ASPECTS OF THE BIOLOGY AND POPULATION DYNAMICS OF FRESHWATER MUSSELS IN LAKE KARIBA AND LAKE MCILWAINE

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ABSTRACT

Following preliminary observations in 1975 the Lake Kariba Fisheries Research Institute implemented a research program in March 1976 to investigate various aspects of the biology and population dynamics of the mussel crop of Lake Kariba, with a view to greater understanding of their status in the lake, and establishing a basis for management, if required. Aspects investigated were densities, distribution, species composition, predation by fish, reproduction, age and growth, gross biochemical composition and crude production rates. The mussel community comprised four species, a small pill clam, Corbicula africana, and three mussels, Caelatura mossambicensis, Aspatharia wahlbergi and Mutela dubia. Only the latter three were studied. Mussel beds occupied all the gently shelving cleared and uncleared areas, and the bulk of the populations occurred from 3 m - 9 m depth, but extending to 11 m. Predation by fish was found to be extremely low. The reproduction study showed two species bred all year - C. mossambicensis and M. dubia, whereas A. wahlbergi bred seasonally during the rainy season. The two year-round breeders were repetitive spawners, capable of breeding several times a year. Indications are that A. wahlbergi is essentially a fluviatile species, with a life cycle adapted to taking advantage of riverine conditions. Sex ratios in all three species were approximately 1 : 1 , with females predominating slightly. Fecundity in one species, C. mossambicensis, was investigated. The complete parasitic cycle of M. dubia was elucidated and found to be similar to that of M. bourguignati, as described by Fryer (1961). Host species were noted amongst
the cichlid and mormyrid families, and the conclusion drawn that the species is not host specific. Various aspects of the life-cycles of the other two species were noted, but complete life-cycles were not successfully elucidated. Population composition according to age showed the most common species, *C. mossambicensis*, to be comprised mainly of 2 - 5 year-old individuals, indicating a young and vigorous population. Juvenile pre-adult mussels were very scarce. In the population of *A. wahlbergi*, older mussels formed a greater proportion of the biomass than in the population of *C. mossambicensis*, and young were also scarce. *M. dubia* were not recorded in sufficiently large numbers to estimate age composition accurately. The production rate (whole wet mass) of the most common species, *C. mossambicensis*, was calculated to be 2,45 kg ha\(^{-1}\) day\(^{-1}\) in the Sanyati East cleared area (30,5 km\(^2\)), while the overall production rate of all three species was calculated to be 3,34 kg ha\(^{-1}\) day\(^{-1}\). Calorific values of all three species were obtained, while gross body composition in terms of water, fat, protein, ash and amino acid composition were determined. The ash component of *A. wahlbergi* was analysed.

The Lake Kariba results were supplemented by a follow-up study of the composition of the mussel population of a eutrophic, highveld dam, Lake McIlwaine, in 1978/1979. This much smaller lake was populated by only two mussel species, *M. dubia* and *C. mossambicensis*, although *A. wahlbergi* and *Unio caffer* were recorded in the riverine upper reaches. Observations on seasonal breeding of the two lake species were made. A detailed study on the draw down zone of a gently shelving beach showed that at the time the extreme shallows
had been dominated by *C. mossambicensis*, whereas from a depth of approximately 1.6 m *M. dubia* dominated very significantly. Falling lake level was found to trigger off migratory responses, thus placing a proportion of individuals in deeper water and improving chances of survival.

The mussel composition of Lake Kariba and Lake McIlwaine was considered in conjunction with preliminary observations of mussel distribution and composition in other water bodies, and some inferences drawn regarding the ecological factors which appear to influence the composition and diversity of the mussel fauna in rivers and lakes.
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GENERAL INTRODUCTION

Following a broad benthic sampling program of Basin Five of Lake Kariba, Begg (1971) reported the presence of two freshwater bivalve species in the lake, *Aspatharia wahlbergi* (Krauss) and *Corbicula africana* (Krauss), but did not elaborate on either their density or distribution. Thereafter the status of bivalves in Lake Kariba remained unknown until the summer of 1973 / 1974 when an exceptionally low lake level revealed large numbers of *A. wahlbergi* stranded on the Lakeside shoreline of Basin Five. Further interest in the bivalve fauna was stimulated in 1975 following the recording of yet another species *Mutela dubia* (Gmelin) (Junor, pers. comm.), also from the Sanyati Basin. Free and aqualung diving in the Charara area then revealed the presence of a fourth species, *Caelatura mossambicensis* (von Martens) not hitherto recorded in the Sanyati Basin, and a sample density of mussels in this area of 45 per square metre. This stimulated further interest, and a follow-up sampling tour of Basin Five (the Sanyati Basin) showed that concentrations of bivalves existed in all areas examined, particularly in the flat, cleared areas and the uncleared areas adjacent to them.

This investigation of the bivalve stocks prompted a decision by the Department of National Parks and Wildlife Management to initiate a program of research into the status of the bivalve stocks in Lake Kariba, with a view to determining the potential for commercial cropping. This program started in March 1976 with the primary aim of determining the
stock characteristics in general terms (distribution, species composition, abundance) and to decide from this whether the potential for harvesting was sufficient to proceed with further studies on other aspects of their biology. It soon became apparent that a very large standing crop of bivalves existed in the lake, and a program of research was then drawn up to cover the aspects of their biology which would yield data necessary for the utilization and management of the resource.

The following aspects were to be investigated:

1. Distribution and species composition over a wide area.
2. Relative and absolute densities, according to area and depth.
3. Size and age structure of the populations.
5. Morphological aspects and gross biochemical composition.
6. Fish predation on the mussel crop.

Initially all four species of bivalve mentioned above were to be studied, but frequent interruptions to the program from security force commitments necessitated the exclusion of the smallest species, *C. africana*, from the project. Obviously the whole lake could not be sampled in detail, and one area, the Sanyati East cleared area, was
selected for more detailed study. The essential aim of the study was to provide a broad foundation of biological knowledge upon which a program of utilization and management could be built. The idea of utilizing a mussel resource commercially is a new concept in Southern Africa, without precedent, and hence no previous program or research experience existed to draw on for the project. Preliminary sampling was done in October 1975, but the main research program started in March 1976 and continued until late 1977, when the Lake Kariba work was then written up. Further research work was then undertaken on Lake McIlwaine in 1978 and 1979, with the purpose of providing comparative data from another lake. This research came to a close in October 1979 and was combined with the Lake Kariba data to provide the substance of this thesis.

Results of the study are presented in three main sections. PART ONE describes the stock of Lake Kariba and Lake McIlwaine; PART TWO describes various aspects of the breeding biology of the three species; and PART THREE presents the results of morphological, biochemical and age analyses - aspects which are used for initial standing crop and production calculations. The final discussion concludes the thesis with a general examination in ecological terms of the factors which have influenced the development and nature of the mussel faunas of the two lakes under consideration.
LITERATURE REVIEW

While a great deal of research has been undertaken on freshwater bivalves in the Northern Hemisphere, covering nearly all aspects of their biology, a review of the available literature shows a relative paucity of biological studies on Southern Hemisphere bivalves.

In Africa the majority of contributions, dating back to the middle of the last century to the comparatively recent 1950's, are primarily concerned with the collection, description and identification of freshwater molluscs from the freshwater systems of Central and East Africa. Doubtless the colonial occupation by European powers of many of these African countries was the primary instigation for this research, as many of these papers are from French, Belgian or German authors. On Lake Tanganyikan molluscs there are contributions from Smith (1880 a & b, 1881 a & b, 1904); Crosse (1881); Bourguignat (1890, and some earlier notes); Germain (1905); Ancey (1906); Schoutenden (1935); Schwetz (1943); and Leloup (1950). On other regions there are contributions from Woodward (1859), von Martens (1883), Preston (1910) and Haas (1929), on the shells and molluscan fauna of Central Africa; from Boettger (1913), Pilsbry and Bequaert (1927), van den Berghe (1936), and Schwetz (1949) on the aquatic molluscs of the Belgian Congo; from Schwetz (1949) on freshwater molluscs of Ruanda-Urundi; from Smith (1881 a) on Lake Nyasa shells, and Franc (1949) on Unionids of West Africa. More general papers are those of Ortmann (1918) and Bloomer (1932) on the anatomy of African naiades.

