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ASPECTS OF THE BIOLOGY AND POPULATION
DYNAMICS OF FRESHWATER MUSSELS IN LAKE
KARIBA AND LAKE MCILWAIN²¹—

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the contrary in the text is his own original
work and that it has not been submitted for
any other degrees



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. bourquignati, 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 km²), 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.
4. Reproduction.
5. Morphological aspects and gross biochemical composition.
6. Fish predation on the mussel crop.
7. Estimates of standing crops and production rates.

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.

More recent contributions on molluscs in African waters are those of Mandahl-Barth (1954, 1972) on the fresh-water molluscs of Uganda and adjacent territories, and Lake Malawi; of Fryer (1959, 1961) on the developmental history of a bivalve species from Uganda; of Azevedo et al (1957, 1961) on the molluscs of Mozambique; of Yonge (1962) on a fresh-water oyster species; of Dejoux et al (1969, 1971), Dupont and Leveque (1968), and Leveque (1968, 1971, 1973) on the benthic fauna of Lake Chad; and of Woodward (1974) on the molluscs of Lake Chad.

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; Darteville (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.

NOMENCLATURE

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) wahlbergi (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 synonymy 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 synonymy with M. dubia.

The family Unionidae is the largest family of freshwater mussels, containing some 85 genera and approximately 1 000 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

STUDY AREAS

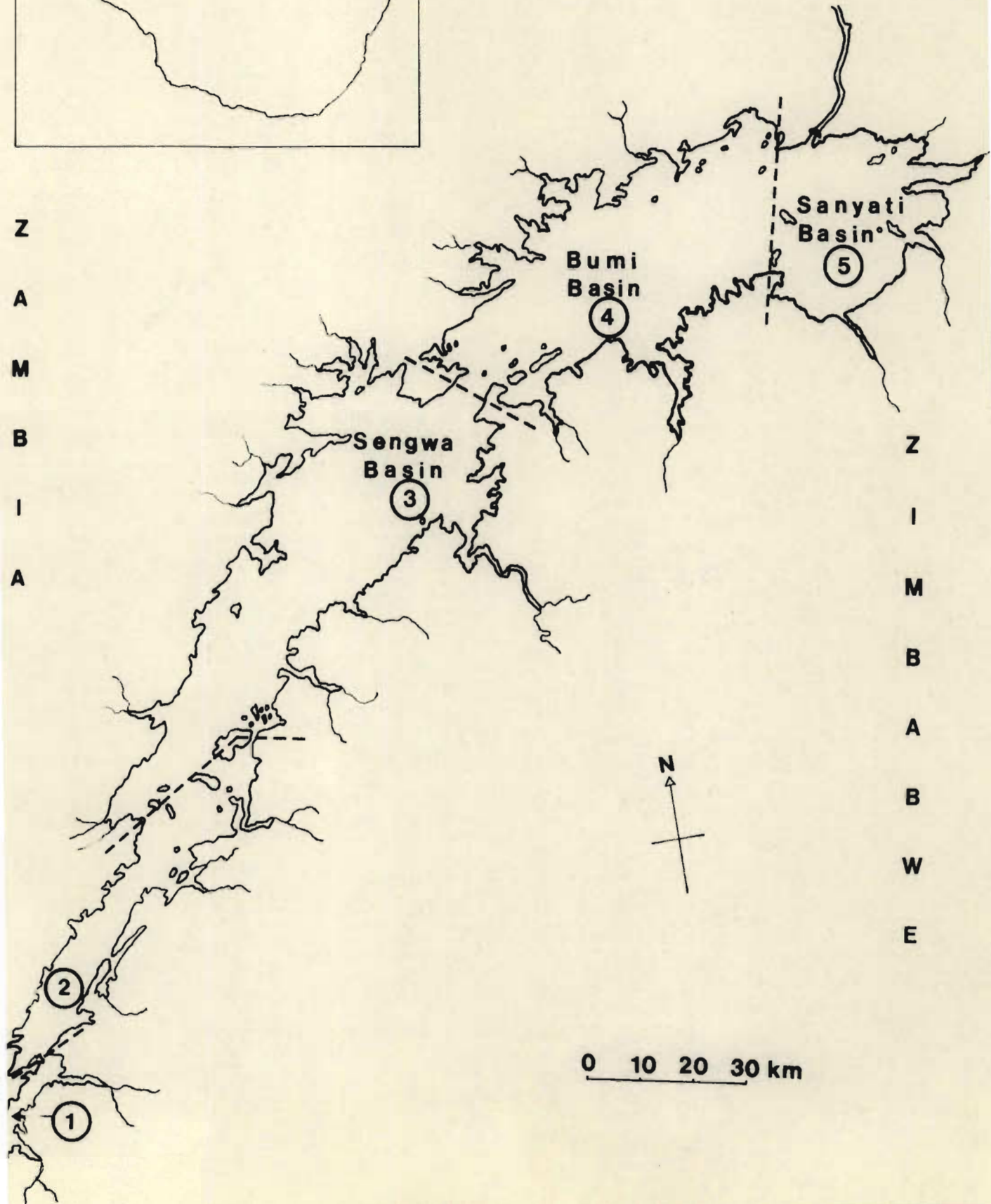
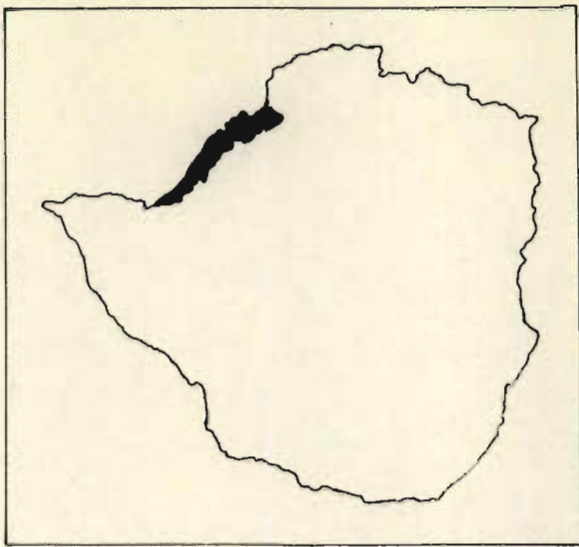
1. Description Of Lake Kariba

General:

Lake Kariba (Fig. 1) lies in the Middle Zambezi Valley, situated between latitudes $16^{\circ}30'S$ and $18^{\circ}06'S$ and longitudes $26^{\circ}40'E$ and $29^{\circ}03'E$, 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 $5\ 250\ km^2$ 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 $663\ 817\ km^2$ 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



Z
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0 10 20 30 km

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 southern most 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):

	%
Molteno Series (grits, sandstone)	41
Forest sandstone	17
Lower Karroo Sandstone	8
Fine red marley sandstone	2
Basalt and interbedded sandstone	15
<hr/>	
TOTAL Karroo rocks	83%

	Gneisses	14
	Pebbly arkose	2
	Sandstone (? Kalahari)	1
		—
TOTAL	Pre- and Post-Karoo rocks	17%

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 accomodate incoming Zambezi floods.

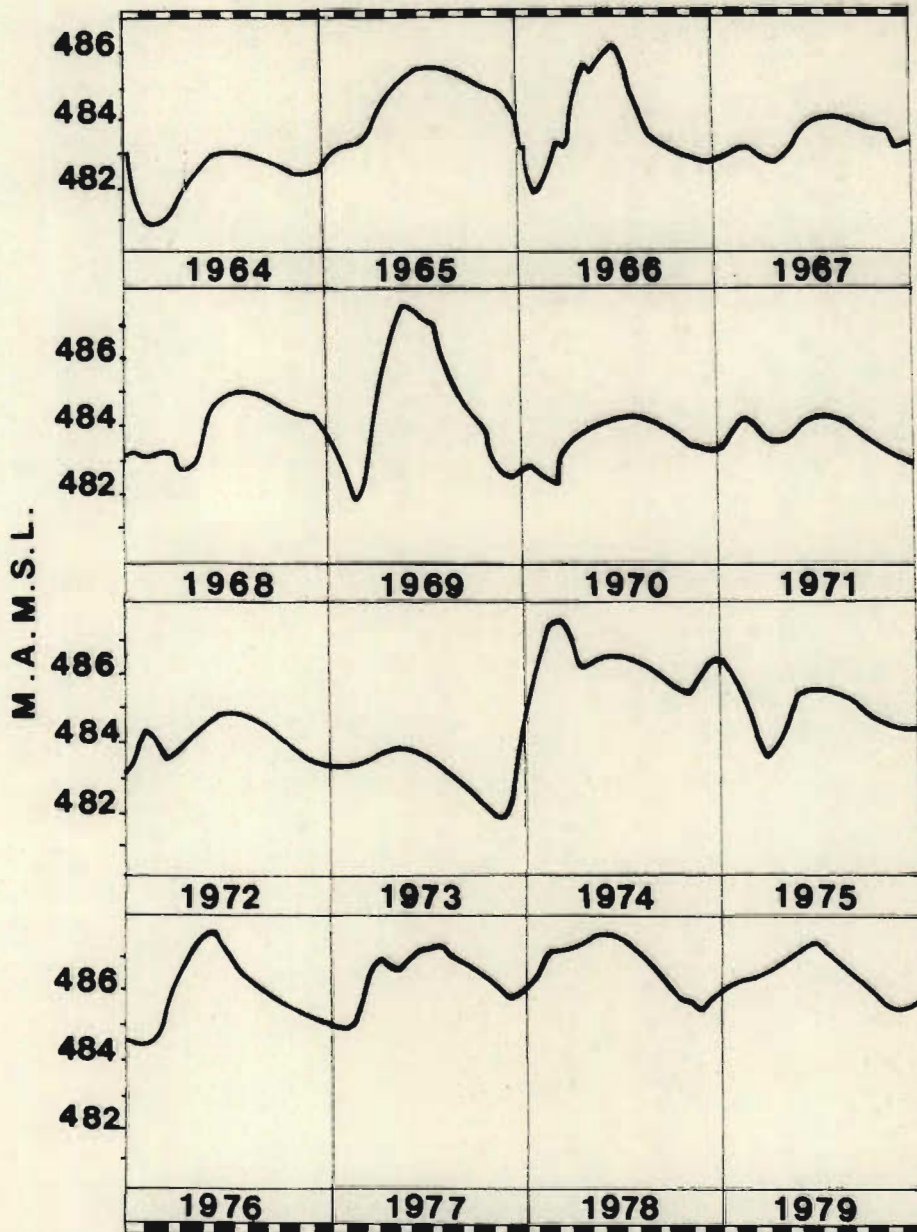


Figure 2: Lake level fluctuations from 1964 to 1979

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.

