of the African Rift Valley (Ojany and Ogendo 1973) geographically isolates the Lake Baringo catchment from Lake Victoria and the Nile system where the species occurs naturally, which may explain the natural absence of lungfish in the lake.

The marbled lungfish is a recent introduction in Lake Baringo. Its introduction occurred in 1975 but is not documented in the scientific literature. Interviews with a Fish Scout, Mr. Pius Bernard Awiti Malit (Pers. Comm.), who served with the District Fisheries Office (DFO) at the Lake Baringo Fisheries station, indicate that he introduced three juvenile specimens of unknown sex from Lake Victoria into Lake Baringo. The introduction was not planned and indeed can be regarded as an incidental event. Four juvenile lungfish earlier obtained from Lake Victoria and exhibited at the Nakuru ASK (Agricultural Society of Kenya) Show, were transported to Lake Baringo, where one ended on the then District Fisheries Officer's dinner plate, while the remaining three were released into the lake (P. B. A. Malit Pers. Comm.). The incident was largely forgotten until almost ten years later in 1984 when local fishermen started noticing strange "snake-like creatures" among their catches. Although early catches were from gillnets, immigrant Luo fishermen at Kampi Ya Samaki (fishing camp) introduced long lining primarily targeting the lungfish. Perhaps due to the new lungfish fishery, fishermen abandoned the bottom set gillnet fishery that caught *Labeo cylindricus*, hence its disappearance from commercial landing records (DFO 1996). Quite remarkably, the transplantation (*sensu* Shafland and Lewis 1984) of only three juveniles had resulted in a commercially exploitable population in the lake.

The Lake Baringo population represents the only incidence where lungfish have become established in a natural environment outside its natural distribution range. The introduction of the lungfish created a new fishery in the lake. First recorded in Lake Baringo fishery landings in 1984 (Ssentongo 1995, De Vos *et al.* 1998), lungfish gradually became an important species in the commercial fishery and often dominates annual landings by weight (see chapter 2). Initially the local fishing community feared that lungfish would wipe out the Baringo tilapia and other native species, much like the Nile perch (*Lates niloticus* L.) eliminated many native cichlid species in Lake Victoria (Ogutu-Ohwayo 1990, Leveque 1995, Olowo and Chapman 1999, and many others). However, now more than 25 years since it was first introduced into the lake, all indigenous species that were commercially exploited prior to the introduction are still landed in the commercial fishery. According to unpublished data at the Kenya Marine and Fisheries Research Institute (KEMFRI) the non-exploited indigenous species also still exist in the lake.

The marbled lungfish, or "kamongo" as it is popularly known in Kenya, is an important food fish, especially among members of the Luo ethnic community living along the shores of Lake Victoria (Smith 1931, Goudswaard et al. 2002). Local communities around Lake Baringo were initially reluctant to eat kamongo because of its strong smell, but this gradually changed and currently lungfish are very much appreciated as a food fish by many people around the lake. Indeed it can be said that the food habits and arguably the nutritional well-being of the local community also saw a change for the better following the introduction of the lungfish. Lungfish became an alternative source of cheap animal protein, which is a boon among the largely pastoral communities as it meant they could keep more of their livestock, whose numbers confer superior social status as a sign of wealth (Meyerhoff 1991). Among most members of the local II Chamus (also known as Njemps, Meyerhoff 1991) community, for example, the lungfish has become increasing preferred to the native tilapia. In the words of one Elijah Persalach (Pers. Comm.), "the lungfish is good especially because children can partake of its flesh without one worrying about them getting choked by bones as is often the case with tilapia".

The lungfish is now naturalized and appears to be suited for the Lake Baringo environment. From the economic standpoint, the introduction of the lungfish into Lake

Baringo, while unplanned can be considered a great success. Non-existent in commercial landings as recently as late 1984, the recorded commercial catch indicate lungfish production reached 66 metric tons in 1995, when for the first time it exceeded the annual landed weight of the indigenous Baringo tilapia (De Vos et al. 1998). The highest annual catch was 199 metric tons in 1999, which at the official price of KSh. 22.00 per kg of fresh weight, had a market value of about 4.4 million Kenya shillings. As described above, the lungfish fishery has also been a significant contributor to the nutritional wellbeing of the local communities as an alternative and cheap source of dietary animal protein. Clearly the maintenance of a viable lungfish fishery in Lake Baringo is of significant importance to the local community and the nation at large. The formulation of management policies for a fishery requires such information as good catch statistics, biological parameters and indices of abundance of the exploited species (Ogutu-Ohwayo 1990). More detailed knowledge of the biology and ecology of the lungfish population in Lake Baringo is required in order to understand what is happening to the lungfish fishery and to provide scientific information upon which its rational exploitation and management can be based.

Goals of the present study

The primary goals of this study are to describe the life history characteristics of the lungfish population in Lake Baringo and provide baseline scientific information to guide formulation of policies for the rational exploitation and management of its fishery. An important component of the present study is the use of ultrasonic telemetry to determine, for the first time, movement patterns and use of space by lungfish in open waters of the lake. Together this information will help provide knowledge needed to formulate rational exploitation policies for the lungfish fishery and biological data for comparison with other populations.

Chapter 2 Study Area, Physical/Chemical Data, Biota and Fishery

This study was conducted in Lake Baringo; the only lake in Kenya (and probably in the world) that has a commercial fishery based on an introduced and now naturalized population of the marbled lungfish *Protopterus aethiopicus*. This chapter provides general climatic and hydrological information of the study area. Data on some physical and chemical parameters of the lake measured in the present study are analyzed and described in context of secondary data to provide a basic understanding of the limnology of the lake.

To determine trends in catches and hence evaluate the relative importance of lungfish in the Lake Baringo fishery, data on annual fish catches obtained from the Department of Fisheries Office (DFO) at Kampi Ya Samaki were analyzed from the time lungfish first appeared in commercial catch records. In addition, information on the lungfish fishery was obtained through informal interviews with fishermen and women fish processors, and through personal observation of fishing and fish processing activities during the study period.

2.1 Location

Lake Baringo, together with Lake Naivasha, are the only two freshwater lakes found within the eastern arm of the African Rift Valley in Kenya (Beadle 1932). The lake is situated between latitudes 0°32' and 0°45' N, and longitudes 36°00' and 36°10' E at an altitude of 975 m above mean sea level (Ssentongo 1974). Outstanding features are the

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numerous islands of various sizes (Fig. 2.1); of which two (Kokwa and Parmalok) are inhabited by members of the Il Chamus (also known as Njemps, Meyerhoff 1991) community. These islands are remnants of an early Pleistocene volcano (Beadle 1932) and the smaller ones are often submerged during periods of high water.

2.2 Watershed characteristics

2.2.1 Soils

Except for small parts of its northwestern shore that are rocky, the lake is bounded by a zone of low gradient fluvio-lacustrine plains, the Njemps flats, which extend southwards to the alkaline Lake Bogoria (Bryan 1994). Soils in the lowland areas are generally poorly developed consisting of alluvial sand, gravel and lacustrine silt derived mainly from weathering of rocks in adjacent highlands (Kamar 1992). Members of the II Chamus, Pokot and Tugen communities sparsely populate the area, with population density being $20 - 40 \text{ km}^2$ (GOK 1997). However, in line with their pastoral way of life, they keep large numbers of livestock including cattle, sheep and goats. The resultant high grazing pressure exposes the soil while hooves loosen it, thus rainstorms fall mostly on bare ground generating surface runoff that carries the soil into the lake (Kallqvist 1987).

2.2.2 Climate: air temperature and rainfall

The area experiences high air temperatures, due to strong solar radiation (Sunderland *et al.* 1991). Air temperature data obtained from the Rehabilitation of Arid Environments (RAE) Trust headquarters at Kampi Ya Samaki indicate that daily minimum temperature



Fig. 2.1 A map of the study area: Lake Baringo, Kenya. Sites where depth and water temperatures were monitored are shown. Geographic position at depth marker = $0^{\circ}30'$ N, $36^{\circ}30'$ E.

ranges from 21 to 28 °C, and the maximum temperature from 28 to 39 °C. However, higher maximum temperatures (42 - 48 °C) are common during droughts especially in the usually drier months of February and September. These high temperatures are associated with high evapo-transporative moisture loss, which Sunderland *et al.* (1991) estimated to be greater than 1.5 times seasonal rainfall for the Lake Baringo area. The lake experiences a regular pattern of winds with the stronger northeasterly winds blowing from late afternoon to early evening while the weaker southeasterly winds blow in early morning hours (Beadle 1932, Kallqvist 1987).

Rainfall, as typical for a tropical semi-arid region, is limited and unreliable (Meyerhoff 1991, Bryan 1994). The rainfall pattern exhibits high variability attributed to a few high intensity storms (lasting 30 – 50 minutes) accounting for most of the total rainfall (Rowntree 1988). Annual total rainfall ranges from 300 to 700 mm for the lowlands surrounding the lake (Meyerhoff 1991), however, adjacent highlands such as the Tugen hills where altitude reaches up to 2,700 metres, receive between 1,200 and 1,500 mm of rainfall per year on average. Figure 2.2 shows the total monthly rainfall recorded at RAE Trust offices in Kampi Ya Samaki during the two years of this study. The total annual rainfall was 471.5 mm in 2001 and 366 mm in the subsequent year, with most rainfall received between the months of March and August. February and September were the driest months in both years with no rainfall in February and less than 15 mm in September. Total annual rainfall was highest in 1996 and 1997 (Fig. 2.3), while 1999 and 2000 were drought years, during which the area received low rainfall.



Fig. 2.2 Monthly rainfall recorded for the Kampi Ya Samaki area during 2001 (solid bars) and 2002 (open bars). No measurable rain was recorded in February of either year or in December 2001.



Fig. 2.3 Total annual rainfall recorded at the Rehabilitation of Arid Environments Trust offices in Kampi Ya Samaki from 1990 to 2002 (data from RAE Trust).

2.2.3 Streams

Lake Baringo receives water from several streams draining the Mau ranges and Tugen hills to its west, and the Laikipia escarpment to the east. According to Kallqvist (1987) the total watershed area of the lake is 6,820 km². The major streams include Endao, Ol Arabel, Mukutan, Perkerra, and Molo (Fig 2.1). Only the latter two are perennial; however their flow is high during and shortly after rainfall episodes but reduces to trickles during periods of extended drought largely due to abstraction of water, damming and diversion for irrigation purposes (Muchiri 1997, Kimakwa 2000). The streams bring in considerable amounts of sediment because of poor land use practices in the watershed (overstocking of livestock and clearing of vegetation for arable farming and human settlement) (Kimakwa 2000). This results in extreme turbidity, giving Lake Baringo waters their brownish colouration (Plate 2.1), which according to Ssentongo (1995) is "the most significant limnological characteristic of the lake". The lake has no surface outlet and its freshwater status has been attributed to a possible existence of a subterranean outlet towards its northern end (Beadle 1932, Muchiri 1997).

2.3 Physical and chemical data for Lake Baringo

The size of the lake was estimated from a digitized topographic map (Sheet 91/3, Edition 3-DOS, GOK 1982) of Lake Baringo. Physical and chemical parameters measured during the present study included water depth, transparency, temperature, conductivity and dissolved oxygen, with measurements taken at randomly selected sites during routine fish tracking (Chapter 4) and experimental fishing (Chapter 5).



Plate 2.1 The waters of Lake Baringo: dirty brownish due to high levels of suspended inoganic sediments

Water depth was measured using a graduated, weighted rope, whereas a Secchi disc (Wetzel and Likens 2000) was used to determine water transparency. Dissolved oxygen and water temperature were measured using a YSI model 55/12 FT (Yellow Spring Instruments Co. Inc) dissolved oxygen meter, while a Hanna Instruments (HI) conductivity meter was used to measure conductivity. Between July 2001 and April 2002, bottom and surface water temperature data were recorded on Stow-away temperature data loggers (Onset Computer Corporation 1997) placed *in situ* at each of an inshore and offshore site (Fig. 2.1). The two sites were selected for their proximity to the Moi University Fieldhouse as a measure to safeguard against their removal and loss. The lakeshore at this site is rocky and adjacent lake waters among the deepest in the lake. As on other rocky shores, receding waters have left permanent marks on the rocks along the shore, with rocks that had been submerged being brownish as evidence of past higher lake water levels (Plate 2.2).

At each site, a pair of temperature data loggers was set to record near-surface and near-bottom water temperatures at two-hour intervals. The probes were mounted on a rope suspended by a float (marker) and anchored at the bottom by a rock such that each probe was about 10 cm from the surface or bottom respectively. The depth of water when the probes were initially deployed was 1.6 m and 1.9 m at the inshore and offshore sites respectively, but water depth varied over time as described in section 2.3.1 below.

2.3.1 Size and depth

Based on dimensions of the digitized topographic map (Sheet 91/3, Edition 3-DOS, GOK 1982), Lake Baringo has a surface area of about 137 km². Its maximum length along



Plate 2.2 A rocky shore on the northwestern part of Lake Baringo. Notice light brown rocks close to the water-line which were submerged during periods of high water levels in the past.

the North-South axis measures about 20 km while it is approximately 10 km at its widest on the East-West axis.

Lake Baringo is shallow, with the bottom consisting of soft mud in most parts. Depth measurements taken at sites where gillnets were set during experimental fishing (see Chapter 5) ranged between 0.60 and 2.80 m, with a mean of 1.56 m (\pm 0.04 m SE). Depth data reported in various previous studies (Table 2.1) indicate that the mean depth of the lake has decreased over time, which is probably related to sediment deposition and higher evaporation than inflow rates (Sunderland *et al.* 1991). A depth contour map (Fig. 2.4) based on depth measurements taken at positions lungfish were located during ultrasonic tracking (section 4.1.2.2) showed that the deepest waters are found in the central part of the lake.

Water depth fluctuated considerably over time, generally increasing after rainfall episodes followed by gradual decrease. Depth measurements taken regularly for a period of 11 months at one site (Fig. 2.1) where an ultrasonic tag lost from a lungfish (section 4.1.2.2) was located were used to study temporal changes of water level in the lake. The monthly mean water levels fluctuated over time with low water recorded between February and May, and again in September 2002 (Fig. 2.5). The lowest water level at the site was 1.8 m recorded in February 2002 while the highest (2.9 m) was recorded in November of the previous year. The water level fluctuations caused dramatic shifts of the lakeshore location in the shallow and gentle sloping southern part of the lake.

Table 2.1	Summary data on water level depth reported for
	Lake Baringo by various workers (* not reported).

Period	Mean depth (m)	Maximum depth (m)	Source
1930 - 1931	*	<7.5	Beadle (1932)
1969	5.6	<7.5	Ssentongo (1974)
1977-1979	*	5	Kallqvist (1987)
1988-1989	4	*	Patterson & Wilson (1995)
1997	3.5	*	Muchiri (1997)
2000	2.7	3.7	Kemfri (Unpublished data)





Fig. 2.4 A depth contour map of Lake Baringo, Kenya. Note: Contours are based on depth measurements taken at 452 positions where ultrasonic-tagged lungfish were located between September 2001 and September 2002.



Fig. 2.5 Monthly mean depth (m) recorded at one site in Lake Baringo during the study (vertical bars represent standard error of the mean).

2.3.2 Transparency

Lake Baringo waters are extremely turbid and brownish. Secchi disc transparency measurements ranged between 3.0 and 6.5 cm. The highest Secchi depth ever reported for Lake Baringo is 20 cm by Beadle (1932), and again much later by Kallqvist (1987). Odhiambo and Gichuki (2000) reported Secchi disc depth ranging from 4.0 to 6.0 cm in their study conducted between May 1994 and April 1995, whereas Muchiri (1997) reported an average Secchi depth of 3.5 cm for readings taken in March 1996. More recent data by Oduor *et al.* (2003) indicated transparency ranged from 5 to 8 cm (mean = 7 cm) for reading taken between May and August 2000. The low transparency is related to presence of sediment that is maintained in suspension by regular early morning and late afternoon wind action.

2.3.3 Dissolved oxygen and conductivity

Table 2.2 presents mean dissolved oxygen concentration and conductivity values of the lake water as determined from measurements taken at different sites during experimental fishing in 2002. The dissolved oxygen concentration ranged from 2.20 to 7.30 mg Γ^1 with a mean of 4.30 mg Γ^1 (\pm 0.15 SE). Oduor *et al.* (2003) reported a mean dissolved oxygen concentration of 6.8 mg Γ^1 (range 6.0 – 9.7) in their 2000 study. Conductivity varied considerably ranging from 263 μ S cm⁻¹ recorded in March to 2863 μ S cm⁻¹ in June. The overall mean conductivity for the period between February and October 2002 was 1473 μ S cm⁻¹ (\pm 103 SE). This compares well with the mean conductivity of 1222 μ S cm⁻¹ reported in Oduor *et al.* (2003). Other previous studies have reported different

Table 2.2 Mean dissolved oxygen concentration and conductivity measured at various sites during experimental fishing in Lake Baringo in 2002.

	Dissolved oxygen (mg/l)		Conductivity (uS cm ⁻¹)	
Month	Mean	range	Mean	range
Feb	4.33	2.90 - 7.30	953	409 - 1668
Mar	4.55	4.10 - 5.10	621	263 - 841
May	4.22	2.70 - 5.02	440	328 - 609
Jun	4.47	2.20 - 6.70	2068	1447 - 2863
Aug	3.96	2.70 - 4.90	2168	1913 - 2390
Sep	4.48	2.30 - 7.00	1668	1165 - 2447
Oct	4.08	2.20 - 6.15	1896	952 - 2653

values for conductivity of Lake Baringo. Kallqvist (1987) reported values ranging from 520 to 1090 μ S cm⁻¹, whereas Wilson (1989) reported a mean conductivity of 790 μ S cm⁻¹. The variation in conductivity of the lake water is probably related to the interplay between water inflow on the one hand and evapotranspiration on the other.

2.3.4 Water temperature

Surface and bottom temperatures at the inshore and offshore site differed and showed consistent diel fluctuations. Surface and bottom water temperature profiles for the inshore and offshore sites are presented in Fig. 2.6 and Fig. 2.7 for the periods July-December 2001 and January to April 2002 respectively. Both surface and bottom water temperatures showed fluctuations, however surface temperatures were more variable. For example, surface temperature at the inshore site ranged from 22.6 to 37.4 °C (mean = 26.10 °C \pm 0.06 SE) compared to 22.5 – 27.5 °C (mean = 24.05 °C \pm 0.02 SE) at the bottom. Bottom temperatures at the inshore site were generally less variable and cooler by as much as over 10 °C during the day. Differences between surface and bottom water temperatures were much less at the offshore site. On two separate occasions, the surface and bottom probes at the offshore site became entangled and both ended up on or near the bottom until they were retrieved and redeployed. This explains the similar temperatures recorded by the two probes around September 2001, and again from the later half of December 2001 (Fig. 2.6) to early February (Fig. 2.7).

Beadle (1932) showed that Lake Baringo was thermally stratified during the day but isothermal at night. Kallqvist (1987) reported temperature profiles, which showed



Fig. 2.6 Surface (blue) and bottom (red) water temperatures at inshore and offshore site from July to December 2001.



Fig. 2.7 Surface (blue) and bottom (red) water temperatures at the inshore and offshore site from January to April 2002.

uniform cooler surface to bottom waters in the morning but presence, in the afternoon, of a warmer surface layer with the steepest temperature gradient between 0.2 and 0.5 m. The daily temperature profiles in Fig. 2.8 are consistent with these two earlier studies and indicate that the water column stratifies and then re-mixes almost daily. Surface and bottom water temperatures were uniform through the night and early morning but surface waters started becoming increasingly warmer than bottom water from 1000 hours onward. The temperature difference between surface and bottom waters was greatest at around 1400 hours, indicating stratification of the water column by this time. The break down of thermal stratification later in the afternoon is largely due to action of northeasterly winds, which regularly started blowing between 1500 and 1600 hours. The surface and bottom waters were usually completely mixed by 1800 hours and the water column remained isothermal through the night. However on a few days the late afternoon winds were either non-existent or weak, hence the entire water column was not mixed.