Further south on the continent the available literature is again largely concerned with molluscan distribution in general, the monograph by Connolly (1939) being perhaps the best known and most important of these works. Other contributions are those of Melville and Ponsonby (1898) on the non-marine molluscan fauna of South Africa; Connolly (1912, 1925, 1931) on the non-marine molluscan fauna of South Africa, Portuguese East Africa and South West Africa, respectively; Dartevelle (1939) on freshwater molluscs of the Kunene; Kuiper (1964) on South African Pisidium species; Schutte and Frank (1964) on the freshwater molluscs in the South-Eastern Transvaal and adjacent Northern Swaziland; Oberholzer and van Eeden (1967) on the freshwater molluscs of the Kruger National Park; Brown (1967) on the freshwater molluscs of Natal; Pretorius et al (1975) on the molluscs of the Pongola River flood plain pans; Marshall (1975) on the bivalve fauna of Lake McIlwaine (Zimbabwe); Heard and Vail (1976) on the systematics of Unio caffer; and Appleton (1977) on the freshwater molluscs of Tongaland and a note on
molluscan distribution in Lake Sibaya. Donnelly and Grobler (1976) have commented on predation by otters on bivalves in the Bulawayo region (Zimbabwe), while Jubb (1976) has commented on the distribution of Unionidae in South African inland waters. A useful collation of records and some systematic notes on the Unionacea of South - Central Africa has been provided by Appleton (1979).

At the time of writing there is no published literature on the bivalves of Lake Kariba, although they are briefly mentioned by Begg (1971) and Bowmaker (1973 a) in an unpublished report and thesis respectively; by Kenmuir (1978); by French (1980, unpublished report) in connection with stranding on the lake shore; and more recently the stock has been briefly described by Kenmuir (1980, in press).

The literature on bivalves from other parts of the world is fairly comprehensive, and no attempt will be made here to review it. References appear throughout the text in the relevant sections.
Only four bivalve species were recorded in Lake Kariba during this study. The four species are:

**Family Unionidae**
1. *Caelatura mossambicensis* (von Martens, 1860)

**Family Mutelidae**
2. *Mutela dubia* (Gmelin, 1793)
3. *Aspatharia (Spathopsis) wahlbergii* (Krauss, 1848)

**Family Corbiculidae**
4. *Corbicula africana* (Krauss)

It is possible that three further large mussel species may occur in Lake Kariba, these being *Caelatura kunenensis* (Mousson, 1887), *Unio caffer* (Krauss, 1848) and *Aspatharia (Aspatharia) pfeifferiana* (Bernardi, 1860).

They are reported from the Zambezi above the Victoria Falls (Appleton, 1979) and if any do occur in Lake Kariba they are most likely to be found in the lake in proximity to the inflowing Zambezi River. *U. caffer* has also been recorded from the Gwaai River (Appleton, 1979) which is an important tributary of the Zambezi near the Western-most end of the lake, and also in the Ruziruhuru River (Hulley, pers. comm.), which flows into the large Sengwa Basin (Basin Three). It is possible therefore that this species may occur in the lake as far East as the Sengwa Basin. Bowmaker (1973a) recorded *Mutela rostrata* from the Mwenda River. According to Appleton (1979) this species is now considered to be *M. dubia*. 
Identification of the Lake Kariba species has come from various sources. Species 1 - 3 were identified by Appleton (pers. comm.), formerly of the Bilharzia Field Research Unit in the Transvaal, who had his identification of numbers 1 - 2 subsequently confirmed by Dr. Mandahl-Barth of the Danish Bilharzia Laboratory, Denmark. Species 2 was originally named Mutela mabilli (Rochebrune), but has now been placed into synonomy with M. dubia (Appleton, 1979). Species 3 and 4 were identified earlier for Begg (1971) by Prof. van Eeden of Potchefstroom University, while Dr. G. Oberholzer also of Potchefstroom University confirmed Appleton and Mandahl-Barth's identification of Species 1 and 2.

Identification of Lake McIlwaine bivalves was undertaken by Marshall (1975) and was based on Connolly (1939), supplemented by Oberholzer and van Eeden (1967) and Leloup (1950) and subsequently confirmed by Oberholzer in personal communication. As mentioned above the species M. mabilli has now been placed into synonomy with M. dubia.

The family Unionidae is the largest family of freshwater mussels, containing some 85 genera and approximately 1000 species (Morton, 1967). The large number of genera contained by this family is thought to be because they were the first bivalves to enter and colonize freshwaters, encountering no competition and negligible predation which led to a major phase of adaptive radiation in the freshwater systems of the world (Purchon, 1977). This is thought to have occurred first in the New World and, more
specifically, in the general area of the Mississippi drainage basin, for the greatest diversity of species occurs here. Five to six hundred species of Unionidae are found in the United States (Pennak, 1953). They are characterized by having parasitic glochidia larvae which are brooded in the gills.

The Mutelidae are freshwater mussels of the Southern Hemisphere. Like the above family they also have parasitic larvae (on fish) which are brooded in the gills and are commonly referred to as lasidial or haustorial larvae.

Plate 1: Showing the freshwater mussels mentioned in the text. From left to right, top row: Aspatharia wahlbergi and Caelatura mossambicensis; middle row: Unio caffer; bottom row: Mutela dubia and Corbicula africana
1. **Description Of Lake Kariba**

**General:**

Lake Kariba (Fig. 1) lies in the Middle Zambezi Valley, situated between latitudes 16°30'S and 18°06'S and longitudes 26°40'E and 29°03'E, with the longitudinal axis roughly NE/SW along the international boundary between Zimbabwe and Zambia. This boundary runs along the submerged Zambezi river bed and divides the lake into approximately equal areas. The river followed a large rift valley overlooked on both sides by a steep escarpment. This valley, now mostly under water, was bordered at the Eastern end by a large mass of gneiss through which the river cut a deep and narrow gorge (the Kariba Gorge), extending for 16 km.

The dam wall was built at the Southern end of this gorge, construction beginning in 1956 and continuing until 1960, although closure was already affected in December 1958, in time for the 1958/1959 seasonal floodwaters. Impoundment resulted in a lake some 280 km long, with a maximum width of 40 km and a mean width of 20 km. The lake has an area of 5 250 km² at the normal operating level of 484 above mean sea level and the impounded water has been estimated to weigh 160 000 million tons, the largest weight man had ever placed on the earth at the time. The lake is fed from rainfall on a catchment area of 663 817 km² extending over the countries of Angola, Zambia, South West Africa, Botswana and Zimbabwe.
Figure 1: Map of Lake Kariba showing the three Basins sampled, and locality of the lake (inset) on the Northern border of the country
The maximum depth is 120 m, while the mean depth is estimated at 29.5 m and approximately one quarter of the lake is less than 12 m deep.

The original valley was largely covered by Mopane woodland (*Colophospermum mopane*). Before flooding 97 126 hectares of this woodland was cleared, approximately half on each side of the lake (at a cost of six million dollars), for future fishing operations.

