

**ASPECTS OF THE ECOLOGY AND REPRODUCTIVE
BIOLOGY OF THREE CICHLID FISH SPECIES OF
SOUTHERN LAKE MALOMBE (MALAWI)**

By

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Thesis

Submitted in fulfilment of the requirements for the Degree of

Master of Science

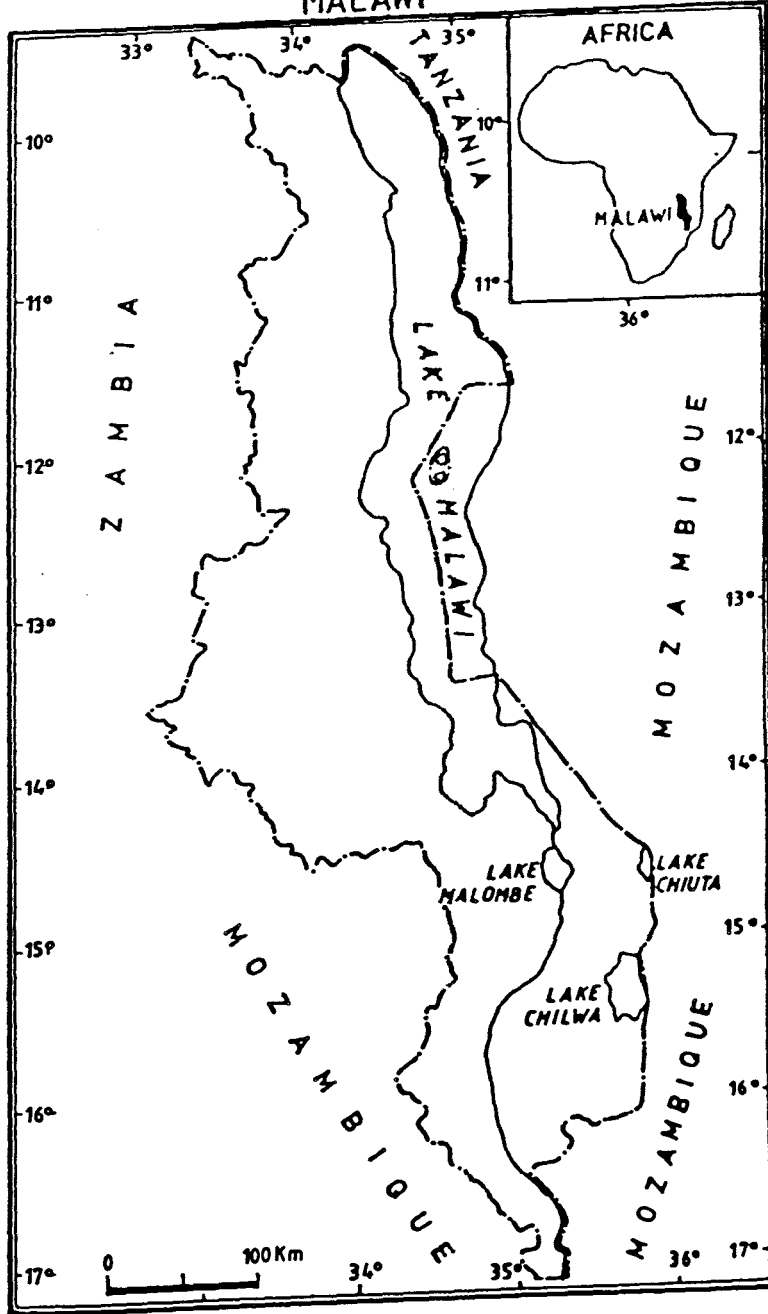
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DEDICATION

This thesis is dedicated to my parents Elias and Eda, for their genuine endurance support and encouragement during the early stages of my education.

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(ii)

ABSTRACT

The three major species *Lethrinops "pinkhead"*, *Otopharynx argyrosoma "red"* and *Copadichromis. cf. virginalis* which used to dominate the catches (by weight) of Lake Malombe in the past decade were investigated. In order to make rational recommendations regarding size and boundary of the existing sanctuary area (lightly fished), distribution and abundance, population structure and reproductive biology of the three species were related to habitat types of the southern part of the lake (south western side and south eastern side).

Analysis of catch composition showed that species richness was higher in the south eastern side than in the south western side of the lake. Rare species such as *Labeo mesops* and *Opsaridium microlepis* were observed in the south eastern side and there was visual absence of such species in the south western side of the lake.

The overall fish abundance was significantly greater in the south eastern side than in the south western side of the lake. In the south eastern side, the catch per unit effort (CPUE) was twice that of the south western side ($P < 0.05$). Seasonal fluctuations in CPUE were also prominent, with the highest peak occurring during September-October period. However, there was an indication of weak relationship among CPUE, phytoplankton biomass, temperature and water depth.

The length-weight relationships revealed that growth of the three species closely followed the cubic law for isometric growth in both sides of the lake. Differences in regression coefficients between sides were not significant (t-test, $P > 0.05$). The length-frequency distribution analysis revealed that the three species had the same growth rate regardless of habitat type. However, females grew faster than males.

An investigation of reproductive biology showed that the three species have low fecundity and they are asynchronous spawners, with a breeding peak during August and September period. Furthermore, the length-fecundity relationships for *L. "pinkhead"*, and *O. argyrosoma "red"* indicated that fecundity

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was more closely related to length in the south eastern side than in the south western side.

Based on the above characteristics of *L. "pinkhead"*, *O. argyrosoma "red"* and *C. cf. virginialis*, and the substrate types, it was strongly suggested that the existing sanctuary (lightly fished) in the south eastern side of the lake could immediately be enlarged to conserve the fish stocks, favourable substratum and aquatic animals that may be of tourists concern.

CHAPTER 1

GENERAL INTRODUCTION

1.1 INTRODUCTION

The Lake Malombe fishery has been under severe fishing pressure since 1986 (FAO 1992, Coulter 1993). The fishing community has expressed concern about the collapse of the fishery and indicated that the only way they could catch more fish is by reducing the mesh sizes (Bell & Donda 1993). The collapse of the *Oreochromis* spp. stocks in the last few years and the current decline in the catches of the small haplochromine species (kambuzi) have caused a major social and economic imbalance, resulting in fisheries management problems.

The fishery of the lake has provided the cheapest protein to the entire population surrounding the lake and directly employs 4,660 people (Frame Survey 1995). In the 1970s and first half of the 1980s, catches were dominated by *Oreochromis karongae* and *Oreochromis squamipinnis*. The two species are locally known as "chambo". During this period, the average annual catches of chambo were estimated to be 5,000 tonnes out of a total of 6,000 tonnes (FAO 1992). However, in the second half of the 1980s the stocks of the high value chambo in the lake started declining and kambuzi began to dominate the catches (Tweddle *et al.*, 1994). In the early 1990s about 67% of the 6,000 tonnes of fish caught in Lake Malombe comprised kambuzi while the chambo fishery only contributed about 530 tonnes, equivalent to about 5% of the total catch (Mwanyama 1995). Kambuzi is a collective name for the smaller haplochromine species in the lake and are caught mostly by seine nets. The most important kambuzi species include *Lethrinops "pinkhead"* *Otopharynx argyrosoma "red"* and *Copadichromis cf.*

virginalis. Since the collapse of the chambo fishery in 1986 the kambuzi fishery has been the most important fishery in Lake Malombe. The decline of chambo prompted artisanal fishers to use small meshed nets with which to target the kambuzi. Recent studies on the kambuzi fishery have shown that the increase in fishing effort, the use of small mesh nets and siltation are now threatening the sustainability of the fishery (FAO 1992, Mwanyama 1993). Recent results from Fisheries Department Annual Frame Surveys indicate that the catches of kambuzi have declined from 20 kg per haul in the late 1980s (Tweddle *et al.*, 1995) to 3.5 kg per haul (personal observation), indicating that the fishery has been severely overexploited.

The current overall collapse of the Lake Malombe fishery threatens both the livelihood of the rural people who depend on fish as their sole source of animal protein and employment, as well as the nation's animal protein supply as a whole. Presently, there is clear evidence of over-exploitation and it is essential that steps be taken to ensure the future of the fish stocks, and the people who depend on them. According to Tweddle *et al.*, (1995), the current catch rates can not be sustained as the fishery is increasingly reliant on small and immature fish. However, Coulter (1993) argues that the recovery of heavily exploited species can be achieved by extending the existing sanctuary area (which was first proclaimed in 1976) in the south eastern side of Lake Malombe. He stressed that the effectiveness of the sanctuary area can be attained through participatory fisheries management programmes (PFMP), in which resource control and management is vested in the community.

To establish a responsible management strategy of the fishery and to form a communal access fishery, the Malawi Fisheries Department in collaboration with International Agencies viz.; Overseas Development Administration (ODA), United Nations Development Programme (UNDP) and Malawi-Germany Fisheries and Aquaculture Development project (MAGFAD) has adopted a community participatory approach. Within the context of the PFMP, classical fishery management strategies of catch and effort which have been used in the past decade have been integrated with closed area methods and local community participation (Bland & Donda 1994). In support of a closed area method, Coulter (1993) suggested that by enlarging the closed area and by proper management, the stocks in Lake Malombe could be rebuilt.

For the accrual of long term benefits from closed areas, scientific information on abundance, size structure, species composition and relative proportions of species present in the area is required (Davis 1981, Alcala & Russ 1990, Attwood & Bennett 1994). This study was aimed at investigating some ecological aspects of the three important species in the kambuzi fishery and in particular, to concentrate on differences in the biology of the fish in the lightly fished area, in the south eastern side and the heavily fished area, in the south western side of the lake. Referring to the works of marine reserve scientists, Bohnsack (1982), Bell (1983), Koslow *et al.*, (1988), Buxton & Smale (1989), it was my hypothesis that there would be significant differences in the diversity, abundance, size distribution and biology in the "sanctuary area" in comparison to the heavily fished area. It must be born in mind however that some fishing effort does occur in the "sanctuary area". This is mainly a consequence of poor control mechanisms. Nevertheless, the fishing effort in the "sanctuary area" in the south eastern side of the Lake Malombe is much less than in the heavily fished area in the south western side of the Lake. It is estimated that fishing effort in the south western side of the lake is

approximately 72% less than in the south eastern side of the lake (personal observation).

1.2 HISTORY OF THE LAKE MALOMBE FISHERY

Fish Resource Exploitation

The small haplochromine species (kambuzi) are mostly exploited by means of kambuzi beach seines and nkacha offshore seine nets. Both types of nets are small meshed, with recommended minimum mesh size of 19 mm. The kambuzi beach seines are mostly over 250 m long and less than 1500 m. These nets are laid by boat and pulled onto the beach by 24 people. The nkacha offshore seine nets are usually less than 250 m long and are used in open waters. Four people on board, two on each side pull the nkacha net simultaneously while two divers "purse" the net by pulling and tying together the weights on the foot rope.

Analysis of catches from Lake Malombe indicate that these two types of fishing gear target around 50 species. (FAO 1992, Banda 1994). In 1995, there were approximately 375 small meshed nets operating in the lake of which 2% were mosquito nets, 14% were kambuzi beach seines, and 84% were nkacha seines nets.

The total annual fish catch in Lake Malombe increased rapidly from the mid 1970s to late 1980s. During this time the cichlids were dominated by chambo. In the early 1990s, three smaller haplochromine species replaced chambo in the catches. The three principal species that replaced chambo were *Lethrinops "pinkhead"*, *Copadichromis cf. virginalis* and *Otopharynx argyrosoma "red"* (FAO 1992). These species used to contribute more than 75% to the total catch (8,000 tonnes). The overwhelming increase in importance of

kambuzi from 4% of the total catch (4,900 tonnes) in 1976 to 90% of 10,300 tonnes in 1991 was largely due to the introduction and use of small meshed nets by most artisanal fishers (Mwanyama 1993, Tweddle *et al.*, 1995).

Research has indicated that recruitment and growth overfishing have led to the decline of the fishery (FAO 1992, Tweddle *et al.*, 1994, Banda 1994 and Mwanyama 1995). According to Coulter (1993), Tweddle *et al.*, (1994), Banda (1994) and Mwanyama (1995), too many of the haplochromine fish are caught too early in life. This implies that fishing mortality on the recruits has increased greatly which may ultimately contribute to the total collapse of the fishery.

In addition, human population increase in Malawi (approximately 3.7% per annum), the common property and open access nature of the fishery, and limited alternative income generating activities have exacerbated the pressure on the fish resources of Lake Malombe.

Management

The management strategies for Lake Malombe, through the period 1970 to 1992, dwelled much on the biocentric legacy of "fish first" rather than "fishers first" (Bland & Donda 1994). During this period, closed seasons, gear restrictions, mesh size restrictions and licensing were the principal elements of the Lake Malombe fisheries management strategy.

Closed seasons

Closed seasons are widely used as fisheries management strategies as they are comparatively easy to enforce as infringement is usually highly visible to the public (Newman 1984). Lake Malombe fishers are familiar with the strategy and appear to have partly adhered to them. The Lake Malombe fishery has two closed seasons per year, one for kambuzi (January to March) and the other for chambo (October to December). Nkacha offshore nets are not allowed to operate during the kambuzi closed season while gill nets, that target chambo are permitted. The closed seasons have not been strictly adhered to by the fishers. This is principally because the closed season for kambuzi (January to March) coincides with the months of greatest social and economic hardship, i.e. just prior to the harvest of agricultural products. During this time most families are deprived of their everyday necessities including a cheap source of protein. These factors might have contributed a great deal to the failure of the kambuzi closed season.

Gear type restrictions

Several types of fishing gears are used in Lake Malombe. These include gill nets, chambo seine nets, kambuzi seine nets, mosquito nets, nkacha seine nets, traps, and hand lines. Since the late 1980s the majority of fish in Lake Malombe have been caught with nkacha and kambuzi seine nets. Gear restrictions have been inefficient and incompatible with the poorer fishing folk's fishing methods (Bland & Donda 1994). A ban on gear that are destructive to spawning grounds and efficient at catching fish such as mosquito nets and big seine nets has been in operation on Lake Malombe since 1990.

Mesh size restrictions

Mesh size restrictions still remain a popular management strategy in Lake Malombe. This strategy has been widely used in many fisheries to ensure that yield per recruit from particular fisheries are maintained at an adequate level (Newman 1984, Buxton & Smale 1989, Bennett & Attwood 1991).

Small meshed kambuzi beach seines were banned in 1990 in Lake Malombe to reduce the catch of undersized kambuzi and to reduce damage of the littoral aquatic environments (habitats that are preferred as breeding and nursery areas by chambo and all shallow water haplochromines (FAO 1992). This was followed by another ban on small meshed nkacha offshore seine nets in 1991. All seine nets currently operating in the lake are restricted to the recommended minimum mesh size of 19 mm. The essence behind this restriction is to control the size of fish at first capture. However, artisanal fishers are using mesh sizes less than 19 mm to maximise their catch. Approximately 45% of the gear operating offshore in the south eastern side of Lake Malombe, and 65% in the south western side have a mesh size less than 19 mm. It appears that mesh size in Lake Malombe cannot be effectively controlled by the Fisheries Department enforcement section. As stated elsewhere (FAO 1992, Bland & Donda 1994), it is difficult to determine the best mesh size for a multispecies fishery because no mesh size can be entirely suitable for all the species.

Licensing

This is a way of identifying all commercial and artisanal fishers and the owners of all registered fishing boats and fishing gear (Arnold 1986). It allows for the control of the number of boats, fishers or gear units that may operate in each fishery and provides objective means by which entry criteria can be specified and applied in the licensing of individual nets and boats.

By law all fishers of Lake Malombe have to be licensed. The current fee for nkacha seine nets is MK150 (\$13) per 50 metres and kambuzi beach seine nets is MK100 (\$9) per 50 metres. All licences are issued at the beginning of the financial year (April) and expire on 31 March of the following year. In the context of Lake Malombe fisheries, the licensing system has successfully limited entry and effort.

Community participation

The Fisheries Department of Malawi recognised difficulties in implementing the classical management strategies described above. Bell & Donda (1993) and Coulter (1993), have recommended the use of the local community in planning and managing the Lake Malombe fishery. The outcome of a detailed consultancy led to the adoption of the 'participatory fisheries management' approach in 1993, with the main objective of reversing the trend towards the use of very small meshed nets that target small cichlid species (Bell & Donda 1993). Through this approach, thirty fishing community groups called beach village committees and a community liaison unit within Fisheries Department, have been formed.

The beach village committees provide channels of communication between user communities, traditional leaders and community liaison unit. They also provide the basis for community control over access to the fishery and function as fora in which users identify their problems, formulate solutions, organise implementation of solutions, evaluate progress and adjust management strategies. Figure 1 shows a simplified conceptual framework for the Lake Malombe participatory management strategy.

Within the context of the participatory approach the Malawi-Germany Fisheries and Aquaculture Development (MAGFAD) project has provided loans to beach village committee members to buy new nets of recommended minimum mesh size (19 mm), in order to replace nets of smaller mesh size.

It should be emphasised that the major regulatory measures applied to Lake Malombe had been developed to address problems associated with commercial fisheries. This probably explains why classical management strategies have not been adequately adhered to by artisanal fishers in Lake Malombe. All the classical management strategies stated above have been ineffective due to wide spread violations. The Fisheries Department of Malawi has failed to police the regulations attached to such management strategies due to a lack of personnel, well-trained staff, equipment and financial constraints (Bland & Donda 1994). This failure has led to a perpetual decline in catches and size of fish caught in Lake Malombe and the South East Arm of Lake Malawi (Tweddle & Magasa 1989, FAO 1992).

1.3 THE RATIONALE, HYPOTHESIS AND OBJECTIVES OF THE STUDY

RATIONALE

The establishment of protected areas which are closed to fishing, sometimes called sanctuary areas, has been promoted by many as a viable alternative tool of managing a fishery especially, where other forms of management are impractical (Wallis 1971, Davis 1981, Buxton & Smale 1989, Bohnsack 1990). Roberts & Polunin (1991) summarised potential advantages of sanctuary areas as; protection of the spawner biomass, providing recruitment source for adjacent areas, maintain natural population structure, maintenance of undisturbed habitat and insurance against management failures in fished areas.

Bennett & Attwood (1991) documented evidence of general stock recoveries of exploited fish species in a shallow habitat following protection within the De Hoop Nature Marine Reserve on the southern coast of South Africa. Following establishment of the reserve, CPUE of *Coracinus capensis*, *Diplodus sargus*, *D. cervinus*, *Lithognathus lithognathus*, *Rhabdosargus holubi* and *Sparodon durbanensis* increased. The catch rates of *Coracinus capensis*, and *Diplodus sargus*, improved 5 fold within 2 years of protection, attaining catch rates equivalent to unexploited catch rates. The recoveries of the other four species were slow and reached 60% of the unexploited level after 4.5 years.

Russ & Alcala (1989) documented that Sumilon Island Reserve in Philippines provides some of the best evidence to date, for the efficacy of protective management. Overall densities in the reserve were approximately double those on unprotected reefs of the island before the collapse of the protection in 1984. By 1985, densities in the reserve had fallen by approximately 25%

due to exploitation, however, large increases in overall abundance were reported in the reserve after a one year period of protection. Alcalá (1988) however argued that such increases might simply reflect good recruitment during that year. Russ & Alcalá (1989) noted that observed increases would indicate that population sizes might have responded quickly to the protective management. Similar results have also been reported for freshwater lakes. Sanyanga *et al.*, (1995) showed that the mean catch per unit effort and mean size of *Pseudocrenilabrus philander*, *Hydrocynus vittatus* and *Brycinus lateralis* caught in protected areas of Lake Kariba were larger than in the exploited areas.

Many of the perceived benefits of sanctuary areas still remain untested due to lack of suitable control areas for comparisons (Bennett & Attwood 1991, Roberts & Polunin 1991). However, recent world wide studies have shown that reserve areas, closed to fishing, function as fishery replenishment areas (Wallis 1971, Davis 1981, Foster 1986, Buxton & Smale 1989, UNEP/IUCN 1988, Clark *et al.*, 1989, Polunin 1990).

Coulter (1993) was the first who recommended the use of sanctuary areas in Lake Malombe on the assumption that such areas would function as buffers against long-term depression caused by overfishing. He proposed that the least heavily fished part of the lake, near the Liwonde National Park, would be the most suitable area and speculated that setting aside such a protected area in the lake would not mean any significant loss to fishing. He suggested that a fish sanctuary could be created by extending the present boundary of the Liwonde National Park (Figure 2). However, he stressed the importance of scientific research on the present status of stocks within the proposed area and consultation with the Department of Wildlife and National Parks.

The Fisheries Department of Malawi Frame Survey results for 1993 and 1994 revealed that approximately 85% of kambuzi out of the total annual catch of 6282 tonnes was landed in the eastern shore in 1993 and approximately 75% of the total annual catch of 4059 tonnes in 1994.

Analysis of data by stratum and visual assessment indicated that approximately 60% of the fish landed on the eastern shore and approximately 40% landed on the western shore were caught near the south eastern part of the lake (Frame Survey 1995, Tweddle *et al.*, 1995). This has led to a suggestion that the proclaimed sanctuary area in the south eastern corner of the lake has more fish and it is recolonising the stocks in the adjacent fished areas (Coulter 1993). However, without any information on migration into and out of the south eastern area, it would be difficult to justify such claims. Like elsewhere in most marine and freshwater reserves, investigations on fish migration to and from the reserve have not been done in Lake Malombe. Nevertheless, a wide spread consensus that most Malawian cichlids are stenotopic, exhibiting narrow utilisation and tolerance of the intralacustrine environment (Fryer & Iles 1972, Ribbink 1991) gives considerable potential for movement of fishes.

Presently, there is no documented scientific explanation for the high catch rates in areas near the Liwonde National Park. Lack of such scientific explanation has influenced unrealistic expectations in the decision-making system of the participatory fisheries management programme, especially as regards the extension of the sanctuary area. In this context, the following intriguing key questions emerged: Does this area which is close to Liwonde National Park reseed the adjacent fished areas, if so, when? Is it during the closed season or throughout the year? Does this area hold sufficient breeding stock to seed adjacent fished area? Does the area harbour large fish, more

fish and more fish species? Answers to these key questions obtained through scientific research, would be relevant to signify the value of establishing a well managed sanctuary area for managing the kambuzi fishery in Lake Malombe.

In view of these key questions and that little is known about the ecology, biology and life histories of most cichlid species, it was important to acquire sound biological and ecological information on some of the more important off shore kambuzi species; these were *L. "pinkhead"*, *O. argyrosoma "red"* and *C. cf. virginalis* (Figures 3, 4 and 5).

It is also evident from Mwanyama's (1995) findings that the three species do not share the same food niche with chambo (*Oreochromis* spp.) that used to dominate the catches. This implies that species replacement, from chambo to kambuzi, had nothing to do with food competition. If the sanctuary area were to be extended and well managed, the remaining stock of chambo may therefore also be gradually restored. However, this study will focus only on kambuzi.

Moreover, data collected during the present study, prior to effective enforcement of the sanctuary area would form a base line against which future comparisons may be made. Such comparisons would enable future research to compare the reserve and non-reserve areas and probably evaluate the effectiveness of the reserve after strict protection has been implemented.

HYPOTHESIS AND OBJECTIVES

The underlying hypothesis was that the sanctuary area, although only partially respected by the fishers, would have a greater species diversity, and abundance and that the fish in the "sanctuary area" are larger in size, and have a higher fecundity than the heavily fished area.

To test the hypothesis three specific objectives were considered;

1. To compare the species composition, distribution and abundance of the three most important haplochromine species in the south western side (heavily fished) and south eastern side of the lake (lightly fished sanctuary area).
2. To study the reproductive biology of the most important three species with the view of understanding their reproductive seasonality, the size at sexual maturity and fecundity, and to determine whether there are any differences in these characteristics between the heavily fished area in the south western side and the "partial" sanctuary area in the south eastern side of the Lake.
3. To estimate age and growth of the three species to assess if overfishing has affected growth rate and the age structure of the three species in the south western side and the south eastern (sanctuary) side of the Lake.

Given that physical and chemical factors also determine fish abundance, diversity and affect their biology (Fryer & Iles 1972, Beadle 1981, Coulter 1991 and Hecht & van der Lingen 1992) an account of the limnology of southern Lake Malombe was also undertaken.

CHAPTER 2

THE STUDY AREA AND SPECIES STUDIED

2.1 GEOGRAPHICAL AND ECOLOGICAL DESCRIPTION

Lake Malombe is located between 14° 29' / 14° 45'S and 35° 12' / 35°20'E. The lake is fed principally by water from Lake Malawi via the Upper Shire River, and discharges downstream into the Middle Shire River. The south eastern corner of the lake and the upper reaches of the Middle Shire River lie in Liwonde National Park (Figure 2). The lake covers an area of 390 square kilometres and is situated 15 kilometres away from the south east arm of Lake Malawi. Its maximum length is 29 km and its maximum width is 17 km. Its basin lies in the south easterly section of the East African Rift Valley system, with the deepest point of six metres and the mean depth of four metres (Van den Bossche & Bernacsek 1990, Hughes & Hughes 1992).

Within the last 30,000 years, the lake has been subject to considerable fluctuations in water levels (Crossley 1982, McCracken 1987). For example, the lake almost dried out between 1915 and 1935 when large sections of the lake bed were cultivated.

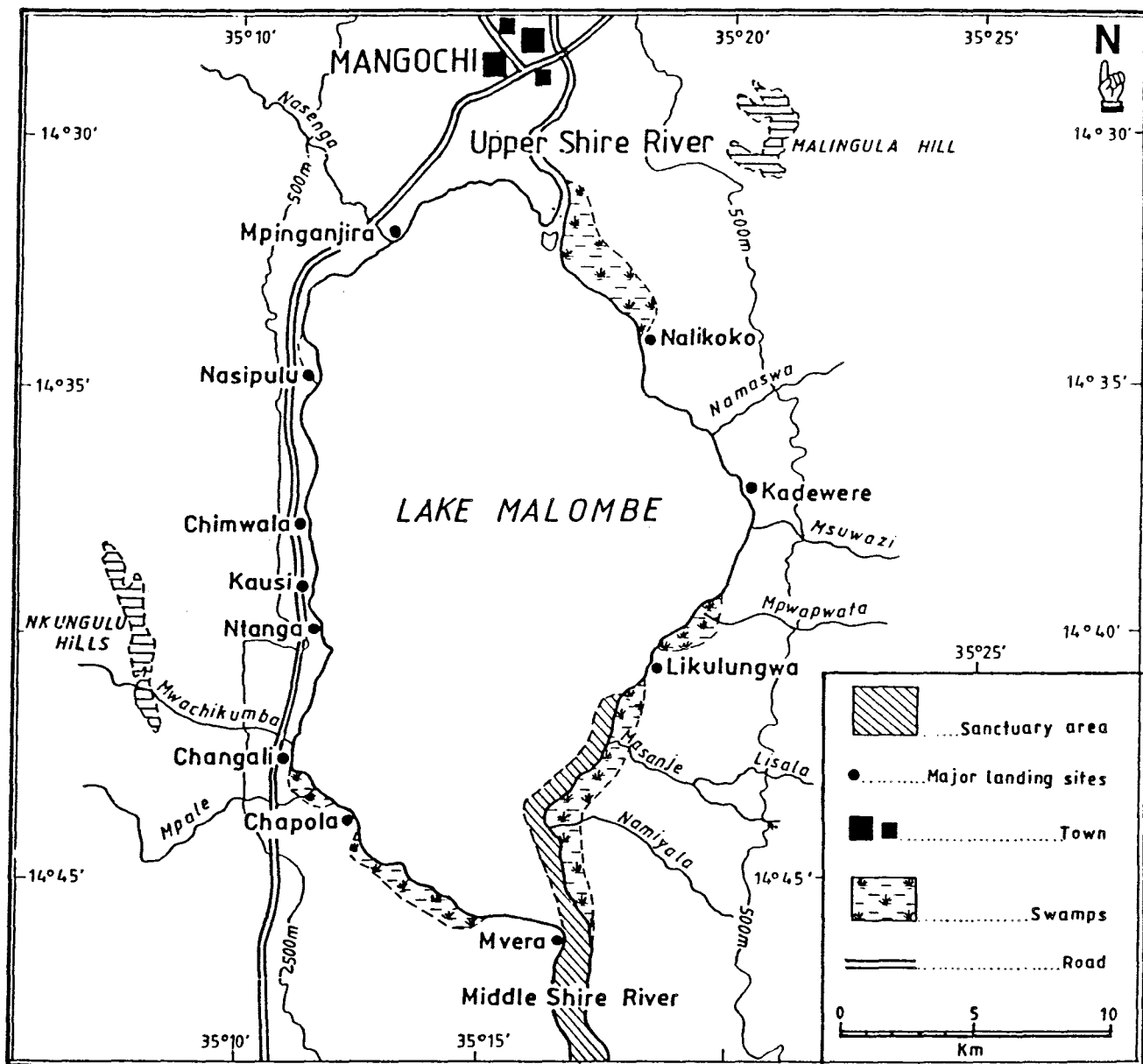


Figure 2. Map of Lake Malombe, showing the drainage system, major fish landing sites and the location of the sanctuary area.

The shores of the lake are covered with typical riverine and floodplain vegetation except in places which have been cleared for beaches. Some shores are covered with small areas of gallery forest containing the palm *Hyphaene benguellensis*. The bordering swamps are dominated by *Typha domingensis* and *Cyperus papyrus* (Hughes & Hughes 1992). The open water is clear of weeds though small floating patches of water hyacinth (*Eichhornia crassipes*) can be seen (personal observation). The surrounding area is mostly covered by savannah woodland.