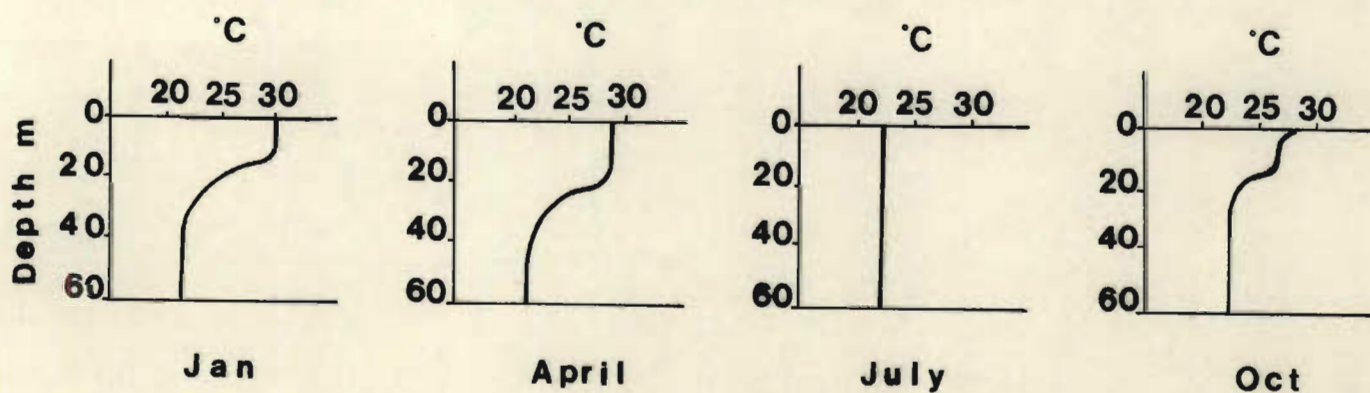


Figure 3 : Temperature profiles for different months in the Sanyati Basin. Mixing of hypo- and epilimnion generally occurs in July (from Begg, 1970)

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 senegalense, Potamogeton octandrus, Potamogeton schweinfurthii, Potamogeton thunbergii, Typha latifolia, and Vallisneria aethiopica. Species occurring seldom or in more restricted habitats, include Lemna perpusilla, Nymphoides indica, Pistia stratiotes, Polygonum aviculata , Polygonum lapathifolium, and

Utricularia sp.

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, Pycneus 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, Hippopotamyrus 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.

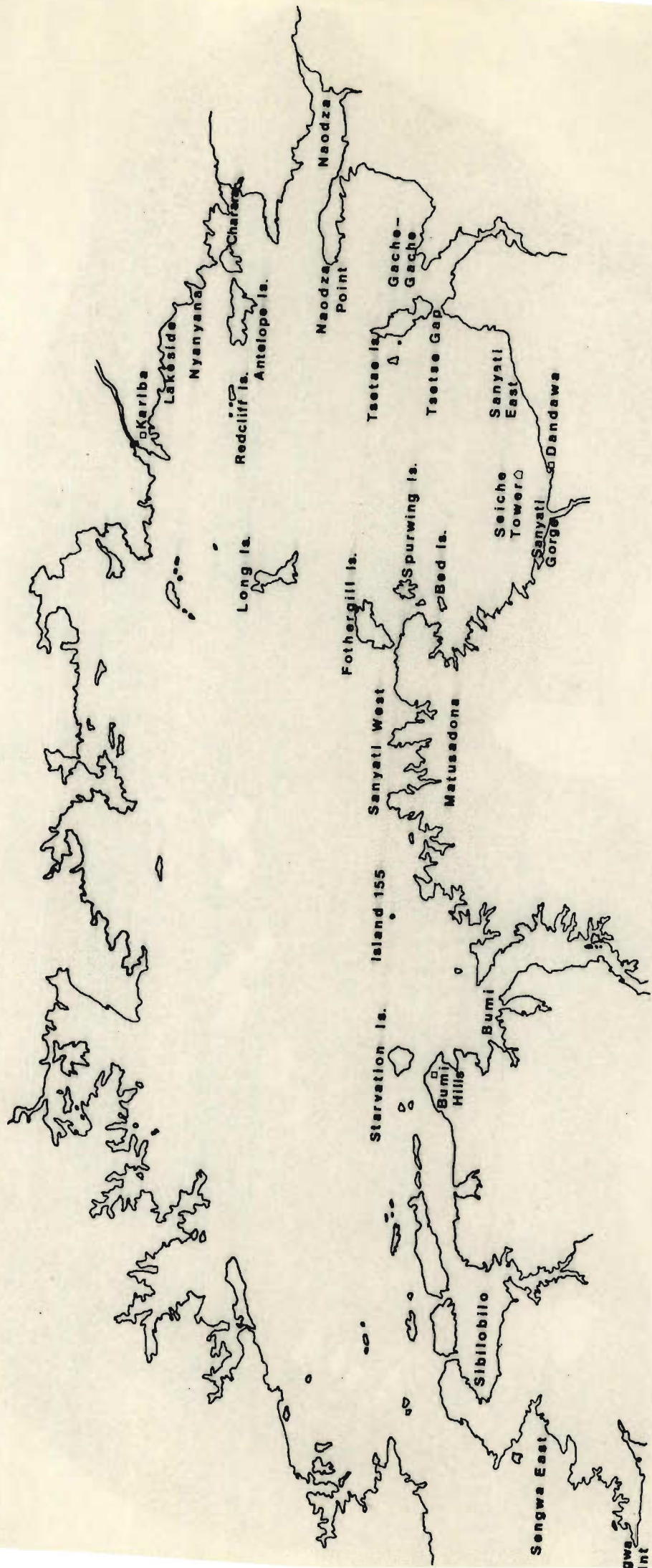
2. Comments on the Main Kariba Study Areas

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:-

	<u>Lakeside</u>		<u>Sanyati East</u>	
% Coarse Sand	7	}	14	}
% Very Fine/Medium	74	}	60	}
		81		74
% Silt/Clay	19		26	

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.)

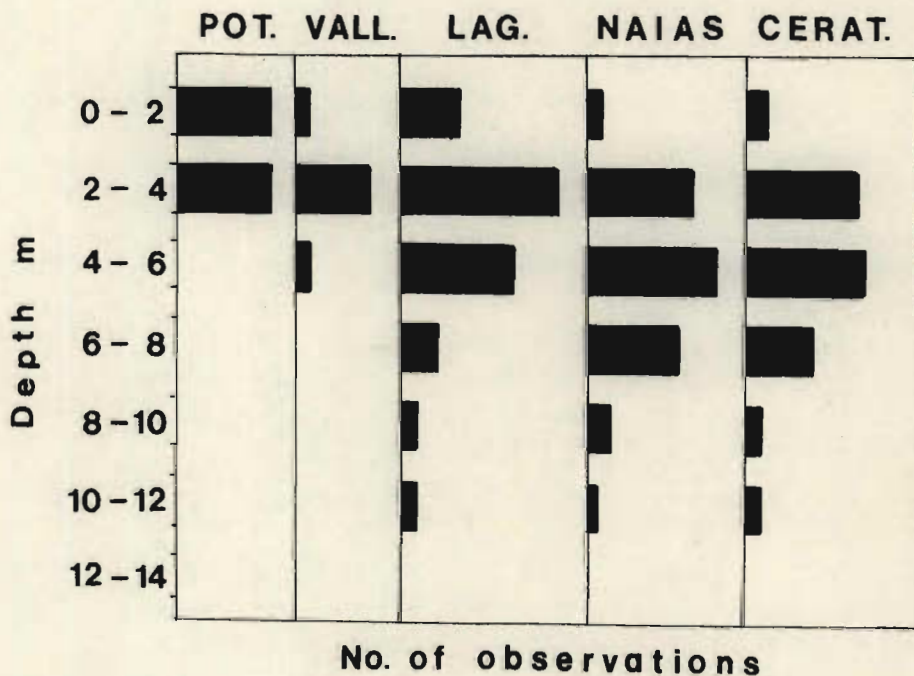


Figure 5 : Depth distribution of plant species in the Sanyati and Bumi Basins. The majority of plants occur in the 0 - 6 m depth range.

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 L I) 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 L I 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 mg l^{-1} will limit fish distribution, and presumably influence other animals as well. He found DO concentrations of 2 mg l^{-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 mg l^{-1} level, one can expect the limits for existence of longer living benthic organism in the littoral 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 (O_m) 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)

STATION	DEPTH	T D S mg l ⁻¹	NO ₃ - N μg l ⁻¹	PO ₄ - P μg l ⁻¹	CATEGORY
Redcliffe	0	60	9,5	3,9	Deep Lake
	11	-	11,2	2,0	
Long Island	0	69,5	4,7	4,3	
	9	-	4,5	3,9	
Lakeside Cleared Area	0	62,5	4,1	10,0	Shallow Marginal
	6	-	4,3	10,4	
Gache Gache Cleared Area	0	75	2,8	11,4	
	7	-	2,8	9,0	
Sanyati East Cleared Area	0	80	3,0	12,9	
	10	-	3,6	9,7	
Gache Gache	0	85	7,2	9,2	Riverine
	7	-	11,5	22,5	
Naodza	0	78	3,0	7,2	
	6	140	6,1	15,0	
Charara	0	88	8,7	7,9	
	6	-	6,1	7,9	

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 $250,4 \times 10^6 \text{ m}^3$, 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 km², and to a lesser extent by the smaller Makabusi and Marimba rivers.