2.4 Primary productivity and biota

In his early account on the limnology of Lake Baringo, Beadle (1932) noted that "the water was greenish in colour, owing to the presence of vast quantities of blue green alga *Microcystis*", but did not give quantitative estimates. Much later Kallqvist (1987), and Odhiambo and Gichuki (2000) described the phytoplankton community to comprise blue green algae (Cyanophyta) and a few species of green algae (Chlorophyta) and diatoms (Bacillariophyta). In their study Odhiambo and Gichuki (2000) indicated that cyanophytes



Fig. 2.8 Daily profile of surface (blue) and bottom (red) water temperature at the inshore and offshore site.

(consisting mostly of *Microcystis aeruginosa*) comprised 90.89% of the total phytoplankton biomass while chlorophytes and bacillariophytes contributed 7.88% and 1.23% respectively. Based on samples collected between May and August 1999, Schagerl and Oduor (2003) reported that the cyanobacteria *Microcystis aeruginosa* appeared to dominate both the phytoplanktonic and periphytic communities of the lake.

The earliest quantitative record of photosynthesis rate for the phytoplankton community in Lake Baringo is 1.6 g O_2 m⁻² d⁻¹ reported by Richardson and Richardson (1972). Kallqvist (1987) reported values ranging between 0.3 and 1.0 g O_2 m⁻² d⁻¹. Patterson and Wilson (1995) reported a higher value of 3.8 g O_2 m⁻² d⁻¹, which is still relatively low for a tropical lake. For example, Lake George in neighbouring Uganda has a gross photosynthesis rate of 15.6 g O_2 m⁻² d⁻¹ (Ganf and Horne 1975). A recent study by Schagerl and Oduor (2003) reported a mean daily productivity of 0.5 ± 0.1 g O_2 m⁻² d⁻¹ for Lake Baringo. The low productivity values for Lake Baringo are probably related to the extremely high turbidity due to presence of suspended inorganic sediment, which scatter and attenuate light (Wetzel and Likens 2000).

Aquatic macrophyte vegetation is sparse and mainly restricted to the southern part of the lake. *Potamogeton* sp. is the major submerged macrophyte (Muchiri 1997). Emergent macrophytes comprising papyrus (*Cyperus* sp.) and a reed (*Paspalidium* sp.) dominate the swamp vegetation (Beadle 1932) near estuaries and along rivers (Plate 2.3). Water lily (*Nymphaea caerulea*), water cabbage (*Pistia stratiotes*) and *Azzola* sp. are commonly encountered on the surface of small bays along the inner edge of the swamp. The latter two are often blown by wind as floating masses all over the open waters of the lake. The



Plate 2.3 Facing upstream near the mouth of the Molo river: one of the streams flowing into Lake Baringo. Notice the brownish waters due to high levels of suspended inorganic sediments and aquatic macrophytes forming a swamp along its edges. Ambatch tree (*Aeshynomene elaphroxylon*) which grows on the outer edge of the swamps (Beadle 1932) is used locally in making fishing rafts (DFO 1996).

Ssentongo (1995) noted that the benthos in open waters are virtually devoid of invertebrate life, which may be related to the settlement of inorganic sediment. The zooplankton community has been little studied. Anecdotal accounts in records at the DFO indicated the presence of a few species of copepods (*Thermocyclops* sp. and *Mesocyclops* sp.), while Pejler (1974) identified seven species of rotifers of which *Keratella tropica* and *Hexarthra mira* were among the more abundant. Schagerl and Oduor (2003) reported low zooplankton species diversity comprising six species of which *Thermocyclops* sp. and *Branchionus patulus* were highly abundant. Six indigenous fish species and the introduced lungfish (*P. aethiopicus*) are known to exist in the lake (Muchiri 1997), which also supports a remarkable assemblage of aquatic birds and is home to populations of the Nile crocodile (*Crocodylus niloticus*) and the hippopotamus (*Hippopotamus amphibius*), a large semi-aquatic mammal.

2.5 The Lake Baringo fishery

2.5.1 Catch composition and trends in commercial fish landings

Commercial fish landings by weight varied considerably over time. Four species namely: *O. niloticus*, *B. gregorii*, *C. gariepinus* and *P. aethiopicus* comprise commercial landings in Lake Baringo (Plate 2.4). Two of these species, *P. aethiopicus* and *C. gariepinus* are landed mostly in the long-line fishery, whereas tilapia (*O. niloticus*) is the primary target species in the gill-net fishery. Table 2.3 presents the annual catch composition by weight of



Plate 2.4 Commercial fishes of lake Baringo: A = P.aethiopicus, B = O.niloticusC = C.gariepinus (top) and *B.gregori* (bottom)

Table 2.3 Annual weight (in metric tons) by species landed in the Lake Baringo fishery from 1984 when lungfish first appeared in catch records.
Data from records at the Baringo District Fisheries Office, Kampi Ya Samaki (* reduced effort due to ban on fishing).

Year	Oreochromis niloticus	Clarias gariepinus	Barbus gregorii	Protopterus aethiopicus	Labeo cylindricus
1984	199	26	46	11	16
1985	226	21	30	30	6
1986	95	17	23	15	2
1987	88	4	19	6	
1988	82	4	3	8	
1989	180	20	17	7	
1990	326	23	10	18	
1991	58	29	6	36	
1992	164	29	6	51	
1993	20	7	1	11	
1994*	4	2	1	L	
1995	20	31	6	66	
1996	24	22	11	16	
1997	145	42	13	11	
1998	235	66	23	50	
1999	131	38	9	199	
2000	145	120	5	196	
2001	49	34	2	34	

species landed in Lake Baringo from 1984 when *P. aethiopicus* was first reported in the commercial catch. Total annual landings by species varied considerably among years, with one species, *Labeo cylindricus*, disappearing from the recorded commercial catch two years after the lungfish first appeared in the catch records.

Figure 2.9 shows the trend in the annual landings by weight for the four fish species that are still commercially exploited in Lake Baringo. Annual fish landings were dominated by *O. niloticus* in all years except 1995, and again in 1999 and 2000 when lungfish was the most landed species by weight. Annual catches of African lungfish were generally low through the later half of the 1980s and early 1990s (Fig. 2.9). An all time low annual catch of 1 metric ton was recorded in 1994, a year of reduced fishing effort, but production increased to a peak of 66 metric tons in 1995 when the lungfish dominated the lake's annual commercial catch for the first time. However, over the next two years lungfish production declined to a low of 11 metric tons by 1997. This was followed by a rather remarkable sharp increase to an all time peak production of 199 metric tons in 1999 that decreased marginally to 192 metric tons the following year. Subsequently landings dropped to only 34 metric tons of lungfish by November 2001 when a ban on all commercial fishing activities in the lake was effected.

2.5.2 Gear and methods used in the Lake Baringo lungfish fishery

Lungfish are usually caught on baited hooks on bottom set long lines left to fish overnight. A long-line in the Lake Baringo fishery typically consists of a 0.3 - 0.4 km long mainline of 8 ply vinylon rope to which standard size 9 hooks are attached at



Fig 2.9 Annual landings by weight of fish species in Lake Baringo from 1984 when *P. aethiopicus* first appeared in commercial catch records.

intervals of between 1.5 and 2 metres. The long-line is anchored at the selected fishing ground by rocks attached to both ends and maintained close to the lake bottom by smaller stones set at regular intervals.

The hooks are usually baited in the afternoon (1430 – 1530 hours) each day. However, depending on the amount of bait a fisherman has, some hooks are not baited and thus do not actively fish on those nights. Long-line fishermen operate individually using small manually powered rafts locally known as gadich (Plate 2.5). The rafts are made locally using dried poles of the Ambatch tree (DFO 1996). Each long-line fishermen also operates a set of gillnets to catch fish (mostly tilapia) that are cut in pieces for baiting hooks on the long-lines. These gillnets are left in the water and thus fish continuously but are inspected twice a day, first in the morning before the fishermen retrieve the previous night's catch from the long-line, and again in the afternoon prior to baiting the hooks.



Plate 2.5 The gadich: a locally made craft used by fishermen in Lake Baringo, with a fisherman holding a lungfish removed from a long-line.
Chapter 3 General biology of the African lungfish in Lake Baringo

Field and laboratory work were conducted to investigate the biology of the African lungfish in Lake Baringo, where the population, which developed from three individuals introduced in the mid-1970s (see Chapter 1), is now the basis of a commercial fishery. Biological attributes studied include: length-weight relationship, condition factor, growth, food and feeding habits, and aspects of reproduction such as sex ratio, gonad maturity and fecundity. The purpose was to gain an understanding of the species' biology and provide baseline biological information relevant to management of its fishery in Lake Baringo.

3.1 Materials and methods

Field and laboratory work were conducted at Lake Baringo between January 2001 and December 2002 inclusive. Most biological data on the African lungfish were collected from commercial fish landings at the Moi-Toronto fish-landing site near the Moi University Fieldhouse (Fig. 2.1), which served as the field laboratory throughout the study. In addition, some length and sex data were obtained from Kampi Ya Samaki and Ngenyin fish landing sites (Fig. 2.1) with the assistance of the Baringo District Fisheries Office (DFO) and Kenya Marine and Fisheries Research Institute (KEMFRI) personnel. Women fish-processors gutted dead lungfish at a designated area near the field laboratory, and gut and gonad samples for food habits and reproduction data respectively were collected at no cost. Although it was desirable to obtain independent fishery data, especially on young lungfish, attempts to capture specimens using a fyke net and minnow traps were unsuccessful. Beach seining of selected swamp fringe areas (Plate 3.1), which have been reported to be the nursery habitats for the lungfish (Greenwood 1958, 1986), yielded no young lungfish.

3.1.1 External examination of lungfish in commercial landings

Lungfish landed in the commercial fishery were examined and incidence of external abnormal development such as possession of extra fins and physical deformities recorded. Because local knowledge among the fisher community was that the position of the cloacal opening distinguished the sexes with male lungfish having a left cloacal opening; data on the position of the cloacal opening among specimens were recorded in the early part of the study. These data and those on the individual's sex later confirmed through internal examination of the gonads (see section 3.1.5 below); were used to test the hypothesis that the position of the cloacal opening was related to sex using a non-parametric chi-square test (Zar 1996). The incidence of physical injury such as tails bitten-off and regenerated tails was recorded and used as a direct indicator of predation.

3.1.2 Length and weight data

Length and weight data were obtained for lungfish landed at the Moi-Totonto fishlanding site and occasionally at other nearby landing sites such as Kampi Ya Samaki and Ngenyin (Fig. 2.1). Dead lungfish were measured for their total length to the nearest 0.1-cm on a 1 m measuring board (or tape-measured for longer specimens) and weighed to the nearest 0.01 kg on a Salter Weight-Tronix digital hanging balance (Plate 3.2). Live lungfish were measured with the help of an assistant who held the fish on the measuring board as



Plate 3.1 Beach seining for young lungfish at an inshore shallow water area in Lake Baringo.



Plate 3.2 Measuring lungfish landed in the Lake Baringo commercial fishery.

length was taken. This was necessary as lungfish bodies are covered with mucus rendering them very slippery. The individual was then transferred into a dipnet (or burlap bag for larger specimens) for weighing.

The length and weight data were used to describe the size of lungfish landed in the commercial fishery and to determine their length-weight relationship and condition. The length-weight relationship in fishes is commonly expressed by the equation $W = aL^b$, which upon log-transformation results in a straight line described by the equation:

$$\operatorname{Log_{10}} W = \log_{10} a + b \log_{10} \mathrm{TL};$$

where W is the body weight, TL is the total length, a is the intercept, and b is the regression constant or slope of the straight line (Le Cren 1951). For most fishes the numerical value of b ranges between 2.5 and 3.5, with a value of 3.0 indicating isometric growth in which the body increases in all dimensions in the same proportions.

The length-weight relationship for lungfish was determined by simple regression of log-transformed weight against log-transformed total length. The relationship was estimated for all lungfish and also separately for the sexes following Anderson and Neumann (1996). Analysis of covariance was used to test whether slopes of the regression lines for the length-weight relationship of males and females were significantly different. Following Gardiner (1997) 95% confidence intervals on the slope were calculated to see whether their range included the value of 3.0 indicating isometric growth. The slope of the length-weight relationship for all lungfish; and those of each sex were each tested for significant difference from 3.0 following the one-tailed t-test procedure in Zar (1996).

The condition of fishes has been described as a measure of their well-being or fatness (Busacker *et al.* 1990, Anderson and Neumann 1996). In the present study, condition was computed using the formula for relative condition (Kn):

$$Kn = W/W';$$

where W is the measured weight of an individual fish, and W' is the predicted lengthspecific mean weight from the length-weight relationship for all specimens combined (Anderson and Neumann, 1996). The mean Kn for lungfish in monthly samples were determined and graphical plots used to study trends over time. Analysis of variance was used to test for significant differences in mean relative condition factor between months, and also between males and females.

Length data were categorized into 6 cm length classes and the frequency or number of individuals in each class determined. Graphs of frequency against length were used to describe the size structure of all lungfish recorded in bimonthly samples landed in the commercial fishery between January and October 2001. Sexed lungfish were also sorted into length categories and the percentage composition of males and females in the different length groups computed for comparison. The sex ratios for different length groups were tested for significant difference from the expected male to female ratio of 1:1 using the non-parametric chi-square test procedure (Zar 1996).

3.1.3 Determination of individual growth of lungfish

Lungfish landed alive were purchased and used as subjects in a mark-mark-recapture study to determine individual growth in the wild. A secondary aim was to obtain information on the dispersion of free ranging individuals. Live lungfish judged to be in good physical condition were purchased directly from fishermen, tagged and released back into the lake. Obtaining live specimens in good condition was a problem initially as most lungfish landed alive were badly injured from clubbing by fishermen because the fish can inflict serious bites and are dangerous to handle in the small local fishing rafts. However, as live lungfish earned more income, fishermen were encouraged to avoid clubbing them, and quickly became adept at maneuvering the lungfish into a burlap bag, after which they cut the leader line above the hook. Following purchase of a lungfish, the hook was carefully removed from the fish after removing the hook's barb with a pair of pliers. The fishermen were supplied with new hooks to replace those removed from their long-lines.

The lungfish were floy-tagged immediately after landing when most were lethargic and could easily be held (on the measuring board) by an assistant as the tag was inserted. Initially all fish were anaesthetized with clove oil before floy-tagging but later only those that were not lethargic and otherwise difficult to handle were anaesthetized. A yellow numbered T-bar Floy-tag was inserted into the dorsal musculature using a fish-tagging gun such that its barbed head passed across the base of the pterygiophores. The length was recorded and the fish transferred into an aquatic dipnet for weight measurement. The fish was then placed in water in a plastic container for release back into the lake. The entire floytagging procedure and measurement took about 2 to 3 minutes on average.

The recovery of Floy-tags was made through the commercial fishery. To encourage tag return, a reward of KSh. 100.00 was placed on each tag returned, and an additional KSh. 50.00 was given if a fisherman brought the recaptured fish to the field laboratory. Where

they were not able to bring a recaptured lungfish to the field laboratory, fishermen were advised to use strings to measure its total length and deliver the same with the floy-tag. Any live recaptures in good physical condition were purchased, measured for length and weight, and released back into the lake. Information about the presence of tagged lungfish and how to report recovered tags was communicated directly to fishermen, and indirectly through the assistance of DFO and KEMFRI personnel at some fish landing sites. More distant fishlanding sites, such as Loruk (Fig. 2.1) were visited periodically to collect any tag returns.

The length and weight measurements of tagged lungfish upon recapture allowed estimation of individual growth of the fish. Growth of individual lungfish was estimated from the respective length and weight increment between the time of release and recapture. Absolute growth rates were determined by dividing the size increment by the number of days between release and recapture (Pauly 1983). Specific growth rate (Ricker 1975) was determined from the length and weight data of the fish at tagging and recapture dates. Thus, specific growth rate for length was computed as:

$$G_{L} = 100(\ln TL_{2} - \ln TL_{1})/t;$$

where TL_1 is the total length at tagging date; TL_2 is the total length at recapture date, and t is the time (in days) between tagging and recapture. The specific growth rate for mass was computed by substituting weight for total length in the formula.

3.1.4 Food and feeding habits

Food and feeding habits were studied by examination of contents of the entire gut. The guts of freshly gutted lungfish were collected from women fish-processors at the landing site (Plate 3.3). For each gutted lungfish, the entire gut was carefully separated from other visceral organs and immediately fixed in 10% formalin in labeled specimen bottles. The guts were later washed and then split open to examine and identify consumed prey. Although *P. aethiopicus* has been reported to lack a distinct stomach (Corbet 1961, Bruton 1998), internally the gut was found to consist of three anatomically distinct sections. The contents of each section were separately emptied into a white-enameled dissecting tray for sorting and identification of prey. Because lungfish usually bite off parts of their prey, identification of prey was largely based on partly digested pieces and remnant bony parts of prey such as scales and other skeletal material. Bony remnants of fish prey were compared with sample skeletal material of species known to occur in the lake to facilitate their identification.

The frequency of occurrence method was the only method used to quantitatively describe the diet of lungfish in this study. The numerical and volumetric methods (Bowen, 1996) were considered inappropriate because lungfish bite and masticate parts of their prey resulting in mixtures of macerated prey along the gut that are difficult to sort and accurately quantify numerically and volumetrically. In the frequency of occurrence method, incidence of a particular prey in a gut counted as one record for that prey regardless of its numbers or mass. The number of guts containing an individual prey was expressed as a percentage of the total number of guts examined (Bowen 1996).



Plate 3.3 Women fish processors at landing sites provided gut and gonad specimens for study

3.1.5 Reproduction

Gross internal examination of gonads was used to sex individuals because lungfish lack external dimorphic sexual characters. Thus, lungfish landed and sold alive for mark-recapture studies (or to agents who preferred buying live lungfish for resale) were not sexed. On internal examination it was easy to distinguish between sexes as even the smallest females in samples had ovaries with discernible eggs as described by Okedi (1971). The sex ratio was determined for all lungfish samples, for fish in monthly samples and also for fish in different length groups. The non-parametric chi-square test (Zar 1996) was used to test for significant deviation from the expected male to female ratio of 1:1.

In fisheries biology, the term maturity stage refers to the degree of ripeness of the ovaries and testes and is a measure of how close an individual is to spawning (Holden and Raitt 1974, Cailliet *et al.* 1986). In this study, gonads were assigned a maturity stage based on macroscopic examination, according to a scheme described by Mosille and Mainoya (1988, Table 3.0). Estimation of the size (total length) at attainment of maturity was based on the percentage incidence of individuals in mature gonad condition (i.e. stages III and IV) among lungfish in different length groups, following Mosille and Manoiya (1988). Thus size at maturity was taken as the minimum length category that 50% or more of the individuals had mature gonads.

Gonads were subsequently carefully removed, blotted on tissue paper and weighed to the nearest 0.01 g on a top-loading electronic balance. For fecundity estimation, sub-samples of ovaries in maturity stage IV were cut, weighed and stored in well labeled plastic specimen bottles containing Gilson's fluid; a solution which hardens

Table 3.0	Stages of gonad maturity of African lungfish (P. aethiopicus).
	(After Mosille and Mainoya 1988).

	Females	Males		
Stage I:	Developing I			
	Gonads very small in size,	Gonads very small size,		
	deep red mass not covering	slender and pale grey.		
	the whole ovary; free side			
	silvery grey in colour.			
Stage II:	Developing II			
	Gonad increased in size,	Gonad increase in size,		
	fat deposition along the	Fat deposition along the		
	gonad begins, individual	gonad begins.		
	oocytes clearly seen.			
Stage III:	Ripening			
	Further fat deposition,	Further fat deposition,		
	ovary increased in size,	testes become greenish.		
	eggs large and brownish.			
Stage IV:	Ripe			
	Eggs become pinkish green,	Testes become pale green,		
	fat deposits increase.	fat appears brownish.		
Stage V:	Ripe and running			
	Eggs appear to be loosely	Testes become pale yellow		
	together in ovarian membrane	fat deposits almost		
	and appear pale yellow.	disappearing.		
Stage VI:	Spent			
	Ovary appear loose or	Testes appear loose or		
	deflated.	deflated.		

eggs and dissolves ovarian tissue (Bagenal 1978, Crim and Glebe 1990). Stage IV of gonad maturity is commonly used in fish fecundity studies because it is the most advanced stage of egg development before spawning (Bagenal 1978, Wooton 1990). Thus, eggs in the ovaries of two females in stage V of gonad maturity in the present study were not counted as some eggs might have already been released.