The catchment area of Lake Malombe is completely surrounded by the valley floor land area with dissected hills and major valleys in the west, and rift escarpment in the east (Bell 1985). Detailed land capability surveys carried out by the Machinga Agricultural Development Division report that the western part of the catchment area of the lake has been subject to inappropriate land use practices. The area has been heavily cultivated by smallholder farmers and estates, mainly from Mulanje and Thyolo (Venema 1991).

The eastern catchment area consists of downthrow fault, broken by many valleys of between 300 and 800m in height in the north east and a low (c. 100m), gently sloping monocline in the south-east (Crossley *et al.*, 1984). The north-east catchment area is classified as non-arable land while the south-east catchment is heavily cultivated.

The lake is fed by eight main rivers. These are Namaswa, Mswazi, Mwapwata, Masanje, and Namiyala rivers in the eastern catchment area and the Nasenga, Mwachikumba and Mpale rivers in the western catchment area (Figure 2), although as mentioned above, the principal source of water is Lake Malawi.

2.2 DEMOGRAPHY

The population of Mangochi district (including the study area) was estimated at 495876 with an annual rate of increase of 5.07% since 1977 (National Statistics 1987). In the study area, the distribution of population is very heterogeneous, with very high densities on the western shore of the lake (470 km^{-2}) and low densities in the eastern shore areas (238 km^{-2}). The high population density in the western shore areas has been associated with the availability of arable land in the western catchment of Lake Malombe, the ease of transport access for fish traders (Bell & Donda 1993) and the availability of fish landing sites. There are more fish landing sites (8) on the western shore than on the eastern shore (3).

2.3 CLIMATIC AND LIMNOLOGICAL CHARACTERISTICS

Lake Malombe, approximately 500 m above sea level, lies in the driest region of Malawi with a mean annual rainfall of less than 813 mm per annum. The annual atmospheric mean temperature for the lake is 24.2°C , with a minimum recorded temperature of 18.6°C and a maximum recorded temperature of 32.9°C .

The limnology of Lake Malombe has not been fully investigated and there is a paucity of quantitative and scientific information. It is quite unfortunate to note that researchers ignored detailed limnological studies for such a productive lake until the fishery had declined. However, Mwanyama's (1993) preliminary work on the lake's limnology provides some very important base line information.

2.4 SPECIES STUDIED

Three small cichlid species *L. "pinkhead"*, *O. argyrosoma "red"* and *C. cf. virginalis*, all of which are probably new to science, were the main target species in this study. All other species were however, included in the analysis of species composition. These three species were chosen because of their importance in commercial and artisanal catches. The three species contribute about 75% to the total annual catch of Lake Malombe (FAO 1992). The only biological information available on the three target species, prior to this investigation is summarised in Table 1.

With the low fecundity levels indicated in Table 1. FAO (1992) and Mwanyama (1993) suggested that recruitment of the three species is likely to be strongly related to adult stock size leading to rapid collapse at a high fishing effort. This coincides with Ribbink's (1987) observations that Malawian lacustrine cichlids are slow to recover from exploitation as they produce a few large eggs, invest heavily in parental care and grow slowly. However, Lewis (1985), Tweddle & Magasa (1989) and Bell & Donda (1993) have convincingly argued that Malawian cichlids can easily recover from exploitation if fishing pressure is reduced. Lewis (1985) and Tweddle & Magasa (1989) based their argument on the fact that most Malawian cichlids exhibit precocial traits while Bell & Donda (1993) based their argument on the fact that the fish community in Lake Malombe has repeatedly recovered after episodic desiccation events within the last century.

Table 1. Relevant biological information of the three species studied in the Southern Lake Malombe (Summarised from Mwanyama 1993).

Species	Maximum Size (TL)	Food type	Fecundity (Eggs/mature female)
<i>L. "pinkhead"</i>	150 mm	Detritus	13 - 36
		Zooplankton	
		Zoobenthos	
		Phytoplankton	
<i>O. argyrosoma "red"</i>	120 mm	Zooplankton	18 - 71
		Zoobenthos	
<i>C. cf. virginalis</i>	160 mm	Zooplankton (<i>Diaptomus</i>)	26 - 61

Lethrinops "pinkhead"

L. "pinkhead" (Figure 3) is metallic silvery with very faint vertical barring and a pink spot above the operculum. However, breeding males show a pattern of intense black bars below the dorsal fin. Its body is deep and compressed, the eye is large and lower jaw weak, with a narrow tooth band. The form of the premaxillae is diagnostic; the tooth bearing surfaces turn upwards towards the symphysis to give a "hare lipped" appearance.

It is widely distributed in Lake Malombe and more abundant in the offshore regions of the lake than in the inshore areas. This species is the main component of the demersal ichthyofauna of the lake, sometimes contributing over 60% to the total catch.

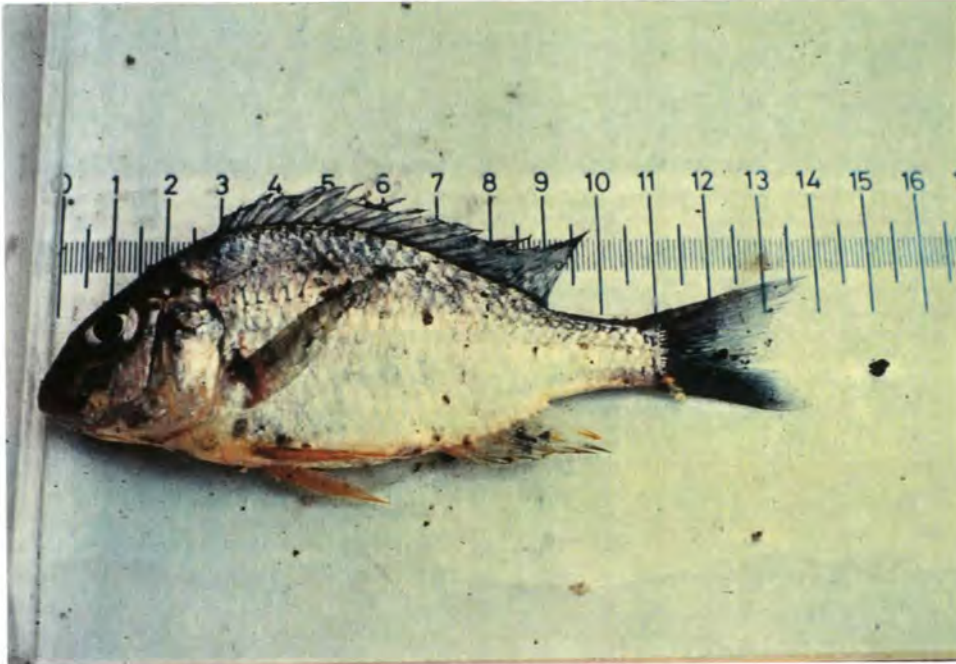


Figure 3. *Lethrinops "pinkhead"* from southern Lake Malombe, June 1995.

***Otopharynx argyrosoma "red"* (Mayland 1982)**

O. argyrosoma "red" (Figure 4) has a silver shiny body. Females and immature males are silvery on the dorsal and the anal fins have yellow edges. Breeding males have scales of flanked with gold and fringed with blue. Throat is usually white or yellow, often with dusky patches. Pelvics are dusky, with white leading edge. This species is widespread and common around the lake off sandy beaches. It is most abundant in the shallower waters which are muddy and is commonly caught in the small meshed beach seines and offshore seine nets which operate in the shallow waters of less than one metre deep.

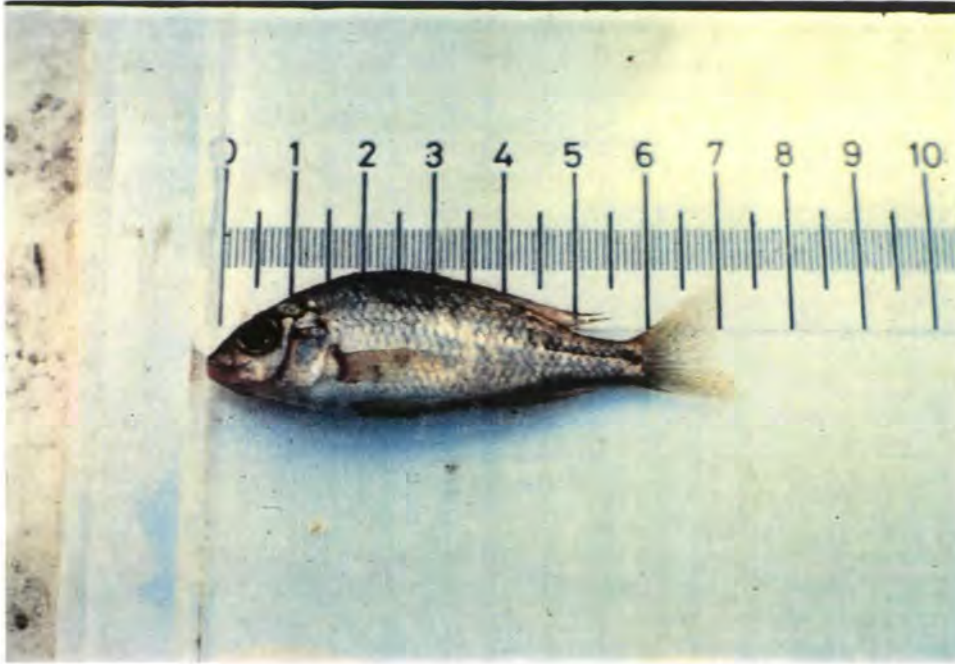


Figure 4. *Otopharynx argyrosoma* "red" from southern Lake Malombe, June 1995.

Copadichromis cf. virginalis (Iles, 1960)

The fish belongs to the "utaka" group (zooplankton feeders). It lacks lateral spots although faint vertical bars may be present. (Figure 5). This species differs from the other "utaka" without spots or stripes in having 21 or more gill rakers on the lower outer arch in comparison to less than 20 gill rakers.

Males are more colourful during the breeding season than their female counterparts. Usually breeding males are intense black with a white or yellow band from top of the snout extending along the distal part of the dorsal fin.

In Lake Malombe this species is found in all habitats but the offshore habitats are more preferred than the inshore. According to Fryer (1984) the tendency or behaviour of this species to congregate in breeding areas might have increased their vulnerability to fishing and inflicted damage to the stock which is out of proportion to the number caught.

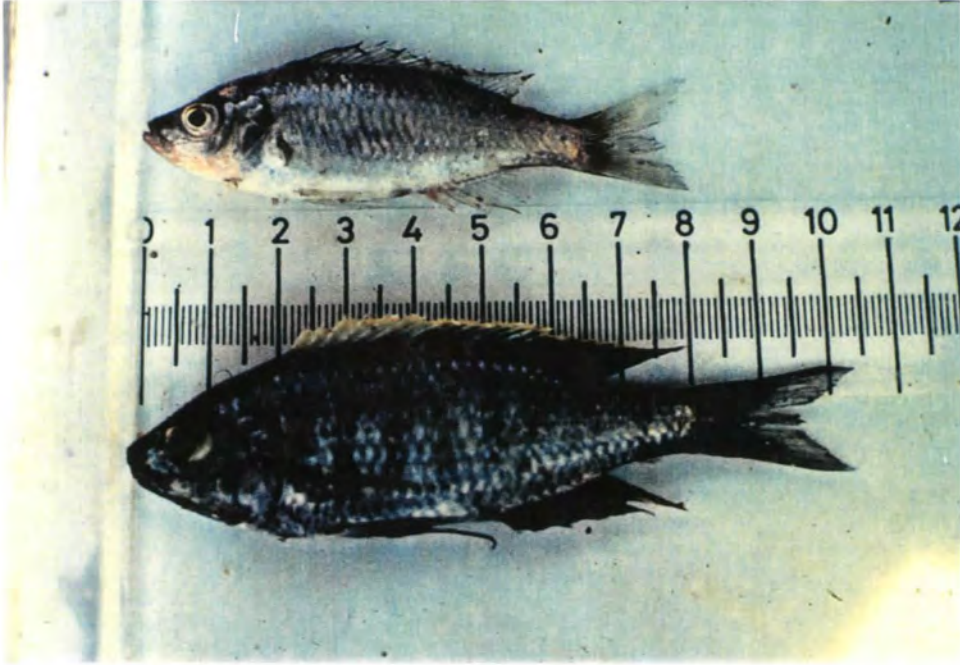


Figure 5. *Copadichromis cf. virginalis* from southern Lake Malombe, June 1995.

CHAPTER 3

SAMPLING STATIONS AND GENERAL METHODS

3.1 LANDING SITES AND CONSTRAINTS

The field work for this project was conducted from June 1995 to June 1996. Four fish landing sites (Kadewere and Likulungwa on the eastern side, Ntanga and Chapola on the western side) were used as departure or landing stations (Figure 6). The whole southern part of the lake was the main study area, however, eight sampling stations on two transects, were identified as main sampling sites.

There were numerous constraints and logistical problems during the sampling period. These included finding divers to purse the net, inclement weather, not being able to get to the source of the landing sites during the rainy season with the research vehicle (Figure 7), misunderstandings on fish sampling during closed season between Fisheries Department of Malawi and the local community leaders and crocodile attacks. In addition, it was observed that the sanctuary area was not strictly controlled or adhered to by the fishers (Figure 8).

Nevertheless, despite these constraints, the scientific information presented in this thesis does represent the first attempt in acquiring sound ecological and biological data for the three dominant fish species, with particular emphasis on the heavily fished areas in the south western side and the lightly fished areas in the south eastern "sanctuary area" side of Lake Malombe.

3.2 SAMPLING STATIONS

The sampling stations that were chosen to study the ecology of the three species were located along two transects across the southern part of the lake (Figure 6). On each transect, two sampling stations were situated on the western side and the other two sites on the eastern side. The sampling stations on the eastern side (Ss1, Ss2, Ss7 and Ss8) represented the lightly fished areas while sampling stations on the western side (Ss3, Ss4, Ss5 and Ss 6) represented heavily fished areas (Figure 6). Sampling at all eight sampling stations was conducted on four randomly chosen days per month, stratified to 2 weekdays and 2 weekend days. Table 2 shows the characteristics of the sampling stations, including water depth, distance from the shore, substrate type and submerged aquatic vegetation. Land marks were used to locate the sampling stations.

Prior to the sampling activities of this study, the general characteristics of the substratum and macrophytes of each side of the lake were also determined. Mud samples were collected from each sampling station once a month for 12 months, using a standard mud grab sampler. According to the criteria described by Laevastu (1965), the substratum was classified into two soil types; muddy and sandy. Visual assessment of macrophytes was also done and few patches of submerged aquatic weeds were noted in the south eastern side of the lake.

3.3 FISHING NET

A standard offshore net (locally known as nkacha), 250 m long and 9.0 m deep was used at all sites on each sampling trip. The nkacha net is a rectangular net with gradation of mesh sizes from bunt to wing and as such the net had stretch mesh sizes of 19 mm, 25 mm and 39 mm (Figure 9a). Given that seine nets act as a barrier into which fish can be concentrated and then hauled, and that the selection is mainly for small fishes, the nkacha net has a gradation of mesh sizes in order to catch fish of different sizes.

All worn out parts of the net were repaired before each sampling trip to minimise bias that could occur if worn out parts had not been repaired. Much attention was put on the middle portion of the net, which retains fish during the hauling process.

The operation of the nkacha involves two wooden boats, and seven crew members. The procedure entails one boat with four fishers casting the net out into water perpendicular to the second boat. After casting, the net is set in a semicircle covering an approximate sampling area of 4974 m² (Figure 9a, b). The net is then pulled together at the foot rope by divers and weights are tied together to "purse" the net (Figure 9c).

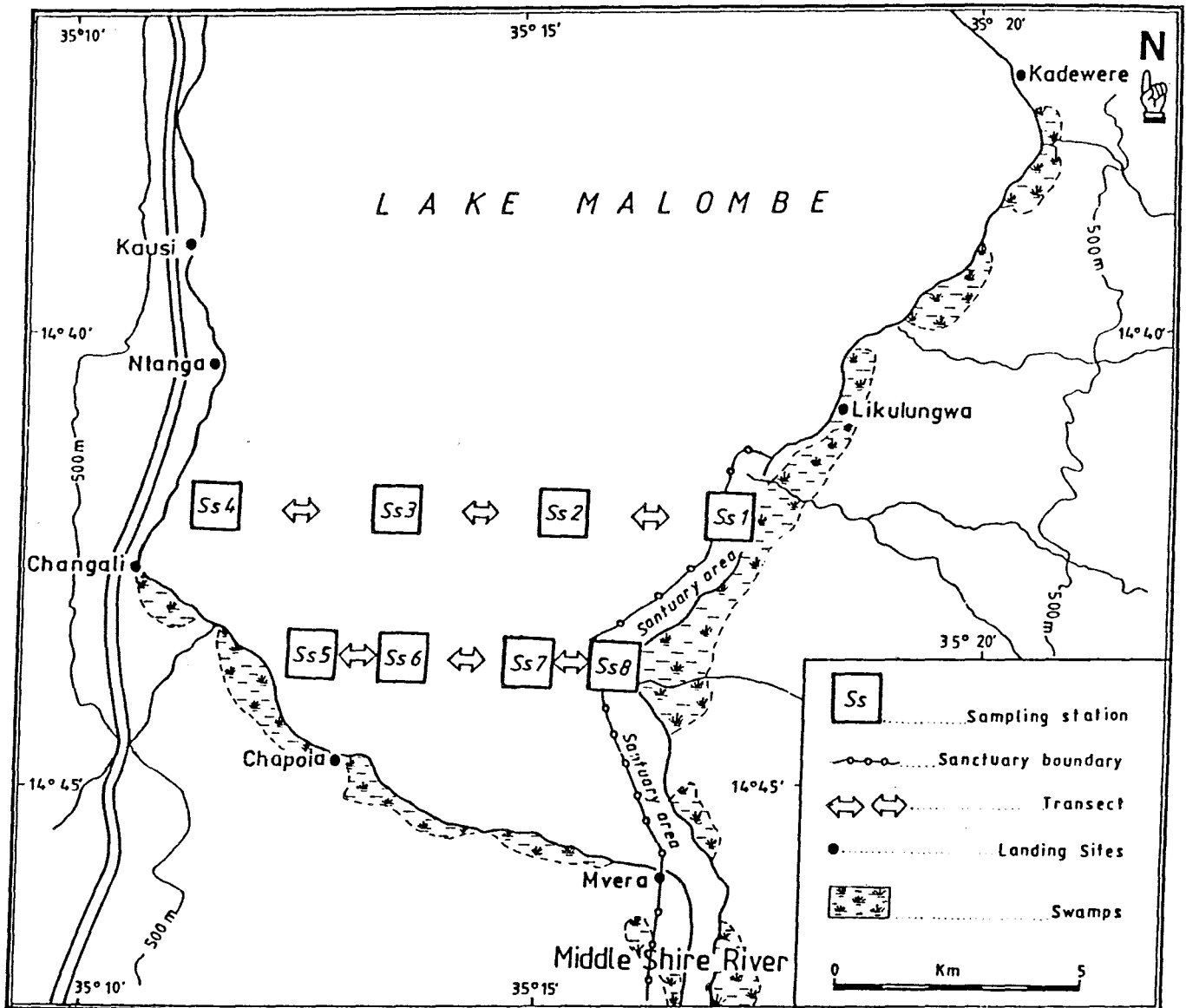


Figure 6. Map of southern Lake Malombe showing the location of all major landing sites and sampling stations used throughout this study. Ss refers to sampling stations along the two transects.

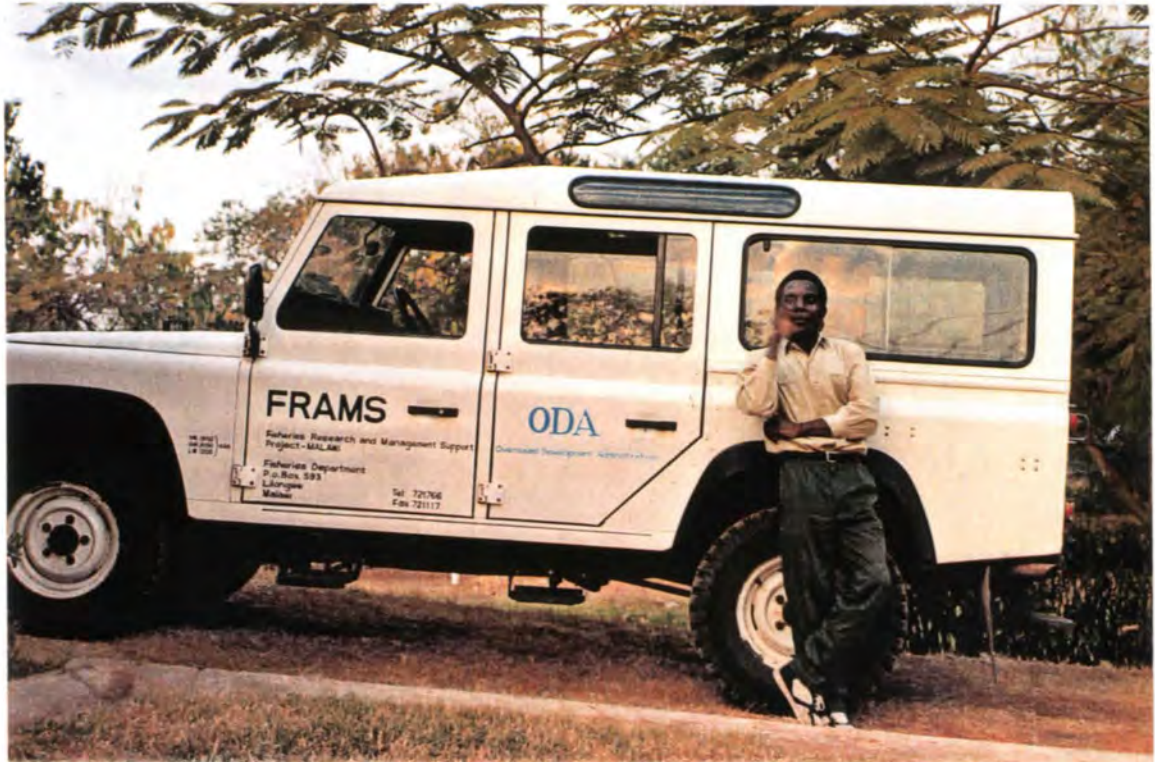


Figure 7. The research vehicle used during the study period, June 1995 to June 1996.



Figure 8. Poachers fishing in the "sanctuary area". This was approximately 4.5 Km south of Likulungwa, May 1995. The smallest mesh size was 10 mm, which is less than the recommended (19 mm). The visual impression of the littoral habitat type of the "sanctuary area" can be also be observed in the background.

Table 2. Some physical characteristics of the eight sampling stations in southern Lake Malombe. ES refers to the eastern shore and WS refers to the western shore.

Sampling Station	Distance	Transect	Mean depth	Substrate	Aquatic weeds
Ss 1	50 m from ES	1	1.2 m	muddy	common
Ss 2	2500 m from ES	1	1.6 m	sandy/snails	rare
Ss 3	2500m from WS	1	2.3 m	sandy/snails	rare
Ss 4	50 m from WS	1	1.7 m	sandy/snails	rare
Ss 5	50 m from WS	2	1.5 m	sandy/snails	rare
Ss6	1500m from WS	2	2.1 m	sandy/snails	rare
Ss7	1500 m from ES	2	1.7 m	muddy/sandy	common
Ss8	50 m from ES	2	1.3 m	muddy	common

A complete haul of a standard nkacha net took approximately thirty minutes. On each sampling trip, two hauls were made at each sampling station, which gave a total number of 16 hauls per month, 20 hauls per sampling station for the whole period of study and 160 hauls for the whole study period.

3.4 FISH SAMPLES

A subsample of approximately 30% of the fish caught in two hauls on each sampling occasion per station was collected for further analysis. Each subsample was immediately labelled and placed in separate plastic bags containing ice and stored in a cooler box until it was transported to the laboratory. In the laboratory the fish samples were stored in a refrigerator. The fish were then identified, sorted, weighed and analysed. Five specimens of each species were preserved in 10% buffered formalin solution for further references and the rest were discarded after they had been washed up.

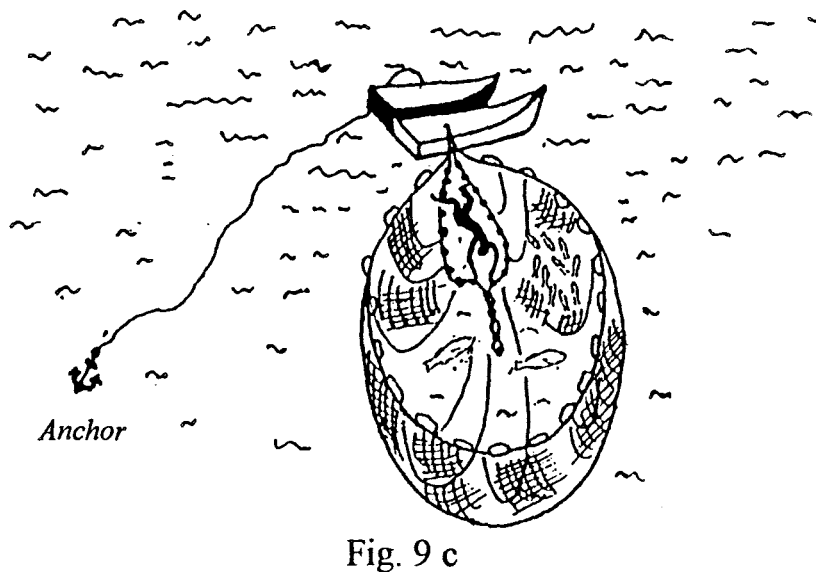
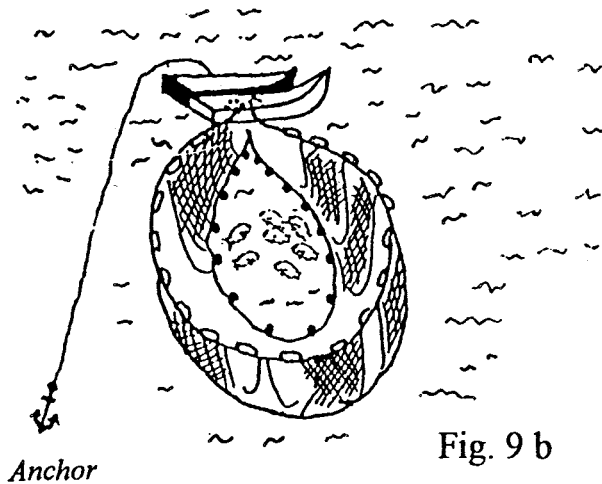
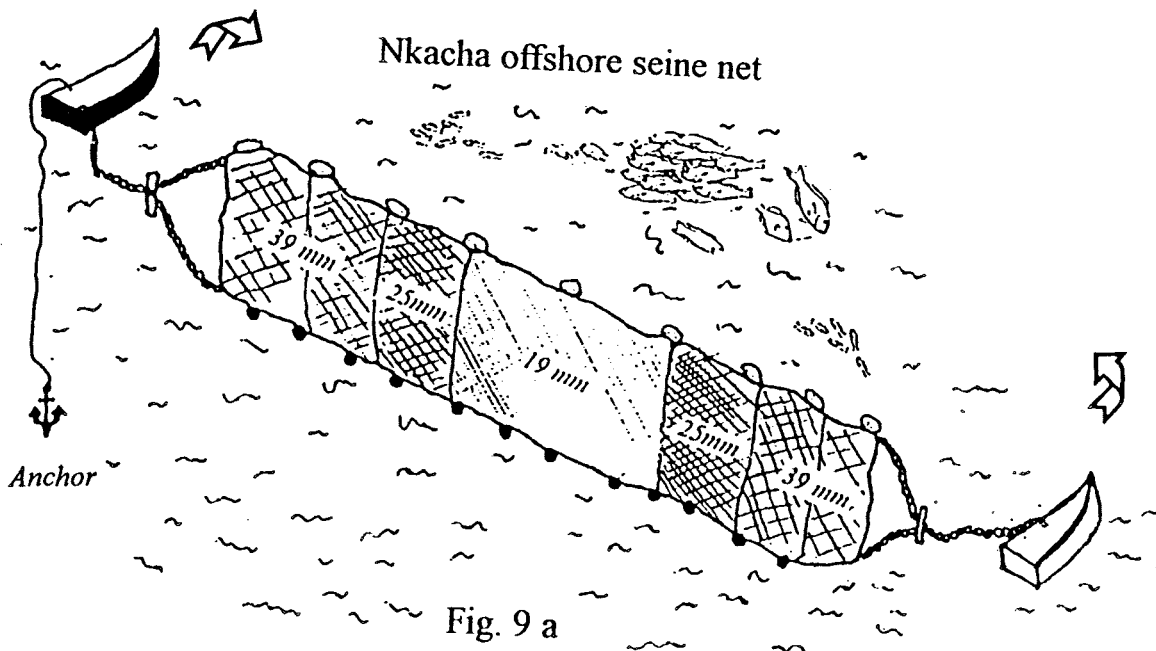


Figure 9. An illustration of nkacha offshore seine net showing its shape, stretch mesh sizes, and operation in the open waters.