Geology:

The mid-Zambezi Valley constitutes the southernmost extremity of the East African rift system, while the Gwembe Valley (i.e. the valley in which Kariba lies) can be considered as structurally a huge asymmetrical faulted syncline with the steep limb on the Zambian side (Gair, 1959). The present form of the valley floor was generated by erosion adjusted to the underlying structure. Soft Karroo sediments (Sandstone and Escarpment Grit) dominate most of the Mid-Zambezi Valley floor and the Lake Kariba area (Coche, 1974). A rough estimate of the percentage composition of the Rhodesian shoreline has been provided by Bond (1965):

<table>
<thead>
<tr>
<th></th>
<th>%</th>
</tr>
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<tbody>
<tr>
<td>Molteno Series (grits, sandstone)</td>
<td>41</td>
</tr>
<tr>
<td>Forest sandstone</td>
<td>17</td>
</tr>
<tr>
<td>Lower Karroo Sandstone</td>
<td>8</td>
</tr>
<tr>
<td>Fine red marley sandstone</td>
<td>2</td>
</tr>
<tr>
<td>Basalt and interbedded sandstone</td>
<td>15</td>
</tr>
<tr>
<td><strong>TOTAL</strong></td>
<td><strong>83%</strong></td>
</tr>
</tbody>
</table>

13
The Karroo sequence in the Mid-Zambezi valley consists of several thousand metres of sediments (Reeve, 1963). The thickness of these deposits taper off in depth toward the outer valley margins. Thermal and mineral springs closely associated with Karroo formations are present in the valley (Mauffe, 1933).

Climate:

Climatically Kariba has two main seasons - the wet season lasting from December to April, and the dry season, from May to November (with occasional very slight precipitation during this period). The warm and cool seasons more or less coincide with these seasons, being from October to March, and May to September respectively. During the warm season 24 hr monthly mean air temperatures range from 22°C-29°C. During the cool season the lowest mean temperatures of 15°C-19°C are reached in June and July.

Between April and August cold and dry south-east winds blow over the lake. From September onwards they are replaced by warm and variable northerly winds. These winds are controlled by the prevalent synoptic atmospheric conditions and cover a large area. Other types of wind
which occur in the area are land and sea breezes, katabatic winds, and local winds and squalls associated with thunderstorms.

Evaporation is high and is estimated to range between 2 500 mm and 2 600 mm annually. Rainfall varies from 610 mm - 813 mm at the Kariba end, to 406 mm - 619 mm at the Binga end.

Lake History:

With the closure of the floodgates in December 1958, at the time of the incoming summer floods, the lake level rose rapidly from its river bed level of 391 m above mean sea level, and by July 1959 the lake was 58 m deep at the dam wall (449.97 m above mean sea level). Thereafter the lake level rose in a stepwise fashion with static and rising phases coinciding with the dry and wet seasons until July 1963, when the lake level rose above its normal operating level and reached 487.81 m a.m.s.l. The lake then dropped approximately 7 m over a period of four and a half months from September 1963 as water was released through the floodgates to excavate the stilling pool below the wall.

Since then (Fig. 2) fluctuations have been cyclic and of a lesser magnitude, generally between 2 m - 5 m resulting mainly from floodgate discharge to accommodate incoming Zambezi floods.
Figure 2: Lake level fluctuations from 1964 to 1979
The Central African Power Corporation's main aim has been to draw the lake level down to about 484 m by the end of December each year, and allowing the lake to rise to a level of about 487 m by the following May. Higher than normal inflows would require spilling between January and May. With the North Bank power scheme now operating it can be expected that retention level will be kept much higher, with water level fluctuations being much reduced.

Thus the lake has had two important phases in its history. The first covered the period from December 1958 to September 1963, when the lake was filling, and the second the period of cyclic fluctuations of between 2 m - 5 m each year. The first phase was marked by an increase of total dissolved solids in the water from 26 ppm in the old river to 65 ppm in the new lake (Harding, 1966) and represented one of extremely high productivity characterized by an explosive growth of many organisms, including plankton blooms, the water fern, *Salvinia molesta*, and various species of fish (Balinsky and James, 1960; Jackson, 1960; Hattingh, 1961; Boughey, 1963; Harding, 1964).

The second phase was marked by a decline in total dissolved solids (Harding, 1966), development of aquatic weed beds and a corresponding change in the invertebrate fauna (McLachlan, 1969), and changes in the composition of the ichthyofauna with the appearance of species not hitherto recorded in the lake (Donnelly, 1970; Bell-Cross, 1972; Balon, 1974; Kenmuir, 1977). *S. molesta* declined steadily during this period to a fractional proportion of its initial
highest density level in 1962.

Limnology:

Limnological data on Lake Kariba has been contributed by Harding (1961, 1962, 1964, 1966); Coche (1968 and 1974); Begg (1970) and more recently by Bowmaker (1976), who concentrated on the Mwenda River mouth.

Thermal stratification in the lake was recorded as early as November 1959, less than a year after it began filling, and thereafter this pattern was repeated each year, i.e. October, November, December with stratification forming at the beginning of the hot season in September and being well established throughout the ensuing summer months (Harding 1961, 1966). Following the rainy season (November to April) and the cool season Harding found that the thermocline had moved to a greater depth and turnover normally took place in winter in July, after which dissolved oxygen penetrated to the bottom. Harding also found that the period of de-oxygenation of the hypolimnion after the thermocline had formed grew shorter each successive year; this was attributable, he felt, to the gradual decline in the biological oxygen demand, as productivity of the lake and thus decomposition in the hypolimnion decreased. Hydrogen sulphide, for example, was found in the hypolimnion for a period of several months before turnover in 1960 and 1961, but by 1964 it was first detected only three months before turnover.
Also of interest at this time (1962 and 1963) was a "pool" of colder water found near the bottom throughout the "deeps" in all parts of the lake. Conductivity measurements indicated that it was water of a different type and origin from that of the overlying lake, and it was suggested this water originated from the Zambezi inflow.

Coche (1968), on the basis of data collected in 1965, defined Lake Kariba as a warm monomictic reservoir whose physical characteristics were dependent upon the Zambezi River (upper third of the lake) and the climatic conditions (lower half of the lake). He found the annual thermal range of the water mass from 17°C - 32°C, with homothermy occurring at 22°C - 25°C, and overturn taking place between March and July at about one month intervals from one basin to the next lower one (i.e. moving towards the dam wall). The main metalimnion (thermal drop equal or greater than 0.2°C m⁻¹) was rarely found at a depth greater than 35 m and involved a water layer less than 10 m thick. Great variations in chemistry (pH, total alkalinity, and specific conductivity) were found to exist from basin to basin, with dissolved inorganic nutrients increasing from the upper basin towards the lower end of the lake. Hydrogen sulphide was found only in the hypolimnion in deep valleys and only towards the end of the stagnation period.

Begg (1970), on the basis of work conducted in 1967, confirmed much of Coche's work, and described Lake Kariba as monomictic and mesotrophic, with five well defined basins (Fig.1) each of which exhibited its own individuality.
The two upper basins he defined as riverine, flushed out in May by the Zambezi River floods and assuming turnover characteristics earlier than the other three basins, which he regarded as lacustrine in nature, with turnover induced by temperature. He found great amplitude of variation in water chemistry existed in relation to the basin locality, biotope (river, estuary, cleared area, open water), time of year and depth. Generally, values of dissolved oxygen, conductivity, alkalinity and pH fell from surface to bottom. Dissolved oxygen in the hypolimnion was depleted four to five months after turnover, with a sharp oxycline at the thermocline, as had been noted by Coche (1968). Surface oxygen values decrease at turnover as a result of mixing.

Figure 3: Temperature profiles for different months in the Sanyati Basin. Mixing of hypo- and epilimnion generally occurs in July (from Begg, 1970)
Bowmaker (1976) concentrated his studies on the Mwenda River mouth, and drew attention to the fact that this river, and hence presumably other rivers, was an important source of potassium, phosphorous and nitrogen to the lake. Nitrate concentrations were found to be of the order of ten times the concentration found by Coche (1968) elsewhere in Lake Kariba. Bowmaker also found an oxycline occurred in association with the thermocline, unless disrupted by density currents originating from the river. He states that the established thermal regime of the warm monomictic Lake Kariba follows a regular annual cycle, where the water mass overturns and reaches homothermy at between 21.4°C and 23.4°C between March and July, with restratification normally starting in September and the metalimnion thereafter moving progressively towards the bottom. In most cases the top of the metalimnion reaches 20 m by February of each year.