Preserved ovary sub-samples were periodically shaken vigorously to help liberate eggs from the ovarian tissue. After about two months, each sub-sample was subjected to serial washing with water and decanting of supernatant liquid 4-5 times to replace Gilson's fluid with water. The washed eggs were transferred into a white-enameled tray and hand counted. Since mature ovaries of *P. aethiopicus* had eggs at different stages of development in the maturation cycle, only the larger mature eggs i.e. those that would have been released in the immediate spawning, were counted. In addition to their larger size, these eggs were also identifiable by their pale green appearance compared to the whitish, smaller eggs.

Fecundity for individual lungfish was computed using the formula for "subsampling by weight" (Kipling and Frost 1969):

F = N x (Wt/Ws),

where F is fecundity, N is number of eggs in the sub-sample, Wt is total ovary weight, and Ws is weight of ovary sub-sample. The mean number of eggs per female was determined. Regression analysis was used to investigate the relationship between fecundity and total length, and also between fecundity and body weight.

The gonadosomatic index (GSI) was determined using the formula:

GSI = 100 x (GW/BW);

where GW is total gonad weight, and BW is body weight (Wooton 1990, Hutchings 2002). Mean GSIs were computed and graphical comparisons were made between males and females in different stages of gonad maturity.

3.1.6 Statistical analyses

Most statistical analyses were carried out using the Minitab statistical software package (Minitab Inc.). The $\alpha = 0.05$ level was used to determine significance for all statistical tests.

3.2 Results

3.2.1 External characters

Lungfish exhibited asymmetry in the position of the cloacal opening i.e. the cloacal opening occurred on the right side of the body in some individuals and on the left in others. Analysis of data on 181 individuals whose sex was confirmed through internal examination of gonads showed that the position of the cloacal opening was not related to sex (chi-square test, $\chi^2 = 0.324$, df = 3, p = 0.956). There was no significant difference in the number of individuals with a left or right cloacal opening among female (chi-square test, $\chi^2 = 0.005$, df = 1, p = 0.942) and male (chi-square test, $\chi^2 = 0.093$, df = 1, p = 0.942) and male (chi-square test, $\chi^2 = 0.093$, df = 1, p = 0.093) lungfish. The number of individuals with a left-sided cloacal opening was not significantly different from that of lungfish with a right-sided cloacal opening (chi-square test, $\chi^2 = 0.069$, df = 1, p = 0.793).

Physical injury, involving bitten tails was often observed among lungfish landed in the commercial fishery. Some individuals had fresh injuries but others had healed wounds, with either fully regenerated or regenerating tails (Plate 3.4). A total of 37 lungfish had either fresh injuries or regenerated tails, which represented 4.6% of the 799 lungfish recorded at landing sites between January and October 2001. Regenerated tails were recognized by their lack of scales. A total of 12 lungfish had developmental abnormalities (e.g. Plate 3.5, Table 3.1).



Plate 3.4 Lungfish with a freshly excised tail (A) and regenerating tail (B and C) in Lake Baringo commercial landings.



Plate 3.5 Abnormal development of the pectoral fin (A) and tail (B) among lungfish landed in the Lake Baringo commercial fishery.

Table 3.1 Some developmental abnormalities observed amongAfrican lungfish (P. aethiopicus) in Lake Baringo.

Type of abnormal development	Number of fish
Possession of two tails	2
Forked pectoral fin	3
Lack of right eye	3
Lack of left eye	2
Extra pelvic fin	1
Deformed head	1
Total	12



3.2.2 Length-weight relationship, condition and length-frequency distribution

Total length and body weight measurements were obtained for 493 lungfish between January and October 2001 while the commercial fishery was open. The average size of lungfish landed in the commercial fishery was 80.9 cm (\pm 0.94 SE) in total length and 2.67 kg (\pm 0.12 SE) in weight. The longest individual measured 145.0 cm and weighed 17.32 kg, whereas the smallest measured 43.0 cm and weighed 0.26 kg. Monthly samples varied in total number of individuals and mean size (Table 3.2), however, analysis of variance showed no significant differences for both mean total length (F = 1.06, p = 0.390) and mean weight (F = 1.06, p = 0.387) for lungfish measured in different months. Figure 3.0 shows the variation in mean total length of lungfish in monthly samples. Among sexed individuals; the longest, heaviest specimen was a male (140.5 cm, 15.82 kg), but females were on average both longer and heavier than males (Table 3.3). These differences were not significant for either total length (ANOVA, F = 3.48, p = 0.063) or weight (ANOVA, F = 0.41, p = 0.525).

3.2.2.1 Length-weight relationship

Lungfish with regenerated tails were not included in the regression analysis to determine length-weight relationship. Data were pooled to derive the length-weight relationship because analysis of variance found no significant differences in mean size between monthly samples or between sexes (see section 3.2.2 above). Simple linear regression of log-transformed length and weight data showed the length-weight relationship based on 493 lungfish was best described by the equation:

Table 3.2Mean total length and body weight (and their standard error, \pm SE) of African lungfish (*P. aethiopicus*) in
monthly samples from the Lake Baringo commercial fishery in 2001.

	Total lengt	h (cm)	Weigh		
Month	$Mean \pm SE$	Range	$Mean \pm SE$	Range	Number of fish
Jan	$\overline{79.95}\pm\ 5.43$	43.0 - 130.0	2.63 ± 0.57	0.26 - 8.94	21
Feb	82.13 ± 2.95	47.0 - 138.5	2.76 ± 0.35	0.30 - 13.78	57
Mar	81.14 ± 2.54	44.6 - 145.0	2.91 ± 0.38	0.18 - 17.50	78
Apr	76.31 ± 3.20	46.0 - 129.1	2.20 ± 0.34	0.28 - 9.42	38
May	$87.16\pm~3.82$	47.8 - 137.0	3.54 ± 0.47	0.20 - 12.20	45
Jun	79.46 ± 3.53	46.2 - 140.2	2.59 ± 0.47	0.18 - 14.72	37
Jul	78.86 ± 2.93	43.5 - 117.2	2.43 ± 0.29	0.30 - 7.72	47
Aug	76.94 ± 2.47	50.0 - 121.3	2.19 ± 0.29	0.32 - 11.22	55
Sep	83.10 ± 2.73	48.0 - 144.0	2.79 ± 0.37	0.32 - 15.00	47
Oct	82.29 ± 2.04	49.9 - 137.0	2.51 ± 0.24	0.36 - 12.84	68
All fish	80.92 ± 0.94	43.0 - 145.0	2.67 ± 0.12	0.18 - 17.50	493



Fig. 3.0 Mean size of lungfish in monthly samples from the Lake Baringo commercial fishery in 2001 (vertical bars represent 95% CI).

Table 3.3 Mean total length and body weight of 86 male and 161 female lungfish in the Lake Baringo commercial catch.

	Total leng	th (cm)	Body weight (kg)		
- 201	Male	Female	Male	Female	
Mean \pm SE 76.68 \pm 2.48		81.87 ± 1.54	2.39 ± 0.32	2.60 ± 0.16	
Range	43.5 - 140.5	43.0 - 130.0	0.18 - 15.82	0.26 - 9.42	

Log W = -6.41 + 3.52 Log TL (n = 493, r² = 0.972, p < 0.001).

The 95% confidence interval for the slope was between 3.467 and 3.573. A one tailed t-test showed the slope was significantly greater than three (t = 19.245, p < 0.001) and the data conformed (r^2 = 0.972) closely to the regression line (Fig. 3.1). The non-log transformed length-weightrelationship is described by the equation:

$$W = 3.89 \times 10^{-7} TL^{3.52}$$
.

The equations that best described the relationship between total length and body weight for males and females were:

Log W = -6.38 + 349 Log TL (n = 86, r² = 0.970, p < 0.001) and

Log W = -6.36 + 3.49 Log TL (n = 161, r² = 0.976, p < 0.001) respectively.

Analysis of covariance demonstrated that slopes of the length-weight relationship were not significantly different between sexes (ANCOVA, F = 0.14, p = 0.706). The 95% confidence interval for the slope for males was between 3.357 and 3.623, whereas for females, it was between 3.405 and 3.575. The slopes for males (t = 7.345, p < 0.001) and females (t = 11.382, p < 0.01) were significantly greater than three.

3.2.2.2 Relative condition actor

The relative condition (Kn) factors for the 493 lungfish ranged from 0.62 to 1.86 (mean = 1.01 ± 0.01 SE). Table 3.4 presents mean Kn for lungfish in monthly samples. When plotted against time (month), mean Kn for all lungfish did not show much variation from unity (Fig. 3.2).



Fig. 3.1 Length-weight relationship for the African lungfish (*P. aethiopicus*) from the Lake Baringo commercial fishery (n = 493).

Month	Mean \pm SE	Range	Number of fish
Jan	0.99 ± 0.03	0.74 - 1.23	21
Feb	0.96 ± 0.02	0.75 – 1.26	57
Mar	1.03 ± 0.02	0.62 - 1.86	78
Apr	1.02 ± 0.03	0.74 - 1.55	38
May	1.01 ± 0.03	0.63 – 1.66	45
Jun	1.01 ± 0.03	0.67 – 1.84	37
Jul	1.05 ± 0.03	0.73 – 1.58	47
Aug	1.00 ± 0.02	0.73 - 1.39	55
Sep	1.01 ± 0.02	0.72 - 1.53	47
Oct	1.03 ± 0.02	0.78 - 1.54	68
All Fish	$\textbf{1.01} \pm \textbf{0.01}$	0.62 - 1.86	493

Table 3.4Mean relative condition (Kn) factor for lungfish in monthly samplesfrom the Lake Baringo commercial fishery.



Fig. 3.2 Mean relative condition (Kn) factor for monthly samples of the lungfish landed in the Lake Baringo commercial fishery in 2001 (vertical bars represent 95% CI).



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The Kn for 86 males ranged from 0.64 to 1.86 (mean = 1.02 ± 0.02 SE) compared to 0.72 - 1.56 (mean = 1.02 ± 0.01) for 181 females. The mean Kn for females and males were about unity and did not vary during the ten months of commercial fishing in 2001 (Fig. 3.3).

3.2.2.3 Length-frequency distribution

Length measurements were obtained for 762 lungfish between January and October 2001 when the ban on commercial fishing was put in place due to low catches. Of these, 215 were recorded at two fish-landing sites namely: Kampi Ya Samaki and Ngenyin (see Fig. 2.1) by assisting DFO and KEMFRI personnel. Table 3.5 shows the respective number of lungfish recorded at each of the above fish-landing sites. No lungfish were recorded at the Kampi Ya Samaki fish-landing site between August and October 2001 as fishermen who operated from this site abandoned fishing for other economic activities due to low catches. For the same reason, Ngenyin fishermen had abandoned fishing much earlier in May 2001 (Table 3.5).

Figure 3.4 presents the bimonthly length-frequency histograms for the 762 individuals measured during the ten months of commercial fishing activity in 2001. There were no discernible modal progressions in the length-frequency histograms. The size range for all lungfish was between 36.0 and 145.0 cm total length, however, the histograms show that most (>75%) lungfish were in the range between 56.0 and 96.0 cm total length. Lungfish shorter than 40.0 cm total length occurred only in March to June



Fig. 3.3 Monthly variation in mean relative condition (Kn) of male and female lungfish in Lake Baringo commercial catch (vertical bars represent 95% CI).

Table 3.5 Monthly number and sex of African lungfish recorded at Kampi Ya Samaki and Ngenyin fish-landing sites before the ban on fishing in October 2001 (N.S. = not sexed, * no fish landed, fishermen abandoned fishing activities).

Month		Kampi Ya S	amaki			Ngenyin		
	Male	Female	N.S.	Total	Male	Female	N.S.	Total
Jan	10	14	3	27	4	11	3	18
Feb	15	20	3	38	7	10	2	19
Mar	9	16	0	25	5	9	0	14
Apr	8	17	0	25	2	9	0	11
May	8	8	2	18	*	*	*	÷
Jun	4	8	1	13	*	*	*	*
Jul	4	3	0	7	*	*	*	*
Aug	*	*	*	*	*	*	*	*
Sep	*	*	*	*	*	*	*	*
Oct	*	*	*	sie.	*	*	*	*
Total	58	86	9	153	18	39	5	62



Fig. 3.4 Length-frequency histograms for lungfish in bimonthly catches landed in the Lake Baringo commercial fishery in 2001.

samples, whereas those in the 112.0 - 145.0 cm size range occurred in all bimonthly samples but in relatively low numbers (Fig. 3.4).

3.2.3 Recaptured floy-tagged lungfish

3.2.3.1 Tag returns and dispersion of floy-tagged fish

Fishermen at different landing sites reported tag returns indicating considerable dispersion by some tagged individuals from the site of release. A total of 178 lungfish were floy-tagged and released by the end of October 2001 when a ban was imposed on all commercial fishing activities in the lake. Fishermen fishing in the vicinity of the point of release caught about 75% of the released fish; the remaining came from fishermen operating at the Ngenyin fish-landing site (Fig. 3.5). Floy-tagged lungfish ranged from 45.2 to 116.0 cm in total length and weighed between 0.18 and 7.14 kg at the time of release.

Most floy-tagged lungfish recaptures were caught close to the point of release. Fishermen operating near the fish release point reported thirteen tag returns or 54.2% of all recaptures (Fig 3.5), which represented 7.3% of all floy-tagged lungfish. Six returns (or 25% of all tag returns) were reported at the Loruk fish-landing site, while one tag was reported by a fisherman operating near Longicharo on the eastern side (Fig. 3.5).

Table 3.6 shows the number of lungfish that were floy-tagged and released into the lake each month between February and October 2001, and the monthly recaptures reported over the same period. A total of 24 recaptures were returned through the commercial fishery; thus 13.5% of the 178 floy-tagged lungfish released were recaptured



Fig 3.5 A map of Lake Baringo showing the general areas (enclosed in dotted line) where floy-tagged lungfish were recaptured. Numbers represent percentage of total recaptures.

Table 3.6Monthly statistics on tagging and recapture of African lungfish
(*P. aethiopicus*) in Lake Baringo (* does not account for
natural mortality or unreported tags).

	Number	Number	Number still	Catch rate
Month	tagged	recaptured	at large*	(% per month)
Feb	7	0	7	0.0
Mar	47	i	53	1.9
Арг	21	2	72	2.8
May	15	6	81	7.4
Jun	22	4	99	4.0
Jul	18	2	115	1.7
Aug	15	3	127	2.4
Sep	10	2	135	1.5
Oct	23	4	154	2.6
Total	178	24		Mean = 2.7
				SE = 0.68

by October 2001, when commercial fishing in the lake was closed. The monthly tag returns ranged between 0.0 - 6.0 (Table 3.6), which represented catch rates of between 0.0 and 7.4 fish per month (mean = 2.7 ± 0.68 SE). Catch rates increased between February and May 2001 but were lower later despite increased number of floy-tagged fish from subsequent tagging and release, likely reflecting the declining effort as fishermen abandoned fishing (Table 3.5).

Table 3.7 shows days recaptured lungfish were at liberty, method (gear) and general locations of capture and recapture. Most recaptured lungfish were caught on long-lines. Several floy-tagged lungfish returned to the same general area of their original capture; one was recaptured on the same long-line! One floy-tagged lungfish (Floy-tag no. 00347) was recaptured twice, 20 days after its initial release and again 42 days after its subsequent release. The time between release and recapture varied considerably among individual recaptures ranging from 2 to 136 days (Table 3.7).

3.2.3.2 Individual growth of recaptured lungfish

Of the 24 recaptured floy-tagged lungfish, length and weight measurements were obtained on nine and six respectively. Although fishermen had been advised to take measurements of total length using a string whenever they could not bring recaptured lungfish to the field laboratory, most are illiterate and only returned the floy-tags for the cash reward. In two instances where fishermen returned floy-tags together with strings for total lengths of lungfish they had recaptured, the strings turned out to be much shorter than the respective length of the lungfish at release. Thus growth estimates were based on

	Floy-tag	Recapture	Days at	Capture	Recapture	Capture	Recapture
S.no.	no.	date	liberty	area	area	gear	gear
1	00291	03/24/01	11	Ngenyin	Ngenyin	Long-line	Long-line
2	00271	04/27/01	50	Ngenyin	Longicharo	Long-line	Gill net
3	00252	05/21/01	82	Samatian	Lekolos	Long-line	Long-line
4	00292	05/24/01	72	Ngenyin	Lekolos	Long-line	Long-line
5	00289	06/05/01	84	Ngenyin	Rongena	Long-line	Long-line
6	00277	06/09/01	92	Samatian	Kabargolwa	Long-line	Long-line
7	00283	05/14/01	64	Samatian	Samatian	Gill net	Long-line
8	00267	05/09/01	62	Ngenyin	Loruk	Long-line	Long-line
9	00312	05/31/01	3	Samatian	Samatian	Long-line	Gill net
10	00447	05/05/01	11	Samatian	Samatian	Long-line	Gill net
11	00442	04/21/01	7	Ngenyin	Samatian	Long-line	Long-line
12	00306	06/02/01	17	Samatian	Samatian	Long-line	Long-line
13	00316	06/18/01	2	Samatian	Samatian	Long-line	Long-line
14	00304	07/10/01	56	Samatian	Salabani	Gill net	Gill net
15	00302	07/15/01	65	Samatian	Samatian	Gill net	Long-line
16	149.200	07/03/01	136	Samatian	Kichertet	Long-line	Long-line
17	00347	08/11/01	20	Samatian	Samatian	Long-line	Long-line
18	00384	08/15/01	2	Samatian	Samatian	Long-line	Long-line
19	00347R	09/22/01	42	Samatian	Samatian	Long-line	Long-line
20	00328	09/24/01	95	Samatian	Komolion	Long-line	Long-line
21	00393	10/06/01	25	Samatian	Samatian	Long-line	Long-line
22	00326	10/10/01	112	Samatian	Rongena	Long-line	Long-line
23	4058B	10/13/01	7	Samatian	Samatian	Long-line	Long-line
24	00394*	10/30/01	48	Samatian	Samatian	Long-line	Long-line

Table 3.7 Summary data for tagged fish recaptured on various dates through the commercial fishery in Lake Baringo (* fish recaptured on same long-line).

six length-weight measurements that I personally took and three other length measurements recorded by KEMFRI personnel.

Table 3.8 presents growth in length data for nine recaptured lungfish. These fish had a mean total length of 70.3 cm (range 54.8 - 80.5) at release, whereas mean total length at recapture was 72.9 cm (range 55.1 – 85.0 cm). A paired t-test showed these differences were significant (t = -4.11, p = 0.003). The average time of liberty for these fish was 58.6 days (range 17 – 112 days). Absolute growth rate in total length ranged between 0.015 and 0.083 cm day⁻¹ with a mean of 0.041-cm day⁻¹ (Table 3.8). The mean specific growth rate in total length was 0.056 % day⁻¹ (range = 0.027 - 0.108 % day⁻¹).