CHAPTER 4

SPECIES COMPOSITION AND DIVERSITY

4.1 INTRODUCTION

Ecological communities, even within the same ecosystem, do not always contain the same number or type of species, and within its area of distribution the abundance of a species tends to vary with season (Krebs 1978, Pitcher & Hart 1982). In most tropical ecosystems animal life tends to vary more than in temperate regions and Lake Malombe is no exception. The Lake Malombe fish fauna, as with many other African lakes, is dominated by cichlids (Lowe-McConnell 1987, FAO 1992). Approximately 50 cichlid species have been recorded in the lake (Banda 1995). Most of these cichlids do not have a dispersal phase in their life histories and tend to be stenotopic and philopatric (Fryer & Iles 1972). Ribbink (1994) stated that such characteristics may lead to narrow distribution ranges. By implication this means that small sanctuary areas may be very effective management tools.

Most studies on protected areas have tended to concentrate on the primary target species rather on the fish community as a whole. However, Bennett & Attwood (1991) elaborated that more species tend to reside in protected areas or lightly fished areas than in heavily fished areas. They showed that the number of species increased (from 18 to 22) after closure at Koppie Alleen, in De Hoop Reserve (South Africa). Garcia-Rubies & Zabala (1990) also observed that in the Medes Island fish reserve (Spain), where commercial fishing had been prohibited, fish species richness was significantly higher. These two features form a basis for the hypothesis for this

study, that the sanctuary area, though lightly fished, would have more fish species than the heavily fished area in the south-western side of the lake.

Scientific knowledge of species composition needs to be documented for proper management of the existing sanctuary area, and the management of the fishery as a whole. In this study, species composition of the catches was investigated in order to determine whether species diversity and/or richness was higher in the south eastern side (where there is a poorly policed sanctuary area) than in the south western side (heavily fished area).

The hypothesis examined was that the species diversity and richness in the south-eastern side of the lake were greater than in the south-western side. If this hypothesis were to be accepted then it would be fundamental to the fabric of more rigorous law enforcement in the sanctuary extension, through participatory management forums. An inventory of the species occurring in the area would be listed and this would also form the basis on which future conservation decisions could be made.

4.2 MATERIALS AND METHODS

Data collection for species composition analysis was carried out once a month from June 1995 to June 1996 in the southern part of the lake. Four stations were located along two transects across the southern part of the lake (See Chapter 3, Figure 6). A standard nkacha offshore net (Figure 9) was used throughout the study period. At each sampling station, two hauls were made every month, from which a subsample (about 30% of the total catch of the two hauls) was collected for analysis.

In the field, each subsample was placed in a separate plastic bag containing ice and kept in a cooler box for species identification, estimation of percentage numeric and mass contributions of each species. Whenever unique species appeared in a haul, direct numeric counting of that species was done immediately after hauling. Identification of individual species, percentage numeric and mass contributions to the subsamples were carried out in the laboratory two days after each sampling trip. It was assumed that the proportional contribution made by the species in a subsample were representative of the fish composition of that particular sampling station. This assumption was made on the basis that standardised fishing methods were used throughout the study period. It should, however, be stated that the wind direction and strength had an effect on the size and composition of the catch. For example during winter (June-August) when the lake was subjected to strong south-easterly winds, the nkacha seine net became less effective because it was difficult for the divers to pull and "purse" the net underwater. During the calm months (September-December) the operation of the seine net was more effective. Although standardised sampling methods were used in this study, it is was unavoidable to have some bias in the species composition.

All fish caught were identified according to Eccles & Trewavas (1989), FAO (1992) and Banda (1995). The relative species abundance was determined by weighing all fish of individual species to the nearest gram and then expressing it as a percentage of the weight of the monthly total sample. The results presented in this chapter originated from the pooled data of four sampling stations (Ss1, Ss2, Ss7 and Ss8) in the south eastern side and four sampling stations (Ss3, Ss4, Ss5 and Ss6) in the south western side of the lake. These data were used to construct bar charts of species composition

and relative abundance, based on the estimated mass and number of fish caught from the two sides of the southern section of the lake.

Only the five most abundant species were considered in the construction of the bar charts. The other species, that contributed less than 6% to the total catch, on an individual basis, were labelled "others". Detailed information on catch composition and relative abundance of all species recorded, with their catch data, is however provided in Table 3.

The species diversity of any community is to a large degree a function of the total number of species it contains (species richness) and the distribution of individuals between those member species (equitability or evenness) (Putman 1994). Species diversity and its components, species richness and species evenness were assessed (Pielou 1969, Legedre 1983). The equations used were:

$$\textit{Species Diversity Index } (H') = - \sum (p_i) (\log p_i)$$

$$\textit{Species richness Index } (D) = (S - 1) / (\log n)$$

$$\textit{Species evenness index } (J) = H' / (\log S)$$

where p_i is the proportion belonging to i th species of individuals in a sample, n is the total number of individuals and S is the number of taxa. The non-parametric Mann Whitney U - Test was used to test for significant differences between the indices at the various sampling stations (Krebs 1978, Zar 1984).

Similarity analysis between stations was calculated using the Marczewski & Steihaus (1958) equation:

$$S = (w \times 100) / (a + b - w)$$

where: S is similarity index of two sites, w is the total of the lower numbers of specimens of each pair of species common for two given stations, a is the total number of specimens of a species in the first station and b is the total number of specimens of a species in the second station. This analysis was carried out to determine the degree of similarity in fish communities between the sampling stations. Various physical factors of the different sampling stations were considered in this analysis including distance from the shore, substrate type, water depth and presence of aquatic weeds, as presented in Table 2.

4.3 RESULTS

4.3.1 SPECIES COMPOSITION

Overall a total of 49 species belonging to six different families were positively identified in the southern part of Lake Malombe (Table 3). A total of 34 Cyprinidae and 22 Mochokidae were encountered in the catches from the south eastern side. Only one Cyprinid, *Engraulicypris sardella* and no Mochokids were observed in the catches of the south western side of the lake. The family Cichlidae, contributed over 70% of the total catch by mass and number, in the south western and south eastern sides of the lake (Figure 10). Out of 49 species, 37 occurred on both sides of the lake. Two species were exclusively sampled from the south western side and 11 from the south eastern side of the lake (Table 4).

Table 3. The percentage contribution by mass of the species caught in the south western and south eastern sides of southern Lake Malombe between June 1995 and June 1996 using a standard nkacha offshore seine net. Data values less than 0.01% and 0.9 g are omitted and are represented by **. Juveniles* represents those individuals less than 50 mm (TL).

Family	Species	SW (heavily fished)		SE (lightly fished)	
		Catch (g)	%	Catch (g)	%
CICHLIDAE	<i>Astatotilapia calliptera</i>	0	0.00	0.9	0.01
	<i>Aulonocara brevirostris</i>	20.5	0.03	122	0.16
	<i>Aulonocara guentheri</i>	386.7	0.62	289.5	0.39
	<i>Aulonocara macrochir</i>	0	0.00	65.63	0.09
	<i>Aulonocara rostratum</i>	0	0.00	50.7	0.07
	<i>Buccochromis atritaeniatus</i>	1034.7	1.66	749.8	1.00
	<i>Buccochromis nototaenia</i>	281.5	0.45	1266.4	1.69
	<i>Plecodus paradoxus</i>	7.6	0.01	0	0.00
	<i>Chilotilapia rhoadesii</i>	20.4	0.03	304.7	0.41
	<i>Copadichromis chrysonatus</i>	7066.1	11.34	7003.8	9.34
	<i>Copadichromis cf. virginalis</i>	8636.7	13.86	4709.4	6.28
	<i>Corematodus taeniatus</i>	34.3	0.06	205.1	0.27
	<i>Ctenopharynx intermedius</i>	356.7	0.57	2212.2	2.95
	<i>Ctenopharynx pictus</i>	0	0.00	8	0.01
	<i>Dimidiochromis strigatus</i>	37.6	0.06	136.1	0.18
	<i>Fossorochromis rostratus</i>	130.9	0.21	74.5	0.10
	<i>Hemütilapia oxyrhynchus</i>	0	0.00	50	0.07
	<i>Lethrinops "bigeye"</i>	43.2	0.07	21.8	0.03
	<i>Lethrinops "dark"</i>	3064.9	4.92	317.5	0.42
	<i>Lethrinops "pinkhead"</i>	12607.4	20.24	16730.5	22.32
	<i>Lethrinops lethrinus</i>	1980.3	3.18	2644.69	3.53
	<i>Lethrinops nicrodon</i>	64.8	0.10	0	0.00
	<i>Lethrinops parvidens</i>	1909.9	3.07	1529.8	2.04
	<i>Mylochromis semipalatus</i>	0	0.00	88.5	0.12
	<i>Nyassachromis nicrocephalus</i>	86.8	0.14	1044.3	1.39
	<i>Oreochromis shiranus</i>	1320.8	2.12	1306.7	1.74
	<i>Oreochromis spp. (Juveniles*)</i>	407	0.65	3327.5	4.44
	<i>Otopharynx argyrosoma</i>	6245.6	10.03	5501.6	7.34
	<i>Otopharynx heterodon</i>	29.9	0.05	83.9	0.11
	<i>Otopharynx tetrastigma</i>	7670.1	12.31	11224.5	14.97
	<i>Placidochromis subocularis</i>	1173.2	1.88	836.7	1.12
	<i>Protomelas labridens</i>	1745.2	2.80	2748.8	3.67
	<i>Protomelas similis</i>	106.1	0.17	322.1	0.43
	<i>Pseudotropheus elegans</i>	35.8	0.06	130.2	0.17
	<i>Pseudotropheus livingstonii</i>	911.4	1.46	343.3	0.46
	<i>Rhamphochromis spp.</i>	191.9	0.31	561.9	0.75
	<i>Serranochromis robustus</i>	**	**	**	**
	<i>Stigmatochromis woodi</i>	214.5	0.34	526.2	0.70
	<i>Taeniolethrinops furcicauda</i>	64.5	0.10	11.2	0.01
	<i>Tilapia rendalli</i>	0	0.00	21.7	0.03
	<i>Tramitichromis variabilis</i>	**	**	213.4	0.28
<i>Trematocranus labifer</i>	40	0.06	614.3	0.82	
<i>Trematocranus placodon</i>	650.2	1.04	1505.7	2.01	
BAGRIDAE	<i>Bagrus meridionalis</i>	1080.4	1.73	679.1	0.91
CLARIDAE	<i>Clarias gariepinus</i>	2408.2	3.87	2714.7	3.62
MOCHOKIDAE	<i>Synodontis njassae</i>	0	0.00	28.4	0.04
CYPRINIDAE	<i>Barbus trimaculatus</i>	0	0.00	122.9	0.16
	<i>Engraulicypris sardella</i>	124.7	0.20	265	0.35
	<i>Opsaridium microlepis</i>	0	0.00	719.3	0.96
	<i>Labeo mesops</i>	0	0.00	1360.7	1.81
CHARACIDAE	<i>Brycinus imberi</i>	108.8	0.17	176.1	0.23

There were more cichlid species in the south eastern side (40) than in the south western side (36). However, catches from both sides of the lake were dominated by five cichlid species, *L. "pinkhead"*, *C. cf. virginalis*, *O. tetrastigma*, *C. chrysonotus* and *O. argyrosoma "red"*. Differences in contribution by mass and number (expressed as a percentage) of each of these species is shown in Figure 11. The three selected species constituted 44% of the overall fish fauna by mass and 60% by number in the south western side of the lake, and 36% by mass and 54% by number in the south eastern side (Table 3). *Oreochromis* species which used to dominate the catches were encountered in fishers' gill nets (personal observation). This provides a circumstantial evidence that the absence of sub-adult or adult *O. karongae* and *O. squamipinnis* in the catch data was due to the bias and limitations of the sampling gear (nkacha) used in this study.

Table 4. Species exclusively sampled from the south eastern side (SE) and the south western side (SW) of Lake Malombe from June 1995 to June 1996.

Species restricted to SE side	Species restricted to SW side
<i>Astatotilapia calliptera</i>	<i>Lethrinops microdon</i>
<i>Aulonocara macrochir</i>	<i>Plecodus cf. paradoxus</i>
<i>Aulonocara rostratum</i>	
<i>Barbus trimaculatus</i>	
<i>Ctenopharynx pictus</i>	
<i>Hemitilapia oxyrhynchus</i>	
<i>Labeo mesops</i>	
<i>Mylochromis semipalatus</i>	
<i>Opsaridium microlepis</i>	
<i>Synodontis njassae</i>	
<i>Tilapia rendalli</i>	

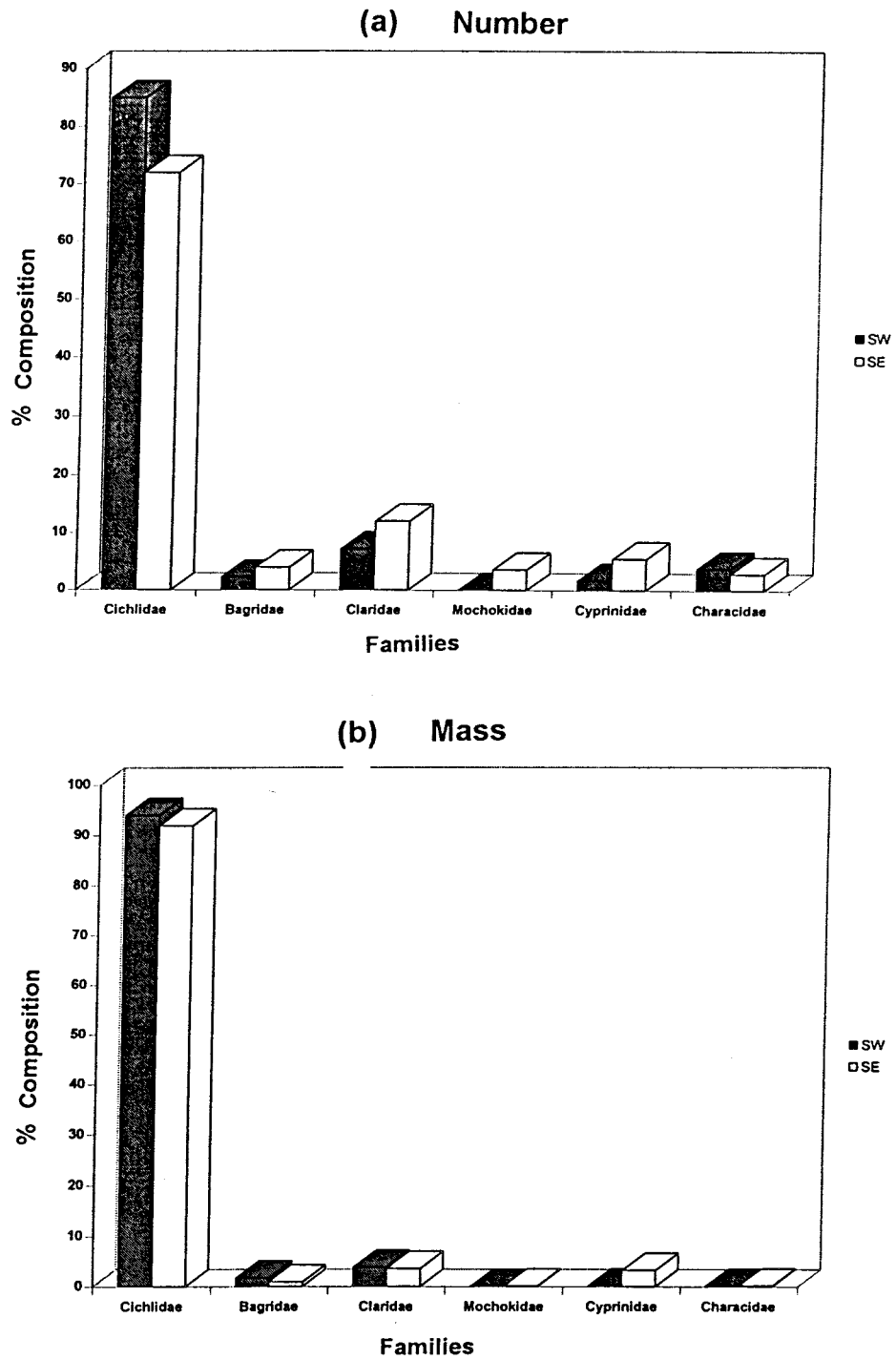


Figure 10. Familial percentage composition by number (a) and mass (b) sampled from the south western (SW) side and the south eastern (SE) side of Lake Malombe from June 1995 to June 1996.

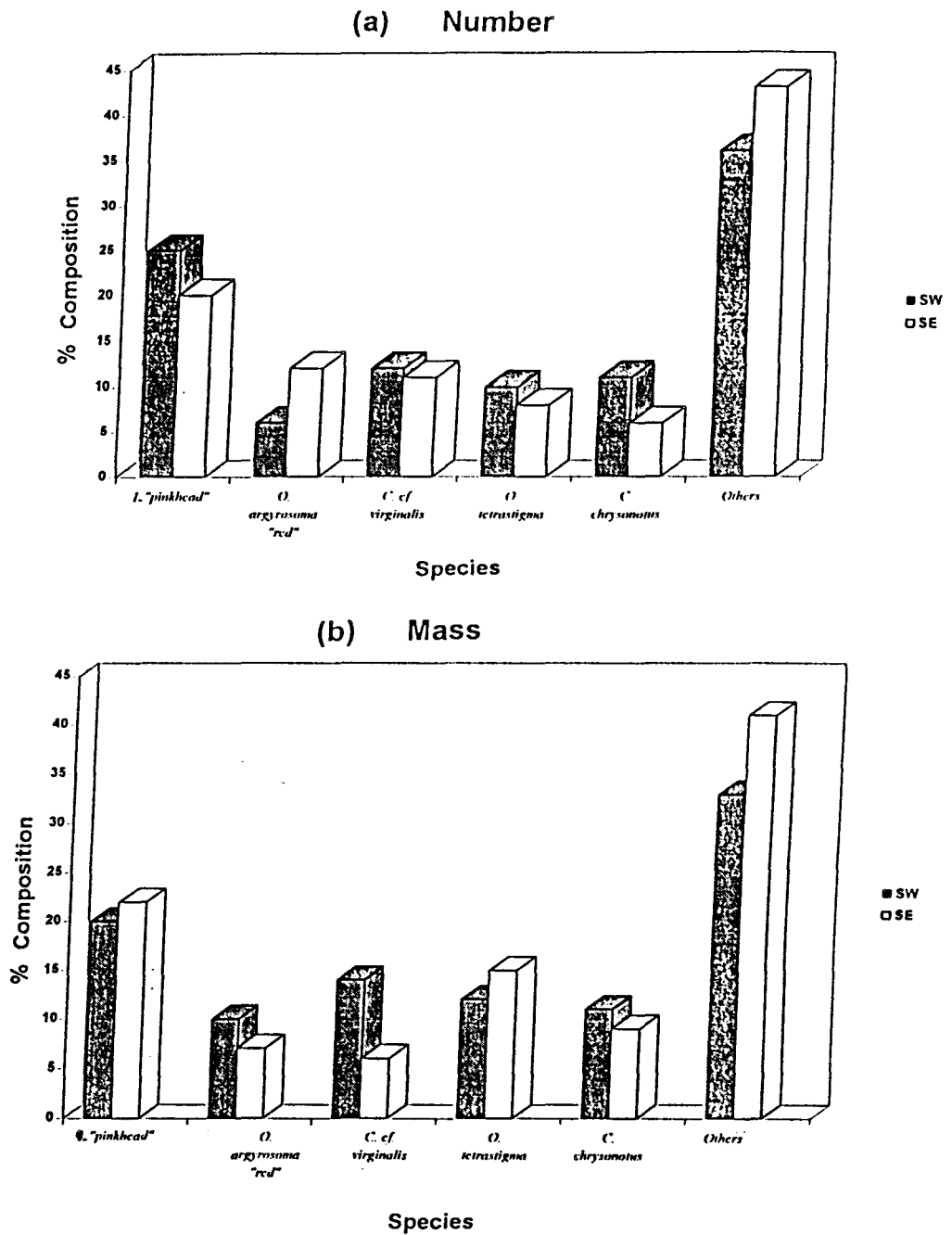


Figure 11. The total number (a) and mass (b) of major species (expressed as a percentage) sampled from the south western (SW) side and the south eastern (SE) side of Lake Malombe from June 1995 to June 1996.

4.3.2 DIVERSITY AND COMMUNITY SIMILARITY

Species diversity, richness and evenness indices for the fish fauna are shown in Figure 12. The species richness and diversity values were slightly higher towards the south eastern side of the lake. The calculated Shannon-Weaver species diversity H' values for the south eastern side were significantly different from H' values for the south western side (Mann Whitney U-test $U = 13$; $P < 0.05$). The species richness (D) mean value (0.75) for the south eastern side was significantly different from that of the south western side of the lake (0.59) (Mann Whitney U-test; $U=14$; $P < 0.05$). Although subsample sizes were in most cases too low for accurate use of these indices, they do nevertheless indicate some distinct trends. On both transects, Shannon-Weaver diversity and species richness indices clearly showed a marked trend in species' diversity increase towards the south eastern side of the lake.

The species evenness values did not vary significantly between the south western side and south eastern side of the lake. It appears the highest values of these indices were all recorded from the south eastern side of the lake; 1.09 for diversity (H'), 0.75 for species richness (D) and 0.65 for evenness (J).

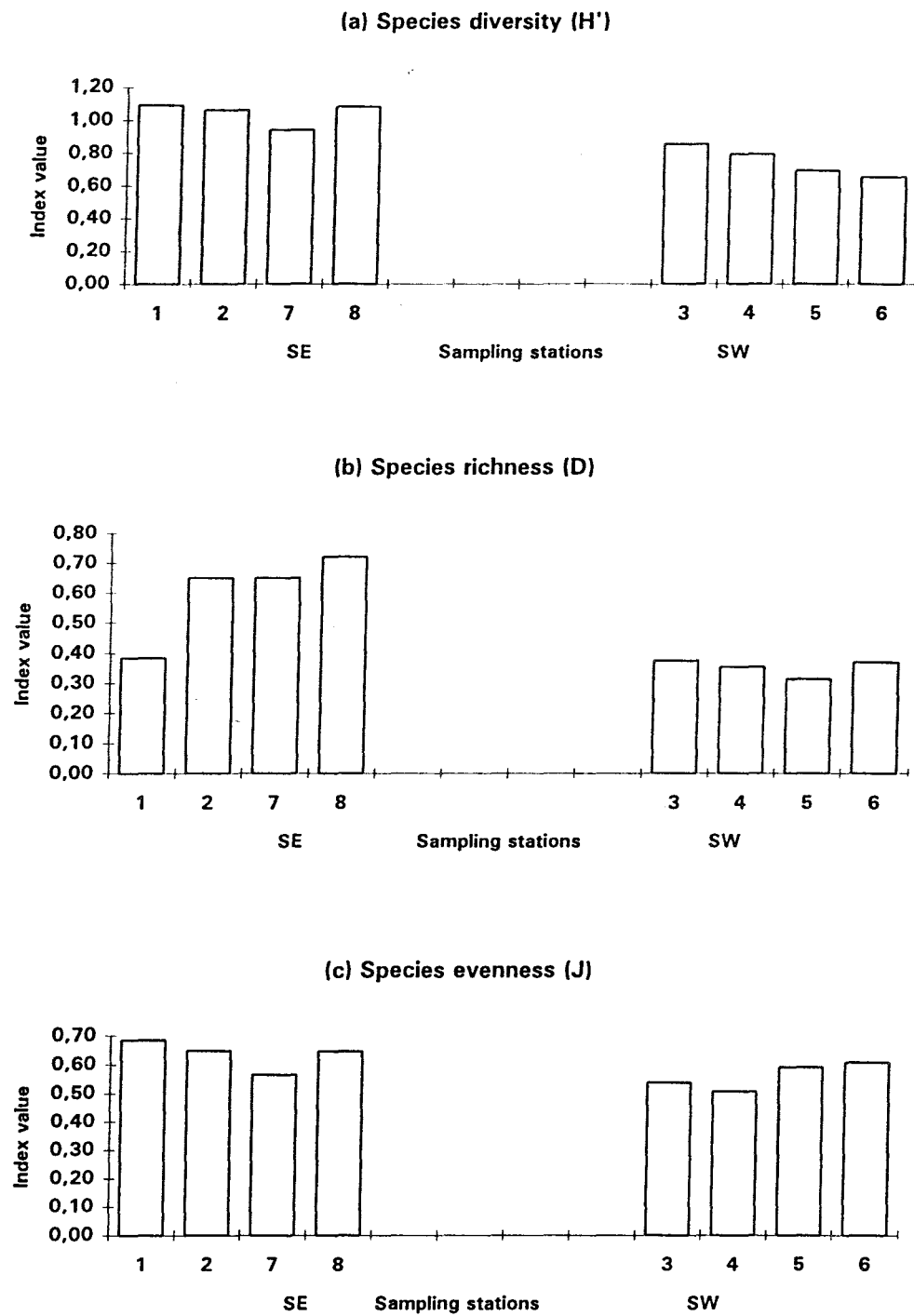


Figure 12. Fish species diversity (a) species richness (b) and evenness (c) values for all sampling station on the two transects. SE refers to the south eastern side and SW refers to the south western side of the lake.

The similarity analysis (Figure 13) separated the sampling stations according to substrate types (mud and sand). These types were separated at a similarity level of 35%. Sampling stations 1, 7 and 8 formed one branch while stations 2,3,4,5 and 6 formed another branch. The relatively short branches of the dendrogram leading to two groups of sampling stations however, showed that these sampling stations are not quite distinct.

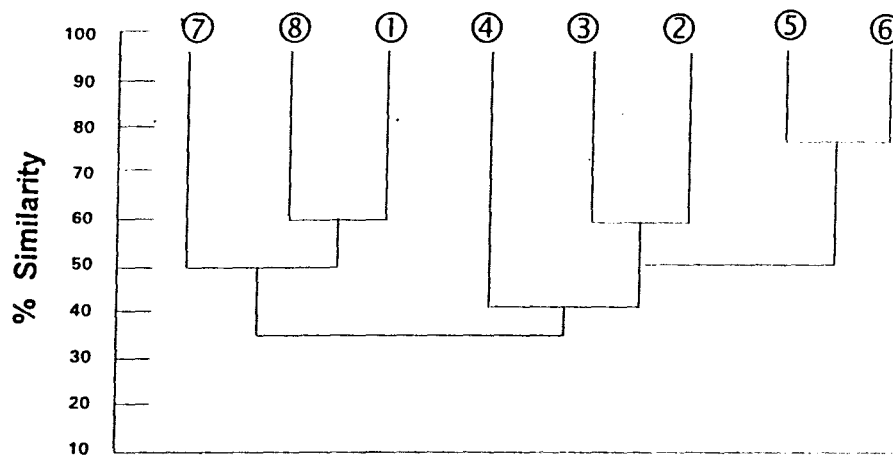


Figure 13. Dendrogram showing similarity of sampling stations for fish species abundance. Sampling stations 1,2,7 & 8 are lightly fished with muddy substrate type except sampling station 2 while sampling stations 3,4,5 & 6 are heavily fished with sandy and snail substrate type.

4.4 DISCUSSION

Catch composition

Results from this study show that more species (48) occurred in the south eastern side than in the south western side of the lake (39), and that 37 species were common to both sides. Overall, five species *L. "pinkhead"* (20%), *C. cf. virginalis* (14%), *O. tetrastigma* (12%), *C. chrysonotus* (11%) and *O. argyrosoma "red"* (10%) were dominant and accounted for 67% of the total catch by weight.

In comparison the study by FAO (1992) on catch composition from the lake identified only 40 species of which three; *L. "pinkhead"* (35%), *C. cf. virginalis* (22%), and *O. argyrosoma "red"* (16%) contributed 73% by weight to the total catch. The results from the Fisheries Research Management and Support (FRAMS) monitoring programme (Banda 1995), on species composition of the western side of the lake (where most fishing takes place), indicated that 45 species contributed to the catch. Five species dominated the catches and together contributed about 80% to the total catch; *L. "pinkhead"* (13%), *C. cf. virginalis* (16%), *O. tetrastigma* (12%), *L. parvidens* (9%) and *O. argyrosoma "red"* (31%). From these results it can be noted that though there is agreement in four of the five dominant species recorded by Banda (1995) and the present study, *L. parvidens* was replaced by *C. chrysonotus* as the fifth most important species. Interpretations of these results need to be treated with caution because catch compositions from the three studies cannot easily be compared since both the FAO (1992) and Banda (1995) studies collected samples from fishers' landings. Nevertheless, it is apparent that catches of the five major species have fluctuated substantially but there is no convincing evidence for changes in composition which might reflect underlying shifts in species' assemblage structure.

The replacement of the bottom feeding *L. parvidens*, by the zooplanktivorous *C. chrysonotus*, as one of the five most important species is an indication that the stocks of these species might have reacted to the higher fishing pressure, which has contributed to substrate degradation. *C. chrysonotus* is confined to inshore waters and most of the breeding males congregate in large schools. Courtship and mating of *C. chrysonotus* takes place in the water column (Eccles & Trewavas 1989). Breeding off the bottom without territories would probably make *C. chrysonotus* less vulnerable to capture by bottom dragging nets than *L. parvidens*.

Species diversity and community similarity

Apparently all the four sampling stations in the south eastern side of the lake have a unique combination of hydrological factors and substrate types (Table 2). Based on the indices of species diversity (H') and species richness (D) for the south western side and south eastern side of the lake and the catch composition data presented in this chapter, it appears that more species prefer the south eastern side than the south western side of the lake. Seven cichlid species and four non cichlid species were restricted to the south-eastern side of the lake. These species appeared in the catches at almost all sampling stations in the south eastern side but were absent from the south western side of the lake.