Plant Life:

Rooted aquatic plant life began developing in 1964 (McLachlan, 1969), and since then the following species have become important in Lake Kariba: *Ceratophyllum demersum, Lagarosiphon ilicifolius, Ludwigia erecta, Ludwigia stolonifera, Naias pectinata, Phragmites mauritianus, Polygonum senagalense, Potamogeton octandrus, Potamogeton schweinfurthii, Potamogeton thunbergii, Typha latifolia, and Vallisneria aethiopica*. Species occurring seldom or in more restricted habitats, include *Lemma perpusilla, Nymphoides indica, Pistia stratiotes, Polygonum aviculata, Polygonum lapathifolium*, and
Marginal fringes of the lake, the draw-down zone, are largely colonized by meadows of the semi-aquatic grass, *Panicum repens*, the extent of these meadows depending on topography. From Sengwa westwards the floating grass *Vossia cuspidata*, makes its appearance. During periods of exceptionally low lake level various species of sedges rapidly colonize the exposed substrate. These include species of *Cyperus*, *Fimbristylus*, *Pycreus* and *Scirpus*. *Scirpus cubensis* is a common colonizer of sudd mats.

The aquatic plants, excluding floating forms, are detrimentally affected by rapid and extreme rises in lake level, and develop best under a regime of minor lake level fluctuations over a period of several years (Bowmaker, 1973b; Kenmuir 1975). Plant life generally extends down to 8 m at normal operating level (484 m.a.m.s.l.), although very small stands may occasionally occur down to 11 m (pers. obs.).

Two species of floating aquatics recorded are *Pistia stratiotes* and *Salvinia molesta*, the former unimportant and usually only found in river estuaries. *S. molesta* reached maximum density level in 1962 and thereafter declined to the extent that today it is confined to small bays and backwaters of river estuaries. The *S. molesta* situation has been monitored in recent years by the Fisheries Research Institute. Comment on its decline in relation to the mussel fauna is made in the final discussion.
Fish Life:

The exact number of species of fish in Lake Kariba at present is in some doubt, due partly to some confusion in identification (notably involving the Labeo species), and partly to the fact that some species may have entered the lake from above the Victoria Falls, or from upland streams. The figure probably stands at about forty-two.

Since impoundment commenced interesting fish population changes have taken place (Kenmuir, 1977). The overall picture has been one of an initial fish population explosion, a gradual decline of those species (Distichodus spp., Labeo spp) more adapted to a riverine habitat (particularly in the more lacustrine East Basins), the establishment of cichlids (Haplochromis codringtoni, Pseudocrenilabrus philander, Tilapia rendalli, Sarotherodon mortimeri) and other stillwater loving species (e.g. members of the family Mormyridae) and the possible arrival of additional species (Haplochromis spp. Serranochromis spp.) in the lake. Initial successful species were mostly fecund herbivorous species (Distichodus schenga, Distichodus mossambicus, Labeo altivelis, Labeo congoro, Sarotherodon mortimeri), while later successful species are mostly benthic invertebrate feeders (Eutropius depressirostris, Haplochromis codringtoni, Hippopotamyrrus discorhynchus, Marcusenius macrolepidotus, Mormyrus longirostris, Synodontis zambezensis). A hitherto empty niche which has been filled in recent years is that of the open water or pelagic zone, where Limnothrissa miodon, the freshwater sardine, has proved extremely successful after its introduction to the lake from Lake Tanganyika in 1967/1968.
2. Comments on the Main Kariba Study Areas

Originally it had been intended to sample the whole of Lake Kariba, but a security curfew imposed on all civilian boat movements west of Bumi Hills made this impossible. Studies have, therefore, been confined mainly to the area east of Bumi, that is, Basins Four and Five, also referred to as the Bumi and Sanyati Basins. (Fig. 1). Some sampling was done west of Bumi as far as the Sengwa Basin, while I was on Security Force duties.

Physical Characteristics:

Basins Four and Five are characterized by having both cleared and uncleared areas with fairly large tracts of very shallow sloping ground and smaller areas of steeply shelving ground usually adjacent to the dip slopes of escarpments fringing the shorelines. The combined area is fed by numerous streams and rivers of which the largest, and only perennial river, is the Sanyati. The four main streams of Basin Five are the Charara, Naodza, Gache Gache and Sanyati while the main streams of Basin Four are the Bumi and Sibilobilo rivers. (Fig. 4). Both areas include a number of islands, usually characterized by having, on opposite sides, steeply shelving and gently shelving shorelines, although a few of the islands (notably Fothergill, Spurwing, Long Island and Tsetse) have all-round shallow sloping gradients. Most of the islands have their origin mainly in geological faulting and as a result are mainly found in chains or lines (Coche, 1974).
Figure 4: Map of Bumi and Sanyati Basins showing localities mentioned in text
Substrates of the study area are composed of varying sand/silt/clay combinations, depending on locality. In most localities the bulk of this combination is composed of medium to fine sand.

Soil samples taken from 7 m depth in two of the main cleared areas, Lakeside and Sanyati East, and analysed in the laboratory by washing them through filter sieves and categorising according to Wentworth's classification (Welch, 1948) gave the following results:

<table>
<thead>
<tr>
<th></th>
<th>Lakeside</th>
<th>Sanyati East</th>
</tr>
</thead>
<tbody>
<tr>
<td>% Coarse Sand</td>
<td>7</td>
<td>14</td>
</tr>
<tr>
<td>% Very Fine/Medium</td>
<td>74</td>
<td>60</td>
</tr>
<tr>
<td>% Silt/Clay</td>
<td>19</td>
<td>26</td>
</tr>
</tbody>
</table>

The greater silt/clay component at Sanyati East is probably attributable to the influence of the Sanyati River, which flows strongly into the lake west of the cleared area during the rains. Winds then blow this water onto the cleared area. The above results agree with soil analyses done by the Government Analyst for Begg (1971), from various stations on the perimeter of the Sanyati Basin, in which medium/fine sand predominated, with lesser fractions of silt/clay, and coarse sand.

Four additional soil samples taken along a transect from 5 - 11 m depth in the Sanyati East cleared area yielded sediments containing 80% - 85% sand (particle size
0.02 - 2.0 mm) and 15% - 20% silt and clay (particle size 0.002 - 0.02 mm) The pH values of these samples, determined by the Government Analyst, gave values ranging from 5.6 - 6.3, slightly acid to near neutral. Two samples from the Nyanyana Estuary had pH values of 5.3 and 5.6 or medium to slightly acid. Begg's samples for Sanyati were comparable at 4.9 - 6.0. In general therefore it would appear that substrate sediments in the study area range from neutral to medium acidity.

Vegetation:

The shorelines generally are covered with the well established lake grass, _P. repens_, and can be classified as good game country; the Matusadona National Park lies adjacent to approximately half of Basin Four, while the area west of the Bumi River also supports considerable game. The Kariba Parks and Wildlife Land lies adjacent to approximately half of Basin Five. The remaining half is Tribal Trust Land where some game still exists. The presence of game on the shores is of more than academic interest since McLachlan (1971) has shown that faeces dropped on lakeside grass by game animals releases considerable nutrients to the water when the lake rises to inundate the grassy shores.