The weight at release and recapture data for six lungfish are presented in Table 3.9, which also shows absolute and specific growth rates in mass over respective periods fish were at liberty. Specific growth rates for mass are presented for only six lungfish, as three lungfish reported by KEMFRI personnel were not weighed at recapture. The mean absolute growth rate in mass was 0.0028 kg day⁻¹ (\pm 0.0002 SE), whereas mean specific growth rate in mass was 0.235 % day⁻¹ (range 0.089 – 0.400 % day⁻¹). Figure 3.6 presents a graphical plot of specific growth rate (SGR) in mass against initial weight of recaptured lungfish. Specific growth rate in mass was strongly negatively related ($r^2 = -0.919$) with initial weight of lungfish and the correlation was significant (p = 0.010, n = 6). Thus smaller lungfish (> 1 kg at initial capture) had the highest specific growth rates, while the heaviest individual (2.74 kg at initial capture) recorded the lowest specific growth rate in mass (Fig. 3.6).
Table 3.8Absolute and specific growth in length of African lungfish recapturedfrom Lake Baringo on various dates in 2001.

Tag No.	Initial TL (cm)	Recapture TL (cm)	Increment (cm)	Liberty (days)	Absolute growth rate (cm day ⁻¹)	Specific growth rate (% day ⁻¹)
00271	74.0	76.1	2.1	50	0.042	0.056
00283	64.0	66.2	2.2	64	0.034	0.053
00302	73.1	78.4	5.4	65	0.083	0.108
00304	58.0	59.8	1.8	56	0.032	0.055
00306	69.5	70.2	0.7	17	0.041	0.059
00326	79.8	85.0	5.2	112	0.046	0.056
00328	80.5	85.0	4.5	95	0.047	0.057
00347	54.8	55.1	0.3	20	0.015	0.027
00394	79.1	80.5	1.4	48	0.029	0.037
Mean (SE)	70.31 (3.17)	72.72 (3.60)	2.62 (0.64)	58.6 (10.3)	0.041 (0.006)	0.056 (0.007)

Tag no.	Initial Wt (kg)	Recapture Wt (kg)	Increment (kg)	Liberty (days)	Absolute growth rate (kg day ⁻¹)	Specific growth rate (% day ⁻¹)
00271	1.32	1.46	0.14	50	0.0028	0.202
00283	1.30	1.48	0.18	64	0.0028	0.203
00302	1.60	1.84	0.24	65	0.0037	0.215
00304	0.76	0.90	0.14	56	0.0025	0.302
00347	0.60	0.65	0.05	20	0.0025	0.400
00394	2.74	2.86	0.12	48	0.0025	0.089
Mean (SE)	1.39 (0.31)	1.53 (0.32)	0.145 (0.026)	50.5 (6.7)	0.0028 (0.0002)	0.235 (0.043)

Table 3.9Absolute and specific growth in mass of African lungfish recapturedfrom Lake Baringo on various dates in 2001.



Fig 3.6 Relationship between specific growth rate (SGR) and initial weight of recaptured floy-tagged lungfish.

3.2.4 Diet of the African lungfish in Lake Baringo

The gut contents of 127 lungfish were examined for analysis and identification of prey items. Externally, the lungfish gut appears as a short, straight, muscular tube of wide diameter extending from the back of mouth to the cloacal opening with no marked distinction between the stomach and the intestine. However, internally it was observed to consist of three distinct regions or compartments. The anterior region is a relatively less muscular chamber with a pale gray inner mucosal lining. In preserved guts, food particles in this region appeared to be enveloped in a whitish mass of what appeared to be digestive secretions, which suggested some form of chemical digestion took place in the region. Muscular folds of the spiral valve marked the beginning of the thick walled middle compartment whose inner lining was distinctively shiny black. At the posterior end, the spiral valve of the middle compartment opened into a third, less muscular rectal region where indigestible food remnants appeared to be stored prior to egestion.

About 35% of all guts examined were empty or had contents in an advanced state of digestion that could not be categorized. Whole prey items were not found among the contents of guts examined in this study. Parts of prey or their remnant indigestible material including scales and other skeletal parts were rarely found in the first compartment but were relatively more common in both the middle and rectal regions. These were identified as belonging to four common indigenous fish species in the lake namely: *Oreochromis niloticus, Clarius gariepinus, Barbus gregorii* and *Labeo cylindricus*. Collectively fish prey occurred in 83 guts, which represented 65.4% of guts examined. However, *O. niloticus* skeletal material was observed in the highest number (52.0%) of guts examined and 79.5% of those with identifiable contents (Table 3.10), whereas scales of *B. gregorii* were found in only one fish gut. The incidence of *L. cylindricus* (7.1%) was noted only among guts of lungfish sampled in August. However, based on the total of 34 guts that were examined in August, *L. cylindricus* was second to *O. niloticus* as most consumed prey, occurring in 23.5% of the guts. An almost entire trunk (head to anal fin) of *L. cylindricus* was found in the first compartment of one lungfish gut. Although the trunk had some bite marks, this prey had evidently been swallowed head first.

No invertebrates or other prey were encountered in the guts examined. Neither were parts that could be identified to belong to lungfish. However, bite marks found on some lungfish with fresh wounds were similar to those observed on a part of the trunk of *Labeo cylindricus* in one lungfish gut. Missing parts of lungfish and scraped scales observed among individuals kept together in holding tanks in the field laboratory were assumed to have been ingested since such parts were not seen anywhere within the tanks. Vegetal or plant material in the rectal region of the guts of two lungfish appeared undigested. No endoparasites were observed in the viscera of lungfish, which was a striking contrast to the masses of these parasites commonly found in the viscera of indigenous species.

Table 3.10 Percentage frequency of occurrence of fish prey in the alimentarytract of lungfish landed in the commercial fishery.

	Number	Percentage frequency (%)			
Prey taxa	of tracts examined	All fish (n = 127)	Fish with identifable contents $(n = 83)$		
Oreochromis niloticus	66	52.0	79.5		
Clarius gariepinus	11	8.7	13.3		
Labeo cylindricus	9	7.1	10.8		
Barbus gregorii	1	0.8	1.2		

3.2.5 Reproduction biology

3.2.5.1 Sex ratio

There were more females than males among lungfish landed in the Lake Baringo commercial fishery. Of 478 lungfish that were sexed, 181 were males and 297 females. The resultant sex ratio of 1 male to 1.64 females was significantly different from the expected 1:1 (chi-square test, $\chi^2 = 28.151$, df = 1, p < 0.001). Sex ratios of lungfish in monthly samples were skewed in favour of females. Figure 3.7 shows the percentage composition of males and females in various length classes. Females did not occur in length classes longer than 132.0 cm while they predominated in most other length classes. Table 3.11 compares the male to female sex ratios among lungfish of different length classes. The non-parametric chi-square test showed significant differences in the sex ratios of lungfish longer than 72.0 cm, but not in those that measured less than 72.0 cm in total length (Table 3.11).

3.2.5.2 Gonad size, GSI and gonad maturity

Gonads of female lungfish were on average larger than those of males. Total gonad weights determined for 115 lungfish: 81 females and 34 males showed mean female gonad weight was 128.8 g (\pm 15.8 g SE), whereas male gonads had a mean weight of 30.5 g (\pm 6.9 g SE). Consequently the mean GSI (gonadosomatic index) for females was higher (3.07 \pm 0.34 SE) than the 0.88 (\pm 0.12 SE) for males. The non-parametric Kruskal-Wallis test showed that the differences in median GSI were highly significant (H



Fig. 3.7 Percentage composition of male (solid bars) and female (open bars) lungfish in different length groups. Males = 86, females = 161.

Size class midpoint (cm)	No. of males	No. of females	Sex ratio M : F	Calculated χ^2	df	p-value	Difference
39	3	3	1:1.00	0.000	1	1.0000	n.s
45	8	5	1:0.63	0.692	1	0.4055	n.s
51	15	21	1:1.40	1.000	1	0.3173	n.s
57	21	26	1:1.24	0.532	ł	0.4658	n.s
63	23	20	1:0.87	0.209]	0.6473	л.\$
69	23	30	1:1.30	0.925	1	0.9332	n.s
75	15	34	1:2.27	7.367	١	<0.0001	S
81	15	30	1:2.00	5.000	1	<0.0001	S
87	17	32	1:1.88	4.592	l	< 0.0001	S
93	11	30	1:2.73	8.805	1	< 0.0001	S
99	8	24	1:3.00	8.000	1	< 0.0001	S
-102	22	43	1:1.95	6.151	1	< 0.0001	S
Total	181	297	1:1.64	28.151	1	<0.0001	S

Table 3.11 Size composition of male and female lungfish in the commercial catch and results of the chi-square test (n.s = not significant, s = significant).

= 27.53, d.f. = 1, p < 0.001). The data in monthly samples were too few to allow meaningful comparison of variation of GSI over time.

Males and females in different stages of gonad maturity occurred in all monthly samples. The status of gonad maturity was determined for 237 lungfish, 89 males and 148 females. Table 3.12 shows the monthly distribution of male and female lungfish in the various stages of gonad maturity. Males and female lungfish in maturity stages I – IV occurred in all monthly samples. There were nine (representing 6.1%) females in stages V (ripe and running) and VI (spent) while no males were found to be in either of these two maturity stages.

Table 3.12 also shows that there were relatively more females than males among fish in later stages of gonad maturity. The two females in the ripe and running condition (stage V) had eggs that had descended in the oviduct. These eggs were pale green and each appeared to be surrounded by a clear jelly coat. In its ripe and running state (Plate 3.6) the ovary was dominated by larger greenish eggs, however a few small orange eggs could be easily discerned amongst the larger ones.

There was considerable overlap in the size (total length) of lungfish among stages of gonad maturity (Table 3.13). For example, females with mature ovaries (i.e. stages III and IV) ranged between 65.2 and 130.0 cm, but an individual measuring 100.0 cm in total length had immature ovaries. Similar results were obtained for males, where a 138.5 cm long fish was in immature gonad condition, although males in mature gonad condition ranged in total length from 72.1 - 112.5 cm. Over 50% of the females in the 70.0 - 76.0 cm length group were mature (i.e. in stages III and IV) indicating that females

	Maturity Stage							
Month	Ι	II	III	IV	V	VI	Total	
Jan	4	0	2	3	0	0	9	
Feb	6	ĩ	10	10	0	3	30	
Mar	2	0	3	3	0	0	8	
Apr	4	1	4	2	0	2	13	
May	2	I	3	1	0	1	8	
Jun	1	0	4	0	0	0	5	
Jul	6	5	1	8	l	0	21	
Aug	14	9	1	2	0	0	26	
Sep	4	5	1	6	1	1	18	
Oct	1	6	2	1	0	0	10	
Total	44	28	31	36	2	7	148	

Table 3.12 Monthly status of gonadal maturity among male and female lungfish landed in the Lake Baringo commercial fishery in 2001.

Males

Females

	A Stan	1.5.1	Maturity	Stage			_
Month	I	п	III	IV	V	VI	Total
Jan	3	0	2	0	0	0	5
Feb	11	3	4	1	0	0	19
Mar	2	0	3	0	0	0	5
Apr	3	1	2	0	0	0	6
May	4	2	2	3	0	0	11
Jun	4	0	0	2	0	0	6
Jul	4	2	1	1	0	0	8
Aug	7	5	0	1	0	0	13
Sep	4	1	4	0	0	0	9
Oct	3	2	2	0	0	0	7
Total	45	16	20	8	0	0	89



Fig 3.6 A ripe ovary of the African lungfish (A). Arrows in B show pale greenish free ova that had descended into the oviduct.

Table 3.13 The size range of lungfish in different stages of gonad maturity

	Females		Males		
Maturity stage	Total length (cm)	n	Total length (cm)	n	
r	43.0 - 74.2	40	43.5 - 138.5	43	
П	68.5 - 100.0	28	70.5 - 107.0	13	
III	65.2 - 101.2	27	72.1 - 112.5	19	
IV	77.0 - 130.0	31	88.0 - 131.2	6	
V - VI	100.0 - 129.1	8			

attained maturity at this size. However, the smallest female with an ovary in mature condition measured 65.2 cm and weighed 1.40 kg. The size range where 50% males were mature was 82.0 – 88.0 cm, but the smallest mature male measured 72.1 cm long and weighed 1.52 kg.

Figure 3.8 presents plots of mean GSI against maturity stages of male and female lungfish landed in the commercial fishery in 2001. The results show that mean GSI for both sexes increased with an increase in the status of gonad maturity. The highest mean GSI values were found in individuals with gonads in maturity stage IV, however individual GSI for these fish varied considerably, ranging from 3.09 – 12.86. One of the two females in maturity stage V had an excised tail that had started regenerating and was not included in the computation of mean GSI. The computed mean GSI of the one female in maturity stage V was 4.56. Females in maturity stage VI had low mean GSI compared to those in maturity stage IV (Fig. 3.8).

3.2.5.3 Fecundity

Fecundity varied among individual females but was positively related to both length and weight. The number of eggs determined for each of 28 females, which ranged between 4,179 and 16,528 eggs (mean = 10,711 eggs \pm 572 SE) (Table 3.14). Of these females, one had a freshly bitten tail while three had regenerated tails and were thus omitted from further statistical analyses. The remaining 24 females ranged in total length from 77.0 to 125.0 cm and from 2.02 to 9.26 kg in weight. Simple linear regression of the log-transformed data showed the following relationships:



Fig. 3.8 Mean GSI (gonadosomatic index) of male and female lungfish in different stages of gonad maturity (vertical bars are standard deviations).

TL (cm)	W (kg)	Number of eggs	
77.0	2.02	4823	
89.0	2.68	6387	
90.2	3.28	8515	
90.8	3.62	8913	
91.2	4.16	9804	
94.5	3.80	9629	
98.0	3.58	8156	
100.0	4.75	10503	
100.0	4.60	11284	
100.3	4.32	12542	
103.2	4.72	8312	
104.5	4.88	10331	
105.3	4.74	12284	
106.0	5.02	13929	
107.0	5.20	10672	
111.5	6.30	11601	
112.0	6.66	10624	
112.5	5.52	11563	
114.5	7.28	12096	
114.5	6.14	10507	
117.0	6.66	12595	
122.0	7.28	15661	
124.0	8.86	15608	
125.0	9.26	14360	
83.5*	2.90	4179	
90*	4.80	7629	
70*	5.60	10867	
*	8.74	16528	

Table 3.14 Fecundity of African lungfish (*P. aethiopicus*) in Lake Baringo (* fish had excised or regenerating tail).

Log F =
$$0.104 + 1.94$$
 Log TL ($r^2 = 0.736$, $n = 24$, $p < 0.001$)
Log F = $3.57 + 0.65$ Log BW ($r^2 = 0.763$, $n = 24$, $p < 0.001$)

Graphs of non-log transformed fecundity and total length, and fecundity and body weight (Fig. 3.9 and Fig. 3.10) showed fecundity increased with both total length and body weight.



Fig. 3.9 Relation between fecundity and total length for the African lungfish (*P. aethiopicus*) in Lake Baringo commercial catch.



Fig. 3.10 Relation between fecundity and body weight for the African lungfish (*P. aethiopicus*) in Lake Baringo commercial catch.

Chapter 4 Movement and Space Use by the African lungfish in Lake Baringo

Information on movement is important in understanding fish behaviour. Such information may help identify critical feeding, reproduction and refuge areas or habitats for a species, which is useful to management of its fishery. In the present study investigations were conducted using biotelemetry techniques to monitor the movement of lungfish surgically implanted with ultrasonic transmitters. The purpose was to describe the species' movement and use of space, of which little is known. Biotelemetry techniques were used because they enable rapid identification and positioning of fish with high temporal and spatial resolution (Winter 1996, Lucas and Baras 2001). Since it was not originally envisioned that a boat for use in tracking would be available, radio telemetry in which tracking could be done from the shore was attempted first, however, tracking radio-tagged lungfish was generally unsuccessful due to poor signal transmission.

4.1 Materials and methods

4.1.1 Laboratory procedures

Radio and ultrasonic tags were surgically implanted into lungfish under anaesthesia. After a period of post-surgery observation subjects were released back into the lake so that their movements could be monitored. Lungfish for transmitter implantation were obtained from among fish landed alive in the commercial long-line fishery. Fish judged to be in good condition were purchased from fishermen and held in holding tanks to recover from the effects of post-capture handling, usually for a period of one to two days. This period of observation became necessary when it was noted that some lungfish that appeared to be in good condition later died before surgery was performed. Some specimens with minor injuries were held for longer periods (between one and two weeks) until they healed before tags were surgically implanted. During this time the water in the holding tanks was changed every two days. Captive lungfish were initially supplied with fresh chunks of fish flesh, but this was stopped as lungfish did not eat the food.

Before surgery a specimen was anaesthetized by being placed in a plastic tub containing 4 litres of lake water to which had been added 1 cc of clove oil in 9 cc of absolute alcohol. The lungfish became agitated approximately 5 minutes after immersion and was immobile after about 15 minutes. The immobile specimen was measured for total length and weighed, and then placed belly up on a v-shaped wooden trough (Plate 4.1). Scales were carefully removed along a line approximately 1 cm off the midventral line and 5 cm anterior to the pelvic fins to allow a 3 cm incision to be made. An activated transmitter, sterilized in absolute alcohol, was inserted into the body cavity through the incision and manipulated towards the posterior of the abdominal cavity. The incision was then closed with three separate sutures using a size 10 ASCO surgical needle and thread. The gills were periodically irrigated with lake water throughout the surgical procedure, which took approximately 10 minutes. If the transmitter was a radio tag, the body wall was punctured about 1 cm posterior to the incision, using a hypodermic needle, to feed the tag's antenna out through the body wall.



Plate 4.1 Preparing for surgery in the field. The V-shaped trough on which lungfish were surgically implanted with transmitter tags under anaesthesia. Notice the tagging gun for attaching an external Floy-tag to subject.

While the subject was still under anaesthesia, a blue (for easy distinction from other externally tagged lungfish) Floy-tag was inserted into the dorsal musculature as described above (section 3.1.3). After surgery, the lungfish was placed in an upright position in a recovery tank with just enough water to cover its body. In addition the tank was slanted to ensure that the subject's head was not completely immersed in water. This was necessary to prevent the fish from drowning, as their initial attempts to gulp air were feeble. It took between 20 and 30 minutes following surgery for subjects to reestablish a regular cycle (every 8 - 12 minutes) of lung ventilation (raising the head to break the water surface and gulp air). Surgically tagged lungfish were normally released back into the lake in the late evening of the same day or early morning of the next day. However, one radio tagged lungfish was held for a longer period of observation and was released 12 days after surgery when the wound appeared to have completely healed. All surgically tagged lungfish were released at the same location; about 50 meters offshore of the Moi University Fieldhouse (Fig. 4.0).

4.1.2 Field procedures

4.1.2.1 Radio-tracking lungfish

Four lungfish implanted with radio transmitters were released into the lake on various days in the early part of the study (Table 4.0). Following release, three radio-tagged lungfish were monitored from a vantage position on shore (a 5 - 6 m high cliff overlooking the release site) using both directional and omnidirectional antennas attached to a Lotek receiver. The fourth lungfish was monitored from a gadich anchored at the



Fig 4.0 Map of Lake Baringo showing the release point for all surgically tagged lungfish and some designated fish landing sites (Note: the Moi-Toronto fish landing site at the Moi University Field house was established and operated only for the duration of this study).

Table 4.0 Details of lungfish that were surgically implanted with radio tags and released on various dates in the early part of the study.

Fish	Date	Date	Date	Radio Tag	Length	Weight
Number	Captured	Tagged	Released	Frequency	(cm)	(kg)
ALF053	02/15/01	02/16/01	02/17/01	149.200	81.0	1.58
ALF061	02/16/01	02/17/01	02/17/01	149.420	74.5	1.16
ALF082	02/25/01	02/26/01	02/28/01	149.400	68.0	1.06
ALF121	02/26/01	02/27/01	11/03/01	149.000	76.5	1.68



release site for first 12 hours following its release. Attempts to locate and monitor all radio-tagged lungfish continued for several days following release from Moi-Toronto and other vantage positions along the shore. This activity was abandoned when radio signals could not be detected for a period of about two weeks after their release.