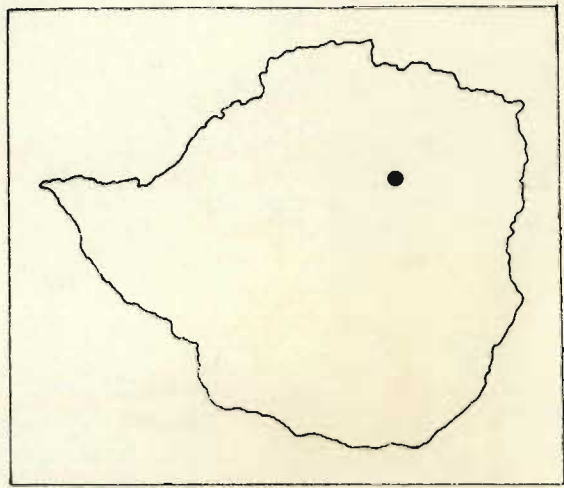
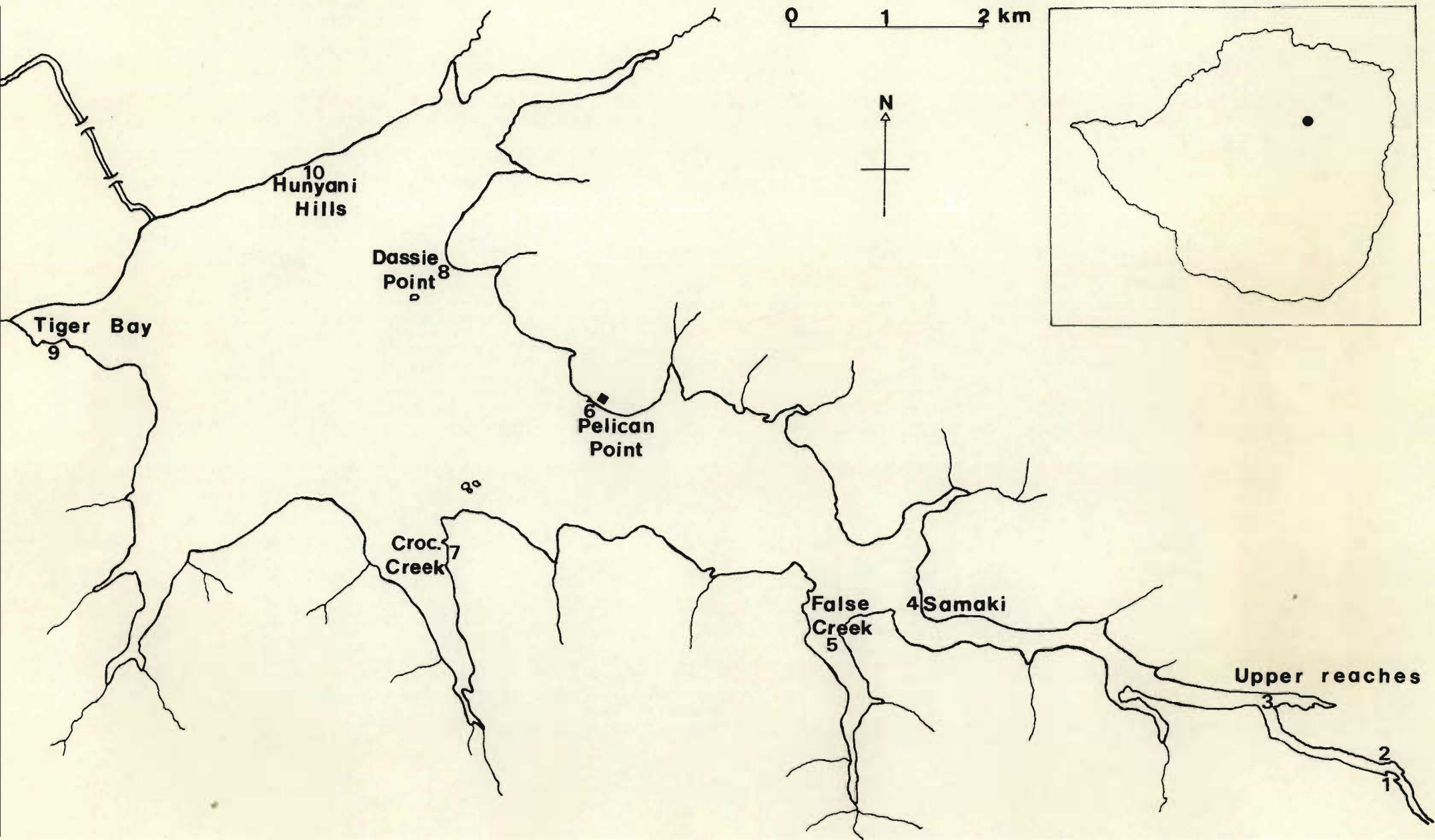
Geology:

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°C, with a mean diurnal variation of about 12°C.

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

(3) The hot dry season, in summer, from September to November, when temperatures average about 22°C, with a mean diurnal variation of about 12°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, 1978 b). 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 1978 b). The most abundant benthic animal was Branchiura sowerbyi with Limnodrilus hoffmeister 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 ($100 \text{ kg ha}^{-1} \text{ year}^{-1}$) 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 Haliaeetus 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 'quantitative' 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 wide-spread 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 $\frac{1}{2}$ m² grid on the substrate and remove all the mussels enclosed by the grid, using aqualungs. 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.

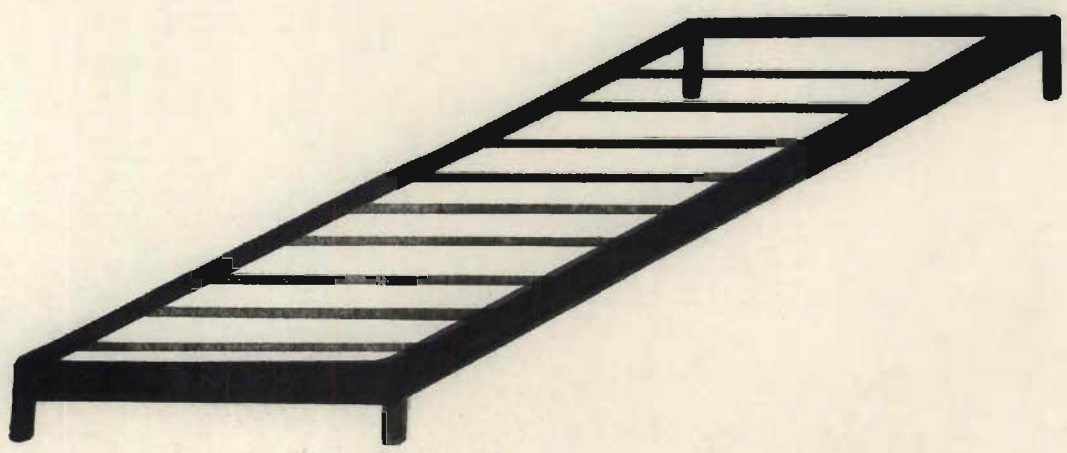
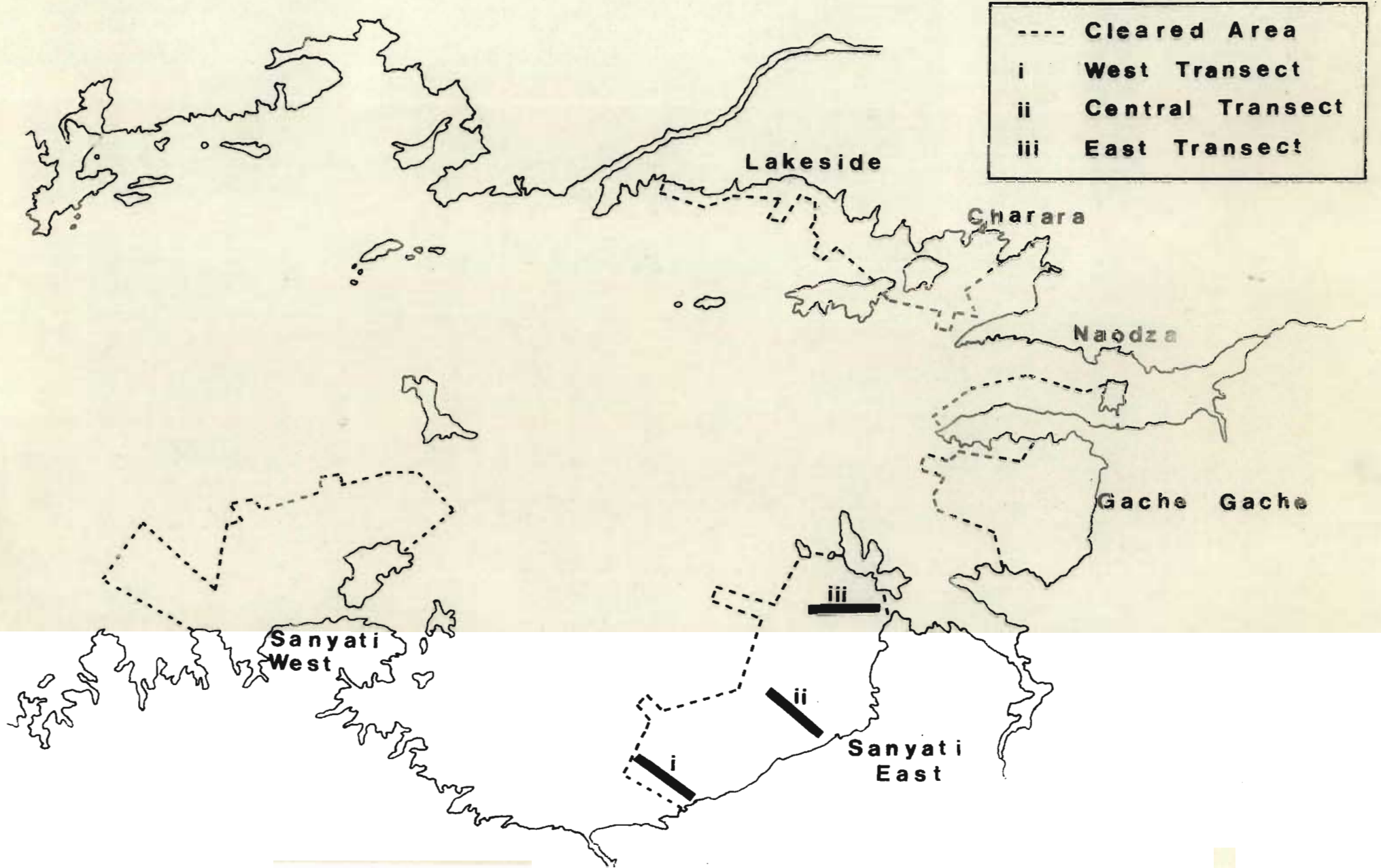