The only submerged aquatic plants recorded in the study area were _Ceratophyllum demersum, Lagarosiphon ilicifolius, Naias interrupta, Vallisneria aethiopica_, and three
species of Potamogeton (P. schweinfurthii, P. thunbergii, P. octandrus). These have been found to occupy rather broadly defined and in some cases overlapping zones in the littoral areas, within the 0 - 12 m depth zone. Observations made prior to this study in 1974 (Kenmuir, 1975) were combined with observations made in this study to produce a histogram (Fig. 5) showing the number of times the main species were observed at various depths (depths determined against a standard depth of 484 m.a.m.s.l.)

Figure 5: Depth distribution of plant species in the Sanyati and Bumi Basins. The majority of plants occur in the 0 - 6 m depth range.

The histogram shows that the main depth zone for submerged plants lies between 0 - 6 m. Below this
depth only 3 species were recorded, while none were recorded below 11 m. The distribution of aquatic plants has some relevance to this study of bivalves and this will be discussed in the appropriate sections later.

The depth distribution of submerged aquatic plants and algae and hence other organisms and animals associated with them is, in the absence of other limiting factors, related to light penetration.

Physico-chemical Limnology:

Coche (1968) did a comprehensive limnological survey of Lake Kariba, which included measuring the Relative Light Intensity (R LI) in various parts of Basins Four and Five. His findings, in summary, were that in most cases 50% of the surface radiation is absorbed within the first two metre layer of water, while the 2% value was recorded at depths ranging from 9 m - 16 m at various times and places. If one considers that the range of R LI which is effective for photosynthesis leading to plant production is from 100 to above 2% (Welch, 1948) the depth at which plants will cease to grow in the study area should be somewhere between 9 m - 16 m, assuming there are no other limiting factors. The 11 m depth actually recorded falls within this range.

The possibility exists that oxygen and not light is the limiting factor involved in the distribution of
heterotrophs, and hence its presence, or lack of it, is relevant to the distribution of flora and fauna. Coche (1974) has stressed the importance of identifying water masses with a low dissolved oxygen (DO) content because of their major impact on aquatic organisms in general, and he considers that, on the basis of other studies on the relationship of animals and oxygen, contents lower than 2 mgl$^{-1}$ will limit fish distribution, and presumably influence other animals as well. He found DO concentrations of 2 mgl$^{-1}$ as shallow as 15 m in January with the depth of such presumably habitable waters decreasing until April/May (approaching turnover), when this DO level can be as shallow as 10 m. Thus the volume of the potential trophogenic zone (down to about 25 m) for organic production will be greatly reduced under such conditions because of the lack of O$_2$ in its bottom half. Taking into account both R L I at the 2% level and DO at the 2 mgl$^{-1}$ level, one can expect the limits for existence of longer living benthic organism in the litteral zone to be somewhere between ten and sixteen metres. In this context, the depth distribution of mussels is discussed in PART ONE, where the tolerance of one species of mussel to low O$_2$ concentrations is also mentioned. The mussel population in fact starts dwindling towards zero at approximately 11 m (Fig. 18). Shorter living animals are not similarly inhibited and colonization of deeper sections of the lake takes place after turnover, when oxygen penetrates to the bottom (McLachlan, 1970; Bowmaker, 1973 a)
Nutrient Status:

In this study, for the purpose of comparing sample populations in terms of mean size of individuals and also density, three basic areas (biotopes) were considered - river estuaries, open marginal areas (away from rivers, generally the cleared areas), and islands. In terms of water quality, the river areas (estuaries) are richest, bringing nutrients into the lake (Caulton, 1970; Coche, 1974; Bowmaker, 1976) and generally increasing biological productivity in their immediate vicinity. The Table below is extracted from Caulton (1970) and gives comparative values of three nutrient categories from three different biotope regions - riverine regions, shallow marginal regions and deep lake stations.

The results in Table 1 show that in most respects the riverine areas have the highest nutrient values, the shallow marginal areas being intermediate and the deep lake areas having the lowest values. This is true in the case of TDS values at the surface (0m) and phosphate phosphorous values below the surface. In the case of nitrate nitrogen values this is highest in the riverine areas below the surface, lowest in the marginal areas, and second highest in the deep lake areas. Presumably the low nitrate nitrogen values in the cleared areas are as a result of the rapid utilization of this nutrient by aquatic plants which are abundant in these areas, and less abundant in the riverine or estuarine areas because
Table 1: Comparative chemical values from three different biotope regions (from Caulton, 1970)

<table>
<thead>
<tr>
<th>STATION</th>
<th>DEPTH</th>
<th>TDS mg 1-1</th>
<th>NO3-N μg 1-1</th>
<th>PO4-P μg 1-1</th>
<th>CATEGORY</th>
</tr>
</thead>
<tbody>
<tr>
<td>Redcliffe</td>
<td>0</td>
<td>60</td>
<td>9,5</td>
<td>3,9</td>
<td>Deep Lake</td>
</tr>
<tr>
<td></td>
<td>11</td>
<td>-</td>
<td>11,2</td>
<td>2,0</td>
<td></td>
</tr>
<tr>
<td>Long Island</td>
<td>0</td>
<td>69,5</td>
<td>4,7</td>
<td>4,3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>-</td>
<td>4,5</td>
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<tr>
<td>Lakeside</td>
<td>0</td>
<td>62,5</td>
<td>4,1</td>
<td>10,0</td>
<td></td>
</tr>
<tr>
<td>Cleared Area</td>
<td>6</td>
<td>-</td>
<td>4,3</td>
<td>10,4</td>
<td></td>
</tr>
<tr>
<td>Gache Gache</td>
<td>0</td>
<td>75</td>
<td>2,8</td>
<td>11,4</td>
<td>Shallow</td>
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<tr>
<td>Cleared Area</td>
<td>7</td>
<td>-</td>
<td>2,8</td>
<td>9,0</td>
<td>Marginal</td>
</tr>
<tr>
<td>Sanyati East</td>
<td>0</td>
<td>80</td>
<td>3,0</td>
<td>12,9</td>
<td></td>
</tr>
<tr>
<td>Cleared Area</td>
<td>10</td>
<td>-</td>
<td>3,6</td>
<td>9,7</td>
<td></td>
</tr>
<tr>
<td>Gache Gache</td>
<td>0</td>
<td>85</td>
<td>7,2</td>
<td>9,2</td>
<td>Riverine</td>
</tr>
<tr>
<td></td>
<td>7</td>
<td>-</td>
<td>11,5</td>
<td>22,5</td>
<td></td>
</tr>
<tr>
<td>Naodza</td>
<td>0</td>
<td>78</td>
<td>3,0</td>
<td>7,2</td>
<td></td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>140</td>
<td>6,1</td>
<td>15,0</td>
<td></td>
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<tr>
<td>Charara</td>
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<td>8,7</td>
<td>7,9</td>
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<tr>
<td></td>
<td>6</td>
<td>-</td>
<td>6,1</td>
<td>7,9</td>
<td></td>
</tr>
</tbody>
</table>
of silt-laden water flowing there for several months of the year and limiting effective light penetration.

Bowmaker's study (1976) of the physico-chemical limnology of the Mwenda Estuary clearly showed that the Mwenda River was an important source of potassium, phosphorous and nitrogen to the Lake. Nitrate concentrations in particular were extremely high.

Human Occupation:

With regard to human occupation and habitation of the study area the cleared areas of both basins are commercially fished with gill nets (with the exception of the lakeside cleared area) while the open waters of Basin Five and Basin Four are fished at night for sardines. Recreational angling takes place in nearly all parts of the study area, in particular the sheltered bays and river estuaries.

The shoreline from the dam wall to the Charara River is the most settled, comprising the Kariba Township area on the Northern coastline and smaller areas of habitation of various types (angling camps, an African township, crocodile farm etc.) on the eastern coastline. A number of African fishing villages are situated between the Naodza and Sanyati Rivers, while westwards of the Sanyati as far as the Bumi the shoreline is virtually uninhabited, including only resident Game Department personnel (at Tashinga Camp)
and two tourist safari outfits on islands offshore. The area between the Bumi Estuary westwards as far as the Kota Kota narrows is also sparsely populated by a few African fishermen, a small settlement of sardine fishermen, and a small settlement at Bumi Hills comprising an hotel and some Government personnel.