4.1.2.2 Tracking and location of ultrasonic-tagged lungfish

Tracking of ultrasonic-tagged lungfish was done regularly to determine their location over the tag's life expectancy. Initially some tracking was done from a gadich, however this became impractical when a lungfish moved more than 3 – 4 km from the release site. When it became available, an open 6 m fibreglass boat powered by a 25-horse power (HP) engine was used to track ultrasonic-tagged lungfish. Ultrasonic tracking was restricted to day light hours because the lake is inhabited by several groups of hippopotamus (*Hippopotamus amphibius*) and the Nile crocodile (*Crocodylus niloticus*) which made tracking at night too dangerous. Initial tracking results indicated that ultrasonic-tagged lungfish tended to move short distances and remained in the same general area for periods of over one month, thus later tracking was usually carried out over a period of at least four consecutive days a week.

Ultrasonic tracking was done using a directional hydrophone attached to a CR-40 ultrasonic receiver (Cai associates inc.) or a VR-60 (Vemco Ltd) receiver. The ultrasonic transmitter tags were of the V16-4H Pinger model by Vemco Ltd and tagged lungfish were identified by the signal transmitting frequency of their tags or when necessary the combination of frequency and pulse rate (Table 4.1). The tags were 15 mm in diameter, 58

Sonic tag no.	Frequency (KHz)	Pulse rate	Fish number	Date of release	Length (cm)	Weight (kg)
4060B	65.5	29.8	65	09/25/01	102.0	4.66
4061B	69	29.6	69	09/29/01	58.0	0.62
4059B	60	30	60	09/30/01	74.0	1.72
4062B	76.8	30	75	10/02/01	89.5	2.56
4057B	50	59.5	50F	10/05/01	81.2	1.90
4058B	50	48.1	50S*	10/07/01	89.1	2.52
4058B	50	48.1	50S	10/22/01	85.9	2.12
4403	50	60	50V	03/20/02	87.2	2.32
4408	76.8	60	75F	03/21/02	78.6	1.64
6751B	53.8	40.3	54F	05/03/02	75.3	1.66
4798B	65.5	40	65F	05/14/02	76.0	1.54
6752B	53.8	29.8	54S	05/23/02	67.5	1.24
4799B	69	39.8	69F	08/01/02	59.0	1.08
6754B	76.8	35.3	75N	08/01/02	66.5	1.14

Table 4.1. Summary data on ultrasonic tags and the size of tagged lungfish released into Lake Baringo on various dates between September 2001 and August 2002 (* fish recaptured on 6th day). mm in length, and weighed 10 g in water; thus the tag weight was always less than 2% of fish weight (Winter 1996) since the smallest lungfish tagged weighed 620 g. To locate a fish, the frequency of its tag was tuned in on the receiver and the directional hydrophone immersed into the water while listening for signals (Plate 4.2). The hydrophone was pointed to different directions to search an area of about 1.5 km radius. The tag frequencies of lungfish yet to be located that day were successively tuned and listened for at every search site. Whenever a signal was detected, the distance of the target lungfish was estimated based on the signal strength; and either the motor or, at short distances, oars used to bring the boat over the fish. The boat was assumed to be over the lungfish when the strength of the signal recorded on the receiver at the lowest gain was equal in all directions. The geographic position of the lungfish was recorded on a handheld Garmin 12XL Global Positioning System (GPS) receiver. The depth of water at each fish location was determined using a graduated weighted rope.

Tracking was usually done once a day, in the morning starting between 0600 and 0730 hours, and continued until either all fish were located or tracking was abandoned due to low fuel, fatigue, or bad weather (e.g. heavy rain). Usually when tracking was done on successive days, each tracking excursion started with a search for the nearest fish based on the previous day's positions. Where tracking was not on successive days all ultrasonic-tagged lungfish would be systematically searched for at each stop (after every 0.5 km) as the previous position of the nearest fish by the last tracking was approached. However, in January and February 2002, three ultrasonic-tagged lungfish were tracked twice a day, once early in the morning (between 0600 and 0830 a.m.) and again in late evening (1600 – 1800)



Plate 4.2 Tracking ultrasonic-tagged lungfish in Lake Baringo: tuning in a tag's frequency on the receiver to detect signals from a subject fish using the directional hydrophone immersed in the water.

to determine if lungfish were active in the day; and whether day and night movements were different.

Signals could usually be detected over a range of approximately 1.5 km. When a fish could not be heard from its previous position, it was first searched for in the direction it was headed as predicted from its previous movement. Repeated stops to search for the fish were made every 0.5 km along a circular route whose radius roughly equaled a distance twice the range of the receiver's detection limit. If not detected on completion of this circular search, the fish was searched for at every subsequent stop in the search for other lungfish. Fish not located on a tracking day were considered as "lost" and were extensively searched for on subsequent excursions after other ultrasonic-tagged lungfish had been located. Usually the "lost" fish were relocated in the open waters of the lake after two to three days, and at distances that suggested they had not moved far from their previous known position but were missed for some other reason. This often occurred when the ultrasonic-tagged lungfish were around the southern assemblage of islands (some smaller ones were often submerged); thus it is possible that these and other underwater obstacles could have contributed to the non-detection of signals.

It was discovered that the CR-40 receiver unit was sensitive to increased heating over the course of the day. Before this, it was common not to be able to locate Fish 60 and Fish 75 on successive days of tracking and then relocating them close to their last known positions on subsequent days. Early results from the morning and late afternoon tracking showed that Fish 60 and Fish 75 were consistently not located during the afternoon tracking. Either fish was, however, easily located at the same general area on the subsequent morning tracking, at times within less that 0.5 km from the previous day's position. This raised the possibility that these lungfish may not have actually moved far from their earlier positions. An all day tracking of Fish 60 at hourly intervals showed that this fish did not move much that day, but the frequency at which the transmitter was detected changed (increased) over time, and was probably related to increasing day temperatures. Generally, the best frequency at which a transmitter's signal was detected shifted by as much as 2 KHz and also the bandwidth became narrower. Appropriate adjustment for this subsequently improved the relocation of these two fish.

All ultrasonic-tagged lungfish were searched for on each tracking day until either the tag's life expectancy expired or it was decided that the tag was stationary on the bottom and thus no longer in a lungfish. The latter appears to have occurred for five ultrasonic tagged lungfish: Fish 69, 50F, 50S, 75F and 54 in the present study. Their transmitters were located at the same position for periods longer than two months, even after a swimmer deliberately disturbed the area.

4.1.3 Data Analyses

4.1.3.1 Determination of distances moved by lungfish

Position data from ultrasonic tracking were analyzed using spatial analysis techniques. Spatial analyses were done using the Animal Movement Analyst Extension (AMAE, Hooge and Eichenlaub 1997), a software program integrated with ArcView GIS (Environmental Systems Research Institute, Inc., Redlands, CA). The Lake Baringo topographic map Sheet 91/3, Edition 3-D.O.S (GOK 1982) was digitized and geo-

referenced in UTM (Universal Transverse Mercator) coordinate system for Zone 37 in ArcView GIS. To enable digitization of the map, actual ground coordinates for several distinctive location features along the shores of the lake and major islands (Fig. 2.1) were taken using the GPS receiver. These position data were used as control points to digitize and geo-reference the map following the procedure detailed in the ArcView GIS User's Manual (ESRI 1996).

Fish position data were converted into decimal degrees and plotted on the georeferenced map in ArcView. Distances between successive daily fish relocations were used as the basis for calculating daily horizontal movement by ultrasonic-tagged lungfish. These were determined by constructing fish movement paths as polylines from the point profile data in AMAE (Hooge and Eichenlaub 1997). This procedure outputs distances between successive locations, which allowed determination of minimum, maximum and mean daily movement. The non-parametric Kruskal-Wallis test was used to test for significant differences between daily movement among fish because the daily movement data comprised extreme values, which greatly affect mean values (Gardiner 1997).

4.1.3.2 Day and night movement of lungfish

Day and night movement data were analyzed to determine whether there were differences in level of activity of lungfish between day and night time. Day and night movements were determined as above i.e. from successive morning-evening and eveningmorning distances between relocations. All day and night time distances were converted into distance moved per hour to allow comparison of day and night movements because on average day time (morning and evening) tracking recorded movement over a shorter time period of 8 hours, as compared to 16 hours between evening and morning tracking. The Kruskal-Wallis test (Gardiner 1997) was used to test for significant differences between day and night movement.

4.1.3.3 Determination of home ranges

Animation of movement based on the relocation data revealed that some ultrasonic-tagged lungfish often restricted their movements within certain areas for extended periods, suggesting existence of home ranges smaller than the entire lake. However, by definition, a study animal can be said to have a home range only if its movements exhibit faithfulness to an area (Hooge and Eichenlaub 1997). Thus the relocation data for a fish in each particular area determined as above were tested for site fidelity using the site fidelity test in AMAE. Site fidelity indicates centralized nonrandom movement, which occurs when the animal's real location data exhibit neither significant dispersion nor linearity (Hooge et al. 1999). The site fidelity test thus tests the null hypothesis of random movement. The procedure first estimates the centre of activity (Hayne 1949) of the distribution of relocations and then calculates the mean squared distance (MSD) of each point from the centre of activity. These are then compared with MSDs generated from 100 random movement paths (Hooge et al. 1999) and fidelity determined at p > 95.00, where p is the proportion of movement paths with higher MSD values than those from the random paths (Hooge et al. 1999). Site fidelity thus indicates that the area utilized by an individual is significantly smaller than the area that would be used if its movements were random.

Each area that passed the site fidelity test was confirmed as a home range, and two home range estimator procedures in AMAE namely, the minimum convex polygon (MCP) and the kernel home range procedures (Hooge and Eichenlaub 1997), were used to estimate its size. The MCP (Mohr 1947) procedure is the oldest and most direct method of estimating the size of a home range, and basically involves connecting outermost locations or position fixes to circumscribe the area. The 100% MCP, which uses all position data for an area, was used since, as was noted by Andersen and Rongstad (1989) not using all points can bias home range size. The kernel home range in AMAE constructs frequency of use polygons based on the concentration of points in areas within the home range (Hooge and Eichenlaub 1997). It is a non-parametric probabilistic technique that makes no assumptions about the underlying statistical distribution of the data. The procedure calculates a fixed utilization distribution (Worton 1989) by placing a kernel over each point, giving higher density where points are concentrated, hence it is a measure of the relative time an animal spends in different parts of the home range. The 95% frequency polygon was used to describe the kernel home range, an area with 95% probability that the fish is inside (Hooge et al. 1999). Use of space within home ranges was investigated using the 50% frequency polygon, which usually represents the probable core area of activity within the home range i.e. where the animal was found most of the time.

4.2 Results

4.2.1 Radio-tagged lungfish

Signals from radio tags were detected in a pattern that appeared to be consistent with the lungfish settling at the bottom most of the time but periodically coming up to the surface to gulp air. The radio signal strength attenuated sharply as soon as the fish entered the water and subsequently the signal could not be heard within seconds after the fish was released. However, after some time a weak signal was detected which quickly became more audible, reached a peak and then rapidly weakened until it again was inaudible. Since the radio tag's antenna protruded ventrally, radio signals could not be heard when the fish settled on the bottom, as its weight buried the antenna into the mud. On average, the time between when a signal was first detected and when it became inaudible was 30 -60 seconds. However, on at least three separate occasions peak signals from two lungfish lasted for as long as 2 - 4 minutes, suggesting the fish remained in the surface waters for that long. Times when signals were detected from radio-tagged fish following their release are shown in Table 4.2. The detection of signals was only possible for a short period following the release of three of the radio-tagged lungfish, while one was never heard from (Table 4.2). The time between peak signals also varied, generally ranging between 2 and 45 minutes but in one instance a peak signal was heard after 126 minutes.

Although not a direct result from radio tracking, a very interesting finding was the recapture of one of the four radio-tagged lungfish (Fish 149.200) on a long-line in a small satellite lake, locally known as Lake Kitchirtet. This small lake lies about 5 km south of Lake Baringo and is best described as a swamp at the confluence of the River Molo and

Fish 149.200		Fish 149.420	Fish 149.400		Fish 149.000	
Time signal heard	Time between signals (min.)	Time signal heard	Time signal heard	Time between signals (min.)	Time signal heard	Time between signals (min.)
07:00		19:15	06:35		07:00	
09:58			06:57	22	07:15	15
10:00	2		07:01	4	07:23	8
10:06	6		07:14	13	07:31	8
10:15	9		08:48	34	07:48	17
10:19	4		09:23	35	07:54	6
10:24	5		10:05	42	08:02	8
10:26	2		10:50	45	08:10	8
10:37	11		10:53	3	08:13	2
10:57	20				08:32	19
11:01	4				10:38	126
16.05	*				17:40	*
19:15	*			586-110	19:00	*

Table 4.2Results from radio tracking showing the times when radio-tagged lungfish were
detected following their release (release time in in bold, * indicates weak signal).
one of its tributary streams. According to local knowledge, this satellite lake formed following the heavy rains of 1994 (Elijah Lekosek Parsalach, Pers. Comm.) and its existence was recently reported on the earth watch website by a team of scientists working on the Kenyan Rift Valley lakes.

4.2.2 Ultrasonic-tagged lungfish

There was considerable variation in the direction and pattern of movement of different lungfish following their release. Fourteen lungfish (ranging in size from 58.0 to 102.0 cm, Table 4.1) implanted with ultrasonic tags were tracked for a total of 121 tracking days between September 2001 and September 2002, with tracking done in all months except April 2002. Occasionally, tracking could not be carried out (for periods of up to three weeks at one time) due to malfunction of the receiver unit.

The shortest duration an individual lungfish was tracked was 5 days for Fish 50S*, which was recaptured on a long-line on the 6th day after its release (Table 4.3). By the time of recapture this fish had covered a total distance of 1.2 km from the point of release. The recapture of this lungfish on a long-line indicated it had resumed feeding activity. Physical examination of its surgical wound at recapture showed no evidence of inflammation indicating proper healing had occurred. A total of 482 relocations or position fixes were recorded for the fourteen ultrasonic-tagged lungfish over the duration of tracking. The number of relocations varied considerably among individuals ranging from 5 to 104 fixes (Table 4.3).

Table 4.3 The number of relocations (position fixes) for ultrasonic-tagged African lungfish (*P. aethiopicus*) tracked for various periods between September 2001 and September 2002 (* caught on 6th day).

Fish	TL	Date		Number
identity	identity (cm) Released		Period tracked	offixes
65	102.0	25/09/01	Sep. 01 – Sep. 02	104
69	58.0	29/09/01	Sep. 01 – Dec. 01	38
60	74.0	30/09/01	Oct. 01 - Sep. 02	99
75	89.5	02/10/01	Oct. 01 – Jul. 02	57
50F	81.2	05/10/01	Oct. 01 – Dec. 01	19
50S*	89.1	07/10/01	08/10/01 - 12/10/01	5
50S	85.9	22/10/01	Oct. 01 - May 02	28
50V	87.2	20/03/02	Mar. 02 – Jul. 02	31
75F	78.6	21/03/02	Mar. 02 – May 02	12
54	75.3	03/05/02	May 02 – Jul. 02	24
65F	76.0	14/05/02	May 02 – Sep. 02	27
54S	67.5	23/05/02	May 02 – Aug. 02	15
69F	59.0	01/08/02	Aug. 02 – Sep. 02	12
75N	66.5	01/08/02	Aug. 02 – Sep. 02	10

Figure 4.1 presents the spatial distribution of positions where all ultrasonic-tagged lungfish were located in the course of this study. The ultrasonic-tagged lungfish collectively utilized an area of approximately 48.6% of the available lake area habitat of about 137 km² as determined from the digitized topographic map of Lake Baringo. The distribution of fixes (relocations) revealed some clustering around the central and southern parts of the lake (Fig. 4.1). None of the ultrasonic-tagged lungfish were located in the northern part of the lake or close to shore for most parts of the lake.

Figure 4.2 shows the depths at different positions where ultrasonic-tagged lungfish were located during the study. Depth measurements at all positions lungfish were relocated ranged between 1.0 and 2.9 metres. Table 4.4 presents details of depths at locations where ultrasonic-tagged lungfish were located. The lake water levels changed considerably over the study period as described in section 2.3.2 above. This probably explains some of the variation in depth where fish were located, however at no time were any of the ultrasonic-tagged lungfish located at depths shallower than 1.0 metres.

4.2.2.1 Daily movement of ultrasonic-tagged lungfish

Both direction and distances covered in the daily movement differed among individual ultrasonic-tagged lungfish. The relocation data showed that the distances moved by lungfish over the first 24 hours after release ranged between 17 and 1,192 metres (mean = 407.6 ± 105.4 m SE) (Table 4.5). Later individual daily movement of lungfish also varied among individuals ranging from virtually no movement to a maximum of about 5.2 km which was covered by Fish 50V (Table 4.5).



Fig. 4.1 Distribution of position fixes of all ultrasonic-tagged lungfish tracked for varying periods between September 2001 and September 2002 in Lake Baringo (circle encloses cluster of fixes near the fish release point, squares represent areas of apparent concentrated use, and broken line (---) encloses the area of the lake utilized by all fish over the study period).



Fig. 4.2 Depth (in metres) at positions where ultrasonic-tagged lungfish were located during the study.

Table 4.4Details on depth at positions where ultrasonic-taggedlungfish were located during the study (S.E. = standarderror of the mean).

Fish	Depth (m)								
identity	Mean	S.E.	Range	n					
65	2.1	0.05	1.1 - 2.9	104					
69	2.7	0.01	2.6 - 2.9	38					
60	2	0.05	1.0 - 2.8	99					
75	2	0.05	1.3 - 2.9	57					
50F	2.1	0.07	1.3 - 2.6	19					
50S	2.2	0.09	1.4 - 2.8	28					
50V	1.7	0.04	1.3 - 2.1	31					
75F	1.8	0.04	1.6 - 1.9	12					
54	2.1	0.06	1.3 - 2.4	24					
65F	1.9	0.07	1.1 - 2.3	27					
54S	1.8	0.1	1.2 - 2.2	15					
69F	1.8	0.05	1.6 - 2.0	12					
75N	2	0.02	1.9 - 2.1	10					

Table 4.5 Initial (first 24 hours) and later daily movement of ultrasonic-tagged

lungfish (** fish lost tag - see text, n.d = not determined).

Fish	ish Date tag Date fish Distance after La		Later	daily movement (i	n)	
number	implanted	released	24 hours (m)	Mean	Range	n
65	09/24/01	09/25/01	185	918.0	18.0 - 3768.0	58
69**	09/27/01	09/29/01	768	299.2	20.7 - 1766.3	34
60	09/29/01	09/30/01	n.d.	662.0	3.0 - 4448.0	66
75	10/01/01	10/02/01	n.d.	522.0	20.7 - 2028.2	36
50F**	10/02/01	10/04/01	600	226.0	19.0 - 1554.0	14
50S*	10/04/01	10/06/01	327	224.0	18.0 - 665.0	4
50S**	10/21/01	10/22/01	1192	366.0	8.0 - 2646.0	20
50V	03/18/02	03/20/02	306	1080.0	11.0 - 5218.0	24
75F**	03/19/02	03/21/02	120	157.7	18.2 - 373.1	7
54**	05/01/02	05/03/02	17	76.3	6.0 - 373.9	17
65F	05/12/02	05/14/02	322	231.5	7.8 - 1102.6	15
54S	05/22/02	05/23/02	845	525.5	17.2 - 1031.1	8
69F	07/31/02	08/01/02	79	45.3	3.3 - 117.2	7
75N	07/31/02	08/01/02	131	1101.5	85.0 - 3059.4	5

The overall mean daily distance for all ultrasonic-tagged lungfish over the study period was 565.7 m (\pm 44.2 SE). However, median daily movements were significantly different among individual fish (Kruskal-Wallis test, H = 80.40, df = 13, p < 0.001). Monthly mean daily distances moved by two ultrasonic-tagged lungfish tracked for the longest period (about a year) indicated that these fish moved longer distances in May 2002 (Fig. 4.3), however data on monthly daily distance moved per fish were too few for further statistical analyses.