Figure 7: The sampling grid used in the Sanyati East cleared area

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 ($1\frac{1}{2} \text{ m}^2 - 2 \text{ m}^2$) could be cleared before the aqualungs 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



- Cleared Area
- i West Transect
- ii Central Transect
- iii East Transect

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.

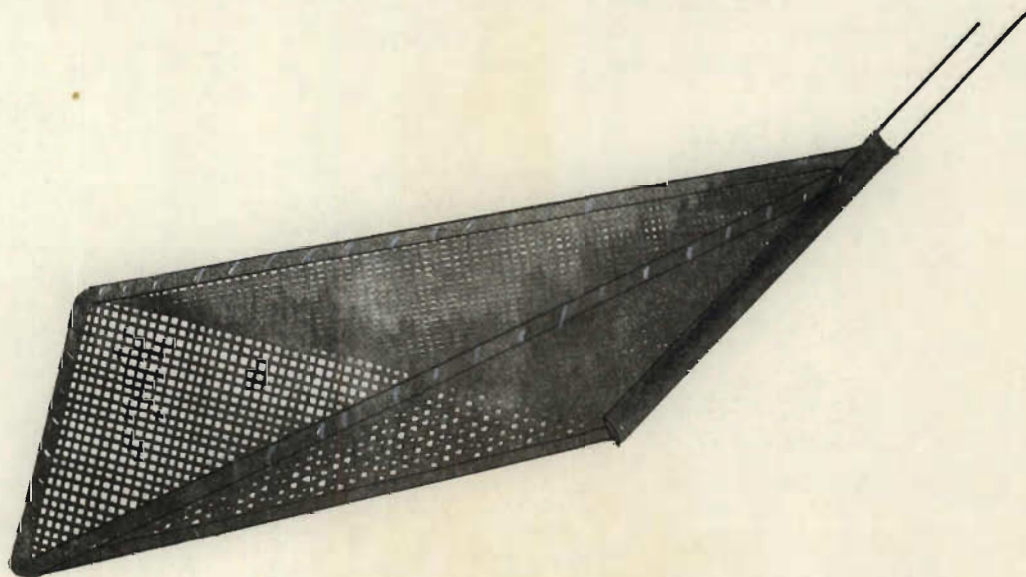


Figure 9: The scoop used to try and collect baby and juvenile mussels

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.

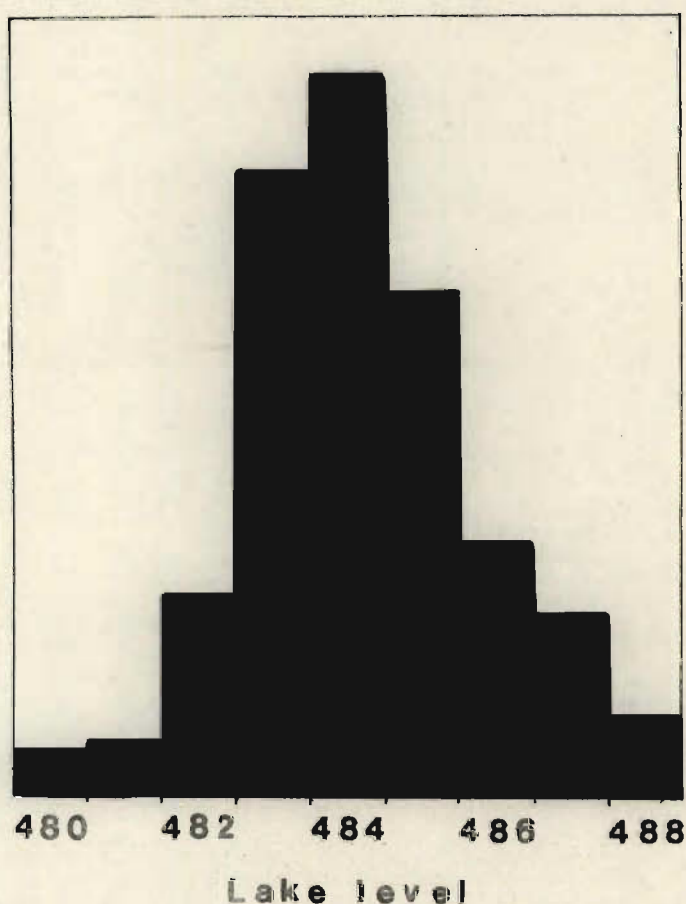


Figure 10: Lake level frequencies, 1962 - 1977

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 (1973 a), Joubert (1975), Mitchell (1976), and Mitchell and Gahamadze (1976).

B. LAKE MCILWAIN

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.

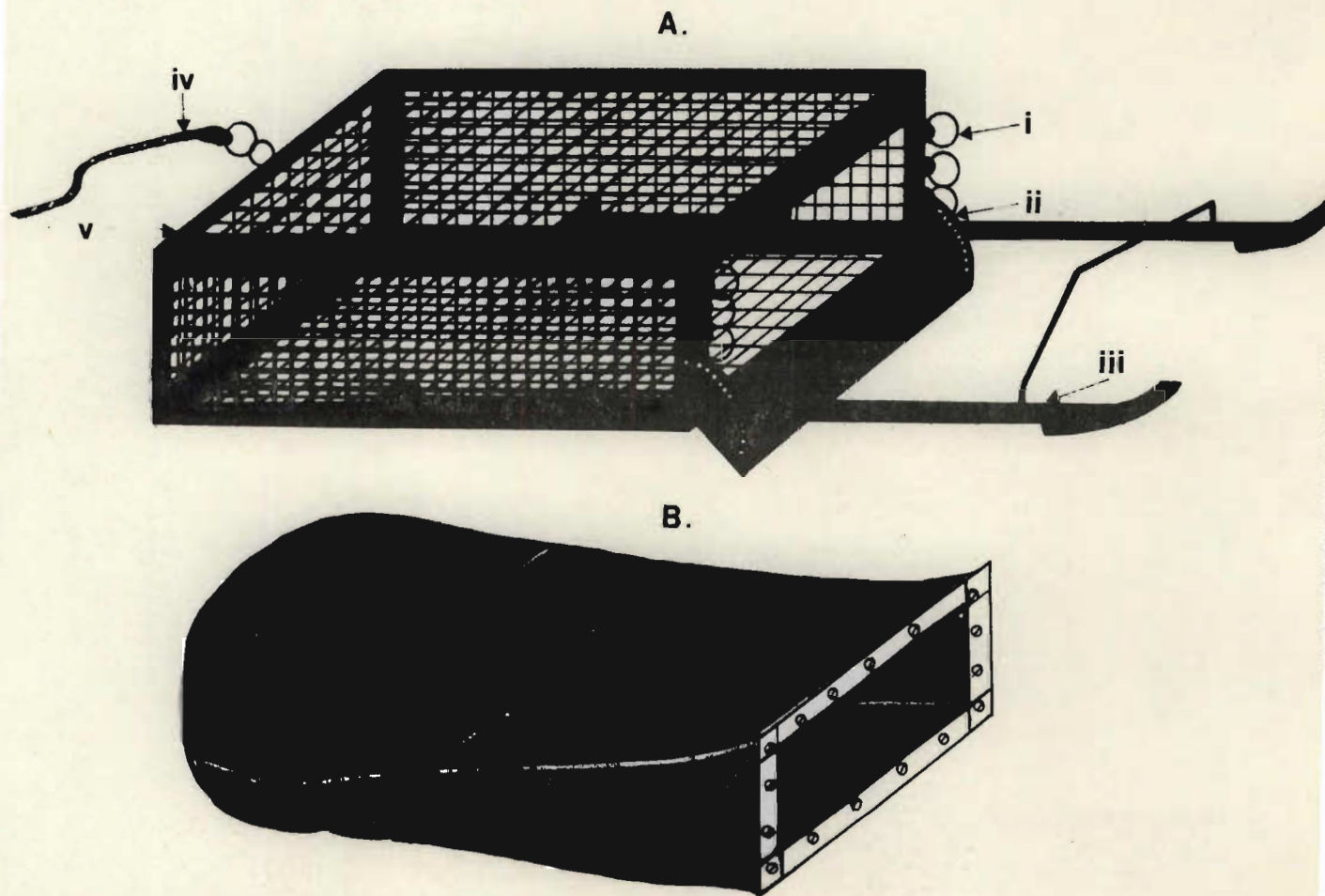


Figure 11: The dredge(A) and catching bag (B) built for sampling in Lake McIlwaine. Components are: (i) rings for towing rope, (ii) adjustable scooping blade, (iii) skid for stability and maintaining even keel, (iv) attachment rope for heavy weight to prevent rear end lift, (v) removable back grid to 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.