Plate 2: Aerial photograph showing the Gache-Gache sub-basin in the foreground, the Gache-Gache Estuary above that, Tsetse Island to the right of Tsetse Gap, which leads into the Sanyati East cleared area, with the Matusadona mountains in the background
Plate 3: An example of a suitable substrate for mussels. The Lakeside cleared area at low level (482 m.a.m.s.l.) in December 1973. Note the shrub stumps remaining which would interfere with dredging operations, the S. molesta being stranded, and the Kariba Township hills in the background. Some of the depressions are T. rendalli nests.

Plate 4: Showing a typical uncleared area (background) with cleared area in the foreground. Charara Estuary, taken in October 1973, when lake level was falling. Note the stranded, brown S. molesta in the foreground, and the white silt deposits in the cleared area.
Plate 5: The Lakeside cleared area at high water level (486.5 m.a.m.s.l.) in April 1974. These shallows are generally transient, overlying vegetation (e.g. P. repens beds) and do not support mussels.

Plate 6: An example of an uncleared area supporting few mussels because of extremely rocky substrate. Entrance to the Yacht Club Harbour, December 1973. Note the complete lack of colonizing vegetation on the exposed shoreline.
3. **Description of Lake McIlwaine**

**General:**

Lake McIlwaine lies 37 km South West of Salisbury on the central Zimbabwean Plateau at an altitude of 1 368.5 m a.m.s.l. and at 17°54'S : 30°48'E. It was built in 1952, primarily to provide water for Salisbury, but is now also utilized extensively for recreational purposes and commercial fishing. It has a surface area of 2 360 ha, a capacity of $250.4 \times 10^6$ m$^3$, length of 14.4 km, maximum width of 8 km, a mean depth of 9.4 m and a maximum depth of 27 m. The main inflow is provided by the Hunyani River, draining an area of 2 230 km$^2$, and to a lesser extent by the smaller Makabusi and Marimba rivers.

**Geology:**

The dam wall is built on banded ironstone, but most of the lake lies over granite. The catchment area is comprised mostly of granite, but outcrops of dolerite and banded ironstone occur. Basement schists are found in the northern area of the catchment (Tyndale-Biscoe, 1957).

**Climate:**

Although within the tropics the climate is generally cool. Broadly speaking there are three seasons:
Figure 6: Map of Lake McIlwaine showing sampling areas and locality of the lake (inset)
(1) The rainy season, in summer, from November to April, when temperatures average about $20^\circ$C, with a mean diurnal variation of about $12^\circ$C.

(2) The cold dry season, in winter, from May to August, when temperatures average about $14^\circ$C, with a mean diurnal variation of about $14^\circ$C.

(3) The hot dry season, in summer, from September to November, when temperatures average about $22^\circ$C, with a mean diurnal variation of about $12^\circ$C. The height of the rainy season is from December to February.

Limnology:

A characteristic feature of the lake is that treated sewage is discharged into the lake with a consequent highly eutrophic state developing (Marshall and Falconer, 1973b) although this has declined somewhat since sewage diversion started in 1968 (Williams, 1970; Marshall, 1978b). Eutrophication has resulted in a permanently high population of blue-green algae, first reported in 1960 (Junor, 1964) and comprised predominantly of *Microcystis aeruginosa* and *Anabaena flos-aquae* (Falconer, 1973).

The lake has a monomictic physico-chemical pattern, with stratification in summer and isothermal conditions in winter (Marshall and Falconer, 1973a). The thermocline however is weakly developed. Beadle (1974) has suggested that de-oxygenation of the bottom water in summer is enhanced by its eutrophic state.
Benthic fauna is influenced by eutrophication and water level fluctuations and consists of few species (Marshall 1978b). The most abundant benthic animal was Branchiura sowerbyi with Limnodrilus hoffmeisteri common in the more organically polluted areas. Chironomid larvae are seasonally abundant, occurring most commonly from December to April (Munro, 1966; Marshall, 1971). The lake is also characterised by a large population of freshwater mussels, which dominates the biomass (Marshall, 1975; Kenmuir, this report). These are affected periodically by lake level fluctuations. The crab population contributes fairly substantially to the benthic fauna in the shallows (Templeton, 1979).

Plant life:

Beds of water lilies, Nymphaea caerulea once occupied about 40% of the shoreline (Munro, 1966) but these are no longer common. Submerged vegetation is scarce to non-existent, a state attributable to the herbivorous fish (Junor, 1969), the shading effect of planktonic algae, and lake level fluctuations. Macrophytic vegetation consists primarily of stands of bullrushes, Typha latifolia, beds of the weed Phragmites mauritianus, Polygonum spp., and various grasses and sedges. Exposed shorelines due to lake drop are colonised rapidly by vegetation, in which Polygonum spp. are important. Floating macrophytes are represented by the water hyacinth Eichornia crassipes which reached epidemic proportions on the lake's surface in 1971, covering more than 30 ha, after control measures had
been relaxed (Marshall, 1978 b). Since then persistent and successful control measures keep this plant restricted.

Fish life:

Twenty five fish species are reported from the lake of which seven are important for angling or commercial fishing. Of these twenty five species four have been introduced, two intentionally, and two accidentally. Sarotherodon macrochir was introduced early in the lakes history, and rapidly displaced the indigenous Sarotherodon mossambicus to become the main commercial species. Tilapia rendalli was introduced as an angling and commercial species, and to control aquatic vegetation, but its importance has declined following the decline of vegetation. The carp, Cyprinus carpio, and black bass, Micropterus salmoides, reached the lake accidentally and have not established well. Of the indigenous species, the tigerfish, Hydrocynus vittatus, Hunyani labeo, Labeo altivelis, and catfish, Clarias gariepinus, are the most important contributing substantially to the commercial fishery and also to a lesser extent to angling. Small important indigenous species are the dwarf bream, Haplochromis darlingi, and the imberi, Alestes imberi, which contribute to the African subsistence fishery as well as being heavily utilized by birds. Total fish production has been estimated by Marshall (1978a) as about 300 tonnes per year (100 kg ha\(^{-1}\) year\(^{-1}\)) of which one third is commercial, the remainder taken by fish poachers and anglers.
Bird Life:

Bird life on and around the lake is prolific. Jarvis (pers. comm.) reports 255 indigenous species recorded at a bird sanctuary on the lake shore. Piscivorous birds include the white breasted cormorant, Phalacrocorax carbo, the reed cormorant, P. africanus and the darter Anhinga rufa, plus numerous king fishers. Nine species of herons are recorded and fish eagles Haliaetus vocifer are present.

Human Occupation:

Being a multi-purpose body of water in which recreation figures prominently, the North bank of the Lake is dotted with a number of recreational resorts as well as the Research Centre plus attendant staff residences. Most of the South bank is game park with tourist facilities and staff quarters. Both the North and South banks of the Upper Reaches are farmland, while at the other end of the lake on the South bank, outside the game park, is a commercial gill-net and seine net fishery.
Plate 7: The exposed beach at Pelican Point, where the depth distribution study was undertaken

Plate 8: The Upper Reaches of the lake where the Hunyani River flow merges with the lake. A greater diversity of mussel species was recorded here
PART ONE - THE STOCK

DISTRIBUTION, SPECIES COMPOSITION, DENSITIES, POPULATION STRUCTURES, MORTALITY

INTRODUCTION

In any management program of a fishery resource, one of the early requirements, in fact a prerequisite, is to identify and describe the stock. In order to determine the various population parameters that would meet this requirement in a vast and heterogenous lake such as Lake Kariba, methods of sampling had to be devised which were (i) quick and easy to implement (ii) adaptable to any habitat the lake could offer, and (iii) would provide meaningful results capable of being interpreted with a reasonable measure of confidence in terms of the distribution and composition of the stock, relative and absolute densities, and the structure of the populations. Painstaking methods which gave an accurate and detailed analysis of a small portion of the lake while neglecting the vast remainder were not applicable, and in fact could well have given a distorted picture if extrapolated to the lake as a whole. A number of methods were tried and assessed before choosing the most suitable for the requirements of this study.