Figures A1 – A12 in Appendix A show the individual movement paths for twelve ultrasonic-tagged lungfish as determined from the tracking relocations during the present study. Examination of the movement paths showed the lungfish made short (<500 m) daily movements and generally remained within 1 – 1.5 km of the point of release for periods between two weeks and one month after their release. For example, the movement path of Fish 50S (Fig. A6) shows a cluster of relocations between 24th October – 26^{th} November 2001 close to the point of release (Fig. 4.1), in contrast to its relatively much longer daily movement between 4^{th} and 6^{th} December 2001. However, the lungfish later moved much further away from the point of release and ranged widely in the central and southern part of the lake (Fig. 4.1). Transmitter tags lost by ultrasonic-tagged lungfish were located at different parts of the lake (Fig. A3, A5, A6, A8 and A9). Based on the date tags were first relocated at sites where loss of tag occurred, the time to tag loss varied among individuals ranging from 51 to 89 days.



Fig. 4.3 Mean monthly distances moved by two ultrasonic-tagged lungfish between September 2001 and September 2002 (vertical bars are standard error of the mean, note: no tracking in April 2002-see text).

4.2.2.2 Day and night activity of ultrasonic-tagged lungfish

Ultrasonic-tagged lungfish were active during both the day and at night. There was no significant difference in movement speed (m/h) between day and night periods (Kruskal-Wallis test, H = 0.30, df = 1, p = 0.582). Table 4.6 gives summary statistics of the hourly day and night movement of lungfish. The mean movement speed for three lungfish that were tracked twice a day between January and February 2002 was 24.0 (± 4.7 SE) metres per hour at night compared to 22.0 (± 5.3 SE) metres per hour during the day.

4.2.2.3 Home ranges of ultrasonic-tagged lungfish

The home ranges of lungfish differed in their location and the duration they were occupied. Based on the results of the site fidelity test, six home ranges were confirmed for four ultrasonic-tagged lungfish. Two home ranges were described for Fish 65, HR1 to the immediate north of; and HR2 to the south of, Kokwa Island (Fig. 4.4). Fish 60 also had two home ranges, which were similarly located due north and south of Kokwa Island (Fig. 4.5). One home range each could be discerned from the distribution of relocation data for Fish 75 and Fish 50V (Fig. 4.6 and 4.7). The duration home ranges were occupied ranged from about 2 to 4.5 months.

The home ranges differed in size, both between individuals and also for the same individual where it had more than one home range (Table 4.7). Based on the MCP home range size estimates, the largest home range (19.8 km²) was the first home range of Fish 65, the largest ultrasonic-tagged lungfish; while the smallest was the first home range of



Table 4.6Comparison of hourly distances moved by ultrasonic-tagged lungfish
during the day and at night.

-		Day time	Night time			
Fish number	Range (m)	Mean (m)	n	Range (m)	Mean (m)	n
65	2.0 - 110.0	19.2	16	1.0 - 81.0	23.9	12
60	6.0 - 42.0	18.3	4	5.0 - 41.0	23.4	5
75	3.0 - 86.0	36.7	4	3.0 - 63.0	25.5	4
Weighted mean		22.0			24.0	



Fig. 4.4 The minimum convex polygon (MCP) home ranges (outlined in bold) and Kernel home ranges (dark green) for Fish 65 in Lake Baringo. Light green area = core area of activity. Duration home ranges were occupied is shown.
Position fixes outside home ranges are also shown.



Fig. 4.5 The minimum convex polygon (MCP) home ranges (outlined in bold) and Kernel home ranges (dark green) for Fish 60 in Lake Baringo. Light green area = core area of activity. Duration home ranges were occupied is shown. Position fixes outside home ranges are also shown.



Fig. 4.6 The minimum convex polygon (MCP) home range (outlined in bold) and Kernel home range (dark green) for Fish 75 in Lake Baringo. Light green area = core area of activity. Duration home range was occupied is shown. Position fixes outside home ranges are also shown.



Fig. 4.7 The minimum convex polygon (MCP) home range (outlined in bold) and Kernel home range (dark green) for Fish 50V in Lake Baringo. Light green area = core area of activity. Duration home range was occupied is shown. Position fixes outside home ranges are also shown.

Table 4.7 Minimum convex polygon (MCP) and Kernel (95%) home range sizes, and core areas of activity (CAA, 50% Kernel) for ultrasonic-tagged lungfish in Lake Baringo.

Fish identity	Home range identity	Number of fixes	MCP (km ²)	Kernel (km ²)	CAA (km ²)
65	F65-HR1	41	19.80	20.20	1.30
102	F65-HR2	22	14.50	30.50	7.10
	F60-HR1	28	5.80	9.40	2.00
60	F60-HR2	27	6.80	6.70	0.60
75	F75-HR	31	9.30	10.90	1.30
50V	F50V-HR	14	14.40	20.40	2.40

Fish 60, which measured 5.7 km². All but one of the home range size estimates based on the kernel home range estimator were larger than the respective MCP home range sizes (Table 4.7).

Within each Kernel home range there were one to two core areas of activity (Fig. 4.4 - 4.7), where the fish were located most frequently. The core areas of activity of lungfish showed that larger MCP home ranges were not necessarily associated with bigger core areas of activity. For example, Fish 65 had the largest core area of 7.1 km² in its smaller second home range. Similar results were obtained for Fish 60. Using the larger MCP home range for fish with two home ranges, home range area was found to be positively related ($r^2 = 0.887$) to fish size although the correlation is not significant (p = 0.113), likely due to the small sample size (Fig. 4.8).

Ultrasonic-tagged lungfish generally exhibited two types of movement behaviours: 1) a series of successive long daily movements and 2) shorter daily movement or no movement between days. For lungfish that possessed home ranges the successive longer daily movements either marked the abandonment of a home range or were considered to be exploratory forays (Burt 1943) if the fish returned to the home range within two weeks or so. The longer distance movements occurred at unpredictable times among individuals. Within a home range, the lungfish at times made little or no movement between days. Over the period of the present study, none of the ultrasonictagged lungfish returned to reoccupy a home range. However, Fish 60 and 65 made at least one exploratory foray to their respective earlier home ranges.



Fig. 4.8 Relationship between fish size (total length at release) and the MCP home range area.

Home ranges of two ultrasonic-tagged lungfish: Fish 60 and Fish 75, overlapped to a considerable degree. Their respective core areas of activity also overlapped to a lesser degree when the fish utilized the same general area between January and March 2002 as Fish 60 was occupying its first home range. Figure 4.9 shows the spatial overlap in the MCP home ranges of the two fish. The extent of spatial overlap was about 3.5 km², which represented 60.7 % of the home range of Fish 60 and 37.6 % that of Fish 75.



Fig. 4.9 Use of space by Fish 60 and Fish 75 showing the extent of spatial overlap (blue area) in their MCP home ranges. Duration home ranges were occupied is shown.

Chapter 5: The long-line fishery and experimental gillnetting

Lungfish in Lake Baringo are primarily targeted by the long-line fishery, however African catfish (*Clarias gariepinus*) are also caught on long-lines. The gillnet fishery which targets tilapia (*O. niloticus*) also catches lungfish and catfish as well as barbus (*Barbus gregorii*) but in relatively smaller numbers. However, DFO personnel collecting fisheries statistics at fish landing sites only record the number of fish by species landed regardless of the fishing method used. As such there are no good catch and effort data for any fishery. A study was therefore initiated to obtain catch and effort data on the longline fishery in Lake Baringo. The catch and effort data were recorded for a group of six fishermen operating from the Moi-Toronto fish-landing site between February and October 2001.

The ban on commercial fishing in the lake in October 2001 eliminated access to fish as well as catch and effort data from these fishermen. Therefore a program of monthly experimental fishing was designed and conducted for 10 months from February through to November 2002. This sampling was undertaken in collaboration with personnel at the Kenya Marine and Fisheries Research Institute (KEMFRI) to obtain information on numbers and distribution of fish species in the lake. The experimental fishing also provided more lungfish specimens for biological data and live lungfish for tagging in the absence of a commercial fishery.

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5.1 Materials and methods

5.1.1 Catch and effort data on the long-line fishery

Catch and effort data on the long-line fishery were recorded and used to determine daily catch rates and to quantify catch per unit effort. Catch and effort data were obtained directly from six long-line fishermen between February and October 2001. These fishermen had set their long-lines in the open waters off the Moi University Field House (Fig. 4.1) and landed their catch at the Moi-Toronto fish landing site, which was established and operated for the duration of this study. The number of hooks actually baited (and therefore actively fishing) was recorded on selected days for the fishermen who went out on the lake to fish and used as the basis for defining effort. Long-lines were usually baited in the afternoon (1430 - 1530 hours) to fish overnight and the catch retrieved the following morning (0600 – 0730 hours), thus the duration of fishing was approximately 17 hours. The catches recorded in the mornings were attributed to overnight fishing for previous day's effort, i.e. the number of hooks baited. On a few occasions some fishermen baited hooks on their long-lines in the morning to fish during the day. The lines were inspected in the afternoon and fish retrieved before the hooks were again baited to fish overnight, and thus effectively fished for about 7 hours during the day. The number of hooks baited in the morning was recorded and afternoon catches were attributed to daytime fishing for the respective day's effort of baited hooks.

Daily catch-effort data were used to estimate the catch-per-unit-effort (CPUE) for the long-line fishery. To allow comparison of daytime and overnight fishing, the unit of effort was defined as a hook-hour i.e. one baited hook fishing for one hour. Thus the number of hooks baited for overnight fishing was multiplied by 17 hours while those for daytime were multiplied by 7 hours to determine the total hook-hours. Daily CPUE was then calculated by dividing the day's total weight (in kg) of fish landed by the respective total hook-hours. Mean catch, effort and CPUE were computed based on the days for which catch and effort data were known. The non-parametric Kruskal-Wallis test was used to test for significant differences between daytime and overnight fishing.

5.1.2 Experimental fishing

Gillnetting was used in the experimental fishing largely because gillnets catch all commercially exploited fish species in Lake Baringo. Also data from the commercial catch landings indicated that gillnets all four commercially exploited species compared to only two, lungfish and catfish, that are landed by long lining. The lake was divided into three zones, south, central and north (Fig. 5.0) and each was fished once per day for one month over three consecutive days. The approximate respective sizes of these zones (Table 3.1) indicate that the central zone, whose area represented about 50% of the lake, was the largest and had the deepest water. This zone separated the nearly equal-sized north and south zones.

Three gangs of gillnets, each made up of randomly linked gillnets of 4.5, 4.0, 3.5, 3.0 and 2.5 inch stretched mesh sizes; were surface-set at haphazardly selected sites within the zone being fished that day. The 3.5 - 4.5 inch mesh nets were 100 m long and 2.5 m wide. The 2.5 inch mesh gillnets were 45 m long and 2.0 m wide, while respective dimensions for the 3.0 inch mesh gillnet were 45 m by 2.5 m. Gillnets were set in the mornings (between 06:30 and 08:00) and left to fish for approximately 8 hours.



Fig. 5.0 A map of Lake Baringo showing the three zones that were fished monthly during experimental gillnetting in 2002.

Table 5.1 The approximate sizes of the zones fished during experimental gillnetting in Lake Baringo in 2002.

	Size	% of Lake
Zone	(km ²)	Area
South	32.60	23.7
Central	68.40	49.8
North	36.40	26.5

Fish caught in gillnets were sorted to species and each individual measured for total length (and standard length where applicable) to the nearest 0.1 cm on a standard fish length measuring board and weighed to the nearest 5 g on a top loading electronic balance. Dead lungfish were dissected to determine their sex. Some live lungfish judged to be in good condition were used as subjects for the ultrasonic telemetry work (see section 4.1.1) while others were tagged with numbered floy-tags and released back into the lake.

The catch composition by weight and by number was determined for monthly samples. Total numbers of fish caught were compared by mesh size. Data for lungfish were analyzed to compare sizes of fish caught in gillnets of different mesh size and to evaluate the possible impact of the gillnet fishery on the lungfish spawning stock.

5.2 Results

5.2.1 Long-line catch composition, effort and CPUE

Fish landed at the Moi-Toronto fish-landing site by the six long-line fishermen comprised only lungfish and catfish. The total weight of fish landed between February and October 2001 was 1,402 kg; of which lungfish contributed 1101 kg or 78.5% of the total weight. Lungfish dominated catches by weights in all monthly landings (Fig. 5.1). Most lungfish were dead when retrieved from long-lines in the morning. However, some were landed alive and these usually provided a higher return to fishermen.

Table 5.2 presents a summary of catch and effort data for the long-line fishery as collected at the Moi-Toronto fish-landing site between February and October 2001. The mean daily catch rates varied considerably between months, ranging from 5.51 kg/day recorded in April to 15.18 kg day⁻¹ for March 2001. The daily catch per fisherman during the period ranged from 0.00 - 35.72 kg, with a mean of 5.5 kg (± 0.4 SE). Mean daily catch per fisherman differed between months (Fig. 5.2), which likely reflected the variation in effort between days.

There was considerable variation in the number of hooks baited per day of fishing. This was largely related to the number of fishermen who went out to fish each day. On the days data were recorded (N = 119), an average of 2 fishermen went out to fish, but this varied from 1 to as many as 5 among days. However, the number of hooks baited was also often limited by the availability of bait fish from gillnets. The mean number of hooks baited per day for the nine-month period ranged from 50 – 590 (mean =



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Fig. 5.1 Monthly total weight of lungfish (open bars) and catfish (solid bars) landed by six long-line fishermen at the Moi-Toronto fish-landing site in Lake Baringo.

Table 5.2	Summary data on catch and number of baited hooks for the Lake Baringo
	long-line fishery.

	Number	Total c	atch (kg)	Baited hooks		
Month	of days	Mean	Range	Mean	Range	
Feb	10	14.38	0.78 - 23.60	140.0	50 - 200	
Mar	16	15.18	0.60 - 35.72	245.6	100 - 500	
Apr	17	5.51	0.00 - 16.03	188.8	100 - 300	
May	15	11.88	1.30 - 22.41	256.3	100 - 440	
Jun	9	11.92	0.82 - 25.21	264.4	110 - 480	
Jul	16	13.17	5.50 - 23.66	298.4	160 - 590	
Aug	13	12.88	3.92 - 25.28	311.9	130 - 580	
Sep	14	11.53	4.56 - 25.18	182.1	90 - 350	
Oct	9	10.69	1.78 - 26.36	215.6	50 - 420	



Fig. 5.2 Monthly mean daily catch in the long-line fishery in Lake Baringo in 2002 (vertical bars represent standard error of the mean).

236.0 \pm 110.5 SD). The overall mean CPUE was 0.003 (\pm 0.003 SD) kg hook-hour⁻¹, but mean daily CPUE differed between months (Fig. 5.3). The highest mean daily CPUE was 0.007 kg hook-hour⁻¹ for February, while April's 0.002 kg hook-hour⁻¹ was lowest.

5.2.2 Daytime long-line fishing

The composition of the catch, by species and by weight, from long-lines baited in the morning to fish during the day, was similar to that of catches from overnight long lining (Table 5.3). The number of hooks baited for the daytime fishing varied between days ranging from 50 - 350 baited hooks. The daily CPUE for daytime fishing ranged from 0.002 to 0.011 kg hook-hour⁻¹ (Table 5.3), with a mean of 0.006 kg hook-hour⁻¹ as compared to the mean CPUE of 0.007 kg hook-hour⁻¹ (range = 0.00 - 0.014 kg hook-hour⁻¹) for the overnight fishing. The non-parametric Kruskal-Wallis test showed no significant difference in the CPUE between day and overnight (H = 3.9, df = 1, p = 0.05).

5.2.3 Gillnet catch composition

Experimental gillnet catches comprised four species namely, *Oreochromis niloticus*, *Clarias gariepinus*, *Barbus gregorii*, and *Protopterus aethiopicus*. A total of 2567 fish weighing approximately 531.4 kg were caught by experimental gillnets between February and November 2002. Numbers of individuals of each species caught varied among months but were dominated by *O. niloticus* by an order of magnitude (Table 5.4). Figure 5.4 shows the percentage composition by total number and weight of



Fig. 5.3 Monthly mean daily CPUE for the long-line fishery in Lake Baringo (vertical bars represent standard deviations).

Table 5.3 Details on catches from daytime	e long-line fishing in Lake Baringo.
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Date	Protopterus aethiopicus (kg)	Clarias gariepinus (kg)	Total catch (kg)	Effort (hook-hours)	CPUE kg hook-hour ⁻¹
3/5/01	21.94	5.70	27.64	2450	0.011
5/27/01	10.36	0.00	10.36	1750	0.006
6/16/01	0.58	3.83	4.41	910	0.005
6/18/01	0.60	0.00	0.60	350	0.002
6/21/01	6.62	0.00	6.62	910	0.007

 Table 5.4 The mean weight and total number of individuals of various species in monthly experimental gillnetting samples from Lake Baringo (SE = standard error of the mean).

	Oreochromis niloticus Barbus gregorii				Clarias gariepinus			Protopterus aethiopicus			Total		
	Mean		Number	Mean		Number	Mean		Number	Mean		Number	number
Month	weight (g)	SE	of fish	weight (g)	SE	of fish	weight (g)	SE	of fish	weight (g)	SE	of fish	of fish
Feb	175.3	13.9	106	306.0	50.2	15	795.0	220.0	5	2013.0	199.0	3	129
Mar	195.3	13.0	134	270.3	31.3	9	605.2	83.8	13	930.0	30.0	2	158
Apr	148.6	8.5	122	225.5	26.3	11	921.0	295.0	6	884.0	202.0	6	145
May	151.0	12.9	81	355.0	31.4	13	450.0	50.0	2	462.5	12.5	2	98
Jun	154.2	5.6	220	242.5	16.5	28	961.0	390.0	4	1360.0	349.0	5	257
Jul	172.6	5.5	261	262.5	47.3	12	425.0	102.0	7	1560.0	780.0	3	283
Aug	142.0	5.1	248	249.2	36.0	12	571.0	114.0	8	918.0	166.0	12	280
Sep	174.7	5.6	384	195.0	20.6	11	558.0	143.0	12	988.0	207.0	13	420
Oct	167.6	5.4	405	188.3	23.6	12	321.3	61.3	8	1237.0	319.0	7	432
Nov	195.0	7.1	342	210.0	36.7	5	468.3	73.4	12	882.0	213.0	6	365
Total			2303			128			77			59	2567

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Fig. 5.4 Percentage composition by number (solid bars) and weight (open bars) of fish species caught in experimetal gillnetting in Lake Baringo in 2002.

the four species in gillnetting catches between February and November 2002. Although *O. niloticus* dominated both by numbers and by weight, its percentage contribution by weight was lower. *Protopterus aethiopicus* occurred in the lowest numbers (2.3% of total numbers), but contributed over 10% of the total weight (Fig. 5.4). The total number of fish caught in monthly experimental gillnetting tended to increase over time (Fig. 5.5). This increase appeared to be largely related to increase in number of *O. niloticus* caught (Table 5.4).

Most fish were caught by gillnets of smaller mesh size than the minimum legal 3.5 inch mesh size (Table 5.5). Collectively the two smaller mesh sizes (i.e. 2.5 and 3.0 inch) caught more than 75% of all fish, with the 2.5 inch mesh catching about twice the number caught by the 3.0 inch mesh (Table 5.5). Generally the number of fish caught decreased with increasing mesh size for all species except *C. gariepinus* which was caught in highest number by the 3.5 inch mesh.

All four species were caught in each zone of the lake, but their numerical abundance varied over time (Table 5.6). The total number of fish caught in the south, central and north zones over the ten month period was 1116, 831 and 620 respectively. *Oreochromis niloticus* comprised more than 90% of all fish caught by experimental gillnets in the south and central zones and 85% in the north zone (Fig. 5.6). Numbers for *Clarias gariepinus* and *Protopterus aethiopicus* were generally low, representing between 2 and 3 percent of the total captures in each of the three zones. This was also true for *B. gregorii* in the south and central zones, however in the north zone *B. gregorii* comprised nearly 10% of all fish caught.