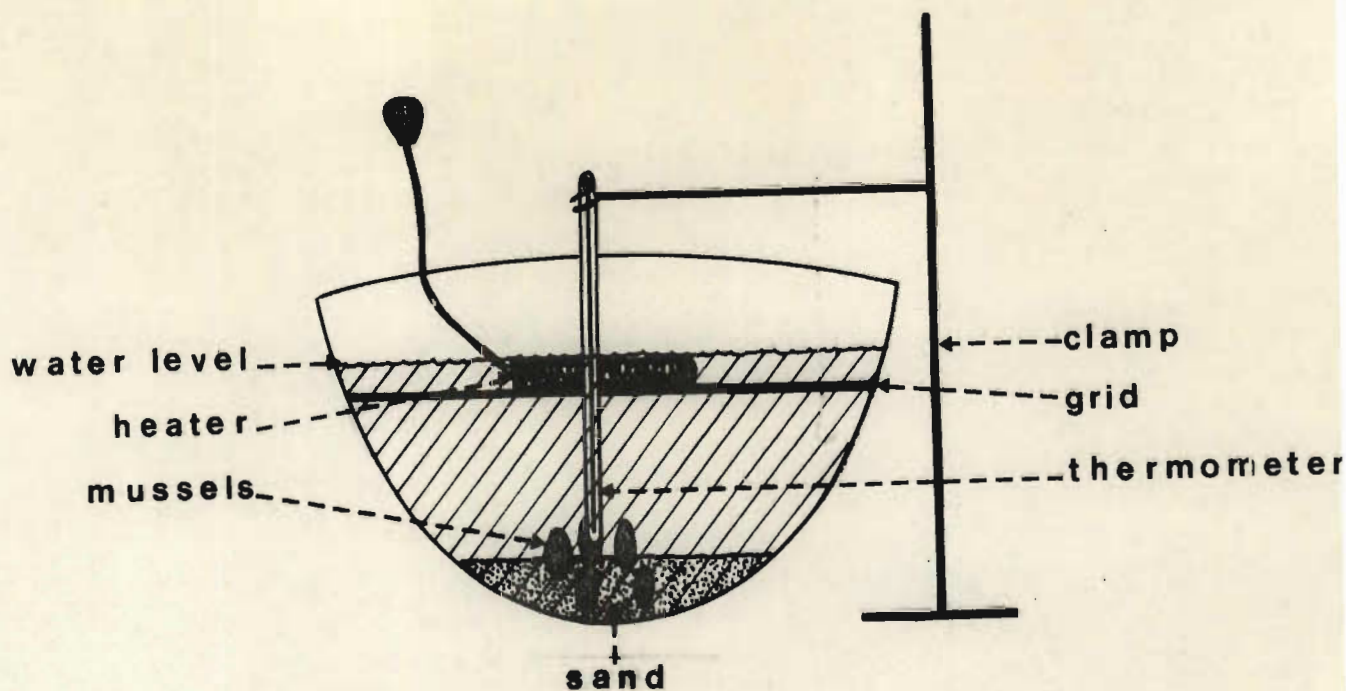


Figure 12: The temperature experiment set up

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.

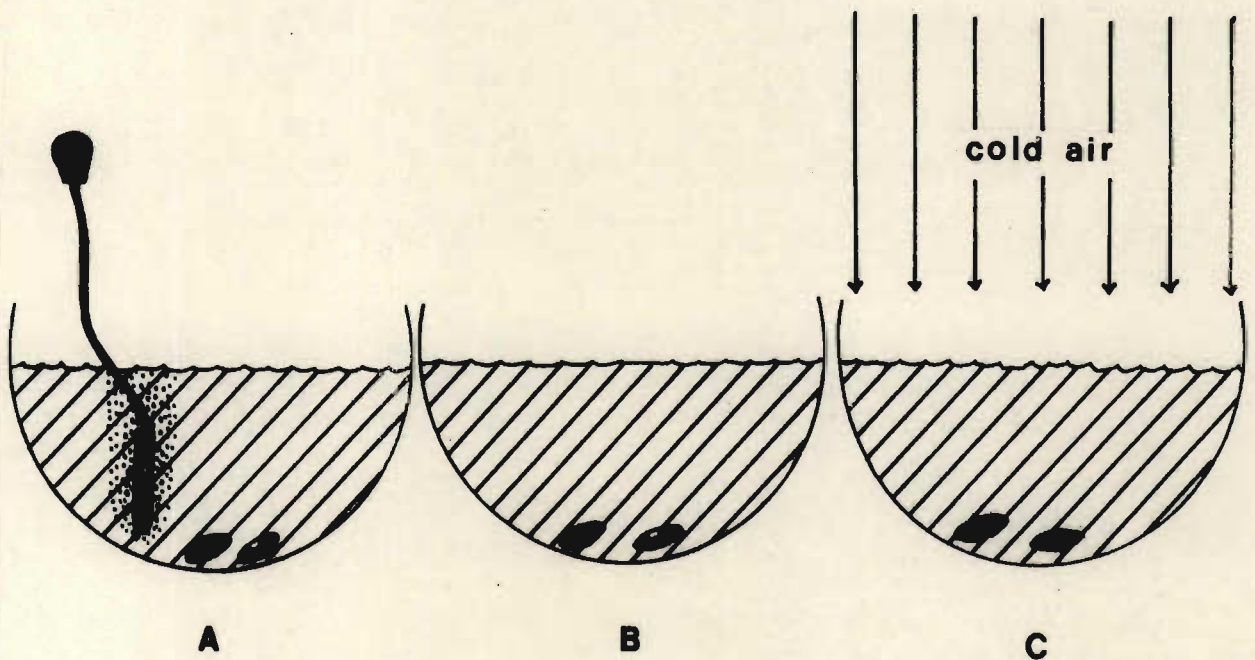


Figure 13: The oxygen experiment - Bowl A : ambient temperature, oxygenated; Bowl B : ambient temperature, no oxygen; Bowl C : sub-normal temperature, no oxygen

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.

RESULTS

A. LAKE KARIBA

Using the data obtained from dive sampling during the period March 1976 to March 1977 distribution maps reflecting percentage composition by numbers and mass for various areas were compiled. (Fig. 14 and Fig. 15).

These maps clearly show C. mossambicensis to be dominant in nearly all areas, and in particular towards the west of the study area. Eighty seven percent of the stations were dominated numerically by this species and seventy percent dominated by mass. Between Fothergill Island and Sengwa West this was the only species recorded at 15 stations sampled, although two specimens of A. wahlbergi were subsequently recorded from the Sengwa Basin, indicating they are present but in very small numbers. Populations of A. wahlbergi were confined to the Sanyati Basin, in particular the shallow cleared areas, and generally had a more restricted distribution than the other two species, not being recorded at several stations. M. dubia had a wide distribution but was nowhere really dominant, except in some of the river estuaries (Charara and Gache-Gache) and at one of the islands (Redcliffe). In the areas where A. wahlbergi were numerically common they figured prominently in terms of mass composition because of their much larger size and greater mass than the other two species. Similarly, M. dubia proportions increased relative to C. mossambicensis proportions when considered in terms of mass rather than numbers.

Figure 14: Species composition (numbers) at
all sampling stations, March 1976
to March 1977