In addition to describing the stock a concurrent study of fish predation on the stock was run in order to determine the impact of this form of mortality, and to evaluate mussels as a dietary component of fish. A low degree of predation would strengthen the argument for commercial
cropping, whereas a high degree might signal caution in interfering with the food resources of animals which are themselves commercially important.

Finally, a follow-up study on the mussels of Lake McIlwaine was undertaken, in order to provide useful comparative data for the Lake Kariba study, and to evaluate the present status of stocks in this lake.

MATERIALS AND METHODS

A. LAKE KARIBA

1. Field

A variety of methods are available for bivalve collection. Limnological textbooks list core samplers, grabs, towing dredges, air-lift pumps and scoop nets, or collection by hand or shovel, as the methods most commonly used. The efficiencies of these various devices are discussed by Flannagan (1970) and McIntyre (1971). The first method considered was the use of a Petersen grab used by Begg (1971) in a survey of the benthos of the Sanyati Basin. The efficiency of this method under conditions at Lake Kariba is revealed in Begg's report, which records only two bivalve species out of a known total of four, in samples taken from a wide area of the lake.

Similarly, in benthic sampling programs conducted
at Lakeside, where sampling during this study has shown four species to occur, both Joubert (1975) and Mitchell and Gahamadze (1976), using a van Veen grab, recorded only one and two species respectively. Bowmaker (1973a), sampling the Mwenda Estuary, had greater success with the van Veen grab, in that he recorded three species, but he remarks on the difficulty of obtaining "good" samples, and cites an occasion where the grab had to be dropped 43 times to obtain 5 acceptable samples. Flannagan's experiments in Lake Ontario (1970) showed that no one sampling device will give satisfactory results in all of the sediments and substrates in lakes, and he warned against placing too much value or faith in 'quantitive' results obtained from these devices.

In the light of these results, (and based on preliminary field trials using the Petersen grab) it was realised that sampling with grabs would not only be extremely time consuming, but also in many cases impractical and inefficient and likely to lead to erroneous results. The idea of using a grab for sampling, other than to provide comparative results, was thus abandoned.

The second possibility was a towing dredge of some sort, along the lines of those tested by Greenway (1969) in the Firth of Thames in New Zealand. Here again, preliminary diving observations had shown that mussels occurred amongst the many trees in uncleared areas, amongst beds of aquatic plants, and amongst rocks in rocky areas. In addition, although the cleared areas are ostensibly "cleared", numerous small stumps and root entanglements remain. Such conditions
would render use of a dredge impractical for sampling purposes in many areas, and consequently this idea was not pursued.

A third method considered, and tested, was the use of an air-lift pump, similar in principle to that described by Pearson et al (1973). In this case the method consisted of feeding air from an air cylinder via a tube to the mouth of a wide bore rubber hose, pressed close to the substrate. Material brought to the surface through the hose was directed through a mesh screen. Preliminary trials showed the method to be effective on soft and yielding substrates but limited in "weed" or "stick" areas where the sucking or inhalent nozzle was apt to become clogged by debris of one sort or another. These tests also showed that the air-cylinders supplying the air were used up fairly rapidly, a factor which could prove to be a continual nuisance and limiting in widespread sampling.

A fourth possibility was to determine distribution and relative abundance by shell collections on the shorelines as used at Lake McIlwaine by Marshall (1975). This method depends on a drop in lake level with resultant stranding of mussels, and such conditions did not occur at Lake Kariba during this study. Lake levels, in fact, were very much higher over the study period than in previous years.

After considering these various methods and undertaking trials the method eventually selected as the most suitable for determining species composition, distribution and relative density over a large area of the lake encompassing
widely differing substrate conditions and depths involved free-diving and collecting mussels by hand from the bottom. The fairly clear visibility of Lake Kariba assisted greatly in the application of this method. An advantage was that the mussels could be actively looked for under rocks, fallen trees, branches and bark, and in the cracks and crevices of the roots of big trees. No mechanical sampler could have recorded mussels in these places, or in the hard rocky or pebbly substrates which occurred in some areas. The number of dives was usually 5 to 10, although occasionally more where mussels were scarce, each dive was timed, and the time taken to reach the bottom and then to return to the surface was taken into account. (This was determined in separate trials). Diving times were from 1 - 2 minutes for each dive, and the actual collecting time somewhat less.

The total collecting time could be related to numbers and mass of mussels collected, and different areas and depths compared. The advantage of this method was that a large number of areas involving any type of habitat could be sampled in a fairly short time. Some care had to be taken in areas where hippopotami, crocodiles, bilharzia, or submerged gill nets were or could have been a hazard. A further factor which influenced the choice of this method is that the future commercial cropping of mussels could be by diving, and hence experimental data collected this way would be of value for predictive and comparative purposes at a later date.

Using this method, sampling over a wide area of
the lake in Basins Three to Five in cleared and uncleared areas, river estuaries and off-shore islands took place from March 1976 to March 1977. Sampling in Basins One and Two was prohibited for security reasons, and, in fact, most of the sampling in Basin Three (the Sengwa Basin) took place while I was stationed there on Security Force duties.

With regard to more quantitative sampling, experiments showed that the most effective and easy method (weather permitting) was to place a $\frac{1}{2}$ m$^2$ grid on the substrate and remove all the mussels enclosed by the grid, using aqua lungs. The oblong shaped grid was divided into "compartments" by bars, and each compartment was thoroughly searched before moving onto the next. When the procedure was complete, it was repeated, and then finally the whole quadrat was given a last quick inspection.

Figure 7: The sampling grid used in the Sanyati East cleared area
At the termination of the collecting the grid was lifted off the substrate by a rope from the research vessel anchored overhead, moved to another position and gently lowered onto the substrate, where the procedure was repeated. Mussels collected were placed in a bag. Generally, three or four quadrats (1½ m² - 2 m²) could be cleared before the aqua-lungs had to be pumped up again.

This grid sampling was done in a selected area, the Sanyati East cleared area, along three transects from shallow (approximately 2 m) to deep water (11m). This sampling was not attempted in water shallower than 2 m because of thick Panicum repens beds (Lake grass) covering the bottom. Because I was diving alone I limited my activities to a maximum depth of 12 m, where the mussel beds were reaching zero densities. The first transect was situated at the western end of the cleared area, adjacent and parallel to the tree line (West Transect). The second transect was situated halfway along the cleared area (Central Transect) while the third transect was situated at the eastern end of the cleared area (East Transect). Two to three square metres were sampled in each depth zone. Ideally the same area should have been sampled at each zone, but frequently adverse weather conditions (mainly wind and wave) necessitated limiting the area to less than was desired in some instances. This sampling was done in February and March 1977, when most of the distribution and relative density sampling involving free-diving had been completed.
Figure 8: Sanyati Basin showing cleared and uncleared areas and transect lines in the Sanyati East cleared area
In addition to grid sampling here some results were also obtained from other areas. It had been my intention to do more intensive grid sampling in selected areas around the lake, but this was not possible because of a transfer. Some Petersen grab sampling was also done in Sanyati East, and in October 1978 a follow-up trip to Lake Kariba was undertaken to sample the Sanyati East area again to see if the stock showed any alterations from the earlier picture obtained. On this follow-up trip, a Petersen grab was again used as well as a mollusc scoop in order to assess any possible mussel recruitment.