The virtual absence of these species from the four sampling stations in the south western side could be related to substratum degradation given that cichlid species have a sufficiently generalised habitat preference, they should be widespread and relatively common throughout the lake (Eccles & Lewis 1977). By implication it could be suggested that the relatively higher fishing pressure in the south western side of the lake, has degraded the substrate type (FAO 1992, Turner *et al.*, 1992). Jennings & Lock (1996) stated that

habitat degradation would affect fish yield, both by causing a redistribution of the exploitable fish biomass and, in severe cases, by reducing total productivity of the fishery.

Furthermore, it can be speculated that the substrate type and availability of aquatic weeds could be the obvious ecological factors influencing the habitat preferences of the Cyprinidae and Mochokidae, although fishing intensity could also play a major role.

Similarity analysis separated the sampling stations into muddy and sandy habitats. Nevertheless, it should be emphasised that this is not an absolute criterion because even muddy habitats had sandy microhabitats and sandy habitats had muddy microhabitats. The dendrogram indicates that in the south eastern side of the lake, sampling stations (1 & 8), had a 60% similarity but a 50% similarity to sampling station 7. However, sampling station 2 had a 60 % similarity to sampling station 3. It is also evident from the dendrogram that amongst sandy habitats, sampling stations 5 & 6 had a 75 % similarity but only a 45% similarity to sampling stations 2 & 3. However, the most noticeable feature of the sampling stations is that they are not significantly different from each other in terms of water depth and availability of food.

From the findings presented in this chapter, it appears that high species diversity and richness in the south eastern side of the lake are due to substrate type (for the non cichlid species) and low fishing intensity (for the cichlids). It is therefore apparent that this study, to a certain extent, has provided quantitative data to support the claim that more individual species reside in the south eastern side than in the south western side of Lake Malombe.

CHAPTER 5

DISTRIBUTION AND ABUNDANCE

5.1 INTRODUCTION

In the Lake Malombe fishery, catches of *Oreochromis* spp. and the three haplochromine cichlid species being investigated have declined significantly (FAO 1992, Banda 1995). This has had a serious economic impact on the fishing community. Total fishing effort in Lake Malombe has been limited by management action (see in Chapter 1), however, the fishers have learnt by experience that fish abundance is not a fixed quantity and that it varies from one place and one time to another, producing spatial and temporal patterns. Under such circumstances and within the context of the open-access nature of the fishery, fishers have exploited almost all accessible habitats in the lake including those in the so called sanctuary area (Bland & Donda 1994).

Welcomme (1992) argued that fishing pressure and environmental degradation have had major modifying effects on fish communities in most freshwater lakes. He pointed out that substratum, water quality and primary production of a lake change due to overfishing, and such effects bring about fluctuations in abundance of fish through time.

The desire to understand the effects of fish reserves on fish distribution and abundance, in order to manage exploited fisheries, has provided a major focus for fisheries research in recent years. With few exceptions, most studies have reported that the abundance of target species in lightly fished areas or reserve areas is greater than in exploited areas (Bell 1983, Russ 1985, McCormick & Choat 1988, Buxton & Smale 1989, McClanahan 1989).

Intriguing questions, related to the Lake Malombe kambuzi fishery, would be: How are the three main species (*L. "pinkhead"*, *O. argyrosoma "red"* and *C. cf. virginalis*) distributed in southern Lake Malombe? Does the south eastern side (lightly fished "sanctuary area") have more fish than the south western side of the lake? Are there differences in the distribution and abundance of the three species in the south western and south eastern sides and if so, are these differences attributable to exploitation? Answers to these questions together with historical changes in fish community composition (discussed by Bell & Donda 1993), would provide information on the changes in the physical environment and factors that might have resulted in the current distribution and abundance patterns of fish in the southern part of the lake. Answers to these questions would also provide the basis for the extension and more efficient management of the "sanctuary area".

Given that part of the south eastern side is a proclaimed sanctuary area and is only lightly fished while the south western side is heavily fished, the null hypothesis being tested in this chapter is that the abundance of fauna in the south eastern side and south western side of the lake is the same.

5.2 MATERIALS AND METHODS

During the period June 1995 to June 1996 fish were sampled on four consecutive days each fortnight. Standard gear (described and illustrated in Chapter 3) was used throughout the period of study. The three main fish species were identified, counted and weighed immediately after hauling. At each sampling station two hauls were made in order to avoid the use of replicates that were not statistically independent (Hulbert 1984). A subsample was then collected from a mixture of the two hauls, and stored in a refrigerator for further laboratory work. Species bigger than kambuzi and all

juveniles less than 15 mm (TL) were counted and weighed without any subsampling.

In the laboratory, subsamples were categorised into species. Fish of each species were counted and weighed to the nearest gram. Habitat characteristics like temperature, turbidity, substrate type and primary production levels were related to the distribution and abundance of the three main species. Correlations between these environmental variables and catch have been found in numerous studies (Skud 1982, Saetersdal & Loeng 1983, Legget *et al.*, 1984, Laevastu 1984).

Water temperature was measured using the main and auxiliary thermometers fitted to the 2 litre Van Dorn bottle, which collects water samples for chlorophyll-*a* analysis, at particular depths. Water temperatures were recorded at standard depths of observation: 0, 1, 1.5 and 2.0 metres. The temperature readings on the main thermometer were read to an accuracy of $\pm 0.01^{\circ}\text{C}$ and the auxiliary to $\pm 0.1^{\circ}\text{C}$. The auxiliary thermometer helped to show the water temperature at the time of reading and served for correction of the actual temperature. For each sampling site, mean temperature was calculated and used because the temperature profiles recorded at particular depths were not significantly different.

Turbidity measurements were made using a standard 20 cm diameter Secchi disk. The Secchi disk was lowered into the water slowly, on the shaded side of the boat, attached to a string marked in metres. The depth at which the disk disappeared was recorded. The exact depth of disappearance was determined by moving the disk slowly up and down at that depth. The depth of disappearance was then converted into extinction coefficients (Laevastu

1965), which were then used to evaluate the turbidity of water in the south western and south eastern sides of the lake.

The depth integrated samples for the study of phytoplankton were collected by a weighted bottle, which fills slowly as it descends. This method was used because it gives a more complete and accurate picture of the phytoplankton composition than a single depth sample (Laevastu 1965).

Catch per unit effort (CPUE) for each sampling station was established to ascertain the demography of the fish population in relation to substrate type and fishing intensity. It should be pointed out that the CPUE was calculated based on the pooled data, from the sampling stations. The underlying assumption of the sampling techniques on the distribution and abundance in this study was that fish were not affected by divers during gear operation (as discussed in Chapter 3) and that all sampling errors were assumed to be similar in all habitats sampled because standardised techniques were used at all sampling stations.

On the basis of the differences in the fishing intensity and substrate type, data from each side of the lake were treated separately. The data for 80 subsamples collected from the south western side (sampling stations 3, 4, 5 and 6) were pooled together, as were the data for 80 subsamples from the south eastern side of the lake (sampling stations 1, 2, 7, and 8).

5.3 RESULTS

5.3.1 Limnology

Temperature

In both sides of the lake, the water temperatures increased slightly between July and August and between September and November. The lowest temperatures occurred in June. Overall, the monthly mean temperatures of the south eastern side were slightly higher than those of the south western side of the lake. However, the differences were not significant (Figure 14).

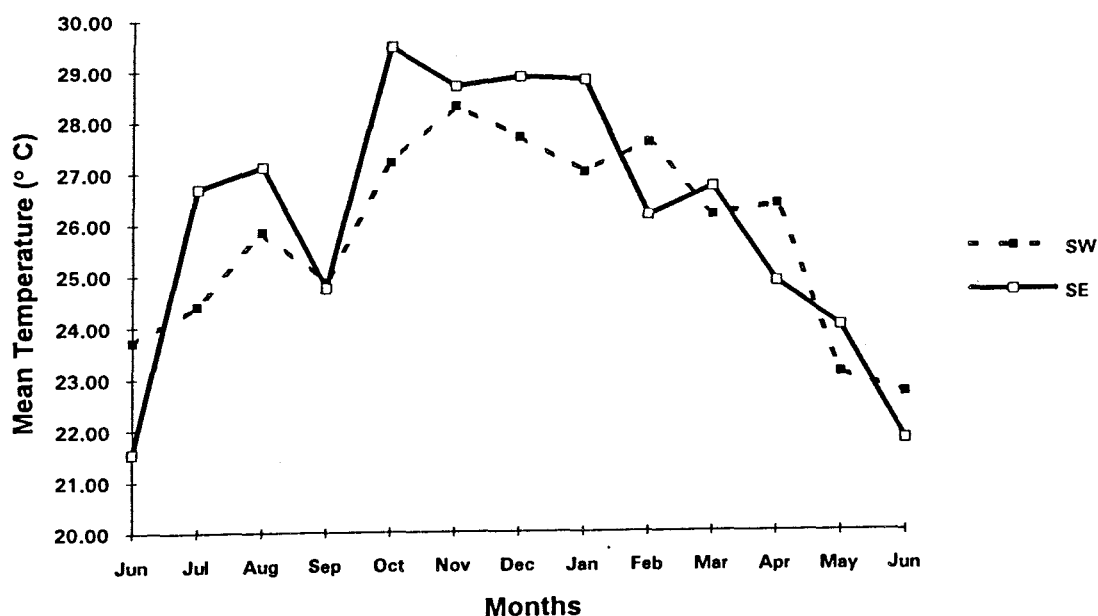


Figure 14. Mean monthly water temperatures of the south western (SW) side and south eastern (SE) side of Lake Malombe recorded between June 1995 and June 1996.

Turbidity

Turbidity of water in the south western side remained relatively constant throughout the study period. The minimum Secchi disk reading (1.6 m) was recorded in June 1996 and the maximum (2.0 m) in December 1995. In the south eastern side of the lake, the fluctuations in turbidity were minimal throughout the study period. Secchi disk readings ranged between 0.2 m, in June 1996 and 0.6 m, in September 1995.

The mean Secchi disk reading (1.6 m) in the south western side of the lake indicated high transparency, while the mean reading (0.3 m) in the south eastern side of the lake indicated low transparency. There was a marked significant difference (t-test, $P < 0.05$) in Secchi disk readings between the south western and south eastern side of the lake. However, the seasonal patterns of the two sides were very similar (Figure 15).

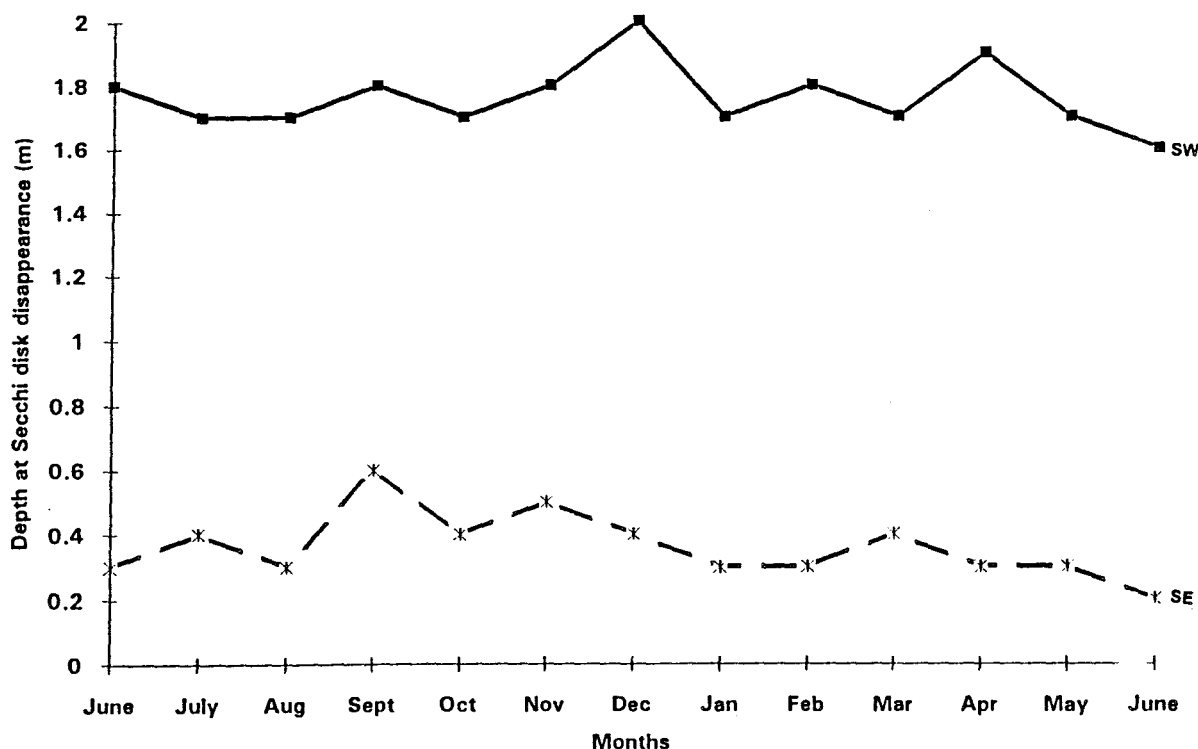


Figure 15. Monthly Secchi disk readings in the south western (SW) side and south eastern (SE) side of Lake Malombe recorded between June 1995 and June 1996.

Phytoplankton

The mean monthly phytoplankton biovolume values for the sampling stations in both sides of the lake showed seasonal variations in phytoplankton. The highest mean biovolume was recorded in August (13800 mm³/m²) in the south western side and (13600 mm³/m²) in the south eastern side. The lowest mean biovolume occurred in September (1600 mm³/m²) in the south western side and in September and October (1800 mm³/m²) in the south eastern side of the lake (Figure 16). Overall, the differences in phytoplankton abundance between the two sides were not significant (t- test, $P < 0.05$).

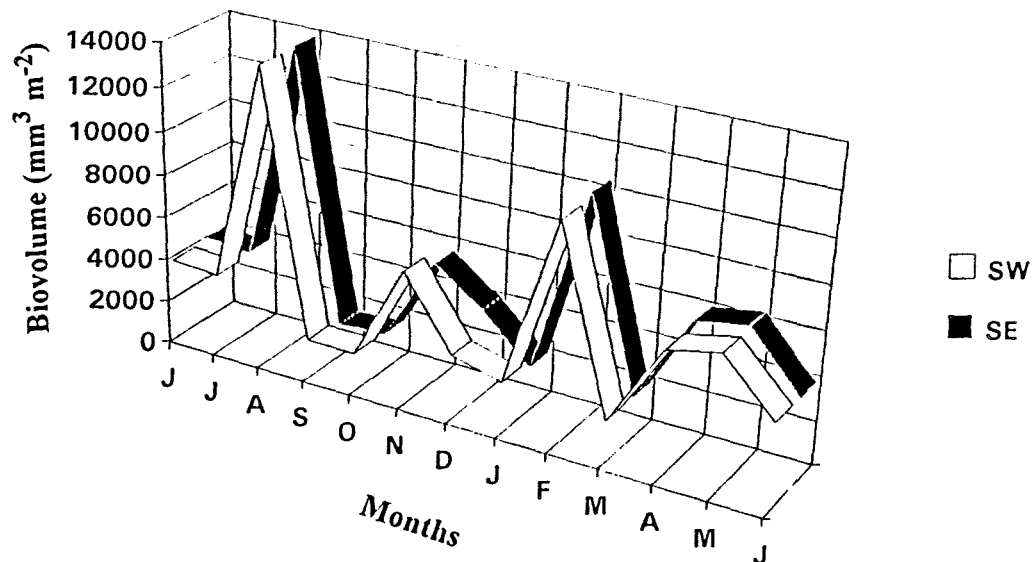
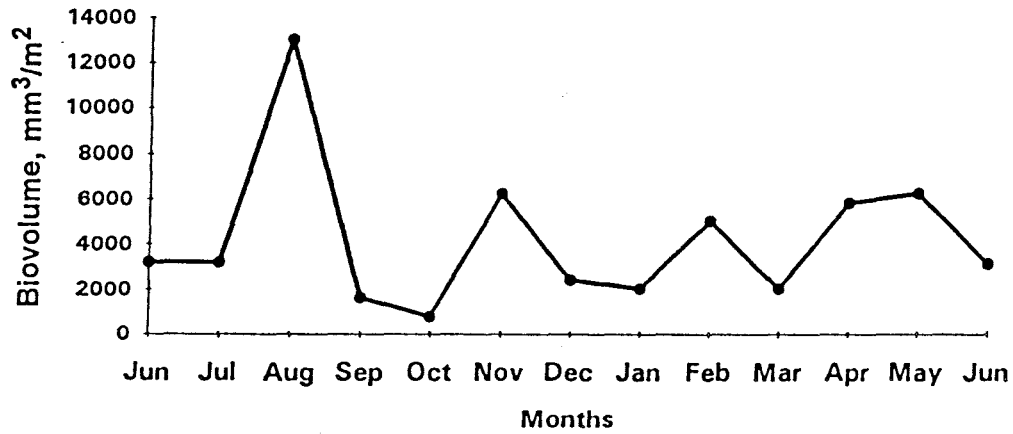


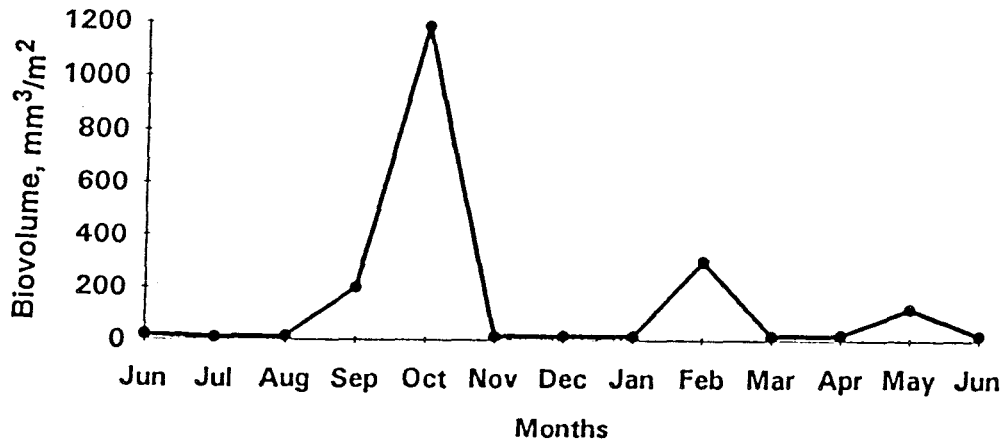
Figure 16. Monthly abundance of phytoplankton in the south western (SW) side and south eastern (SE) side of Lake Malombe recorded between June 1995 and June 1996.

Four main taxa of phytoplankton, Cyanophyta (blue greens), Chlorophyta (greens), Bacillariophyta (diatoms) and Pyrrophyta (flagellates) were identified. The blue greens, greens and diatoms were dominant throughout the year. Mean monthly variations of these taxa are presented in Figure 17.

Diatoms



Blue green



Greens

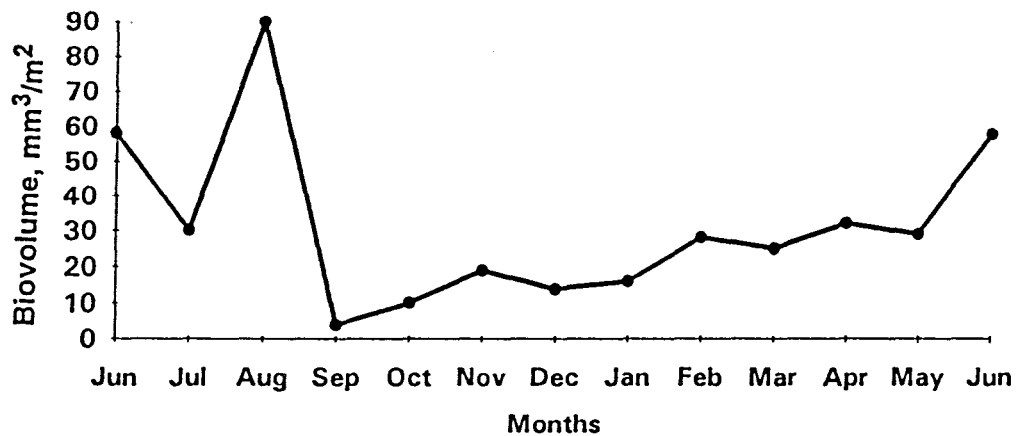


Figure 17. Monthly variations of the three prominent phytoplankton taxa for the south western side and south eastern side of Lake Malombe. Pooled data for all sampling sites were used.

5.3.2 Distribution

Spatial distribution and habitat preferences

The three species *L. "pinkhead"*, *O. argyrosoma "red"* and *C. cf. virginalis* were common at all eight sampling stations. However, the total biomass of *O. argyrosoma "red"* and *C. cf. virginalis* was greater in the south western side than in the south eastern side of the lake (Table 3). Numerically, there were notable differences in the total catches of the three species in both sides, ($F = 9.25$, $P < 0.05$) with highest overall catches in the south eastern side and lowest in south western side (Table 5). Differences in the total number caught on a monthly basis of each species, for the two sides, were analysed for significance with Tukey's t- test at a significance level of $P < 0.05$, and it was found that no marked monthly differences occurred between the two sides for each species. This implies that the mean CPUE results were not seasonally biased. The analysis of variance of the results on monthly catches showed significant deviations from random distribution for all the three species and the total catch (Table 6). This indicates that the distribution of the three species was heterogeneous.

Table 5. Spatial distribution of the three fish species in the south western (SW) side and south eastern (SE) side of Lake Malombe (Based on the number of fish in all the subsamples collected between June 1995 and June 1996).

Species	SW side	SE side
	Sandy substrate	Muddy substrate
<i>L. "pinkhead"</i>	1404	1656
<i>O. argyrosoma "red"</i>	337	993
<i>C. cf. virginalis</i>	675	911
<i>Others</i>	3201	4720

Table 6. Analysis of variance of the nkacha offshore seine net catches, to test the null hypothesis that there was no difference in catch of the three species, at the sampling stations, in the south western side and south eastern side of Lake Malombe.

Species	F-ratio	Probability of F
<i>L. "pinkhead"</i>	4.51	<0.05
<i>O. argyrosoma "red"</i>	3.16	<0.05
<i>C. cf. virginalis</i>	3.01	<0.10
Total	5.12	<0.05

Seasonal distribution

Differences in seasonal distribution of the three main species were observed during the study period. In the south western side, the contribution of *L. "pinkhead"* by mass was greatest between September and November and constituted about 40% of the total catch during this period. The greatest contribution by mass of *C. cf. virginalis* occurred in December and April, contributing approximately 42% to the total catch and *O. argyrosoma "red"* contributed 25% to the total catch in June.

In the south eastern side, the greatest contribution by mass of *L. "pinkhead"* (45% to the total catch) occurred between October and November. For *C. cf. virginalis* it occurred in June and July (15% to the total catch), whilst for *O. argyrosoma "red"* it was almost constant throughout the study period (Figure 18).

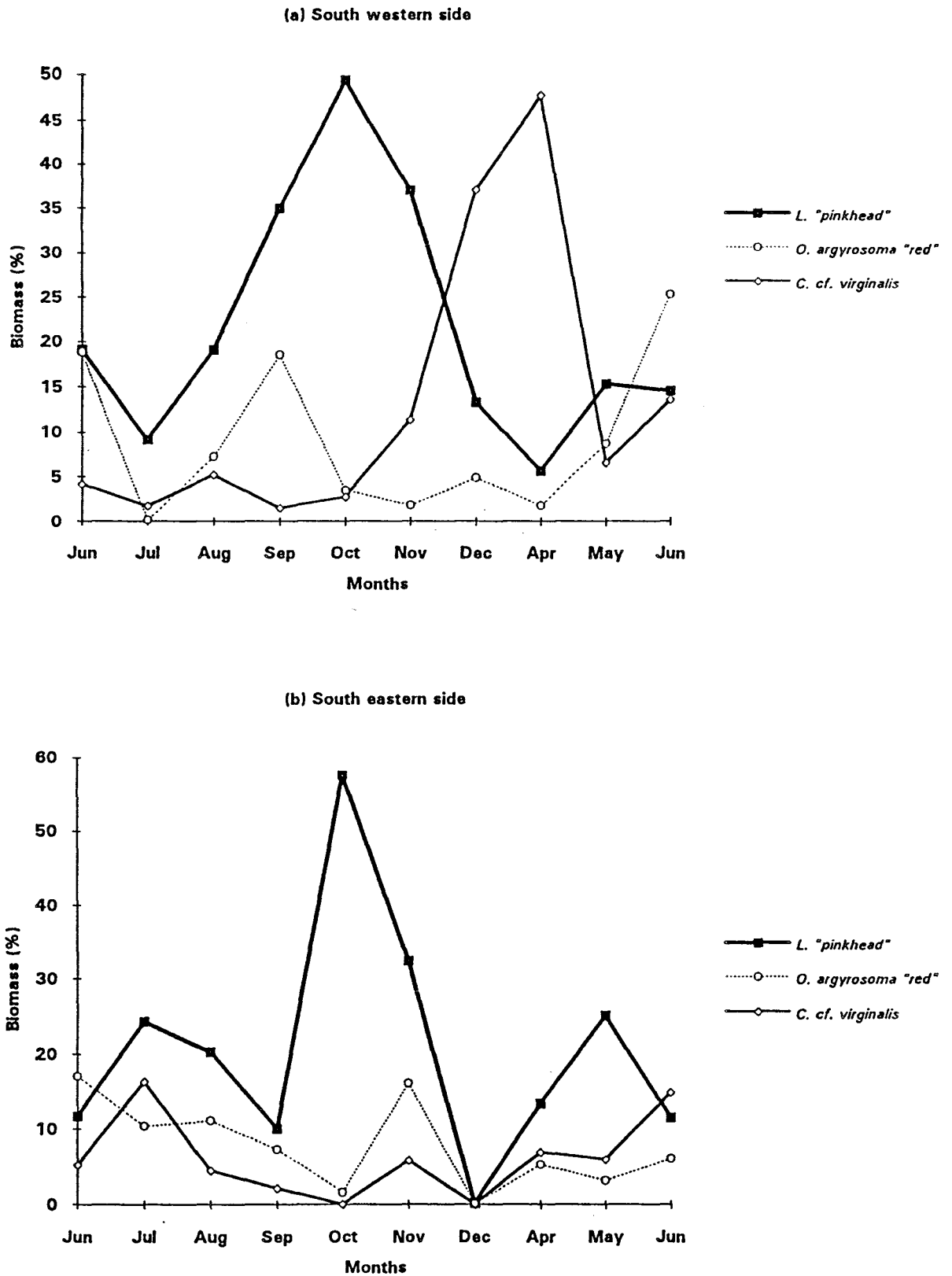


Figure 18. Monthly contribution by mass of the three species to the total catches in (a) the south western side and (b) south eastern side of Lake Malombe between June 1995 and June 1996).

In general terms, monthly fluctuations in the distribution of the three main species were not related to water temperature, water depth and phytoplankton availability (Table 7).

Table 7. Relationships between fish distribution by mass and abundance (CPUE); and water temperature, phytoplankton, water depth and turbidity in the south western (SW) and south eastern (SE) sides of Lake Malombe using Pearson correlation coefficient (r).

Parameters	SW side	SE Side
	(Heavily fished)	(Lightly fished)
CPUE/Temperature	0.035	0.162
Phytoplankton	0.179	0.009
Depth	0.021	0.022
Turbidity	4.250	6.251
Mass/Temperature	0.211	0.321
Phytoplankton	0.221	0.006
Depth	0.022	0.124
Turbidity	5.420	6.125

Size distribution

The analysis of mean lengths of the three species showed a marked absence of smaller and larger length classes in both sides of the lake. The length frequency data for all subsamples showed that the modal length of *C. cf. virginalis* (TL =75 mm - 80 mm) was greater than that of *L. "pinkhead"* and *O. argyrosoma "red"* (TL = 65 mm - 70 mm). Comparing the mean lengths of each species by sex between the two sides, it was found that males on both sides of the lake were of the same size. This was also true for females (Table 8).

However, in the south eastern side of the lake, *L. "pinkhead"* and *O. argyrosoma "red"* males were significantly bigger than females (*t*-test $P < 0.01$). By contrast *C. cf. virginalis* females were significantly bigger than the males (*t*-test $P < 0.01$).