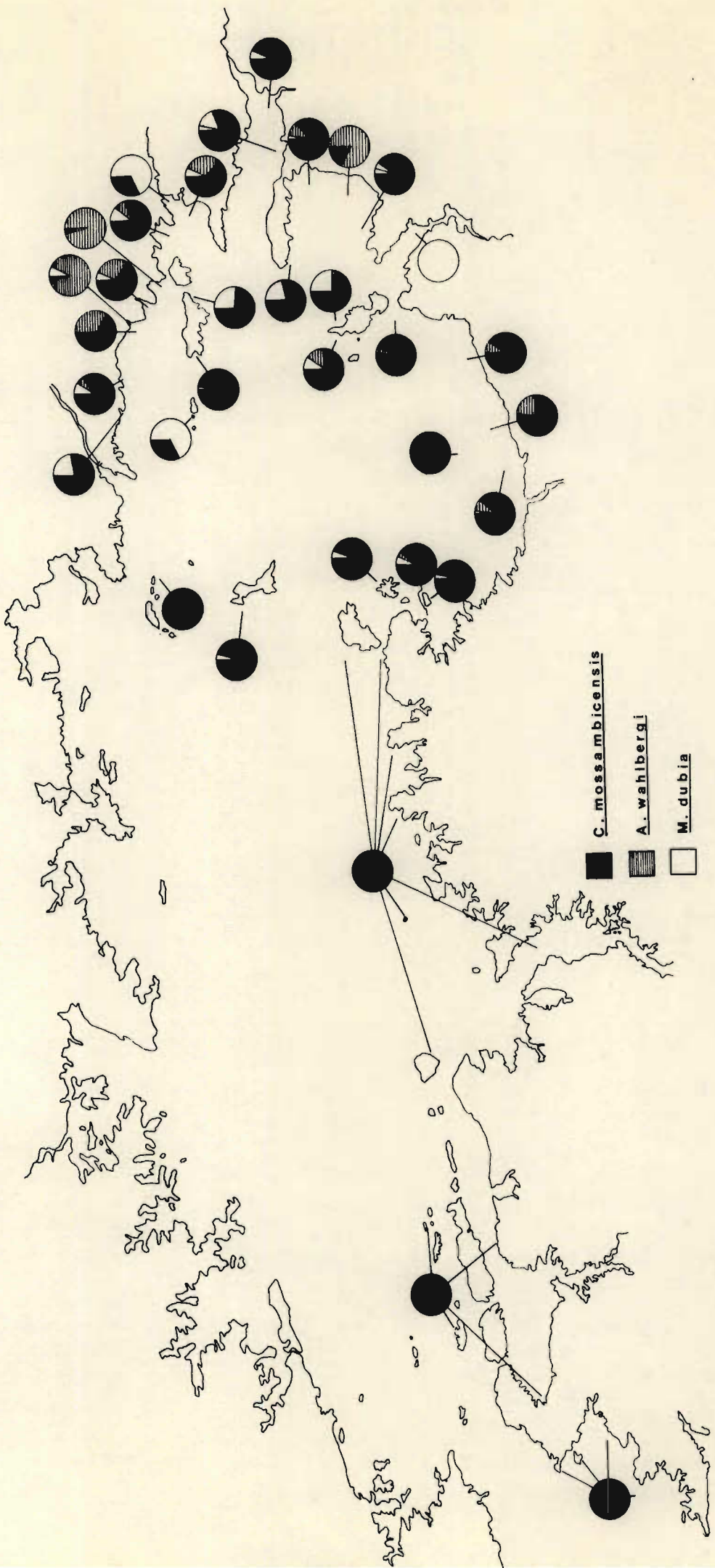
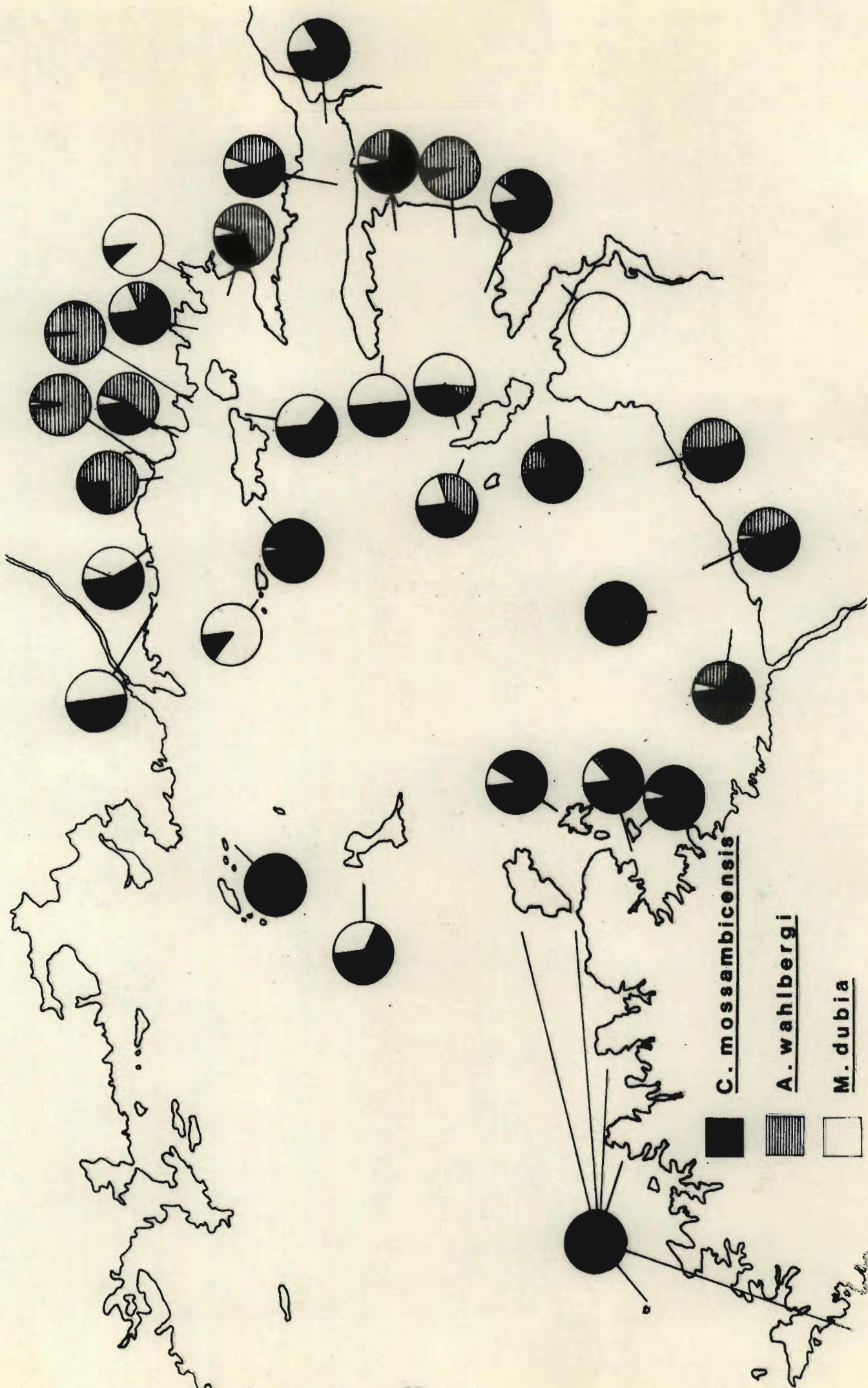


Figure 15: Species composition (mass), March
1976 to March 1977



1. Relative Densities

Using the data collected during dive sampling to determine the distribution and species composition, density maps showing the relative density of mussels in terms of numbers and whole wet mass collected per minute in various parts of the lake were compiled. (Fig. 16 and Fig. 17). The data have been grouped into three classes, representing three categories of abundance.

The maps show that in all cases where high or medium high densities were recorded these were from the shallow cleared areas. These areas correspond to the commercial gill net fishing pitches. Areas showing the lowest densities were in most cases adjacent to islands, or steeply shelving shorelines.

The presence of A. wahlbergi in the populations generally had the effect of boosting mass abundance in relation to numbers abundance, because of their much greater mass than the other species. This is evident in the Nyanyana/Lakeside area, where, although numerical density was not high, mass density was higher than in other areas with equal numbers of mussels because of the presence of A. wahlbergi.

Figure 16: Relative densities (no. min⁻¹) in various localities, March 1976 to March 1977

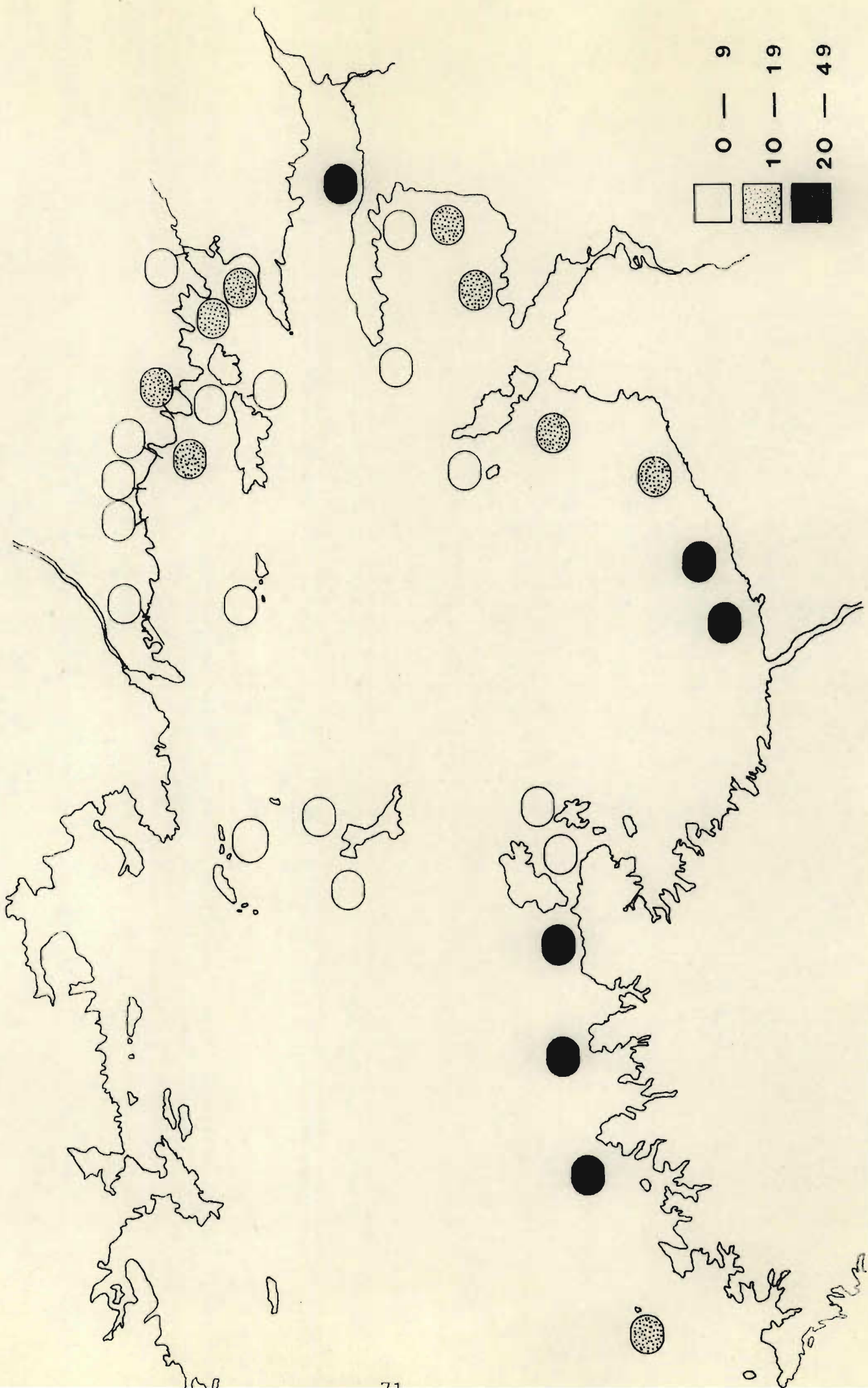
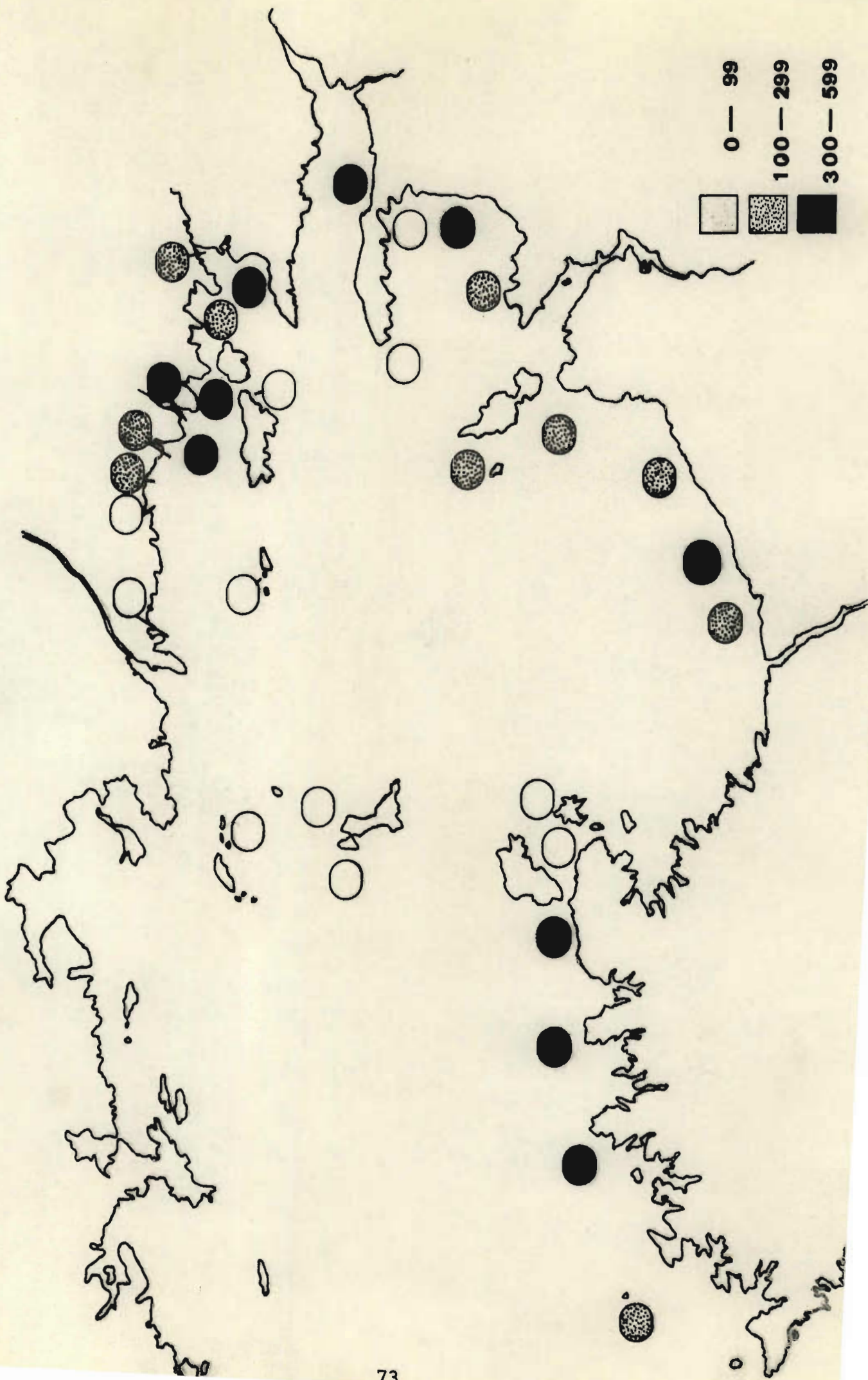