Figure 9: The scoop used to try and collect baby and juvenile mussels

2. Lake Level Fluctuations

A problem encountered during field sampling was a fluctuating lake level. Because of the large area to be covered and demands made on time by security force commitments it was not possible to complete the field
sampling in a relatively short period, thus sampling extended over a period of a year. This meant that lake levels at different times of sampling varied, and 6 m in June in one locality could well be 5 m in August. Since various parameters of the mussel populations were to be examined in relation to depth (mean lengths and density, for example), it was necessary to fix a standard lake level (in metres above mean sea level) to which each sampling area at a particular time could be related.

![Lake level frequencies, 1962 - 1977](image)

**Figure 10:** Lake level frequencies, 1962 - 1977

The lake level which had occurred most frequently between 1962, when lake levels reached 480 m.a.m.s.l., and March 1977, approximately half way through this study, was chosen
as the standard level, since this level would have had most influence on the development of the lake mussel beds.

Using midpoint and endpoint lake levels of each month in this period as data, a histogram was compiled (Fig. 10) which shows the lake level mode to be 484 m.a.m.s.l. This figure is also the official normal operating level. Thus an area with a depth of 6 m at a lake level of 486 m.a.m.s.l. would in fact be at a depth of 4 m at the standard lake level of 484 m.a.m.s.l. All analyses for this particular time would then be related to a depth of 4 m, and not 6 m. In all cases where cited, unless otherwise stated, depth refers to this standard depth and not the actual depth at the time of sampling.

3. Predation

Stomach contents of a number of benthic feeding species caught in a mixed fleet of gill nets in the Nyanyana Estuary of the Lakeside cleared area were examined on a weekly basis from June 1976 to June 1977. This area was chosen because of its proximity to the Research Institute, because diving had shown all four species of bivalves were present, and because benthic feeding fish species are generally well represented in river estuaries. In addition, stomachs of fish caught in a fleet of mixed mesh gill nets set offshore away from the estuary in the Lakeside cleared area were examined from March 1976 to June 1976. (This station designated Lakeside Cleared Area). Nets were also set in a few other localities of the Sanyati Basin (Charara,
Fothergill Island, Tsetse Island and Hydro Bay), and stomachs of benthic feeders caught in those nets examined. The frequency of occurrence methods was used to present the results of the analysis.

In addition to this study, a fairly comprehensive picture of predation on mussels was obtained from the studies of workers who have looked at the diets of a variety of species over the years. These are Matthes (1968), Donnelly (1970), Kenmuir (1970), Begg (1971), Burne (1971), Bowmaker (1973a), Joubert (1975), Mitchell (1976), and Mitchell and Gahamadze (1976).

B. LAKE MCILWAINE

In April 1979 Lake McIlwaine stopped spilling and lake level started dropping slowly. By August the lake level had dropped approximately 1 m, leaving the shallows exposed and mussels stranded on the beaches. Quantitative sampling was undertaken at various points around the lake on the 30th July and 1st August, starting at the juncture of the Hunyani River and the lake. (Fig. 6). The sampling involved measuring out 5 m x 5 m quadrats on the exposed beach, depending on the space available, and collecting all the mussels within the quadrats to establish species composition and density. Where densities were very low additional data was obtained by randomly collecting stranded mussels along the beach and thereby accumulating sufficient length data to establish size structures of the populations,
and species composition. A further sampling trip was undertaken on the 13th and 14th October 1979, when the lake had dropped another metre. Thus a direct comparison, in relation to the lake depth, could be made between the two populations.

Prior to the lake level dropping, thus facilitating mussel sampling and removing the need for sampling gear, a mussel dredge had been designed and built for use in the shallower marginal water.

Figure 11: The dredge(A) and catching bag (B) built for sampling in Lake McIlwaine. Components are: (i) rings for towing rope, (ii) adjustable scooping blade, (iii) skid for stability and maintaining even keel, (iv) attachment rope for heavy weight to prevent rear end lift, (v) removable back grid to attach bag with screws. For quantitative sampling (bag attached) sheet metal plates can be inserted to sides and bottom to prevent loss of substrate.
This was tested off Pelican Point and found to be suitable for sampling - the only proviso being that the digging blade should have been longer as it tended to slice into the bigger *M. dubia*. However, small *C. mossambicensis* were successfully recorded here using this dredge. Although not used in this program it is illustrated here because of its potential for use in sampling sandy or muddy substrates of the deeper waters of rivers, or dams or lakes. The dredge can be effectively towed either by boat, or set in place by boat and pulled from the shore by vehicle.

A more detailed study of the mussel population was made on the beach in front of Pelican Cottage. Mussels here were collected every two or three days as they became stranded and the area of beach exposed was measured at intervals of 7 to 20 days so that numbers and biomass could be related to area, and mean size and species composition related to the altitude or lake level at which they were collected. Observations on migration as lake level dropped were also made here.

C. **LABORATORY**

In order to supplement observations made on mussel distributions in the field a few simple experiments were run in the laboratory. These were merely intended to provide an indication of the ability of mussels to withstand one natural phenomenon or another in relation to their distribution in the field.
Falling lake levels are a common feature in Southern Africa during late winter and early summer and the ability of the three species to survive exposure to air was tested. Five adult specimens of each species were placed on a tray in the laboratory and examined each day for survival. Temperatures ranged from 21°C - 30°C and the duration of the experiment was to be three months coinciding with a fairly normal exposure period for mussels.

Another effect of the climatic regime is high marginal temperatures experienced during the day in the extreme shallows. In the warmer low-lying regions of the country, such as Lake Kariba, these temperatures can rise above 40°C. Conversely, in the higher parts of the country, such as the Mashonaland Highveld, night temperatures in the shallows during winter can drop as low as 5°C, and rise to 34°C during the day, (pers. obs.), giving a diurnal range of 25°C - 30°C.

The ability of the most common species at Lake Kariba, *C. mossambicensis*, to withstand temperatures in excess of 40°C was tested in the laboratory when five adult specimens (mean length about 40.0 mm) were subjected to a temperature rise from ambient temperature, 23.0°C - 42°C, over a period of five hours. (Fig. 12). This time factor and temperature rise was used as it roughly coincides with conditions in the marginal shallows in the summer months (September - March). The response of the mussels was observed throughout the five hour period.
At Lake McIlwaine, *C. mossambicensis* and *M. dubia*, the main species, were exposed to a temperature range from 5°C - 34°C by placing adult specimens in a shallow tray of water and leaving this exposed to day and night temperatures during winter (July) for a period of three days.

A final test was related to the observation at Lake Kariba that the population of mussels in general starts reaching zero density at approximately 11 m. According to Coche (1974) this depth can experience DO concentrations as low as 2 ppm at certain times of the year, and hence this could be a limiting factor to deeper penetration of the lake bed by mussels. The response of *C. mossambicensis* to decreasing levels of DO concentrations was tested by placing 10 mussels in a bowl containing one litre of water at ambient temperature (26°C) and reducing the volume of water each day by 50 mls. This removed water was analysed.
for dissolved oxygen using the Winkler titration method. The decreasing water volume led to a fairly rapid depletion of DO concentration. A control consisted of an identical set up in which the same number and size of mussels were subjected to the same condition of declining water level, but the DO concentration was artificially maintained at a high level with an aerator. A second control also had the same number and size of mussels, subjected to daily decreasing water volume, but at a much lower constant temperature of 15°C, which would depress metabolism as well as maintain a higher absolute DO concentration.

Figure 13: The oxygen experiment - Bowl A: ambient temperature, oxygenated; Bowl B: ambient temperature, no oxygen; Bowl C: sub-normal temperature, no oxygen

All mussels were held in flowing water for two days to eliminate much of the material in the mantle cavity and digestive system before the test.