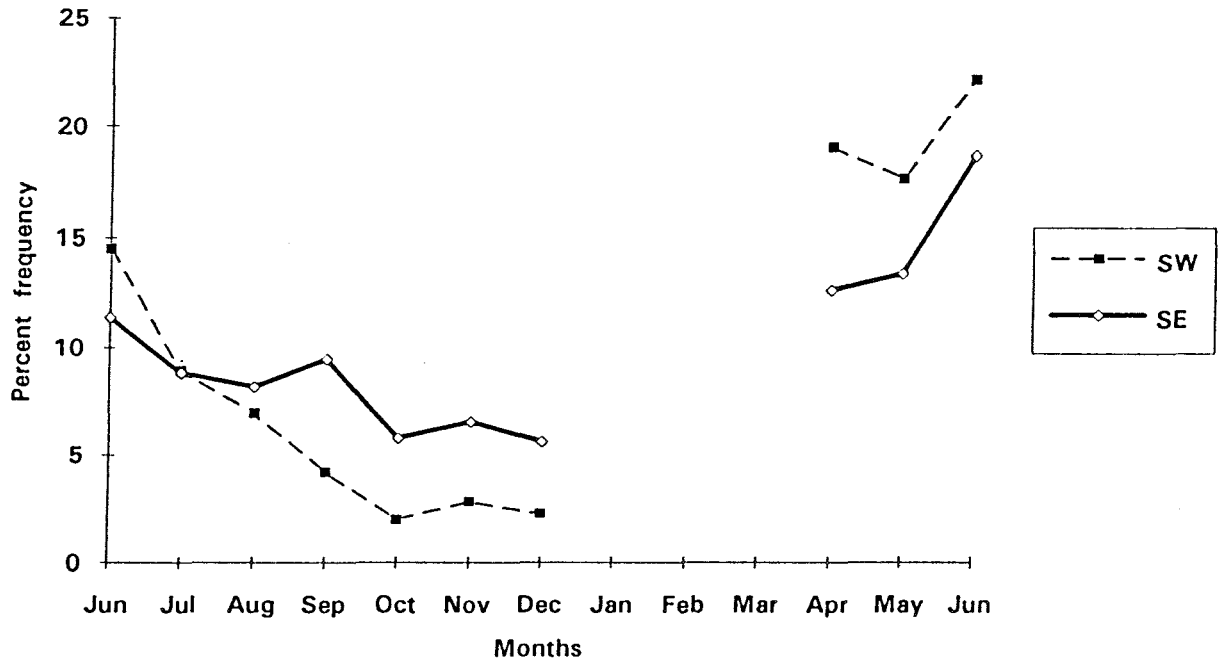
Table 8. Mean length and standard deviation (S.D.) of mature males from Southern Lake Malombe (June 1995 to June 1996) SW refers to south western side and SE refers to south eastern side (Different superscript indicate significant differences at $P < 0.01$).

Species	Sex	SW			SE		
		n	Mean	SD	n	Mean	SD
<i>L. "pinkhead"</i>	♂	207	7.9	0.91	236	7.8 ^a	0.86
	♀	97	6.8	0.64	105	6.8 ^d	0.80
<i>O. argyrosoma "red"</i>	♂	75	8.7	0.96	81	8.9 ^b	0.96
	♀	115	7.3	0.63	85	7.1 ^e	0.86
<i>C. cf. virginalis</i>	♂	157	8.0	0.85	187	7.9 ^c	1.08
	♀	29	8.5	0.97	99	8.4 ^f	1.21

The overall monthly biomass of juveniles ($TL \leq 15$ mm) was greater in the south eastern side than in the south western side of the lake. Based on the total catches of juveniles, the results also showed that the mean monthly biomass was greater in the south eastern side of the lake (0.46 kg per month) than in the south western side (0.26 kg per month). The highest catch by weight and number of juveniles was obtained during the May-June period after which the mean total catches on both sides declined (Figure 19). The Chi-square test analysis confirmed statistical differences in monthly

proportions of juveniles caught from both the south western and south eastern sides of the lake ($X^2 = 18.76$ $df = 9$ $P < 0.05$).

(a) Monthly Frequency (%)



(b) Mean monthly biomass

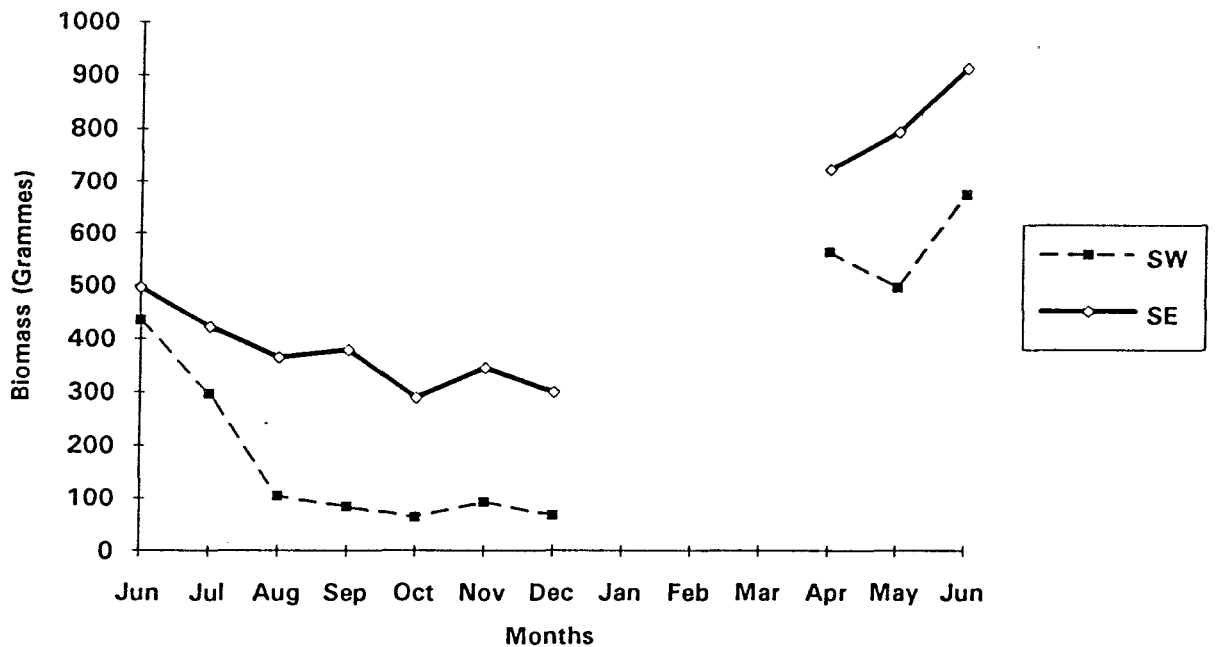


Figure 19. Percent frequency (a) and monthly biomass (b) of juveniles caught in 320 hauls by a standard nkacha net (with minimum mesh size of 19 mm) from June 1995 to June 1996 in the south western and south eastern sides of Lake Malombe.

5.3.3 Abundance

Catch per unit effort (CPUE) was used as an index of abundance and was expressed as kilograms per haul. The overall observed monthly mean CPUE for the south eastern side (13.7 kg/haul) was significantly higher than that of south western side of the lake (8.2 kg/haul) (t - test $P < 0.05$ $df = 9$).

In the south eastern side of the lake, there was a substantial increase in CPUE from 11.3 kg/haul in July to 23.2 kg/haul in October. In contrast, in the south western side CPUE increased from 9.7 kg/haul in September to 16.2 kg/haul (maximum CPUE) in October. After October, there was a rapid decrease of CPUE on both sides of the lake. In the south eastern side of the lake, the CPUE dropped from 14.0 kg/haul to 9.9 kg/haul between November and December. In the south western side of the lake, it dropped from 11.4 kg/haul to 7.3 kg/haul between November and December (Figure 20). Catch effort data were not collected during the closed season (January to March).

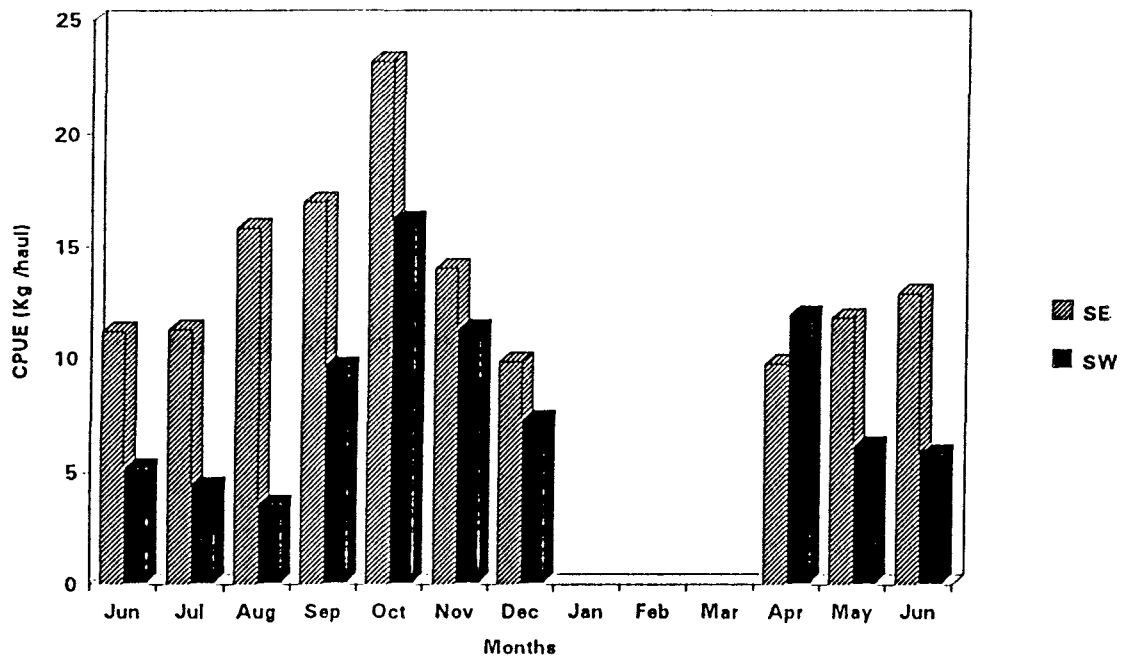


Figure 20. Mean monthly catch per unit effort of the three main species in the south western (SW) side and south eastern (SE) side of Lake Malombe for the period between June 1995 and June 1996.

5.4 DISCUSSION

Distribution

The results from this study clearly show that the three main species, *L. "pinkhead"*, *O. argyrosoma "red"* and *C. cf. virginalis* are evenly distributed over both sides of the lake. However, a greater overall abundance of the three species was found in the south eastern side of the lake. Based on historical and ecological information of the three species (Fryer & Iles, 1972; Mwanyama 1993), it appears that the distribution of *L. "pinkhead"* and *C. cf. virginalis*, in the south eastern side of the lake, may be attributed to the low fishing intensity rather than to the muddy substrate type and the resultant higher turbidity values. However, it is apparent that the distribution of *O. argyrosoma "red"* is related to the muddy substrate type, which occurs in all sampling stations in the south eastern side of the lake.

During the course of the study, rare non-cichlid species (e.g. *Labeo mesops*, *Opsaridium microlepis* and *Synodontis njassae*) were sampled from the south eastern side of the lake but none of these were sampled in the south western side. This uneven distribution of the non-cichlid species possibly indicates habitat preferences for a muddy substratum.

Based on the phytoplankton abundance, it appears that the paradox of food type restriction and water depth as the main determinants of spatial distribution and habitat preferences (Ribbink 1991) has been "refuted". Marginal Pearson correlation coefficients between CPUE, phytoplankton levels and water depth have elucidated that fishing pressure and turbidity are the principal factors which determine fish abundance (see Table 7).

Based on the monthly contribution by mass of the three species (Figure 18), the contribution by mass of *L. "pinkhead"* and *C. cf. virginialis* was greater in the south western side of the lake. The lower turbidity in the south western side (mean Secchi disk value of 1.76 m) may have influenced their distribution. Gradall & Swenson (1982) observed that increased turbidity influences habitat selection in most fish. It is possible that the two species, which are mainly zooplankton feeders predominantly preferred the south western side of the lake, which was less turbid (see Figure 15). Fryer & Iles (1972) pointed out that zooplankton feeders mostly inhabit clear waters of the lake where they easily detect their prey visually and as such, turbidity may reduce feeding efficiency and hence affect their distribution and abundance. However, Hecht & van der Lingen (1992) have argued that in some fish species, a reduction in feeding efficiency would not lead to a decrease in fish abundance in turbid waters. They found that some visual predators such as *Elops machnata* simply change their feeding strategy from feeding on individual prey items to filter feeding.

O. argyrosoma "red" showed a marked preference for turbid water and muddy substrata in the south eastern side of the lake. Based on ecological and behavioural studies, Eccles & Trewavas (1989) and Mwanyama (1995) stated that *O. argyrosoma "red"* is mostly found in the shallow more turbid waters and has a narrow habitat and/or food choice. It could be speculated that such characteristics could make the species more stenotopic in the more turbid waters in the south eastern side than in the less turbid waters in south western side of lake.

This study has shown that *L. "pinkhead"* was most abundant between October and November in both sides of the lake. This period of the year falls just two months after the highest peak of phytoplankton and it is difficult to relate the two parameters unless phytoplankton and zooplankton succession is considered. Unfortunately, zooplankton biomass data was not available.

The water temperatures were slightly higher during this period (Figure 14) and according to Coulter *et al.*, (1986), this could be the warming up phase of the lake, during which fish abundance would theoretically be greater. However, it appeared that there was no relationship between the slight increase in temperature and fish abundance (see Table 7).

In the south eastern side of the lake, *C. cf. virginalis* was most abundant between June and July while in the south western side it was most abundant in December. Observations from this study revealed that from June to July the entire south eastern side of Lake Malombe appears to be subjected to stronger south easterly wind perturbations than any other part of the lake because of its geographical position. Coulter (1991) stated that in most cases this could lead to greater abundance of phytoplankton and zooplankton, which may be utilised as a source of food by the fish, which would as a consequence determine their abundance. However, in December, the abundance of *C. cf. virginalis* in the south western side may have been associated with surface runoff water perturbations caused by water inflows from the catchment area, after the dry season. Such perturbations often cause water stirring (Coulter *et al.*, 1986), hence could encourage greater offshore abundance of zooplankton and phytoplankton which in turn could be utilised by the species in question. In contrast, this study has shown that there is no relationship between phytoplankton and the distribution of fish unless zooplankton peaks occur after phytoplankton.

There was a marked absence of smaller and larger length classes of all the three species in both sides of the lake. This indicates that both growth and recruitment overfishing may have affected the population structure. Numerically, small individuals of *C. cf. virginialis* and *O. argyrosoma "red"* were more abundant in the south western side than in the south eastern side of the lake. The overall presence of many small individuals of these species in the south western side is in agreement with Tweddle's *et al.*, (1995) findings. They found that the fishery was reliant on small immature fish. This is a clear indication that the bigger individuals, in the south western side of the lake, may have been more vulnerable to small meshed fishing gear than in the south eastern side of the lake, where fishing effort is smaller.

Mature males of all three species on both sides of the lake were not significantly different in size. This was also true for females. This gives an impression that both sexes have an equal chance of attaining the same size on both sides of the lake. For females, it could mean that they also have the same reproductive potential because the fecundity depends on the size of females. *L. "pinkhead"* and *O. argyrosoma "red"*, males were significantly bigger than the females. In such a scenario, large males are successful at obtaining a large number of mates (Turner 1993), and this implies that parental care could become prevalent as smaller females could invest more energy in eggs and young rather than in growth. It could therefore be envisaged that the choice of larger males may help in increasing offspring survival (Perrone, 1978, Downhower & Brown 1980, Keenleyside 1985, McKaye, 1986) and this could make *L. "pinkhead"* and *O. argyrosoma "red"* more resilient to fishing pressure than *C. cf. virginialis*.

Juveniles were more abundant in the south eastern side (mean monthly catch of 0.46 kg) than in the south western side of the lake (mean monthly catch of 0.26 kg). It appears that degradation of the substratum in the south western side of the lake (which may be a direct result of the use of destructive small meshed nets) could have substantially reduced recruitment success. Given the assumption that the substratum composition and structure influence the levels of recruitment (Sweatman 1985, Schroeder 1987), the protection of habitats in the south eastern side of the lake could have resulted in higher levels of recruitment.

The high catch of juveniles obtained during the period May-June gives an impression that the recruits from the previous breeding season (August-September) into the fishery are highly vulnerable during the period immediately after the closed season (January-March). Therefore the purpose of the current closed season which is to protect the recruits of less than one year old is useless because the recruits that are protected during the closed season are caught just a few weeks after the closed season. A more sensible closed season would be from October to December during which more breeding adults are particularly susceptible to exploitation.

Abundance

The CPUE in the south eastern side is significantly greater than in the south western side Lake Malombe. These results are in agreement with those of Tweddle *et al.*, (1995). Though Tweddle's *et al.*, (1995) study was based on few samples (3 in the western side and 1 in the eastern side of the lake) and the annual catch per nkacha net, they showed that the catches were higher in the eastern side (46.3 tonnes) than in western side of the lake (24.5 tonnes). Comparing their results with the recent findings, it can be argued that the south eastern side of Lake Malombe is not yet overexploited and should be

protected to serve as a source of recruitment for the rest of the southern part of the lake.

The remarkable increase in CPUE (from 11.3 kg/haul to 23.2 kg/haul) for the September-October period, in the south eastern side of the lake, followed the intense mixing caused by the south easterly winds that occurred in July-August. The south easterly winds bring about heavy upwelling in Lake Malombe every year between May and August (FAO 1992, Mwanyama 1993). Mwanyama (1993) observed that during such windy periods approximately 68% of the plankton is dominated by zooplankton. He also commented that such windy periods are followed by relative calm periods in (November and March) during which algal biomass increases. The increase in zooplankton and algal biomass provides adequate food resources for the fish (Payne 1986) and this could have affected fish abundance.

The increase in phytoplankton, in both sides of the lake, between July and August was followed by an increase in CPUE. There was a rapid increase of CPUE both in the south western side (9.7 kg/haul to 16.2 kg/haul) and south eastern side of the lake (17.0 kg/haul to 23.2 kg/haul) between September and October. However, there was no overall correlation between CPUE and phytoplankton biomass ($r = 0.179$ south western side and $r = 0.009$ south eastern side). This may indicate that the marked difference in CPUE is not absolutely dependent on the availability of phytoplankton.

Despite the above results, the major factor which appears to determine the distribution and abundance of cichlid species in the south western and south eastern side of Lake Malombe is fishing intensity. This conclusion stresses the need for better law enforcement of the "sanctuary area" and for the need to increase the size of the sanctuary.

CHAPTER 6

AGE AND GROWTH

6.1 INTRODUCTION

Sustainable management of fish resources, requires a substantial body of scientific information. One of the most important requirements is knowledge of age and growth (Summerfelt 1987). Ageing fish in modern fisheries research is considered very important because the information on age can be directly incorporated in stock assessment and yield models (Ricker 1975, Pitcher & Hart 1982, Summerfelt 1987).

Most of the published studies of growth in Malawian cichlids are based on length frequency analysis. This is mainly because of the lack of visible annual rings on hard parts such as otoliths and opercular bones (Jackson *et al.*, 1963, Thompson *et al.*, 1995). Despite the protracted spawning season of tropical cichlid species, which makes interpretation of modes in length-frequency data difficult, length frequency analysis has been successfully used in estimating growth rates of these fish in Malawi (Iles 1971, Tweddle & Turner 1977). It was for this reason that length-based methods were used to estimate age in the present study.

The artisanal fishers of Lake Malombe have widely held the claim that the south eastern side (lightly fished) is inhabited by larger fish than the south western side (heavily fished area) of the lake. As such, they have also claimed that fishes in the south eastern side grow faster than those of the south western side of the lake. To the author's knowledge, no previous work has been done on the growth of the three species, in the two sides of the

lake, to assess these claims. It was the overall aim of this study to derive growth parameter estimates of the three species so that the effects of the lightly fished area on fish growth could be determined. Such findings could provide some knowledge that could be essential in the conservation and management of the fishery.

6.2 MATERIALS AND METHODS

All the fish used in this study, *L. "pinkhead"* (2846), *O. argyrosoma "red"* (1819) and *C. cf. virginialis* (1551) were collected using a standard nkacha offshore net. All fishing operations took place as described in Chapter 3. Monthly sampling was undertaken between June 1995 and June 1996. All specimens of 30 mm or more were sexed while those smaller than 30 mm were not sexed because of the difficulty in distinguishing the gonads. For each species, length measurements for each month were pooled into equally-sized length classes. The monthly length frequency distributions (for each sex and combined sexes) and growth parameters were then analysed by the Length Frequency Distribution Analysis (LFDA) software package (Holden & Bravington 1992). Total body weight was measured to the nearest gram and total length (TL) was measured to the nearest millimetre. The length-weight relationship was then expressed in the form of: $\ln w = \ln a + b \ln L$, where w is total body weight, L is total length and a , b regression coefficients.

The Electronic Length Frequency Analysis (ELEFAN V, Brey and Pauly 1986) and Projection Matrix (Holden & Bravington 1992) methods, included in the LFDA, were used to estimate the growth rate (K , Brody's coefficient), asymptotic length (L_∞), and time at which length is equal to zero (t_0) from the length-frequency data. The underlying primary assumptions for these computer packages are that growth is described by a non-seasonal von

Bertalanffy growth curve: $L_t = L_\infty(1 - e^{-K(t-t_0)})$ and that all fish grow at the same rate.

The Petersen method, modified by Bhattacharya (1967), Ricker (1975), Bagenal & Tesch (1978) was also used to assess growth rates. The growth parameters obtained from the three methods were compared in order to minimise biases that occur when only one ageing method is used. MacDonald (1987) and Hoedt (1992) recommended that at least two techniques should be used to improve the precision of results when estimating growth parameters.

The ELEFAN method works by first restructuring the length frequency data in an attempt to identify peaks corresponding to cohorts or age classes. It calculates a score function as a function of the proportion of available peaks that can be explained by a von Bertalanffy growth curve with specified parameters.

In the PROJMAT method, successive pairs of length frequency distributions are compared. The basic idea is successively to project one observed length frequency distribution forward in time, based on an assumed set of von Bertalanffy growth curve parameters, to obtain a prediction of what that length frequency distribution should have looked like at the time the second observed length frequency was collected. The goodness-of-fit of the observed and predicted distributions is then compared and the best estimates of growth parameters are those that lead to the best fit between the two distributions. This method provides no information whatsoever on the parameter of t_0 because it starts with an observed length frequency distribution and projects it forward over a given time interval. Nevertheless, estimates of t_0 for each pair of K and L_∞ values are calculated by the

incorporated Shepherd's Length Frequency Analysis method. The PROJMAT method appears to be very robust to variation in length-at-age because only the movement of data along the length axis, from histogram to histogram, is used rather than the presence of sharply defined peaks in the histograms (Basson *et al.*, 1988).

Both the ELEFAN and PROJMAT methods work by calculating a score function for a data set for specific combination of K , L_{∞} and t_0 . The higher the value of the score function, the better the parameters fit the data set (Holden & Bravington 1992). The values of K and L_{∞} were provided until the best r_n values was obtained. This is an indication of how well the resulting curve coincides with peaks in the length-frequency distributions (Pauly 1987, Morales-Nin 1989). The automatic search routine was then used to optimise parameters until a growth curve best fitting the data was achieved.

The Petersen method involves visual identification of modes in frequency histograms, assigning ages and hence length-at-age to the modes and fitting a growth curve to the resultant length at age data. This method is of course highly subjective and can not make use of any information in the sample other than available from clear modes. However, most investigations especially in tropical fisheries, still continue using this method to evaluate data before trying more sophisticated analyses and often useful preliminary results can be obtained (Roseberg & Beddington 1988).

Estimation of age composition from length-frequencies involved separating each complex length-frequency distribution into cohorts and assigning an arbitrary age to each of those cohorts. Given that such age composition estimates do not always conform to the special von Bertalanffy model (Sparre & Venema 1992), it was assumed that the mode of each age group fits on von Bertalanffy growth curve (Pauly & David 1981).

To smooth out small irregularities the data were rearranged in 50 mm length groups and the original length-frequencies were then restructured to obtain distinct modes. The restructuring process involves "moving average frequency" over 5 length groups (Holden & Bravington 1992). Using the restructuring process the modes became well-structured and easy to identify. However, the results were interpreted with caution since Pauly & David (1981) pointed out that this procedure is subjective and unreliable, unless the age groups are well separated.

6.3 RESULTS

6.3.1 Growth parameters from LFDA analysis

The von Bertalanffy growth parameters calculated from the length-frequency data, using ELEFAN and PROJMAT methods, for each side of the lake are shown in Table 9. The growth parameter estimates of the PROJMAT method appeared to be closer to those obtained using the Petersen method.

Table 9. von Bertalanffy growth parameters for the three species (males and females combined) in the south western (SW) side and south eastern (SE) side of Lake Malombe, as calculated from two LFDA computer packages; ELEFAN (a) and PROJMAT (b).

(a) ELEFAN method

Species	SW (Heavily fished)			SE (Lightly fished)		
	<i>K</i>	<i>L</i> _∞ (cm)	<i>r</i> _{<i>n</i>}	<i>K</i>	<i>L</i> _∞ (cm)	<i>r</i> _{<i>n</i>}
<i>L. "pinkhead"</i>	0.38	11.84	0.121	0.22	10.97	0.163
<i>O. argyrosoma "red"</i>	0.22	10.17	0.252	0.18	10.23	0.271
<i>C. cf. virginalis</i>	0.38	14.60	0.198	0.32	14.34	0.177

(b) PROJMAT method

Species	SW (Heavily fished)			SE (Lightly fished)		
	<i>K</i>	<i>L</i> _∞ (cm)	<i>r</i> _{<i>n</i>}	<i>K</i>	<i>L</i> _∞ (cm)	<i>r</i> _{<i>n</i>}
<i>L. "pinkhead"</i>	0.60	11.84	0.321	0.58	10.97	0.263
<i>O. argyrosoma "red"</i>	0.52	10.17	0.352	0.56	10.23	0.431
<i>C. cf. virginalis</i>	0.88	14.60	0.311	0.84	14.34	0.297

6.3.2 Growth parameters by sex

The von Bertalanffy growth curves for male and female fish of each species revealed that in all three species, females appear to become larger than males. However, males and females attained an asymptotic length at the same age (Figure 21). This implies that females grow faster than males.

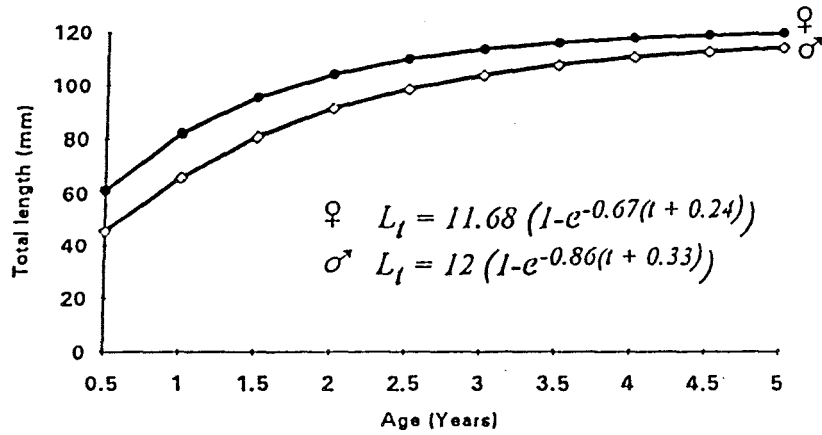
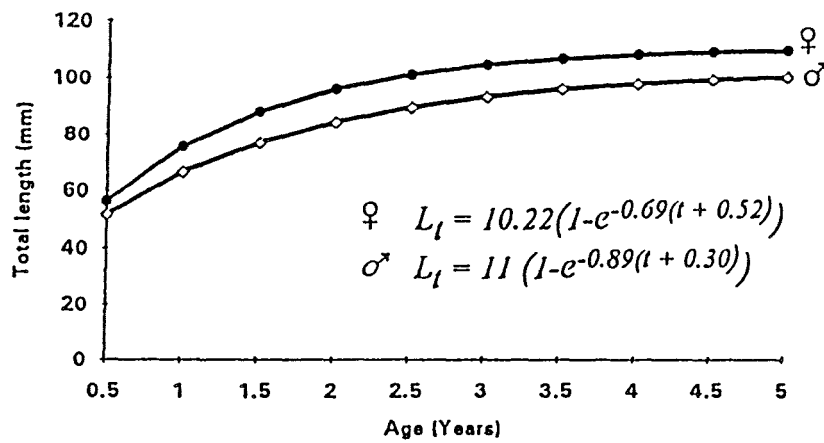
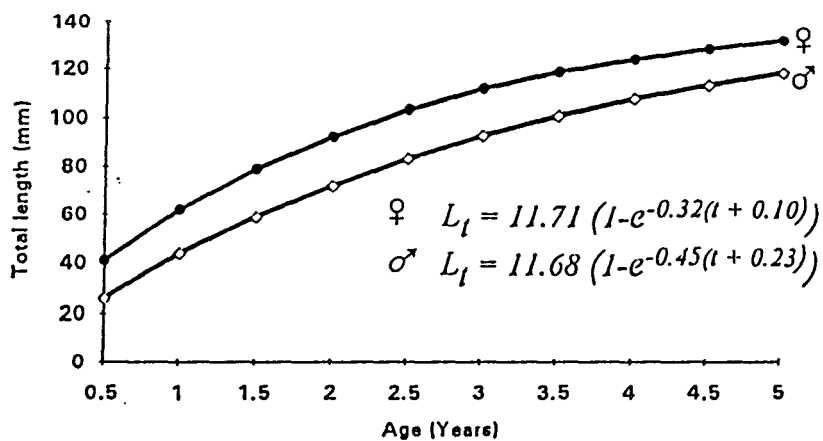
(a) *L. "pinkhead"*(b) *O. argyrosoma "red"*(c) *C. cf. virginalis*

Figure 21. Estimated von Bertalanffy growth curves of *L. "pinkhead"* (a) *O. argyrosoma "red"* (b) and *C. cf. virginalis* (c) irrespective lake side.

6.3.3 Growth rates from Petersen Method

Monthly modal progressions in length-frequency time series for *L. "pinkhead"*, *O. argyrosoma "red"* and *C. cf. virginalis* were not fairly straightforward. Nevertheless, modes representing juvenile fish (Mode *i*) and adult fish (Mode *j*) were identified in all species (sexes combined). On the other hand, modal progressions by sex were difficult to interpret for all species. All specimens of less than 30 mm (TL) were categorised as juveniles because of the difficulty in distinguishing gonads, and the rest were categorised as adults.