Figure 17: Relative densities (g min^{-1}) in various localities, March 1976 to March 1977



2. Depth Densities

In assessing density changes with depth it was assumed that depth related density would be broadly similar in all cleared areas of the lake, and hence studies to determine this were concentrated in only one area, the Sanyati East cleared area. The data were derived from the transect sampling at three stations in the Sanyati East cleared area and is shown graphically below.

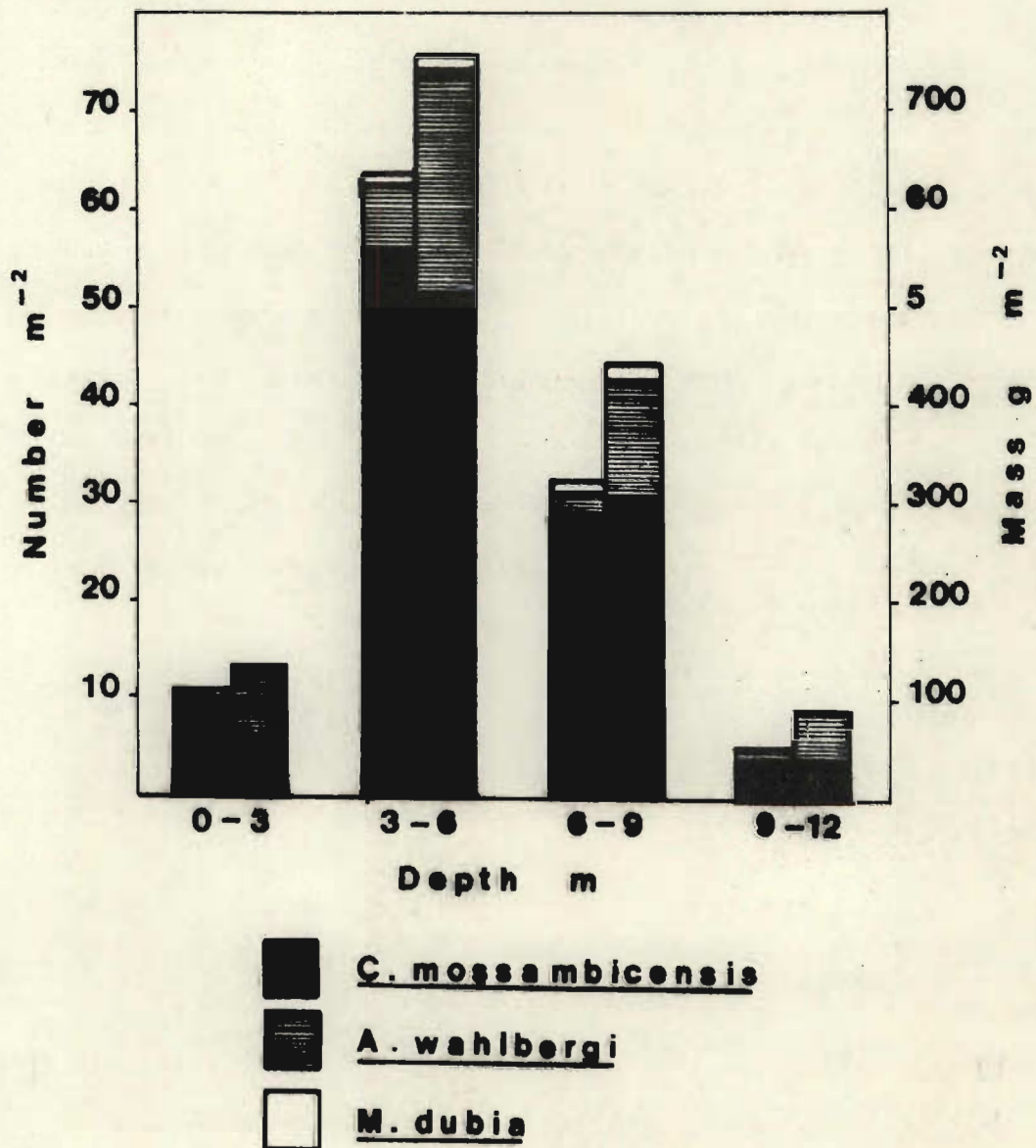


Figure 18: Absolute density and species composition in relation to depth in the Sanyati East cleared area. First column : numbers; second column : mass

This shows numbers and mass per square metre as well as species composition for the different depth categories.

The histogram shows that the bulk of the mussel population occurs from approximately 3 m - 9 m depth. Mussels undoubtedly occur beyond 12 m, but in limited numbers, while in less than 3 m depth they are also well below maximum density. The species composition in general terms is much the same at all depth categories, with C. mossambicensis predominating both numerically and by mass. M. dubia were only recorded between 3 m and 9 m depth, but throughout the area were in such low numbers that no conclusions can be drawn from this. A. wahlbergi were recorded from all depths sampled.

These results are confirmed by dive sampling results recorded in this cleared area. Relative densities at different depths were determined as numbers and mass collected per minute. (Fig. 19).

Figure 19 shows a greatly decreased population density at 10 m - 11 m depth with greatest relative densities at 5 m - 6 m, and 8 m - 9 m. This picture differs slightly from the data shown in Fig. 18 where the greatest density was found to occur at 3 m - 6 m depth, rather than 8 m - 9 m, as in Fig. 19. The difference is attributed to interference during dive sampling in the shallow depths from submerged aquatic plants which proved a hindrance to collecting activities. Visibility was also better in the deeper water.