Fig. 5.5 The total number of fish caught in monthly experimental gillnetting in Lake Baringo.

Table 5.5	The number of fish caught on gillnets of different mesh sizes during
	experimental fishing in Lake Baringo in 2002.

	Mesh size (inches)						
Fish species	2.5	3.0	3.5	4.0	4.5	Total	
O. niloticus	1154	602	382	116	50	2304	
B. gregorii	74	37	13	3	1	128	
C. gariepinus	20	21	23	4	8	76	
P. aethiopicus	15	11	16	11	6	59	
Total	1263	671	434	134	65	2567	

	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Total
South zone											
Oreochromis	48	61	25	59	155	122	139	171	127	108	1015
Barbus	3	3	2	3	13	0	3	8	2	3	40
Clarias	1	7	2	0	1	4	6	10	3	3	37
Protopterus	0	0	0	0	2	2	7	8	3	2	24
Total	52	71	29	62	171	128	155	197	135	116	1116
Central zone						-					
Oreochromis	33	19	48	4	38	109	35	125	200	151	762
Barbus	3	3	4	4	6	2	2	3	2	0	29
Clarias	3	2	2	0	3	0	0	0	3	8	21
Protopterus	1	0	5	1	2	1	3	3	1	2	19
Total	40	24	59	9	49	112	40	131	206	161	831
North zone										1	
Oreochromis	25	54	49	18	27	30	74	88	79	83	527
Barbus	9	3	5	6	9	10	7	0	8	2	59
Clarias	1	4	2	2	0	3	2	2	1	1	18
Protopterus	2	2	1	1	1	0	2	2	3	2	16
Total	37	63	57	27	37	43	85	92	91	88	620
Grand Total	129	158	145	98	257	283	280	420	432	365	2567

Table 5.6Number of individuals of various species caught in the three zones of the lake during
monthly experimental gillnetting in Lake Baringo in 2002.



Fig. 5.6 Percentage composition by number of fish species in experimental gillnet samples from different zones.

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5.2.4 Lungfish data from experimental fishing

Sixty-one lungfish were caught im the experimental gillnets, two of which had freshly excised tails. The remaining fifty--nine lungfish had a mean total length of 63.5cm (\pm 1.6 cm SE) and an average weight \bigcirc f 1.07 kg (\pm 0.09 kg SE). None of the lungfish earlier tagged with numbered floy-tags were caught during experimental gillnetting. There was considerable overlap in the sizes of lungfish caught in gillnets of different mesh size (Table 5.7), however, the mean size of lungfish caught increased with increasing mesh size. The length-frequency distribution of the gillnetted samples differed considerably from that of lungfish cauglint on long-lines the previous year before the closure of the commercial fishery (Fig. 5. \overline{N}). The size range of lungfish caught by gillnets was 43.2 to 90.0 cm total length. Lungfish in the 48 – 66 cm range dominated in the gillnet sample, with 90% of the fish beiing shorter than 80 cm. The length-frequency distribution for the commercial catch showed a peak in the range of 66 - 92 cm (Fig. 5.7). Most (90%) of the lungfish were between 48.0 and 114 cm total length. Lungfish caught on long-lines ranged in total length from 36.0 to 145.0 cm, however individuals longer than 112 cm were relatively few (Fig. 5.7).

Table 5.7The number and size range of lungfish caught on gillnets
of different meshes in experimental fishing (* number
excludes one individual that had an excised tail).

Same in the	Number	Total length (cm)			
Mesh (inches)	of fish	Mean	Range		
2.5	15*	53.2	46.3 - 75.3		
3.0	12	55.9	43.2 - 61.5		
3.5	16	64.3	58.5 - 68.9		
4.0	10*	74.1	63.3 - 82.7		
4.5	6	85.3	82.0 - 90.0		



Fig. 5.7 Length-frequency distribution for lungfish caught in experimental gillnetting and in commercial long lining in Lake Baringo.

Chapter 6 Discussion

6.1 Size and growth of lungfish

Several early workers indicated that mostly adult lungfish occur in open waters of lakes (Greenwood 1958, Okedi 1971). Goudswaard et al. (2002) reported that only lungfish >40 cm total length were commonly caught in the open waters of Lake Victoria. In the present study lungfish smaller than 36.0 cm in total length were not represented in Lake Baringo commercial catches. The absence of smaller lungfish in the open waters is probably related to the species breeding behaviour, in which juveniles remain in the inshore areas where they are spawned (Greenwood 1958). Goudswaard et al. (2002) noted that lungfish of 20 - 40 cm total length were "most abundant within the swamps, particularly swamp lagoons". The size of the smaller lungfish landed in Lake Baringo indicates that new migrants into the open waters are quickly recruited into the commercial fishery. Although lungfish shorter than 40 cm total length occurred in the March to June samples (Fig. 3.4), the presence of 36 - 48 cm lungfish in all monthly samples indicates recruitment of young fish into the fishery throughout the year. There was no evidence of a specific time of year when recruitment of a 'new' year class occurs.

Lungfish in Lake Baringo apparently do not grow as large as has been reported for other populations. The lungfish recorded in this study measured between 36 and 145.0 cm total length, however according to one Fisheries Officer, Mr. David Kemboi (Pers. Comm.), the largest lungfish ever recorded in Lake Baringo measured 154.0 cm total length and weighed 32.0 kg. Greenwood (1986) and Witte and van Densen (1995) noted that the species attains total length of about 200.0 cm in Lake Victoria. Goudswaard *et al.* (2002) reported lungfish measuring 180.0 cm in trawl catches recorded between 1973 and 1990 from the southern part of Lake Victoria. In Lake Baringo, lungfish are mostly caught by long lining, which is considered to be a less size selective fishing method (Witte and van Densen 1995, Goudswaard *et al.* 2002). Thus it is seems likely that the population in Lake Baringo does not contain larger individuals than reported here. Whether this is due to heavy exploitation or other factor(s) is not known.

In Lake Baringo male lungfish attained larger size than females. No female larger than 130.0 cm total length was landed in the commercial fishery (Fig. 3.7). Since males up to 140.5 cm in length and an unsexed individual measuring 145.0 cm and weighing 17.32 kg, were landed, it is clear that the long-lines are capable of catching this size fish. Female lungfish in Lake Baringo therefore probably reach asymptotic size at approximately 130.0 cm total length. These results are similar to those based on samples from Lake Victoria (Greenwood 1958, Okedi 1971) where it was noted that "males grow larger than females" although neither of these authors gave an indication of the respective size attained by each sex.

The lungfish in Lake Baringo exhibited allometric growth i.e. the fish change in shape as they increased in length. The slope or length exponent of 3.52 for the length-weight relationship was significantly greater than 3, indicating individuals become heavier for their length (more rotund) as they increase in size (Anderson and Neumann 1996, Jobling 2002). Mosille and Mainoya (1988) reported a length exponent of about 3.4 for the length-weight relationship of 576 *P. aethiopicus* specimens from the Mwanza Gulf area in the southern part of Lake Victoria. However, it was not indicated whether this value was

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Allometric growth has been reported for the west African lungfish *Protopterus annectens* (Otuogbai *et al.* 2001). In the present study, analysis of covariance showed no significant differences in the length exponents for males and females, indicating similar growth form in both sexes.

There are no procedures yet for aging lungfish. Aging fish in the tropics is difficult but some species show patterns on scales or otoliths that have been correlated to seasonal (i.e. wet vs dry) environmental changes (Weatherley and Gill 1987). Lungfish scales do not show regular growth rings that could be used to quantify growth rates. The tagging and recapture method used to estimate growth in the present study proved to be a successful technique for obtaining information on growth, but was hindered because of the closure of the fishery. Even so, the rate of tag recovery was relatively high (Table 3.6) and the method did provide the only data I am aware of on the growth of individual lungfish in the wild.

The average absolute growth rate as estimated from the mark-recapture data was about 0.04 cm per day (Table 3.8) or approximately 14.5 cm year⁻¹. The size range of the lungfish at release in the present study was 45.2 - 116.0 cm, which (as will be demonstrated later) included immature as well as mature individuals. Results on specific growth showed higher rates of increase in mass than in total length (c.f. Table 3.8 and 3.9), as predicted from the length-weight relationship. The mean specific growth rate in mass was 0.235 % day⁻¹ compared to 0.056 % day⁻¹ for total length. The higher value for specific growth rate in mass is consistent with greater rate of increase in mass than in

length as a fish grows. This makes changes in weight a more precise measure of growth over short periods such as those in the present study. Individual growth in the wild has not been previously reported for *P. aethiopicus*, nor for any of its other three congeners. An overall standard (specific) growth rate in mass of $1.52 \,\% \, day^{-1}$ for the slender African lungfish, *P. amphibius* (Baer *et al.* 1992) remains the only reported growth rate for any of the four African lungfish species. However, that study was under culture conditions and aimed at testing the efficacy of different types of feeds and feeding regimes, so it may not apply to natural conditions.

6.2 Food and feeding biology of lungfish

Lungfishes are often listed among stomachless fishes in the scientific literature (e.g. Bruton 1998). Amongi *et al.* (2001) attributed this to the fact that their guts lack "clear demarcation between the stomach and intestine externally". These authors reported anatomically and functionally distinct stomach and intestinal regions of the gut. In the present study it was observed that towards the posterior end of the intestine the spiral valve opens into a compartment or rectal region, which appears to function as a storage chamber for indigestible prey remnants before egestion. Thus the internal compartmentalization of the lungfish gut into three anatomically distinct parts was confirmed in the present study.

The diet composition indicated that lungfish in Lake Baringo feed primarily on other fishes i.e. are piscivorous. The diet was dominated by tilapia (*O. niloticus*), which is also the most abundant and widely distributed species in the lake, as shown during experimental

fishing. Corbet (1961) and Pabari (1997) reported that lungfish in Lake Victoria consumed mostly molluses, with fish forming a minor component of the diet. However, specimens in these two studies were obtained largely from inshore waters where Okedi (1990) showed that molluses were particularly abundant. This may potentially explain their preponderance in lungfish diet as reported in the above two studies. Lake Baringo lungfish were largely caught in open water areas of the lake whose bottom, according to Ssentongo (1995) is devoid of invertebrates. Thus the piscivorous diet of lungfish from open waters in Lake Baringo may be related to a lack of benthic invertebrate prey. In a recent study Otuogbai *et al.* (2001) reported that *P. annectens* showed a preference for feeding on the young of other fishes breeding in the floodplains of River Niger.

Greenwood (1986) referred to *P. aethiopicus* as an "omnivorous carnivore". It is not clear what is meant by this terminology, but at least the first part of the term implies that lungfish ingest plant material as food. Curry-Lindahl (1956) attributed the presence of vegetal material and bottom sediment to accidental (incidental) ingestion along with prey. Some Lake Baringo lungfish were found to contain plant material in the rectal region of the gut, but it appeared undigested, also suggesting incidental ingestion.

Protopterus aethiopicus reportedly rely on non-visual cues for feeding (Greenwood 1986). It is thought the fish locate their prey by olfaction, supplemented by taste buds on their paired fins, especially the pectorals (Curry-Lindahl 1956, Thomson 1969). In describing the feeding behaviour of lungfish as observed in Lake Edward, Curry-Lindahl (1956) noted:

"the two paired fins of the otherwise motionless fish on the bottom are almost constantly moving slowly in different directions like independent living beings. If these sensitive organs come in contact with something hidden in the mud or a fish or some other animal of suitable size approaching from behind, the *Protopterus* quickly turns towards the prey and sucks it into the mouth".

Greenwood (1986) noted that lungfish probably also use a slow stalking approach when feeding, as an alternative to the lying in wait for the prey to come within sucking range. It is probable that lungfish use chemical cues exuded by fish caught on long-lines or in gillnets to locate such prey. Given the extreme turbidity and low transparency of the Lake Baringo waters, non-visual location of food is necessary for a demersal predator like the lungfish.

Incidences of fish with excised parts in commercial and experimental catches suggested that Lake Baringo lungfish bite off parts of fish caught on fishing gear. Corbet (1961) noted that fish prey in lungfish guts comprised small fragments and concurred with Greenwood's (1955, as cited in Corbet 1961) suggestion that "*P. aethiopicus* bite and damage other fish" caught on fishing gear. However, in the present study remnant body parts of *Labeo cylindricus*, a demersal species (Mann 1974) that is not caught by any of the fishing gear used in the lake were found in digestive tracts, indicating that lungfish also attack fish not caught on fishing gear.

There was no direct evidence of cannibalism from examination of gut contents. Lungfish in landings often had wounds (e.g. excised tails) likely made after being caught, but the large number of lungfish with regenerated tails suggests that lungfish will attack one another even when not caught on fishing gear. Some wounds on lungfish were similar to those observed on a part of the trunk of a *Labeo cylindricus* found in a lungfish gut. Given that no other species in the lake is capable of inflicting such wounds, it appears that lungfish do attack and eat each other. Incidences of missing (bitten off) parts of fins among lungfish in wild populations have been reported in several early studies (see references in Conant 1970) and were attributed to predator attack, likely by other lungfish. Okedi (1971) and Goudswaard *et al.* (2002) also reported missing parts among lungfish in Lake Victoria. Cannibalism among lungfish in their natural environment was reported by Curry-Lindahl (1956) who found remains of fish belonging to four genera: *Clarias*, *Tilapia*, *Haplochromis* and *Protopterus*, in stomachs of *P. aethiopicus* specimens caught by fishermen in Lake Edward. In the present study, additional evidence for cannibalism came from missing fins and scales among individuals kept in the same holding tank in the field laboratory.

The incidence of individuals with two tails and branched pectoral fins found among lungfish in Lake Baringo in the present study can probably be attributed to regeneration following predator attack or other injury. Several lungfish in the fishery landings showed evidence of a remarkable capability to heal and regenerate bitten off parts. Like other fishes, lungfish are known to regenerate lost parts (Conant 1970, 1972). Based on studies in which she mutilated lungfish fins in different ways; Conant (1970) found that regeneration started within 2 - 3 weeks and cut sections were restored in 3 - 4 months, with growth of the regenerating tissue following the typical sigmoid curve. Conant (1972) demonstrated that regenerating fins could form branchial structures i.e. result in bifidism, such as those found in the present study (Table 3.1).

6.3 Reproductive biology of lungfish

The sex ratio of lungfish in commercial landings in Lake Baringo was skewed in favour of females. Available data indicates the sex ratio of lungfish caught in the open waters of Lake Victoria is also skewed in favour of females. Greenwood (1958) and Okedi (1971) reported male to female sex ratios of 1 : 3.31 and 1 : 1.72, respectively for lungfish in the northern part of Lake Victoria, but neither of these workers advanced an explanation for the divergence from the expected 1 : 1 ratio. Similarly, Mosille and Mainoya (1988) did not explain the 1 : 1.98 male to female ratio for lungfish in the southern part of Lake Victoria. However, the sex ratio of 1 : 1.64 determined for fish caught in the open waters in the present study, may not (as discussed below) reflect the natural sex ratio in the Lake Baringo lungfish population.

The skewed male to female ratio in the open waters could be related to the differences in the reproductive behaviour of male and female lungfish. Males migrate from open waters to shallow inshore swamp areas where they prepare nests and provide parental care for eggs and young through their protracted larval stage (Greenwood 1958, 1986). Greenwood (1958) reported that one male in the northern part of Lake Victoria stayed for over two months guarding eggs and young in a nest. In the present study, males in maturity stage V and VI (Table 3.12) were not found in samples obtained from the open waters, consistent with their remaining in swamps providing care to eggs and young (Greenwood 1958). This explanation may best explain the situation in Lake Baringo where a skewed sex ratio was only seen in lungfish longer than 72 cm total length (Table 3.11), probably because males migrate from the open waters to spawning

habitats after attaining sexual maturity. Another factor that may contribute to the skewed sex ratio is differential mortality between the sexes, with higher male than female mortality above 70 cm total length. Males are likely to be more vulnerable to predation by crocodiles during the prolonged nesting and post hatch guarding periods while females are probably in these areas for relatively short periods. The crocodiles, which are known natural predators of adult lungfish (Greenwood 1958), are most abundant in the shallow inshore waters of Lake Baringo.

In contrast, female lungfish presumably spend much shorter periods at inshore spawning sites and hence are caught in greater numbers in the fishery. They do not provide maternal care, thus move to spawning areas only when ready to mate and lay eggs. The times of their inshore movements are not known but females in ripe and running condition were rarely caught in the open waters probably because these individuals move to shallow swamp areas prior to spawning. Other workers have reported females in ripe and running condition in their samples. Greenwood (1958) reported two ripe females in his samples, and Mosille and Mainoya (1988) reported the presence of some females in stage V in their samples, but did not give an indication of the actual number or when they were caught. In contrast, Okedi (971) found no females in this stage of gonad maturity among 836 females caught by bottom trawling in open waters of the northern parts of Lake Victoria. The finding of some females with ovulated eggs in the oviduct (maturity stage V) and also of females in spent condition (maturity stage VI) in open waters in the present study is consistent with females spending shorter time in breeding areas than males.

Female lungfish in Lake Baringo attained sexual maturity at smaller sizes than males. At between 70.0 and 76.0 cm in total length, the size at first maturity for females in Lake Baringo compares well with the 65-76 cm total length reported by Okedi (1971) and Greenwood's (1958) 65-70 cm total length. Okedi (1971) reported that the smallest mature male measured 82 cm in his sample and concluded that females matured earlier than males. However, Mosille and Mainoya (1988) found the converse was true for lungfish in the southern part of Lake Victoria where females matured at between 76 and 86 cm, larger than the 66 - 76 cm for males. The later maturity of male lungfish in Lake Baringo is consistent with their reproductive behaviour, which favours a bigger size that enables individuals to successfully obtain and defend nest sites, and attract females (Wooton 1990). Earlier maturity of females means they produce fewer and perhaps smaller eggs at first spawning (Wooton 1990, Forsgren et al. 2002). By foregoing provision of maternal care and returning to the open waters to feed and grow, these females presumably realize higher subsequent fecundity hence increased overall fitness (Forsgren et al. 2002).

The female lungfish in Lake Baringo are partial or batch spawners. Evidence for partial spawning is the finding that two females with free ova descended in the oviduct had ripe but unshed ova in their ovaries. Mature ovaries with oocytes in varying stages of development occurred in all monthly samples. Other workers including Greenwood (1958), Okedi (1971) and Mosille and Mainoya (1988) have reported presence of oocytes of different sizes in ovaries. In the present study female lungfish between 65.2 and 130.0 cm, and males between 72.1 and 131.2 cm occurred in advanced stages (III-VI) of gonad

maturity (Table 3.13), indicating they were reproductively active (Mosille and Mainoya 1988). The above size range of reproductively active fish indicates that lungfish are iteroparous i.e. breed several times in their lifetime (Wooton 1990).

Lake Baringo lungfish appear to spawn all year round. The monthly distribution of individuals in different maturity stages indicated there was no synchronized pattern in gonad maturation that could be related to seasonal environmental cues. Some workers have suggested breeding seasonality for the lungfish. For example, Greenwood (1986) indicated that P. aethiopicus spawns during periods when local rainfall is heavy and protracted. Mosille and Mainoya (1988) reported an extended breeding period from September to May, for lungfish in the southern part of Lake Victoria; but identified peak spawning times in September, November and March. Greenwood (1958) suggested that rainfall above a certain threshold initiated breeding activity among lungfish in the northern part of Lake Victoria, while Mosille and Mainoya (1988) attributed the onset of breeding to the start of the rainfall season. In Lake Baringo, where rainfall is limited and unpredictable (Meyerhoff 1991, Bryan 1994) males and females in active reproductive state (stage III and IV) were found in all monthly samples consistent with year round spawning. It is possible that due to the unpredictable rainfall pattern lungfish in this lake have spread out their spawning to include most or all of the year.