All three species showed a gradual shift of modes from June 1995 to November 1995 after which another gradual shift occurred from December 1995 to June 1996. The month of June 1995 was arbitrarily chosen as a starting point of modal progression. Most juveniles appeared to be recruited during November and June. However, there was also a remarkable mode of recruits for *C. cf. virginalis* in July (Figure 22, 23 and 24).

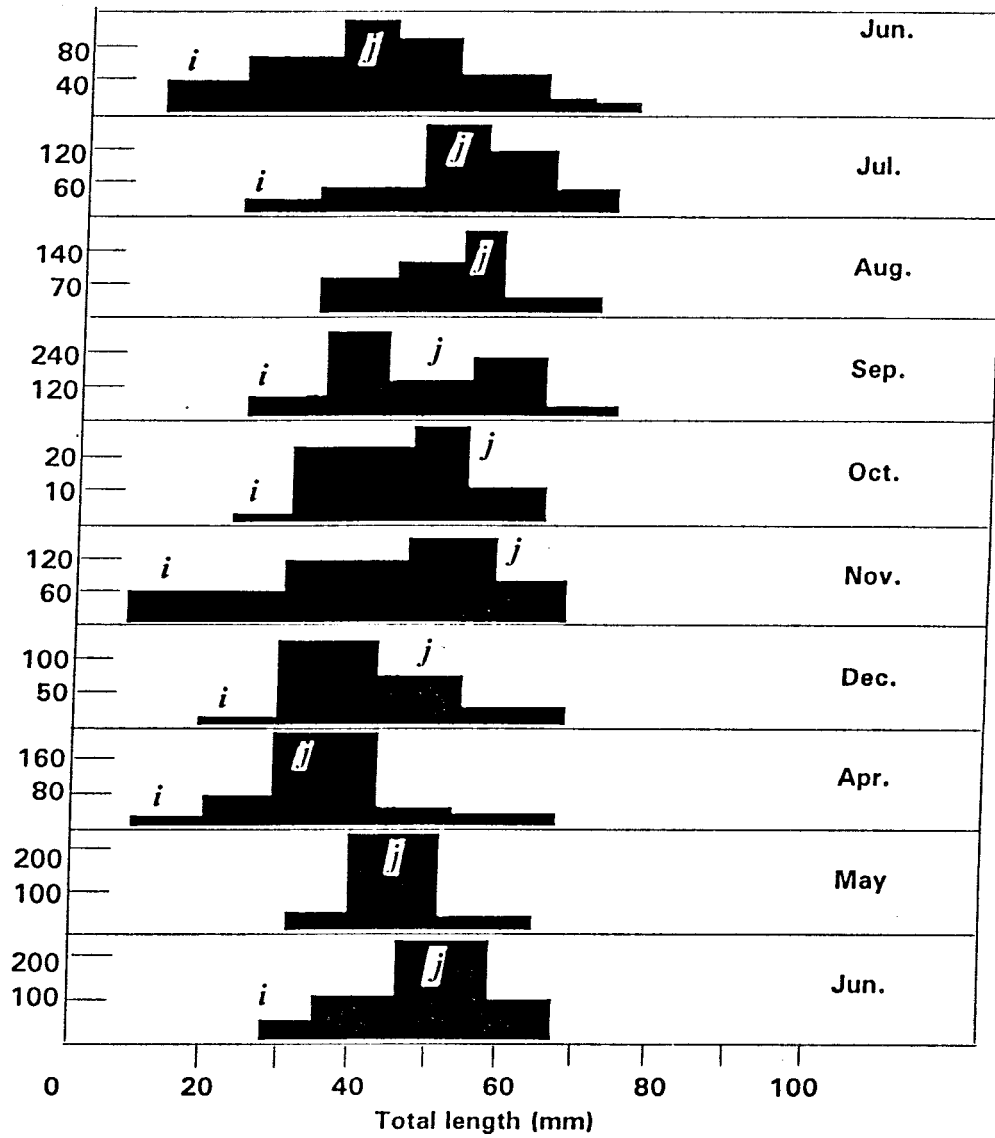


Figure 22. Monthly length-frequency distribution of *L. "pinkhead"*.

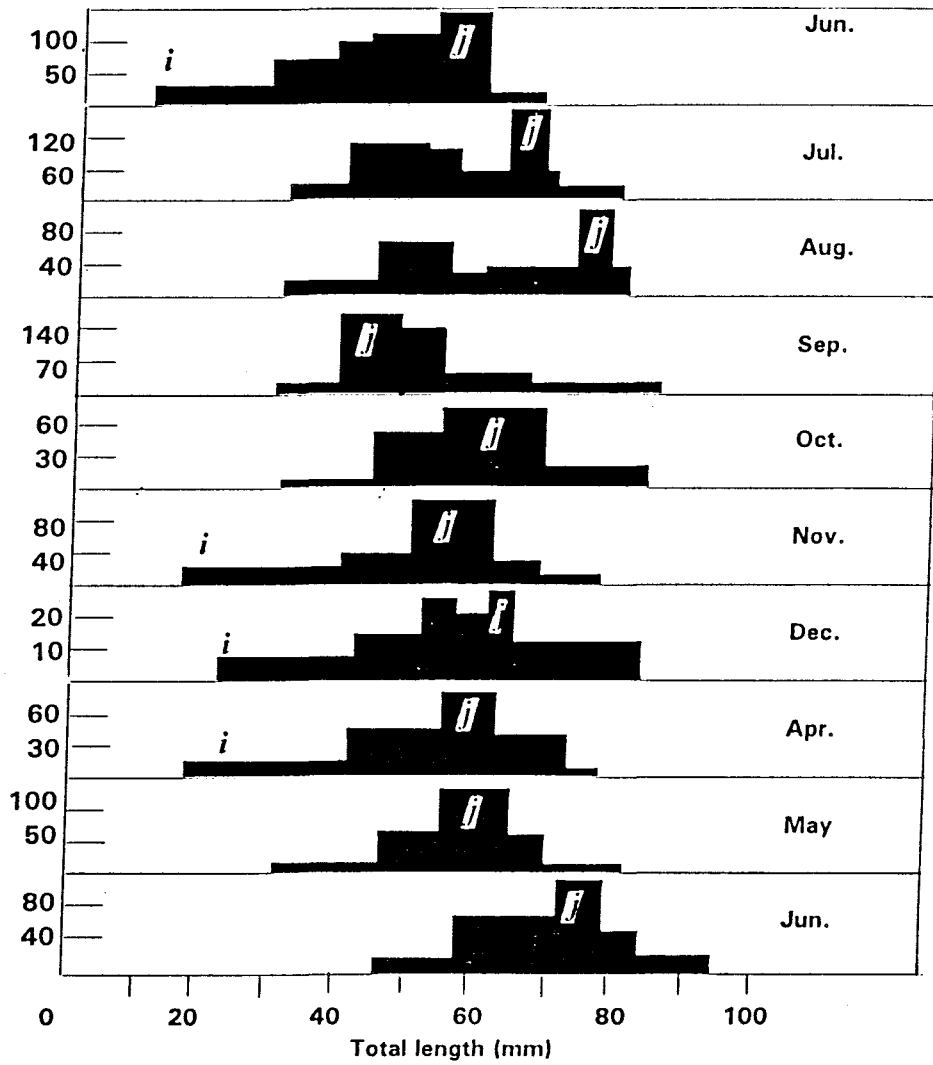


Figure 23. Monthly length-frequency distribution of *O. argyrosoma* "red".

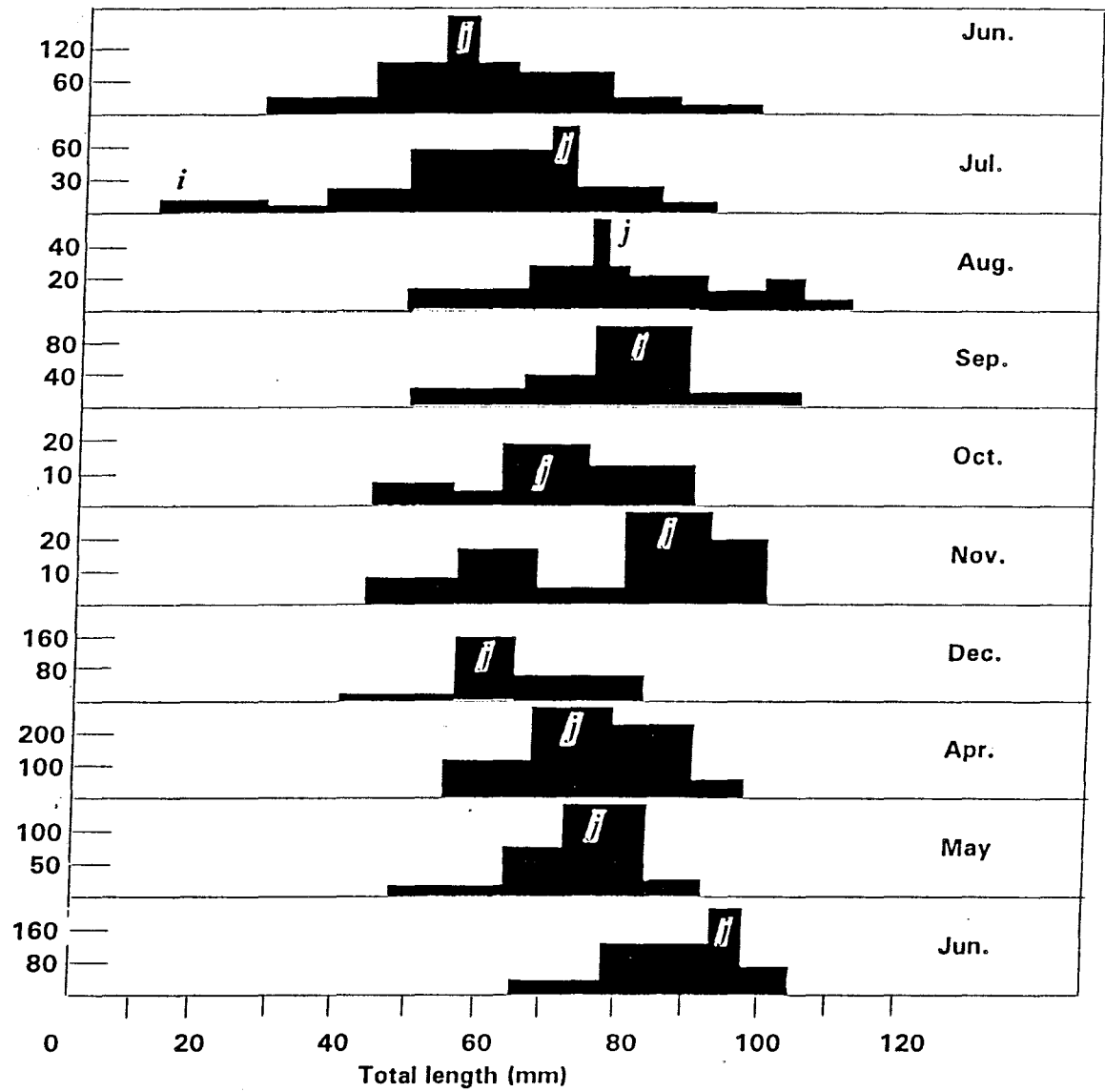


Figure 24. Monthly length-frequency distribution of *C. cf. virginalis*.

Examination of the length-frequency histograms (both sexes combined) for each of the species suggested that their population is comprised mainly of five age groups of which age group 3+ was dominant (Figure 25).

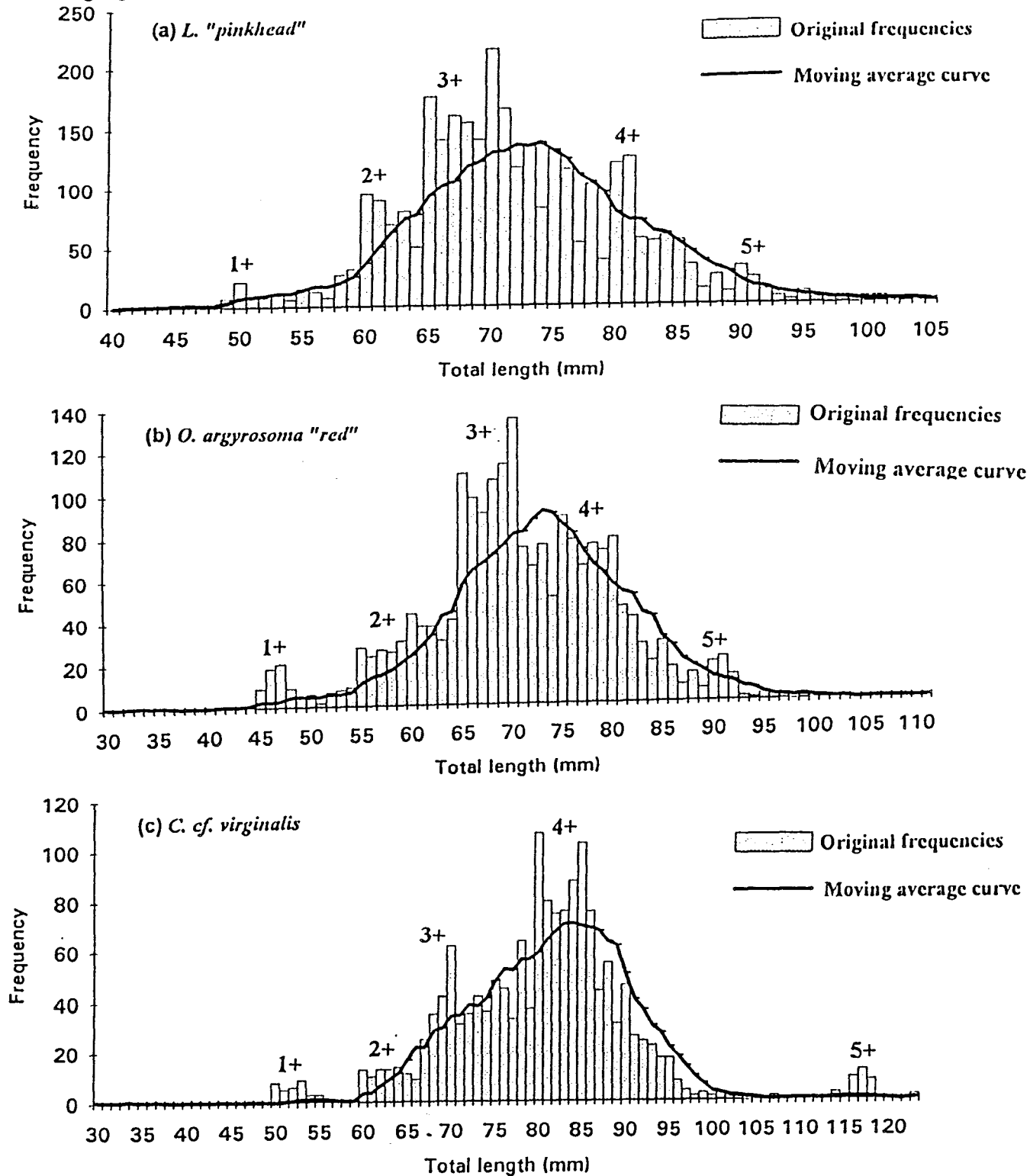


Figure 25. Length-distributions for *L. "pinkhead"*(a) *O. argyrosoma "red"* (b) and *C. cf. virginialis* (c) from offshore catches (June 1995-June 1996). The curves indicate the "moving average" over five length groups and is used to emphasise peaks. The symbol "+" stands for "plus older groups".

6.3.4 Length-weight relationships

The length-weight relationships of the three main species from the south western and south eastern sides of the lake are presented in Table 10. The regression coefficients (*b*) from the two sides of the lake were not significantly different (ANOVA, $P > 0.05$).

Table 10. Length-weight relationships^a of three fish species of south western side (a) and south eastern side (b) of Lake Malombe. Sampled between June 1995 and June 1996).

(a) South western side

Species	<i>n</i>	<i>ln a</i>	<i>SE.</i>	<i>b</i>	<i>SE</i>	<i>s</i>
<i>L. "pinkhead"</i>	1255	-1.67	0.002	2.70	0.004	0.023
<i>O. argyrosoma "red"</i>	740	-1.38	0.061	2.33	0.071	0.115
<i>C. cf. virginalis</i>	660	-1.35	0.054	2.29	0.60	0.091

(b) South eastern side

Species	<i>n</i>	<i>ln a</i>	<i>SE.</i>	<i>b</i>	<i>SE</i>	<i>s</i>
<i>L. "pinkhead"</i>	1250	-1.66	0.003	2.90	0.004	0.023
<i>O. argyrosoma "red"</i>	863	-1.88	0.036	2.93	0.042	0.074
<i>C. cf. virginalis</i>	647	-1.88	0.048	2.89	0.054	0.059

SE stand for standard errors of the regression coefficients (*a*, *b*) and **n** represents number of fish measured. **S** represents the 95% confidence interval of the regression line.

^a Parameters are from a least square regression fit to logarithmic transformed weight (g), and length (mm) measurements.

6.4 DISCUSSION

The estimated growth coefficient for *L. "pinkhead"* (0.68 year^{-1}) was almost identical to the value of 0.65 year^{-1} reported by Banda (1995). This growth rate is also close to that of *L. parvidens* (0.60 year^{-1}), a closely related species (Tweddle & Turner 1977).

The growth coefficient value for *O. argyrosoma "red"* of 0.49 was significantly lower than Banda's (1995) estimate of 0.70. This divergence might be ascribed to different sampling techniques or by the fact that not many juveniles or small fish were retained in the standard nkacha net, which was used in this study. This could directly underestimate K on the realistic assumption that juveniles tend to grow faster than adults. Furthermore, the difference in growth coefficients could have originated from the overestimation of L_{∞} by both the ELEFAN and PROJMAT methods. Pauly (1979) claimed that L_{∞} has often been overestimated or underestimated, especially when fish representing all size classes are absent in the catches. Also, it is possible that the protracted breeding season of the three species may have introduced some error in the shape of the length distributions.

C. cf. virginalis had the largest theoretical asymptotic length (14.6 cm) with a growth coefficient of 0.74. This is in close agreement with the value for K reported by Iles (1972) and Tweddle & Turner (1977) for this species in Lake Malawi (0.66 and 0.49-0.67) respectively and a value of 0.60 in Lake Malombe (Banda 1995).

The overall growth rates of the three species were different and this can generally be attributed to differences in age composition, breeding and recruitment strategies (Nikolskii 1969, Sissenwine 1988).

Based on the growth curves, the estimated growth rates for females were significantly higher than those for males in all three species. The females appeared to grow faster than males in the first year of their life. This could imply that males would reach maturity faster than females because in the early stages of life females seem to invest energy inputs in somatic growth rather than gonadal development (Pitcher & Hart 1982). This growth strategy could enable females to have more eggs because all the available energy could be used for somatic growth prior to sexual maturity (Bagenal 1978).

Based on the Petersen method, the gradual shift of modes from June 1995 to November 1995 and from December 1995 to June 1996 was consistent for all three species suggesting that they have a similar growth pattern. The onset of another well-pronounced series of modal progressions in November may imply that recruitment into the fishery takes place mainly during this time of year. This onset occurred after the phytoplankton biomass peaks (refer to Figure 17), which probably suggests that juvenile growth of the three species does not synchronise with the overall biomass of phytoplankton. However, the overall increase in diatom biomass in November coincided with the highest frequency of juveniles, suggesting that the occurrence of the recruits might have been closely related to diatom biomass (for food) rather than the greens and blue greens.

The regression coefficients of all three species indicate that the weight of fish closely followed an isometric growth pattern. The slightly greater regression coefficients of all species in the south eastern side of the lake suggest that the weight increase in these species, in the south eastern side was higher than in the south western side of the lake. Rapid increase in weight for these species in the south eastern side could be an important adaptation in females, which could lead to a considerable increase in the fecundity of the population. Spanovskaya *et al.*, (1963) and Pitcher & Hart (1982) have reported that fecundity is more closely correlated with the body weight than with length or age.

Whilst it is clear that the regression coefficients of all three species for the south eastern and south western sides were different, the interpretations of results from this study should be handled with caution as they may be biased by immigration, emigration, recruitment and growth fluctuations (Jennings & Lock 1996). In addition, there are size-specific spatial and temporal variations in the distribution of fishes (Jennings & Lock 1996), and fishing techniques used in this study might have not produced samples representative of the population.

The lengths -at-age of one year obtained using the two LFDA methods were compared with those obtained using the Petersen method (Table 11). It appears that lengths-at-age of one year, from PROJMAT growth curves were close to those values obtained from Petersen method.

Table 11. Comparison of length (mm) -at-age of one year, using three different methods. For each species, pooled data for both sexes and from both sides of the lake were used.

Species	PETERSEN	ELEFAN	PROJMAT
<i>Lethrinops "pinkhead"</i>	72.0	30.0	68.0
<i>Otopharynx argyrosoma "red"</i>	69.0	20.0	49.0
<i>Copadichromis cf. virginalis</i>	88.0	35.0	92.0

Finally, it should be noted that the relatively good agreement between growth parameters using the PROJMAT and Petersen methods should be viewed with some caution in the light of possible biases that could have occurred in the interpretation of growth rates from length frequency modal progression data. A more direct validation technique, such as the use of daily growth increments in the otoliths should be used. The discovery of daily growth increments has provided an alternative ageing technique to the commonly used length-frequency method (Pannella 1971). Though Campana & Neilson (1985) have questioned the reliability of daily increments for age determination in fish older than one year, Brothers (1979) noted that, in some tropical species, recognisable daily growth increments can persist for two or three years of life. This gives an impression that if daily growth increments can be observed on the otoliths of the three species, then more precise growth parameters could be estimated.

In conclusion, despite possible sampling biases discussed in this chapter, it appears that all three species have a similar growth pattern regardless of whether they were encountered in the south western side or south eastern side of the lake. It is also appears that *C. cf. virginalis* has the fastest growth while *O. argyrosoma "red"* has the slowest growth.

CHAPTER 7

REPRODUCTIVE BIOLOGY

7.1 INTRODUCTION

The success of any fish species is ultimately determined by the ability of its members to reproduce successfully in a fluctuating environment and thereby maintain viable populations (Moyle & Cech 1988). To understand the reproductive success of the three species, sound knowledge of breeding seasonality, sexual maturation, fecundity and sex ratio is fundamental. Once such knowledge is acquired, protection of spawners and breeding grounds, and formulation of decisions to do with the placing and size of protected areas would be possible (Sadovy 1996).

Roberts and Polunin (1991) argued that in heavily fished areas, populations of large fishes may be severely depleted as a consequence of which the total reproductive output of populations within protected areas may be substantially greater than that of populations in exploited areas, and that this would contribute to recruitment into the fishery. They based their argument on the fact that fecundity is a power function of length, hence increases in average size of females within reserves will result in a larger increase in egg production.

The three cichlid species studied are categorised as polygamous mouth brooders and asynchronous spawners (Fryer & Iles 1972, Balon 1977, Ribbink *et al.*, 1983). They produce relatively few eggs and exercise prolonged parental care. Under such condition the population size of the three species could depend upon high natural survival rates in both adults

and young (Lowe-McConnell 1987). This implies that the populations would be highly sensitive to intensive fishing.

It could be speculated that high fishing intensity in the south western side of the lake might have reduced the average size of the females, resulting in poor recruitment into the fishery. Based on the Fisheries Department of Malawi Annual Reports, Bell & Donda (1993) and Coulter (1993) speculated that fish in the south eastern side of the lake (lightly fished) could provide recruits to the adjacent fished area due to their high reproductive potential. Artisanal fishers have also claimed that the south eastern side harbours more breeding females and juveniles than the south western side of the lake (Bell & Donda 1993 and personal observations). Under the influences of these speculations and claims, the Fisheries Department of Malawi has opted for a sanctuary area as an additional management tool for Lake Malombe fishery. However, the information on the reproductive success of the three species, which is necessary to determine the absolute boundaries, size and position of the protected area has not been collected.

The objective of this study was to assess the reproductive output of the three species with the aim of testing the hypothesis that fish species from the south eastern side of the lake are more fecund and mature at a larger size than those from the south western side where fishing intensity is greater.

7.2 MATERIALS AND METHODS

A sample of 25 to 45 fish per month was collected using nkacha offshore seine net from June 1995 to June 1996 for reproductive biology. For each specimen, total length to the nearest millimetre and total body weight to the nearest gram were measured. Fish mass was taken as the mass of the fish minus gut contents.

The breeding season as well as sexual maturity were determined by a monthly visual appraisal of the gonad activity stages. The visual assessment of gonadal stages was done using the descriptions of Marsh *et al.*, (1986). They recognised four main gonadal development stages for females and three stages for males (Table 12). To eliminate possible error, only those data which were collected during the peak period of gonad activity were used.

To establish the breeding seasonality, the percentage frequency of occurrence of females with active ripe (AR), ripe (R) and spent (S) stages for each species, was plotted against sampling time (months). The breeding season was then identified by comparing peaks of AR, R and S stages. Only mature females with AR, R and S gonadal stages were used in this investigation to avoid the possible masking effect which immature fish could have had on the results.

Table 12. Gonadal development stages used to categorise female and male fish.

Stage	Descriptions of female gonadal stages
Immature (I)	Eggs were elongate, pale yellow / pale orange in colour
Active Ripe (AR)	Eggs were ovoid in shape and they were closely packed and pale orange in colour
Ripe (R)	Eggs were irregular in shape and loosely connected to one another. They were bright orange in colour.
Spent (S)	Ovaries were thin and opaque wall. Red eggs dominated with few bright orange eggs.
Descriptions of male gonadal stages	
Immature (I)	Testes were translucent and almost colourless.
Ripe (R)	Testes were opaque and creamy
Spent (S)	Testes were thin, flaccid and irregular.

To establish the length at 50% sexual maturity, with minimal possible error, the data collected during the period of maximum gonad activity were used. Fish with active ripe, ripe and spent gonads were considered mature. For each species and sex, the percentage frequency of such mature fish was plotted against total length. A logistic curve was fitted to the percentage of sexually mature individuals by length (L), using King's (1995) equation:

$$P = 1/(1 + e^{-r(L - L_m)})$$

where r is the slope of the curve and L_m is the mean length which corresponds to size at 50% maturity. The logistic curve was used in order to minimise unreasonably high estimation of L_m .

To determine the absolute fecundity of each species the ripe ovaries for each fish were separately preserved in Gilson's solution. After keeping the ovaries in Gilson's solution for one week, the number of eggs were counted (Bagenal 1978). The absolute counting method was used because the number of eggs were few and it was not laborious.

The relationship between absolute fecundity and length was determined by regression analysis. The best regression fit was given by the linear equation:

$$F = bL + a$$

where F is the absolute number of eggs counted per individual, L is the total length of fish and a , b are linear equation constants. Relative fecundity (number of eggs per gram fish weight) was used to compare reproductive strategies of the three species.

Sex ratio for each species was evaluated by recording the number of fish sampled by sex. The numbers of males and females were compared using a Chi-square test to determine whether sex ratio differed significantly from unity. This test was done to evaluate if size-selective fishing might have altered the sex ratios of the three species.

7.3 RESULTS

7.3.1 Reproductive seasonality

For all three species, a high frequency of potential breeding females (AR and R) was evident between July and October, with prominent peaks in July and October for active ripe female and in August for ripe females. A high frequency of potential breeding females was also noted for *O. argyrosoma* "red" in December (Figure 26). From these data it is evident that all three species breed mainly from July to August.

7.3.2 Sexual maturity

During the period from June 1995 to June 1996, gonads of 991 males and 979 females were examined. More than 50 per cent of the males, irrespective of species and side of the lake, were mature at approximately the same size (79 mm), thus corresponding to an age of between two and three years. However, they appear to attain 100% sexual maturity at different lengths (TL). In contrast, females of the three species attained 50% sexual maturity at different lengths (*L. "pinkhead"* 66 mm; *O. argyrosoma "red"* 72 mm; *C. cf. virginalis* 83 mm)(Figure 27).

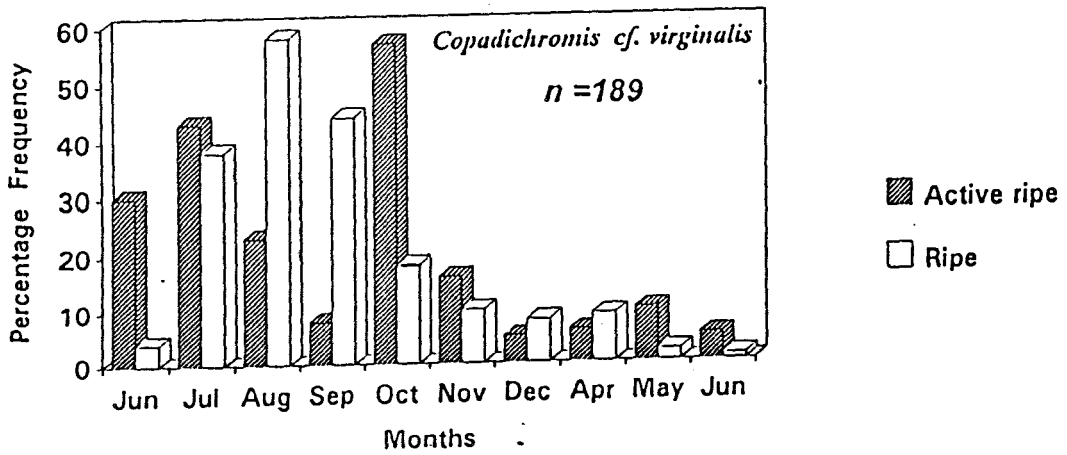
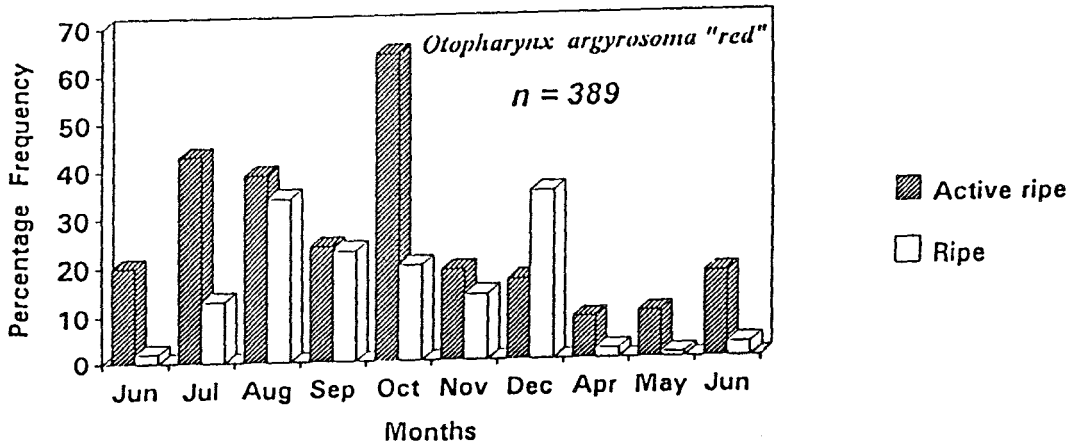
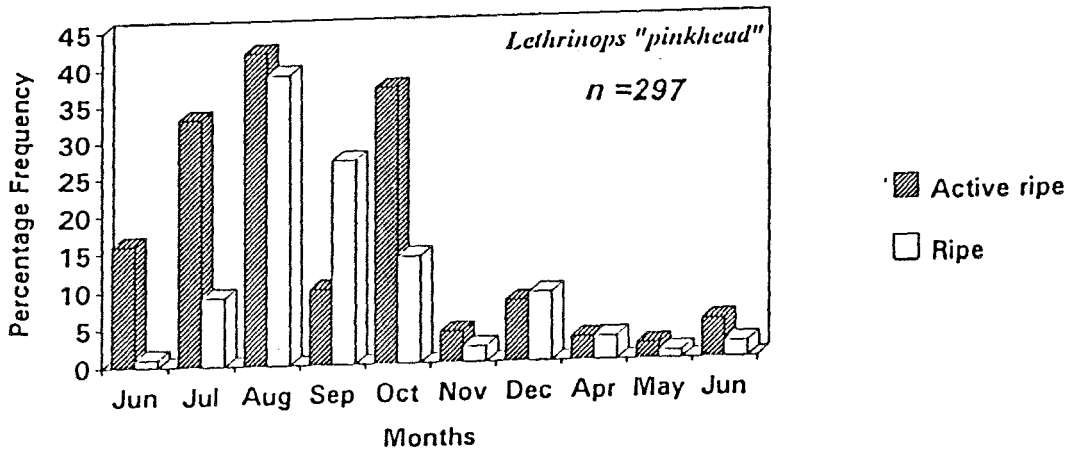
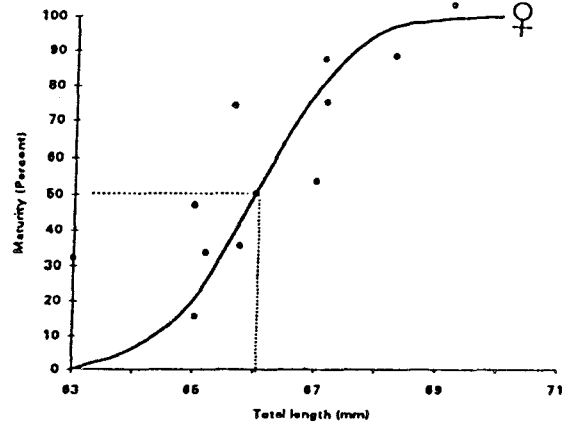
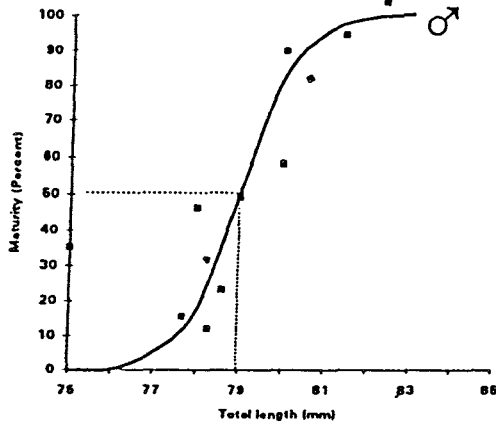
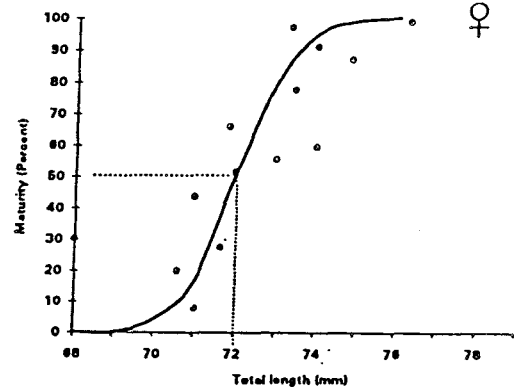
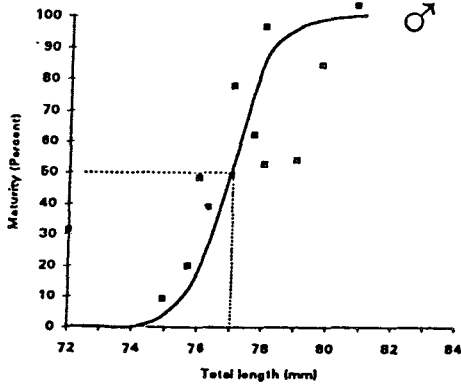


Figure 26. Frequency distribution of female fish with active ripe (AR) and ripe (R) gonads sampled between June 1995 and June 1996.

(a) *L. "pinkhead"*



(b) *O. argyrosoma "red"*



(c) *C. cf. virginalis*

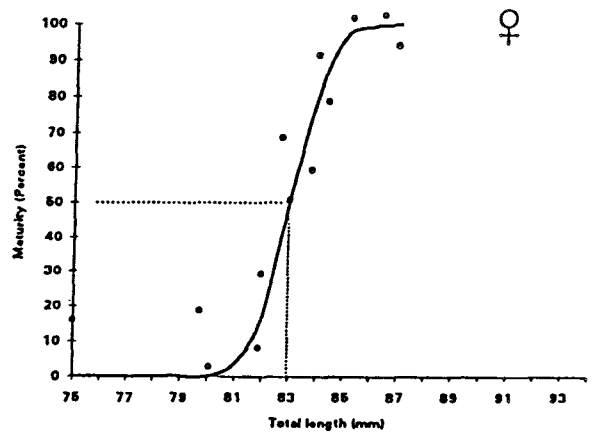
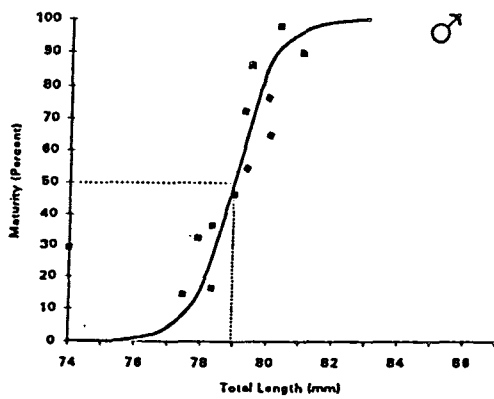


Figure 27. Length at 50% sexual maturity of males and females of three species *L. "pinkhead"*(a), *O. argyrosoma "red"* (b) and *C. cf. virginalis* (c) as a function of total length.

7.3.3 Fecundity

The examination of ripe females revealed that the absolute fecundities of the three species were different in both sides of the lake (Table 13). However, the difference was not statistically different (ANOVA, $P > 0.05$). A linear regression function best described the relationship between fecundity and total length (Figure 28). The length-fecundity relationships indicated that fecundity of all three species increased with increasing total length. However, the fecundity of *L. "pinkhead"* and *O. argyrosoma "red"* increased faster with increasing total length in the south eastern side than in the south western side of the lake.

L. "pinkhead" and *C. cf. virginalis* from the south western side had a higher mean absolute fecundity than those for the south eastern side of the lake. However, the mean absolute fecundity value for *O. argyrosoma "red"* occurred in the south eastern side of the lake (Table 13). The relative fecundities of the three species, in the south western side, were not significantly different from those of the south eastern side of the lake (ANOVA, $P > 0.05$).

Table 13. Minimum (Min) and maximum (Max) absolute fecundities of the three species in the south western (SW) and south eastern (SE) sides of Lake Malombe and their relative fecundities (RF). Figures in parentheses represent mean absolute fecundity.

Species	SW (Heavily fished)			SE (Lightly fished)			F-value
	Absolute Min	Absolute Max	RF	Absolute Min	Absolute Max	RF	
<i>L. "pinkhead"</i>	12	48	6 (28)	6	33	4 (18)	2.25
<i>O. argyrosoma "red"</i>	6	32	5 (21)	21	68	11(47)	1.67
<i>C. cf. virginalis</i>	31	68	10(51)	17	45	5 (25)	3.11

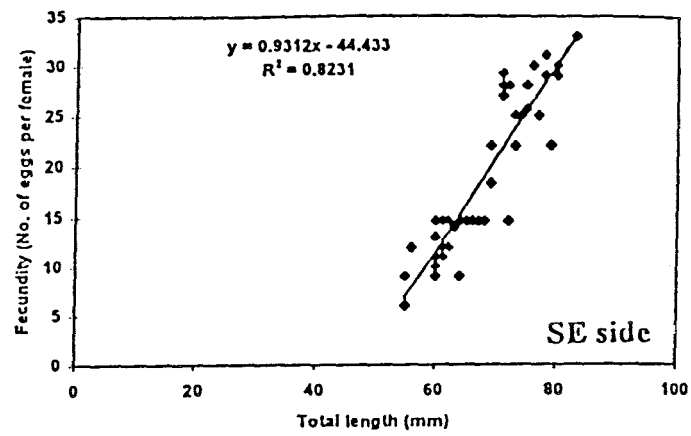
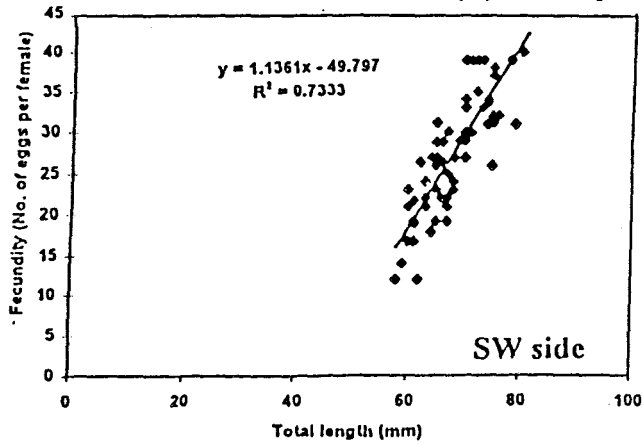
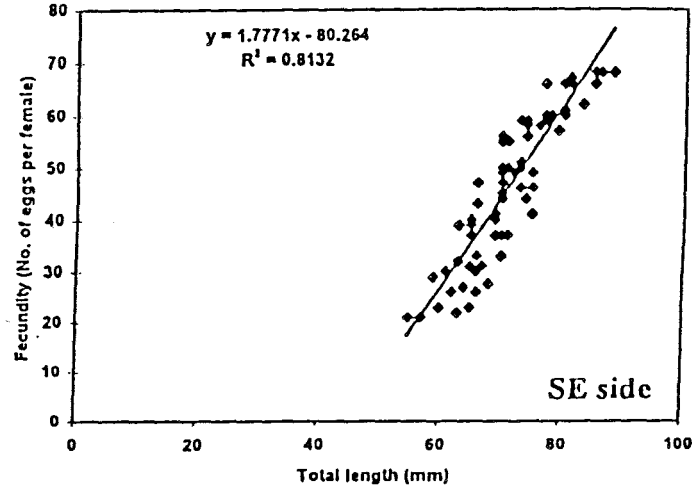
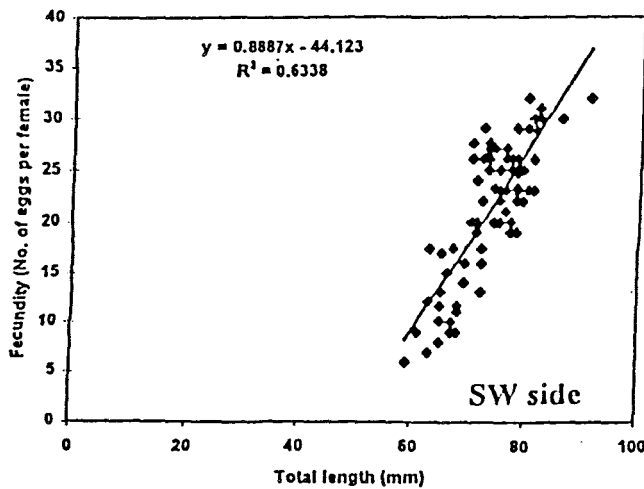
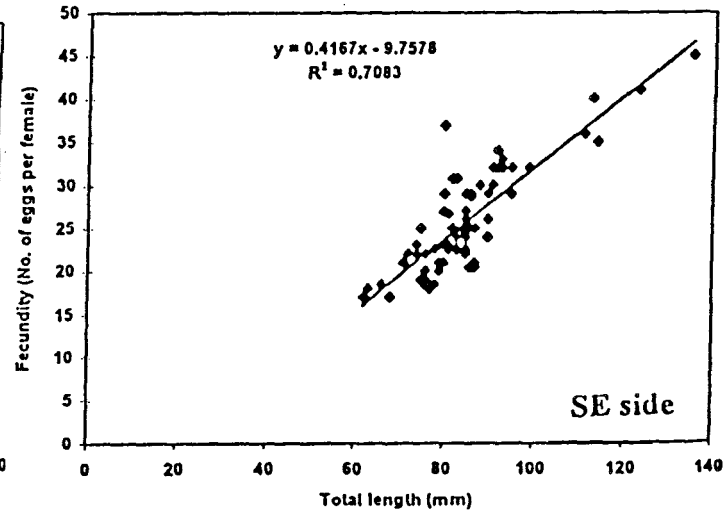
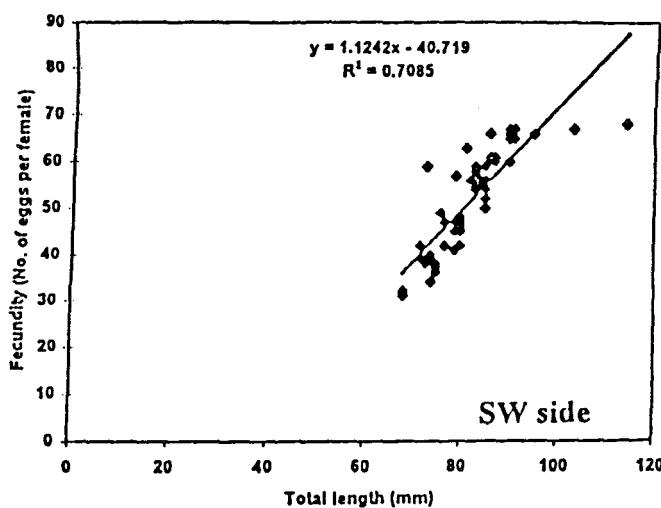
(a) *L. "pinkhead"*(b) *O. argyrosoma "red"*(c) *C. cf. virginalis*

Figure 28. Relationship between fecundity (number of eggs per female) and total length of *L. "pinkhead"* (a) *O. argyrosoma "red"* (b) and *C. cf. virginalis* (c), in the south western (SW) side and south eastern (SE) side of Lake Malombe between June 1995 and June 1996.

7.3.4 Size and sex ratio

Size distribution by sex of mature individuals belonging to the three species are shown in Figures 29, 30 and 31).

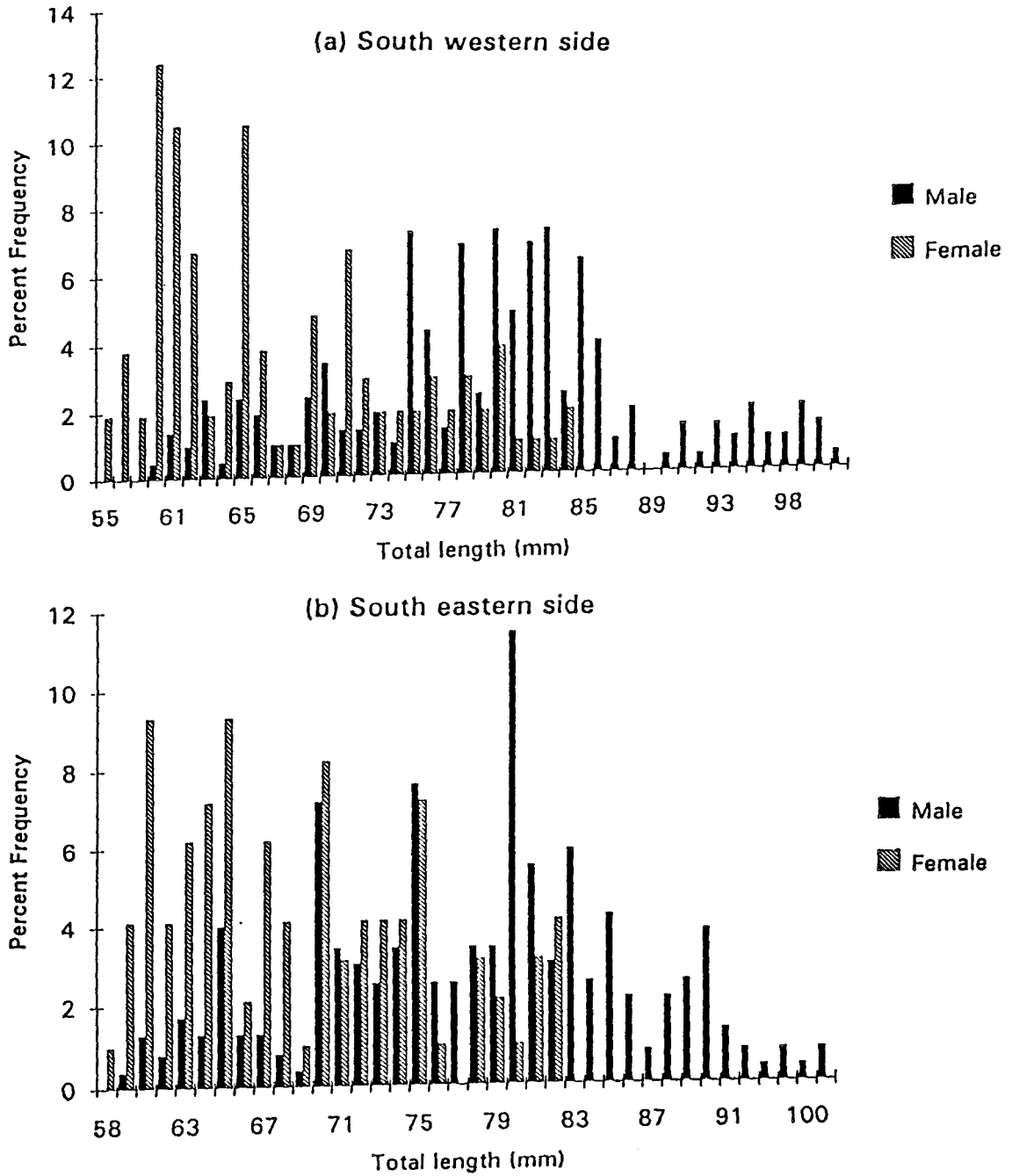


Figure 29. Length-frequency distribution of mature *L. "pinkhead"* in the south western side (a) and south eastern side (b) of Lake Malombe.

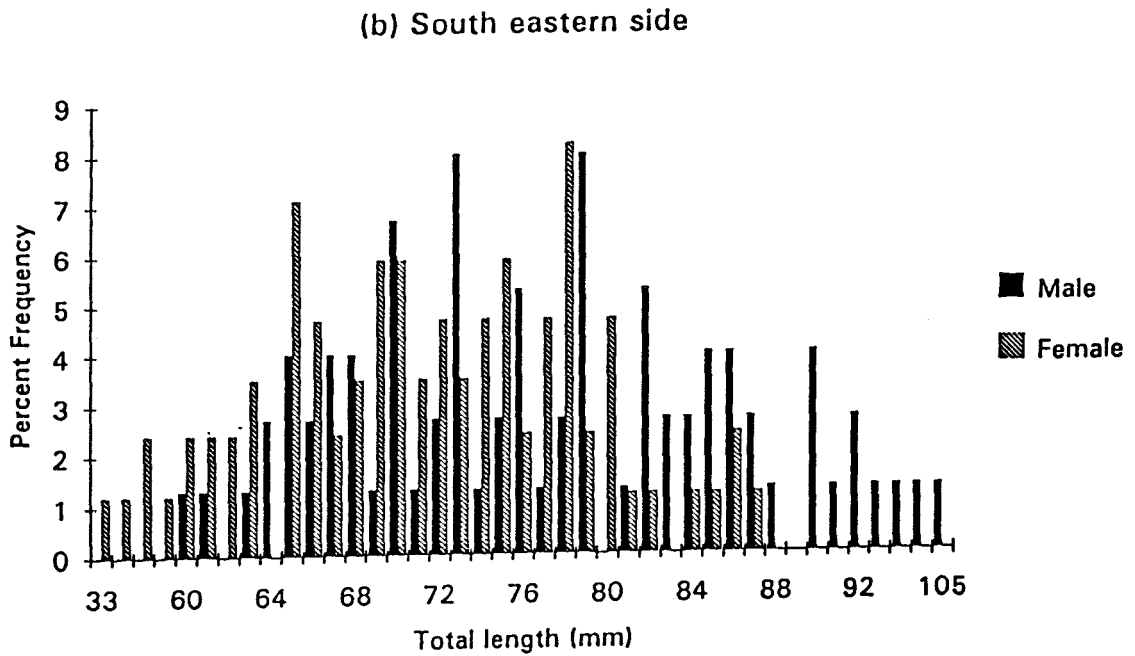
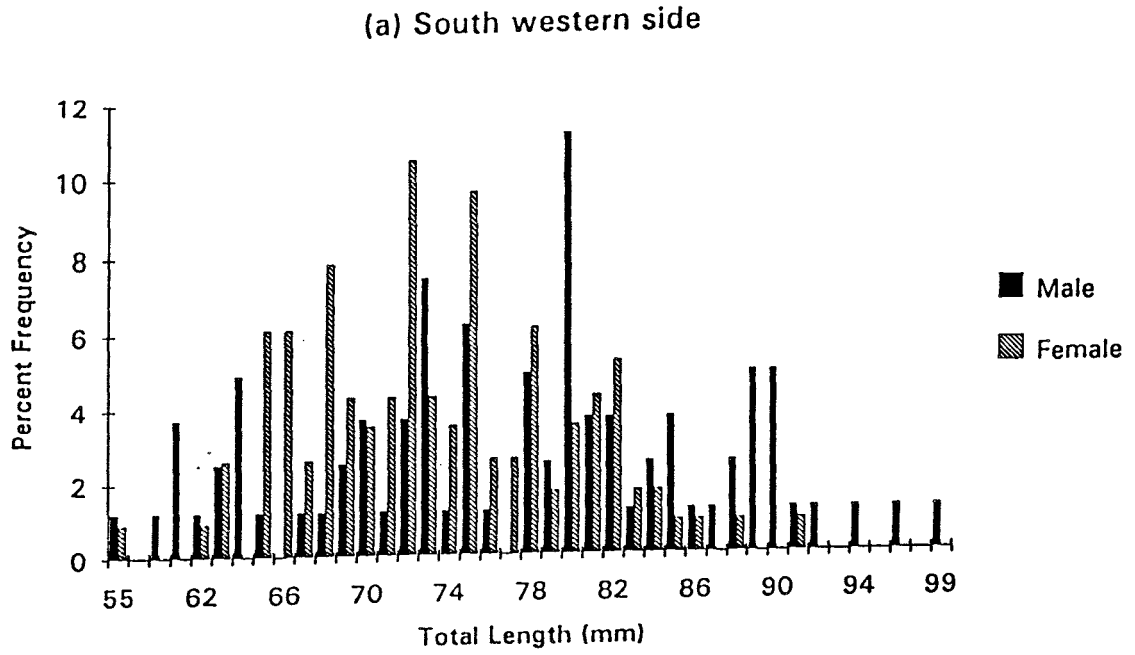


Figure 30. Length-frequency distribution of mature *O. argyrosoma* "red" in the south western side (a) and south eastern side (b) of Lake Malombe.

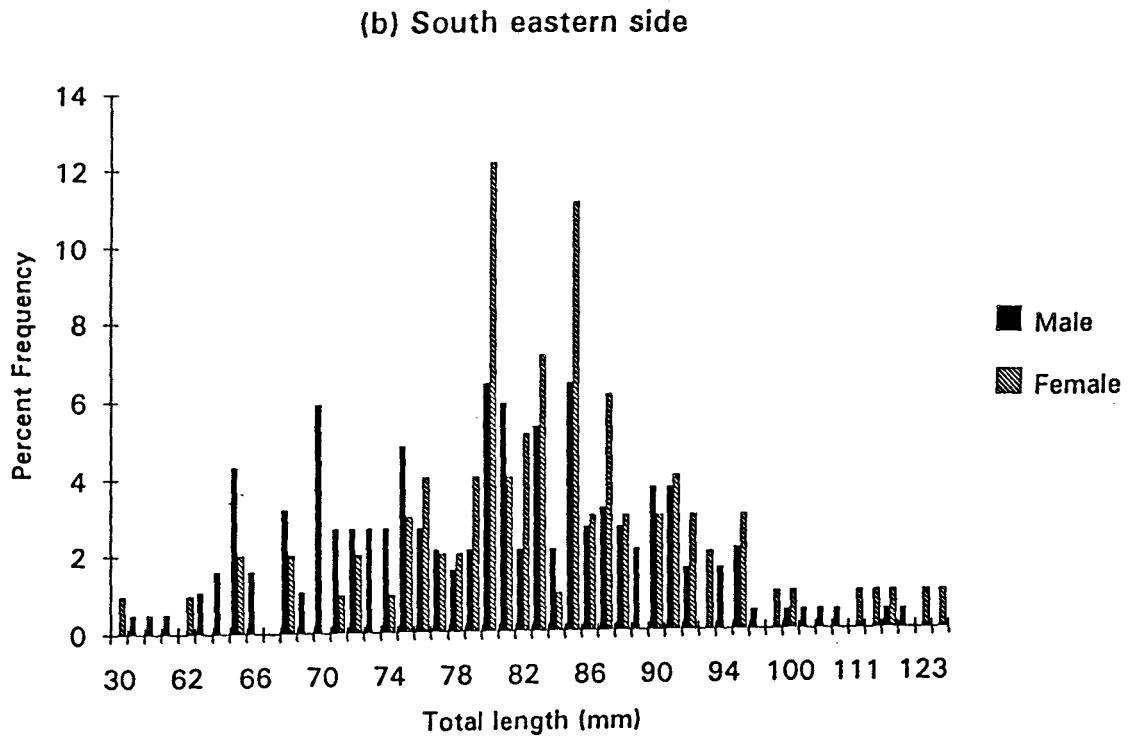
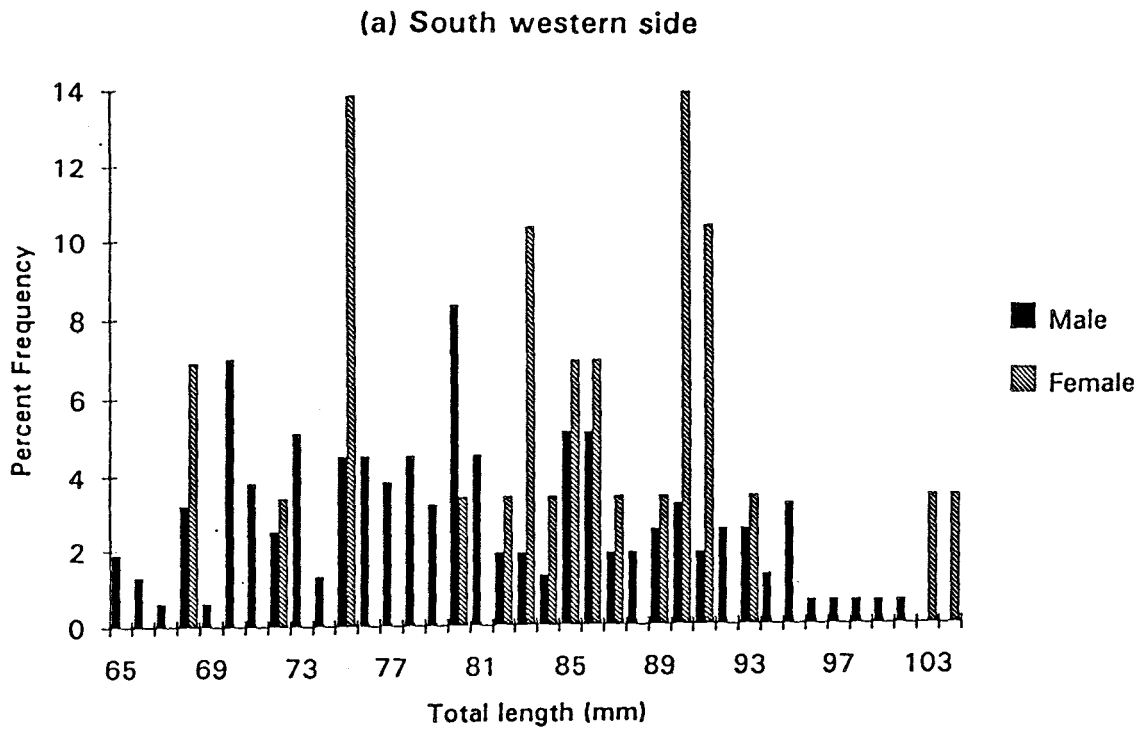


Figure 31. Length-frequency distribution of mature *C. cf. virginialis* in the south western side (a) and south eastern side (b) of Lake Malombe.