The mean gonadosomatic index (GSI) increased with increasing status of gonad maturity up to maturity stage IV among individuals of both sexes, and was low for spent females. The increase in mean GSI is likely related to rapid growth of gonadal tissue resulting in dramatic increase in gonad weight just prior to spawning (Holden and Raitt 1974, Caillet *et al.* 1986) which translates to higher GSI values. Mosille and Mainoya (1988) reported similar findings for lungfish in Lake Victoria. Variation in mean GSI over time is frequently evidence for determining onset of spawning season or periods of peak spawning in fishes (Hutchings 2002). This was not possible in the present study likely because, as argued, above lungfish in Lake Baringo spawn throughout the year with no specific spawning season. Absence of a specific spawning season may also explain the apparent lack of distinct seasonal changes involving increased relative fish condition. Mosille and Mainoya (1988) noted that relative condition appeared not to be closely correlated with reproductive condition in *P. aethiopicus*.

Positive relationships between fecundity, and total length and weight (Fig. 3.9 and 3.10) were found in the present study. Okedi (1971) noted that despite significant variability in egg number even from fish of the same size, egg number increased with the length of females in his samples. The mean number of 10,711 eggs determined for lungfish in Lake Baringo compares well with fecundity values reported by other workers. Greenwood (1958) estimated fecundity of two females at between 5,000 and 6,000 eggs. Okedi (1971) reported a mean fecundity of 8,960 eggs for 189 lungfish ranging in size from 68.0 to 117.0 cm total length, while Mosille and Mainoya (1988) reported values ranging between 705 and 14,922 eggs (mean = 6,000 eggs) in fish 84.0 – 130.0 cm in length.

6.4 Movement and space use by African lungfish

Ultrasonic telemetry proved to be a very useful means of studying lungfish movements in Lake Baringo. Tags surgically implanted into the body cavity remained in two fish for up to about the one-year duration of battery life. The fish showed movement soon after release and resumed feeding at least five days later as evidenced by one individual caught on a long-line on the morning of day 6 following its release. This recapture not only allowed confirmation that the surgical wound was healing properly, but also demonstrated that commercial fishing was likely going to adversely affect the long term study of fish movements. Thus the ban on commercial fishing activity approximately one month after the tracking work was started, while eliminating the supply of lungfish specimens for more biological data, contributed to the success of the movement study, as it enabled the collection of more data than otherwise might have been possible. However, some fish lost their tags in the course of the study. Expulsion of surgically implanted tags has been reported in several studies as reviewed by Jepsen et al. (2002). Possible ways this occurs include 1) through the incision, which is often attributed to post-surgical infection of the wound; 2) through an intact body wall; and 3) resorption into the gut and subsequent expulsion through the anal opening. The later has been reported for catfishes (Summerfelt and Moiser 1984, Baras and Westerloppe 1999). Given that tag loss occurred after 51 - 81 days, any or all of the above three events could have resulted in tag expulsion by lungfish in the present study. However, it seems more likely that expulsion was through the digestive tract. The body wall of lungfish is very thick (> 1 cm), and had the tags been expelled through the incision this would likely have occurred earlier before the wound healed.

Early workers portrayed African lungfishes as sluggish fishes, which moved by either anguiliform swimming or crawling using the paired fins (Johnels and Svensson 1954, Greenwood 1986). Curry-Lindahl (1956) noted that *P. aethiopicus* in open waters occasionally swam to the surface to breathe, and then back to the bottom. Horizontal movements of lungfish in the open waters are largely unknown; although given that they are known to breed in shallow inshore areas (Greenwood 1958, 1986), it has been assumed that adult lungfish make spawning migrations to these areas, the reverse being true of juveniles (Greenwood 1958). Ultrasonic tracking in the present study demonstrated that lungfish frequently made considerable daily horizontal movement and it was not uncommon for a lungfish to move daily distances greater than 1.5 km over several successive days. Thus aside from what is generally well known that lungfish occasionally make vertical movements to access the surface to breathe, lungfish in Lake Baringo make considerable daily horizontal movements. It is very unlikely that such movements involve crawling.

Diel activity of African lungfishes has not previously been studied in any detail. Based on limited field observations in Lake Edward, Curry-Lindahl (1956) reported that *Protopterus aethiopicus* remained largely inactive during the day, except regularly (intervals of 15 – 25 minutes), rising to the surface to breathe. This author noted that the fish became more active during the last hours of daylight, however, there is no indication of the method used to measure activity. Johnels and Svensson (1954) found higher breathing rates in captive *Protopterus annectens* at night than during the day and concluded that the fish were more active at night. Contrary to the above studies sonically tagged lungfish were active during the day in the present study. Consistent with findings of the present study was the fact that long-line fishermen in Lake Baringo were as likely to catch lungfish on freshly baited hooks fished during the day (0800 - 1500 hours) as fished over night.

Fish movement is usually in response to changes such as reduced food availability or increased predation; but movement may also be for reproduction or in response to changes in environmental conditions such as temperature, dissolved oxygen, etc (Lucas and Baras 2001). Because of their air breathing ability, non-visual feeding, and natural occurrence in diverse aquatic habitats of variable salinity and temperature regimes (Goudswaard et al. 2002); lungfish are likely less sensitive to fluctuations in these environmental parameters. Moreover, Lake Baringo is shallow and is regularly (daily) remixed by wind (Fig. 2.8), thus oxygen and water temperature changes occur on a regular short-term time scale. Hence it is unlikely that horizontal movements of lungfish were related to these variables. Given that lungfish in Lake Baringo likely spawn in shallow inshore swamp areas (as discussed in section 6.3 above), their movement within open waters was not directly associated with reproductive activity. Thus it appears that the daily horizontal movements observed in Lake Baringo lungfish are related to predator avoidance, search for food, or both.

The avoidance of shallow water areas by lungfish in Lake Baringo could be associated with the fact that crocodiles, the only known predators for sub-adult (>50 cm total length) and adult lungfish besides man, were most commonly found in shallow inshore waters of the lake. Many fishes show rapid associative learning to avoid predators (Lucas and Baras 2001). In laboratory studies, Pitcher *et al.* (1986) showed that cyprinids alter their foraging behaviour following experience with the predatory northern pike (*Esox lucius*). In a whole lake experiment study, He and Wright (1992) attributed the emigration from the lake to streams of species such as dace (*Phoxinus* sp.) and shinners (*Notemigonus* sp.) to the introduction of the northern pike in a small Wisconsin lake. In the present study it appeared that predation risk accounted for the avoidance of shallow areas by lungfish.

Lungfish movements in deeper waters (>1 m) were likely related to prey availability and abundance. Lungfish movements in the open waters of Lake Baringo frequently consisted of: 1) shorter daily movements or no daily movement between successive days over several weeks or even months, followed by 2) a series of successive longer daily movements over a few days. The shorter daily movements may be associated with an individual having located an area where food is abundant and remaining there for an extended period, whereas the successive longer daily movements could be associated with an individual searching for areas with better food availability. The longest daily movement observed in May for two lungfish (Fig. 4.3), did correspond with low catches of potential prey in experimental gillnets in the lake (Table 5.6). This possibly indicated that less food (fish prey) was available at that time and as would be expected the fish searched wider areas. Longer range movements may enable areas with higher concentration of food resources to be discovered, accessed and utilized; and this may result in adoption of new home ranges (Lucas and Baras 2001). During such movements a fish may go back to a previously used site, probably to explore if the situation has become favourable (i.e. more food). In the present study two lungfish made at least one return to their respective previous home ranges. The successive longer daily movements

of tagged lungfish tended to be directional suggesting they have a map sense of their environment. This is supported by the recapture of one floy-tagged lungfish on the same long-line it had originally been caught on 48 days earlier (Table 3.7). Although collectively these findings can be interpreted to indicate homing (ability of a displaced animal to return to the same site or home), further research is required to evaluate the navigational ability of lungfish.

Sonically tagged lungfish in Lake Baringo utilized areas smaller than the entire lake. Both the size of home ranges $(5.8 - 19.8 \text{ km}^2)$ and their duration of occupation (2 - 4.5 months) varied, possibly reflecting variation in food availability in the respective areas. Lungfish in open waters of Lake Baringo are largely piscivorous. Piscivorous fishes are hunters (Fish and Savitz 1983) and characteristically possess larger home ranges because they forage on mobile prey. However, larger home range size might also be associated with lower prey abundance (Fish and Savitz 1983). Given that the lake was closed to commercial fishing due to low catches during the period of the study, scarcity of prey might have been a factor in the size of home ranges in Lake Baringo as fish would be expected to utilize wider areas when few prey were available. These results might be an indication that prey density and distribution were important factors influencing the size of area utilized by lungfish.

The Kernel home range estimator procedure gave size estimates that were much larger than those based on the 100% MCP procedure. Given that the Kernel home ranges are based on the 95% probability contour, which omits 5% of outermost location data, this procedure seems to overestimate the area utilized and may not be appropriate for describing home ranges for the lungfish. However, the Kernel procedure allowed the determination of the pattern of use of space by the fish within home ranges. Lungfish are ambush predators (Curry-Lindahl 1956, Greenwood 1986) thus would be expected to remain in areas with abundant prey for extended periods. This is consistent with lungfish spending more time and hence being located more often in core areas of home ranges where presumably prey were locally abundant. If prey dispersed, lungfish would abandon the area to search for other areas where prey is more abundant. However given their known cannibalistic behaviour (Curry-Lindahl 1956), agonistic interactions with other lungfish may also have resulted in individual lungfish vacating a particular area. The spatial overlap in home ranges of two lungfish suggested that non-breeding lungfish in open waters are not territorial, contrary to what was suggested by Curry-Lindahl (1956).

While experimental fishing indicated that all lungfish prey species were generally found throughout the lake, more prey were caught in the central and southern parts of the lake. The southern half of the lake has extensive fringing vegetation and is the area where all inflowing rivers discharge their waters (Fig. 2.1). The higher input of nutrients from inflowing rivers may be associated with the higher numbers of fish prey in this part of the lake. Illegal fishing by fishermen living on islands was also rampant in the southern part of the lake. It is possible that lungfish remained in these heavily fished areas where they could prey on fish caught in gillnets and on long-lines. However, the finding that no sonically tagged lungfish utilized the northern most part of the lake is surprising. Fishermen in the northern end of the lake recaptured floy-tagged lungfish released at the same site as the ultrasonic-tagged fish and experimental fishing caught lungfish there as well. Given this, there is no obvious explanation why no ultrasonic-tagged lungfish made excursions into that part of the lake.

Present knowledge indicates the marbled African lungfish is an obligate air breather (Greenwood 1986) and this view is well documented in current ichthyology textbooks (e.g. Helfman et al. 1997, Moyle and Czech 2004). Evidence supporting this comes largely from several laboratory studies (e.g. Jesse et al. 1967, Lenfant and Johansen 1968) following the early report by Smith (1931) that lungfish asphyxiated when denied access to air. However, Greenwood (1958) reported that 20 lungfish about 25 - 28 mm in total length prevented from accessing the surface remained active and alive for over a month. It is not in doubt that captive lungfish regularly use aerial respiration, this is easily observed in laboratory holding tanks and aquaria. Lungfish in their natural habitats have also been observed to break the surface and gulp air (Greenwood 1986, Curry-Lindahl 1956). Indeed in the open waters of Lake Baringo lungfish were occasionally seen surfacing to breathe (personal observation). Lenfant and Johansen (1968) reported that P. aethiopicus relies on air breathing for over 90% of its metabolic oxygen requirements. If lungfish are that dependent on air breathing in their natural habitats, one would expect them to surface frequently and probably at a regular rate to gulp air. Such regular or frequent surfacing was not observed among lungfish in Lake Baringo.

While radio telemetry was not useful in tracking fish it did provide interesting data on aerial breathing by lungfish in their wild environment. Since signals were heard when the fish swam to the surface, this provided a means for gathering information on

aerial respiration. Signals were heard at intervals ranging between 2 and 126 minutes (Table 4.2), indicating irregularity in lungfish air-breathing frequency. Signals were not heard 3 - 4 hours after release, suggesting the earlier surfacing to gulp air was related to the stress of handling and release as the fish re-acclimatized to the lake conditions. In a recent study Seifert and Chapman (unpubl. manuscript) found elevated metabolic rates among lungfish during acclimation in the laboratory; indicating increased use of aerial respiration during stress. In the present study, radio-tagged lungfish subsequently did not use aerial breathing on a regular or frequent basis if at all. That these fish would have stayed within detection range of the radio receiver for at least several days is based on the sonic tracking of 14 similarly handled lungfish released at the same site. These results suggest that lungfish in Lake Baringo that are acclimated to their environment and not under stress are able to meet their metabolic oxygen needs through aquatic respiration. This is contrary to the long held view that *P. aethiopicus* are obligate air breathers and demonstrate the need for more data to elucidate questions on respiration of lungfish in their natural environments. Telemetry studies using ultrasonic tags capable of recording depth data would help answer questions on vertical movements and air-breathing frequency, and help confirm the extent of dependence on aerial respiration of lungfish in

their natural environments.

Sonically tagged lungfish were always relocated in the open waters, however, one radio-tagged lungfish was recaptured on a long-line in a swamp area (locally known as Lake Kitchertet), about 5 km upstream on the Molo River. This provided evidence that lungfish can and sometimes do move upstream from the open waters. Whether they do so to spawn, or while in pursuit of prey such as catfish (*Clarias gariepinus*) which were observed to move upstream to spawn during the present study is not known.

6.5 The fishery: management implications and some recommendations

Lungfish are caught both in gillnets and on long-lines in Lake Baringo. While lungfish in Lake Baringo attain maturity at >70 cm total length, experimental fishing showed that the minimum legal mesh size (3.5 inch) gillnet catches lungfish with an average size of only 64.3 cm total length. Capture of fish before they attain first sexual maturity can result in what has been described as recruitment overfishing i.e. where too few adults are left such that egg production can not sustain recruitment of young fish to the fishery (Pauly 1994). The absence of larger lungfish in the gillnet samples (Fig. 5.6) could be indicative of an effect of overfishing during the previous year. However, Ligtvoet et al. (1995) showed that lungfish longer than about 94.0 cm were not caught by 4.5 inch mesh gillnets. As this was the largest mesh size used in the experimental fishing in the present study, it is possible that larger fish were excluded. There was widespread illegal use of undersize gillnets (personal observation), increasing the fishing pressure on smaller lungfish and other species as well. DFO should effect and enforce use of a minimum mesh size of 4 inches in the gillnet fishery. This would also be good management tactics for the tilapia fishery as well as the other two species, Clarias gariepinus and Barbus gregorii that are commonly caught in gillnets.

As presently practiced, long lining seems to be the most suitable method for exploiting the larger sized lungfish and catfish species in the lake. However, use of alternative bait such as offal from commercial butcheries should be promoted, instead of fish that are caught in small mesh size gillnets currently used illegally by most fishermen. Pieces of meat from butchered animals are effective bait and are indeed often used by fishermen unable to catch bait fish in their gillnets.

A management goal for the lungfish fishery should be to increase the number of lungfish landed live as these are worth at least twice as much as dead lungfish of the same size. Currently most (>80%) lungfish are dead or moribund when landed. However, live lungfish earn more income and have even higher demand as they are readily purchased by agents and transported live to larger cities such as Nakuru, Nairobi and Eldoret for sale as fresh fish, which is quite popular especially among the urbanized members of the Luo community. The high incidence of dead lungfish in catches can be attributed primarily to their drowning before they are retrieved from the long-lines. While under normal conditions lungfish may not need to come to the surface to breathe, this becomes necessary for individuals caught on a long-line. In this situation, the increased oxygen demands from exertion and the stress of being caught can not be met through aquatic respiration. The long-line could be modified such that hooks are attached to leaders instead of being attached directly to the line. This would allow captured lungfish to access the surface to breathe, thus helping prevent them from drowning.

In conducting this work I found it very difficult to get accurate fisheries statistics. DFO needs to direct more effort towards obtaining better statistical data on the fishery. My experience during the present study is that existing fishery statistics collection methods in Lake Baringo, while perhaps suitable for providing general information on the fishery, are of doubtful accuracy and are lacking in detail. Fish are not weighed and numbers by species are the only data recorded by DFO personnel at fish landing sites. In addition fishermen often landed when DFO personnel were not present, while others landed at undesignated, hence unmanned, sites. Effort data is limited to the number of fishermen's and fishing craft (canoes and rafts) licenses purchased from the DFO. However, these licenses are mostly purchased by women fish processors owning fishing crafts and gear used, who then issue the licenses to fishermen they hire to fish for them. In Lake Baringo most fishermen turn to fishing when they are not able to find employment in other forms of economic activity. Thus the number of fishermen fishing on a particularly day is not known, let alone data on the number and mesh size of gillnets or the number of baited hooks being fished in the case of the long-line fishery. For these reasons, the current fisheries statistics were not very useful. As fisheries statistics are used widely in advising and formulating fisheries policy both by government and nongovernmental organizations, the need for accurate fisheries data collection cannot be overemphasized.

Based on catch and effort data, a mean daily catch rate of 5.5 kg per fishermen was determined for the Lake Baringo long-line fishery. According to long-line fishermen this was very low compared to the previous year's catches. The decrease in daily catch per fishermen between February and April (Fig. 5.3); probably reflected decreasing numbers of lungfish in the lake. The decreasing catches seem to be the reason most fishermen at other landing sites abandoned fishing. Because of low catches, the fishermen at the Moi-Toronto landing site fished only during the times I was at the Field house and appeared to be motivated by the ready market my work provided, especially for live lungfish; and the prospect of a cash reward for catching a tagged lungfish.

Climatic factors strongly affect the population dynamics of Lake Baringo fish and this has significant implications for the overall management of the lake's fishery resources. Located in the so-called ASAL (Arid and Semi-Arid Lands) region of Kenya (Bryan 1994), the lake experiences high temperatures and receives little and unreliable rainfall as described in section 2.2.2. Reduced inflow from streams and high evaporative loss during prolonged drought results in significant reductions of water levels in the lake. This has a significant impact on fish populations as it virtually eliminates the reproductive activity of fish species, since most if not all spawn either upstream or in fringing swamp vegetation areas. In times of severe drought, fishing regulations are suspended to allow people to catch fish for survival. Because the lake area is then shrinking, fish become increasingly concentrated in a smaller area and hence catchability is significantly increased. This occurred during the drought of 1999 and 2000 when the area received little annual rainfall (Fig. 2.3), and likely contributed to the high annual lungfish catches realized in those years (Fig. 2.9), as most people then targeted the lungfish because of its relatively bigger size. On the other hand episodic high precipitation input, such as the 1997 - 1998 El Nino rains quickly raises lake water levels and restores breeding grounds for the fish species, leading to recovery of fishable stocks. Consequently, the fishery of Lake Baringo, like those of other Rift Valley lakes, experiences periodic fluctuations in catches (Muchiri 1997), with periods of prolonged drought coinciding with low catches and often leading to closure of commercial fishing activity, as happened towards the end of the first year of this study.

Maintenance of a viable lungfish fishery in Lake Baringo is dependent on the protection and conservation of shallow inshore riparian areas along the shores of the lake and along the lower reaches of inflowing streams. These are important breeding areas for the lungfish as well as other species in the lake. Human activities including vegetation clearing for human settlement and farming in the catchment, diversion and damming of streams for irrigation (e.g. the Perkerra Irrigation Scheme) (Kallqvist 1987, Kimakwa 2000) likely contribute to the general decreasing mean water levels in the lake (Table 2.1). Mitigation against these human influences requires a whole catchment restoration approach, and active community participation to protect and conserve the lake and its fishery resources.

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Appendix A The individual movement paths of ultrasonic-tagged lungfish.



Fig. A1 The movement path of Fish 65.



Fig. A2 The movement path of Fish 69.







Fig. A4 The movement path of Fish 75.



Fig. A5 The movement path of Fish 50F.



Fig. A6 The movement path of Fish 50S.



Fig. A7 The movement path of Fish 50V.



Fig. A8 The movement path of Fish 75F.



Fig. A9 The movement path of Fish 54.



Fig. A10 The movement path of Fish 65F.



Fig. A11 The movement path of Fish 54S.



Fig. A12 The movement path of Fish 75N.