In general, the frequency of occurrence of smaller mature females was greater in the south eastern side than in the south western side. The length-frequency histograms showed that females of *L. "pinkhead"* and *O. argyrosoma "red"* dominated in the smaller size classes (66-75 mm) while females of *C. cf. virginalis* dominated in the larger size classes (78-90 mm). These results suggest that more of the immature females in the *L. "pinkhead"* and *O. argyrosoma "red"* populations were vulnerable to the standard nkacha net. However, there was no significant difference in size between sexes and sides (ANOVA) $P > 0.05$ (Table 14). Similarly, the sex ratio of the three species did not differ significantly from 1:1, X^2 test; $P > 0.05$ (Table 15).

Table 14. Mean lengths (mm) of potential breeding males and females in the south western (SW) side and south eastern (SE) side of Lake Malombe between June 1995 and June 1996.

Species		SW (Heavily fished)	SE (Lightly fished)	F- Values
<i>L. "pinkhead"</i>	♂	78	78	2.57
	♀	67	67	2.34
<i>O. argyrosoma "red"</i>	♂	71	76	2.33
	♀	72	71	2.22
<i>C. cf. virginalis</i>	♂	79	80	2.64
	♀	83	83	2.67

Table 15. Sex ratio of the three species sampled from southern Lake Malombe, irrespective of the sides (June 1995 - June 1996).

Species	♂	♀	Ratio	x ²
<i>L. "pinkhead"</i>	1450	1441	1:1.03	0.55
<i>O. argyrosoma "red"</i>	801	1014	1:1.23	0.63
<i>C. cf. virginalis</i>	749	802	1:1.07	0.52

7.4 DISCUSSION

Breeding seasonality

It appears that all three species breed throughout the year with one or two distinct peaks occurring from August to September for *L. "pinkhead"* and *C. cf. virginalis* and in September and December for *O. argyrosoma "red"*. The high frequency of occurrence of potential breeding fish throughout the year, provides further evidence that the three species breed throughout the year.

From the frequency of occurrence data of spent ovaries, it may be assumed that the three species are probably asynchronous spawners, spawning twice during the reproductively active period from August to October and again during the period of April and June. These results confirm the findings of Fryer & Iles (1972), Tweddle & Turner (1977), Mwanyama (1993) and Banda (1994) who found that the main breeding season for most Malawian cichlids falls between August and September.

It also appears that the breeding peaks of the three species occurred during the phytoplankton biomass peaks (Figure 32). This could be a strategy which synchronises the breeding behaviour with availability of food. Lowe-McConnell (1987), Mwanyama (1993) and Eccles (1974) have indicated that more nutrients are available during the period June to September from sediments pertubated by the south easterly winds and between February and March during the rainy season. These findings provide some evidence that the synchrony in breeding of the three species may reflect a direct response to food availability. Similar relationships have also been found for cichlid species elsewhere (McKaye 1984 and Marsh *et al.*, 1986).

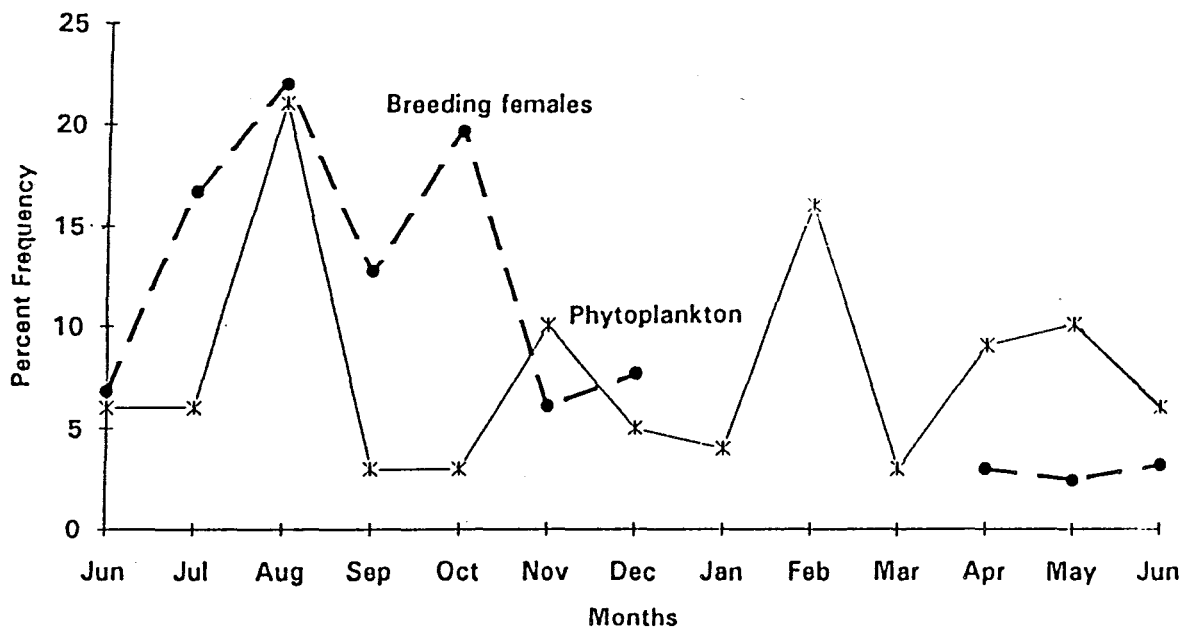


Figure 32. The frequency of occurrence of phytoplankton and breeding females in the south western and south eastern sides of Lake Malombe.

The spawning period of *O. argyrosoma "red"* coincided with the onset of the rainy season in December. This species belongs to a group of small zoobenthic feeders, substrate spawners and it is most abundant in the shallower parts of the lake (Eccles & Trewavas 1989). During the rainy season the preferred habitats for *O. argyrosoma "red"* had high turbidity values. Considering the fact that high turbidity does not prohibit breeding of some haplochromines (Greenwood 1974), it appears that breeding of *O. argyrosoma "red"* coincides with high water turbidity.

Sexual maturity and sex ratio

Analysis of the data, using non pooled data, showed that the size at 50% maturity of female fish, from both sides of the lake, were not significantly different. Results for the three species have shown that the females mature approximately six months to one year before the males. Male *L. "pinkhead"* and *O. argyrosoma "red"* appear to approach 50% sexual maturity during their second year while male *C. cf. virginalis* attain 50% maturity in their third year (Table 16). The early maturing of females is considered to be advantageous to the reproductive potential of the three species because females could breed at least once before they are exploited in their second year of life.

Table 16. Comparison of length at 50% sexual maturity (Lsm) in millimetres and length-at-age 1 (L-at-1) in millimetres for both sexes of the three species studied in the Southern Lake Malombe between June 1995 and June 1996).

Species	Lsm ♂	L-at-1 ♂	Lsm ♀	L-at-1 ♀
<i>L. "pinkhead"</i>	79	67	66	86
<i>O. argyrosoma "red"</i>	77	69	79	89
<i>C. cf. virginalis</i>	79	32	83	45

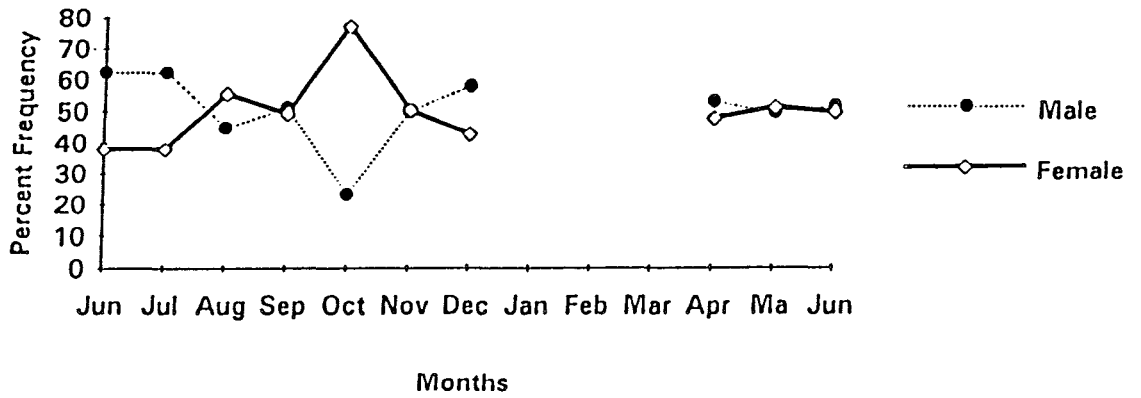
Cichlid females maturing at a small size could also mean a reduction in absolute population fecundity (Fryer & Iles 1972, Pitcher & Hart 1982) resulting in insufficient recruitment levels from such small and early maturing females. However, some scholars have argued that while mouth brooding cichlids may mature at a small size and lay few eggs, recruitment is guaranteed due to the fact that the young are painstakingly cared for by the parent. This implies that although females of the three species are maturing early, at a small size, they may still have a good recruitment potential, which may however need to be conserved by protecting the breeding grounds.

Studies on sexual maturity of related species such as *Haplochromis virginalis* (107 mm), *H. quadrimaculatus* (164 mm) and *H. pleurostigmoids* (130 mm) have shown that they all matured during their third year (Fryer & Iles 1972). Tweddle & Turner (1977) who investigated the sexual maturity of *Lethrinops parvidens*, *L. longipinnis*, and *H. anaphyrmus* (closely related to the species studied here) also postulated that they breed in their third year.

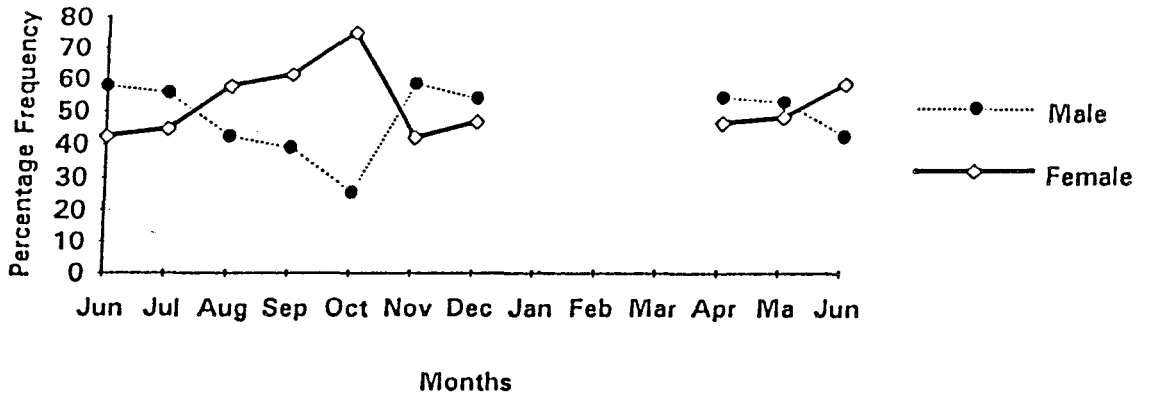
According to Fryer & Iles (1972), reduction in size at 50% maturity in all female individuals might have been a direct adaptation to heavy fishing. It appears that the reduction in size at sexual maturity for *C. cf. virginalis* has been compensated by a faster growth rate (Chapter 6). Pitcher & Hart (1982) and Gulland (1988) pointed out that a smaller size at sexual maturity coupled with an increasing growth rate offers the potential for compensatory adjustment to offset declining spawner stock size. This phenomenon could probably explain why these three species have been resilient to heavy exploitation and give an impression that the fishery could be restored if there is a substantial curtailment of fishing and proper management.

For all three species the overall sex ratio is approximately 1:1 at 95 % confidence interval. This suggests that there was an equal removal of both sexes by the standard fishing gear in southern Lake Malombe. However, it was apparent that for all three species, males slightly outnumbered females two months prior to the breeding season (Figure 33). This may be a reproductive strategy that could increase the reproductive success of the females through the exercise of mate choice. Lande (1981) quoted by McKaye (1986) and Turner (1993) emphasised that such preponderance of males satisfies the polygynandry of mouth brooding cichlids, whereby females have numerous males from which to choose and apportion their eggs and hence achieve greater mating success. Another explanation could be that males, as in *Tilapia moori* (Konings 1988), move about in groups prior to and during the spawning period whilst females are solitary in less accessible breeding grounds. Such a breeding behaviour could contribute to males dominating the catches during and/or prior to the breeding season.

(a) *L. "pinkhead"*



(b) *O. argyrosoma "red"*



(c) *C. cf. virginalis*

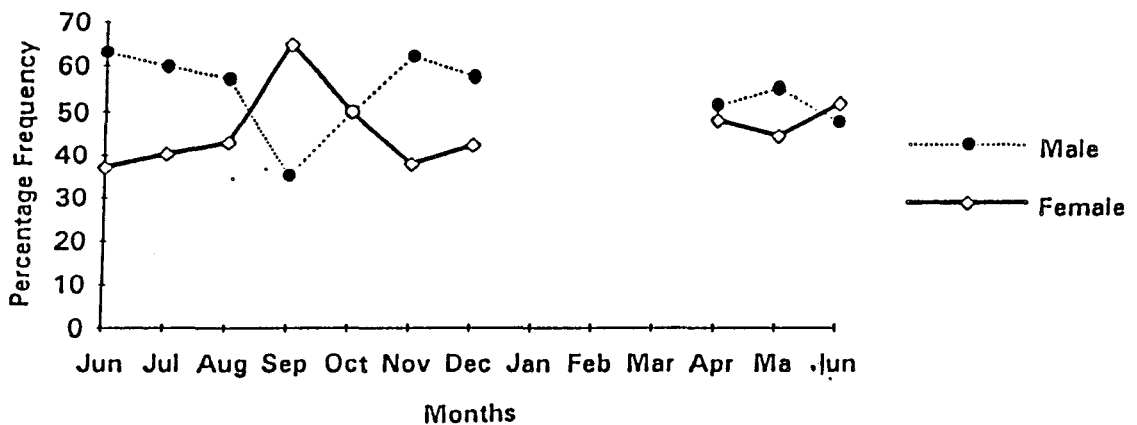


Figure 33. The monthly frequency of potential breeding *L. "pinkhead"* (a), *O. argyrosoma "red"* (b) and *C. cf. virginalis* (c) sampled in the south western side and south eastern side of Lake Malombe based on pooled data collected between June 1995 and June 1996.

Fecundity

Fecundity is the main determinant of reproductive potential and varies according to the body and egg size of the female parent (Welcome 1967, Nikolskii 1969, Lowe-McConnell 1987). Bagenal (1978) and Pitcher & Hart (1982) consider absolute fecundity to be a function of length and is either allometric or isometric. In this study, the linear function best described the significant relationship between absolute fecundity and length. However, the relationships for *L. "pinkhead"* and *O. argyrosoma "red"* were poorer in the south western side than in the south eastern side of the lake. The possible explanation for such a poor length-fecundity relationship in the south western side could be that the high fishing intensity has influenced a shift in the size distribution of these species resulting in the impairment of reproductive output (Sadovy 1996).

The relative fecundity value of *C. cf. virginialis* was significantly higher in the south western side (10 eggs g⁻¹) than in the south eastern side (5 eggs g⁻¹). In contrast, *O. argyrosoma "red"* had a higher relative fecundity value in the south eastern side (11 eggs g⁻¹) than in the south western side (5 eggs g⁻¹) where as the relative fecundity values of *L. "pinkhead"* for the two sides (6 eggs g⁻¹ in the south western side and 4 eggs g⁻¹ in the south eastern side) were not significantly different (t-test, P>0.05).

These results suggest that relative fecundity is variable among the three species and between the sides of the lake. Considering the fact that mean weights for each species, in both sides of the lake were not significantly different (t-test, P>0.05), it appears that the higher values of relative fecundity for *C. cf. virginialis*, in the south western side, might have been a reproductive adaptation to high fishing pressure. Pitcher & Hart (1982) and Sadovy (1996) pointed out that changes in reproductive strategy are expected to involve

increases in relative fecundity at a given size and age when fish populations are subjected to high fishing pressure.

The lower value of relative fecundity of *O. argyrosoma "red"*, in the south western side, could be an indication of poor habitat breeding conditions for this species in the south western side. Based on the information of substrate type (Chapter 3), it could be speculated that the sandy substratum of the south western side of the lake may have contributed to the low values of relative fecundity of *O. argyrosoma "red"* while the muddy substratum of the south eastern side of the lake may have contributed to the better habitat conditions for reproductive success of *O. argyrosoma "red"*.

Absolute fecundity values for all three species ranged from 6 to 68 eggs per mature female irrespective of the side of the lake. This range is closely analogous to Mwanyama's (1993), who documented a range of 13 to 78 eggs. The slight difference might have originated from sampling artefacts and period of sampling. Comparisons of absolute fecundity values of each species with respect to sides of the lake showed that *L. "pinkhead"* and *C. cf. virginalis* had the highest mean values of absolute fecundities (28 and 51 eggs respectively) in both sides of the lake, where as for *O. argyrosoma "red"* the highest mean value was observed in the south eastern side of the lake. Considering these results, it is evident that all three species studied here have relatively low fecundity irrespective of side (a typically *k*-selected trait), which suggests that proper conservation measures have to be imposed to sustain the fish stocks.

CHAPTER 8

GENERAL DISCUSSION

The Kambuzi fishery in Lake Malombe has been of great importance to the economy of the artisanal fishers surrounding the lake since 1976. Of the three main water bodies, the Upper Shire River, South East Arm of Lake Malawi and Lake Malombe, the Lake Malombe fishery contributes approximately 60% (US\$400,000) to the economic output of the three water bodies (FAO 1992). Between 1980 and 1986 the number of fishing crafts had doubled to 650 and since then the fishery has been under severe exploitation (Bland & Donda 1993). It is evident that besides ecological and limnological factors, overfishing has been the main contributing factor to the decline of the fishery (Coulter 1993). In addition, continued eutrophication and siltation, because of bad land use practises in the catchment area, may increase the abundance of the exotic and macrophytic water hyacinth, *Eichhornia crassipes*. Accumulatively, these factors would have serious consequences on the Kambuzi fishery. Given the 64% decline in the yield of the fishery during the 1988-1994 period, which has been ascribed to recruitment and growth overfishing and substratum degradation, there is doubt whether the fishery will be sustainable in the long term unless appropriate and effective management strategies are introduced. The classical management strategies (such as closed season, mesh size restriction and licensing) that have been in place since 1983 are now recognised as having been ill-conceived and not adhered to by the fishers. The only strategy that enjoys support by fishers is community participation management. It is hypothesised that this is the only option for the future management of the fishery.

Approximately 45 species of Kambuzi are harvested by traditional fishers in Lake Malombe, of which five dominate the catches. Cichlids dominate the catches on both sides of the lake. It was also shown that there is a significant lower species richness in the south western side in comparison to the south eastern side of the lake. Koslow *et al.*, (1988), Russ & Alcala (1989) and Attwood & Bennett (1991) have also documented significant decreases in species richness in heavily fished sites in comparison to lightly fished areas. Findings from previous catch data investigations (Banda 1995, Mwanyama 1995), indicate that species richness is low in exploited areas. This supports the argument that the low species richness in the south western side of the lake was attributed to the greater fishing effort as well as to the degradation of the substratum and aquatic vegetation as a consequence of habitat-destructive fishing techniques.

Catch composition data collected from the south western side and south eastern side of Lake Malombe revealed that *L. "pinkhead"*, *C. virginalis*, *O. tetrastigma*, *C. chrysonotus* and *O. argyrosoma "red"* constitute approximately 67% of the total catch by weight. It was also shown that *C. chrysonotus* has replaced *L. parvidens* as the fifth important species in the south western side of the lake (see Chapter 4).

The distribution of the three species (*L. pinkhead*, *O. argyrosoma "red"* and *C. c.f. virginalis*) was found to be uniform on both sides of the lake. However, comparing the current numerical abundance and biomass data, with those from previous studies (FAO 1992 and Banda 1995), there is an indication that fishing pressure may have caused the decline in catch rates and catch per unit effort in the south western side of the lake. Spatial comparisons between the south western and south eastern sides, which are subjected to different fishing intensities have revealed that in the south eastern side of the lake

(lightly fished), CPUE is twice that of the south western side (heavily fished) of the lake. Similar findings have been reported for marine protected areas and sanctuaries (Kawaguchi 1974, Buxton 1983, Munro 1983, Alcala & Russ 1990).

Growth rate estimates of the three species in the south western side were not significantly different from those of the south eastern side of the lake. According to Gulland (1988), this could suggest that both sides have similar conditions for growth. Based on length-frequency histograms, it was predicted that all three species are capable of reaching ages of 5 years. Growth curves indicate that all three species have a similar growth pattern and females grow faster than males in the first year of their life. By comparison, growth rate estimates of *L. pinkhead* and *C. cf. virginialis* from this study are not significantly different from those obtained by Iles (1972), Tweddle & Turner (1977) in Lake Malawi and Banda (1995) in Lake Malombe (see Chapter 6).

The three species breed throughout the year with distinct peaks occurring between August and October. The frequency of occurrence of potential breeding females suggest that the three species are asynchronous spawners, spawning twice, between August and October, and again during the period of April to June. Furthermore, it also became evident that the breeding peaks of the three species coincide with the phytoplankton biomass peaks, suggesting that intraspecific competition for food between adults and juveniles is reduced during the period of greater fish abundance.

Of the three principal species, it appears female *L. "pinkhead"* and *O. argyrosoma "red"* reach 50% sexual maturity at a smaller size than males. It also appears that, irrespective of species and side of the lake, males of all three species attain 50% sexual maturity at approximately the same size (79 mm) which corresponds to an age of between two and three years. The relative small size at sexual maturity is of an advantage for the population because females are given a chance to spawn at least once before they are caught. However, the benefits of early maturation are limited in Lake Malombe due to the high fishing pressure. Jennings & Beverton (1991) pointed out that a fished population would only maintain its evolutionary fitness by a reduction in size at 50% sexual maturity. They also stated that such an adaptation could be a direct consequence of overfishing or a response to physical and biological characteristics of the environment. Lewis & Tweddle (1990) have shown that similar species mature at a greater size in Lake Malawi. These views provide room for speculating that both changes in substratum and high fishing intensity may have caused a reduction in size at sexual maturity of *L. "pinkhead"* and *O. argyrosoma "red"*.

Implications of the study for fisheries management

The present information on catch composition and catch rates show that the species richness and CPUE are greater in the south eastern side than in the south western side of the lake. Differences in CPUE in the south western and south eastern sides of the lake are thought to reflect the impact of overfishing and substratum degradation. Considering these findings, the current idea of extending the existing sanctuary area in the south eastern side of the lake would be advantageous in maintaining the species richness and abundance of fish.

From the von Bertalanffy growth curves, it appears that females of the three species grow faster than males. This could imply that females become sexually mature at a bigger size because in the early stages of life they would invest energy inputs in somatic growth rather than gonadal development (Pitcher & Hart 1982). Relating lengths -at-age 1 to the mean length at first capture of the three species (approximately 24 mm), it is clear that the recruits are caught at age of less than one year and do not have a chance to breed before they are subjected to fishing mortality. From this it is clear that the minimum mesh size regulation for all Kambuzi seines in Lake Malombe is of limited benefit. As mentioned earlier the mean size at 50% sexual maturity for the three principal species is 76 mm TL, which is approximately three times the mean length at first capture. It is therefore strongly recommended that the present minimum mesh size of 19 mm for all Kambuzi seines should be increased to at least 25 mm. This mesh size will be selective for larger sizes of Kambuzi (FAO 1993). Considering the gear selectivity experiment which showed that a 19 mm mesh size gear catches about 40% of immature fish, it is clear that the implementation of a 25 mm mesh size will reduce the catches of the immature Kambuzi. Nevertheless, the reduction in the percent of immature fish caught in a 25 mm seine net would obviously have to be determined empirically. A further increase in mesh size would however undoubtedly meet with resistance from the fishers.

The main breeding season of the three species is between August and October during which time the CPUE is also at its highest. This indicates that all three principal species are more vulnerable to fishing during their breeding season. According to Buxton (1987), such a period would be appropriate for a closed season. Unfortunately, during this period most of the people around the lake need additional income for traditional festivals, such as weddings and initiation ceremonies, that also occur in the August-September period.

From a fishery perspective, the coincidence of greater CPUE and breeding season during the open season, suggests that the present closed season (1 January - 31 March) is ineffective in protecting the breeding females. This provides a basis for a suggestion that there is an urgent need to proclaim a closed season over August-October period, when breeding females are particularly susceptible to exploitation. However, based on the high frequency of occurrence of juveniles sampled between November and December, it could also be suggested that the closed season should even be proclaimed over November-December period, in order to protect juveniles. Considering the roles of closed seasons (Buxton 1987 and FAO 1992), it is recommended that a closed season for the kambuzi fishery should be shifted from January-March to October-December every year, during which more breeding females and juveniles would be protected. Such a closed season would also not clash with traditional activities mentioned above.

The Lake Malombe fishery is a typical example of a multispecies fishery. In other multispecies fisheries (Smale & Buxton 1985, Ruddle *et al.*, 1992 and Attwood & Bennett 1996), classical management measures such as closed seasons, mesh size and gear type restrictions have been found to be impracticable. It is recommended that besides the existing strategies, the sanctuary area should be promoted to a greater extent as an additional and more effective management strategy to protect fish biomass and species biodiversity. This can however only be achieved through the active participation and willingness of the fishers to get involved in the resources and by better dissemination of research findings.

It should, however, be pointed out that the extension of the protected area must also consider social, economic and political issues. Alongside the extension of the sanctuary area, there is need to focus on the livelihood

activities, resource access rights and rules, family characteristics and social dynamics in relation to the Fisheries Department and the Beach Village Committees' management activities. There is a great need for education, among the local communities on the importance and value of sanctuary areas, before any extension is considered. Fundamental to this study is that the management of the Lake Malombe fishery is not limited to considerations on the resource only. The human element is crucial. As commented by Hilborn (1985) human beings are, after all, the reason why fisheries exist and why fisheries management is necessary. Attwood & Bennett (1996) also commented that a management strategy is only successful if it can meet the criteria of ensuring the sustainability and utilisation of the fish stocks and accepted by the resource users.

It is my contention that the extension of the sanctuary would only be beneficial if there is a high degree of involvement and support by people at the local level. It is also anticipated that the existing participatory management approach could easily accommodate the task of extending the sanctuary area without jeopardising the lives of the fishing community, because it appears that the beach village committees have nurtured self help spirit and support towards the idea of enlarging the existing sanctuary area in the south eastern side of the lake.

If the recommendation that the protected area, situated in the south eastern side of the lake, should be larger than it is at present, it must be borne in mind that poor enforcement or uncontrolled poaching could also contribute to the failure of the larger sanctuary area to conserve valuable fish populations. On account that the sanctuary is within Liwonde National Park, policing activities of the sanctuary area should involve a direct collaboration between the Fisheries Department, Parks & Wildlife Department of Malawi and the fishers.

The implementation of an enlarged sanctuary area should be monitored to determine if the desired results are achieved. In addition, further research should be done on the relationship between spawner biomass and recruitment, tagging to investigate migration and enforcement monitoring to evaluate compliance with the sanctuary regulations.

In conclusion, the south eastern side of the lake is characterised by low fishing intensity, muddy substratum and aquatic macrophytes. These factors appear to be the main factors that have been associated with a higher adult fish abundance, species richness and a higher frequency of occurrence of juveniles. It is therefore recommended that the existing sanctuary should be extended.

It is appreciated that the optimum size of a sanctuary area has to be scientifically established. However, given the seriousness of the situation, it is recommended that the sanctuary area boundary be increased immediately, but in consultation with the fishers. Considering the fact that the muddy substratum encompasses about 1.5 kilometres offshore and that aquatic macrophytes are also common within a distance of 1.5 kilometres offshore in the south eastern side of the lake (see Chapter 3), it is recommended that the sanctuary area boundary should be increased by 1 kilometre. Increasing the present boundary by 1 kilometre will effectively double the area of the existing sanctuary area. This implies that the enlarged protected area, with a boundary established 2 kilometres offshore, will encompass an area of 25 Km² (6% of the entire lake). It is anticipated that the enlarged sanctuary will protect the aquatic environment and fish stocks, hence prevent the total collapse of the fishery.

On the basis of the *k*-selected reproductive traits shown by the three principal species, it appears that if fishing pressure was reduced through a well managed sanctuary, the species could have the capacity to recover from the low population size that has been caused by overfishing.

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