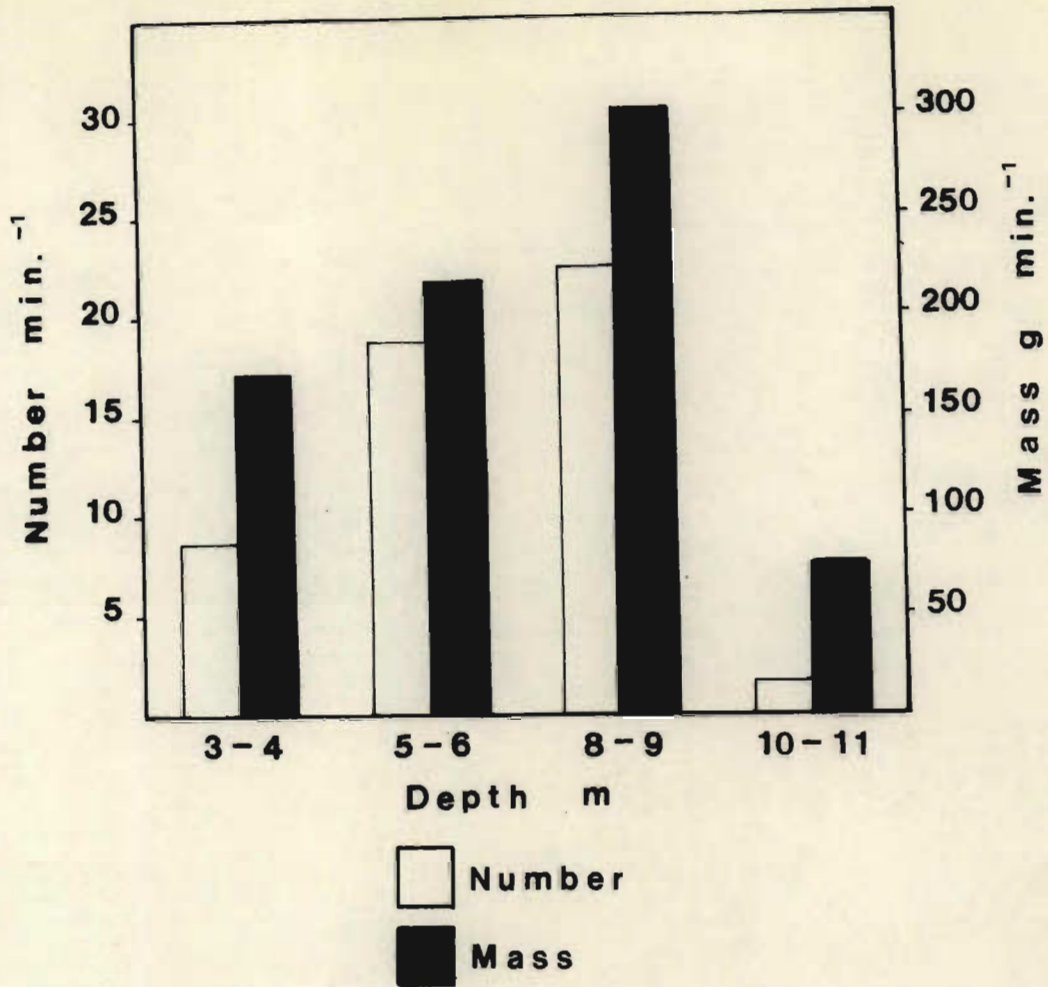


Figure 19: Relative density of the mussel population in relation to depth determined by dive sampling in the Sanyati East cleared area

Because of the risk from bilharzia and also from submerged gill nets along this particular stretch of shoreline, the 0 m - 2 m depth diving was done off Tsetse Island, where conditions were better, although P. repens grass covered most of the bottom. Only C. africana were recorded at this depth. The populations of the species studied only start appearing at 2 m - 3 m depth as shown by the grid sampling.

3. Absolute Densities

a.) Sanyati East

Data derived from the three transect lines have been summarized in Table 2 to show the mean densities obtained for each species at each of the transect stations, the overall calculated absolute density for the Sanyati East cleared area, and the overall species composition for the three transects.

No standard errors have been applied to these means as these would be rather meaningless in view of the wide range of densities obtained in moving from unproductive to very productive depths.

The overall density for the whole Sanyati East cleared area has been calculated from the three transects to be 28,9 mussels and 378 g per square metre, (the figures underlined in Table). Obviously mean densities in the intermediate depth zones are very much higher than this, (shown in Fig. 18 to exceed 60 m^{-2} at 3 m - 6 m depth), with one quadrat yielding 192 mussels m^{-2} and another 96 mussels and a biomass of 1 625 gms (excluding C. africana).

A factor emerging from the results was the difference in both densities and species composition at the three transects.

Table 2: Summary of population density data from the three transects in the Sanyati East cleared area

TRANSECT	<u>Caelatura mossambicensis</u>		<u>Aspatharia wahlbergi</u>		<u>Mutela dubia</u>		<u>All species</u>	
	No m ⁻²	g m ⁻²	No m ⁻²	g m ⁻²	No m ⁻²	g m ⁻²	No m ⁻²	g m ⁻²
1. (WEST)	17,2	176	3,3	134	0,8	11	21,3	321
2. (CENTRAL)	25,7	253	5,0	186	0,5	11	31,2	450
3. (EAST)	35,4	308	2,5	78	0,2	5	38,1	390
MEANS	24,8	236	3,6	133	0,5	9	<u>28,9</u>	<u>378</u>
%	87,2	65	11,4	33	1,4	2		

Proceeding from West to East along the Sanyati East cleared area, the overall absolute density of mussels (numbers) increased from 21,3 at Transect One to 38,1 at Transect Three, with an intermediate value of 31,2 at Transect Two. Biomass did not follow such a clear-cut increase because of differences in species composition, with inflated values at Transect Two because of higher numbers of A. wahlbergi here.

Also of interest are the distinct changes in density of the individual species, proceeding from one transect to another. C. mossambicensis shows a clear increase in numbers from 17,2 m⁻² at Transect One to 35,4 m⁻² (more than double) at Transect Three, with an intermediate value of 25,7 m⁻² at Transect Two. Similarly, and conversely, M. dubia declines in density from 0,8 at Transect One to 0,2 at Transect Three, with an intermediate value of 0,5 at Transect Two. A. wahlbergi increases from Transect One to Two, where it has its highest value. These changes in density, with species composition at each transect are shown in Fig. 20.

There is an almost exact and converse linear relationship of density to location for C. mossambicensis and M. dubia, suggesting that species density and composition are inter-related in such a way that where the density of one species increases the density of another declines. The relationship between total density (all species) and location also very nearly gives a straight line.

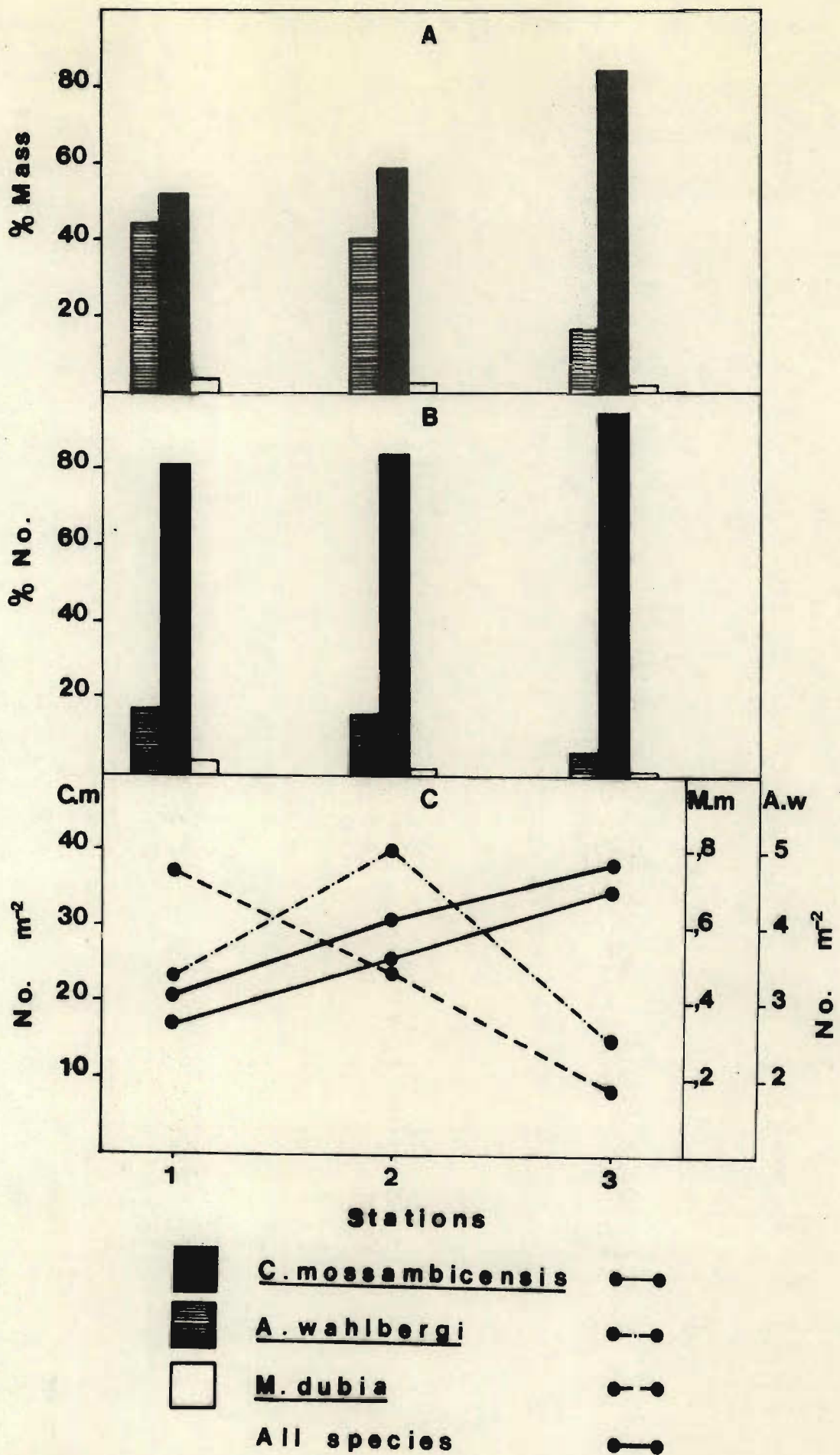


Figure 20: Species composition at Transect Stations One, Two and Three (A and B) and the relationship of species density to Transect Station locality (C)

However , regression lines with only three co-ordinates must be treated with caution.

The species composition histograms also show that differences exist from one transect to another. In the East, C. mossambicensis clearly dominates, whereas in the West, A. wahlbergi is almost as important, in terms of biomass. M. dubia has its highest proportion in the West and lowest in the East.

b.) Other localities

Some grid sampling was done in other areas of the lake, and the results are summarized in Table 3 .

Most of the sampling was done in fairly shallow water, and it is possible greater densities would have been recorded at these stations in deeper water. Unfortunately, time did not allow further grid sampling, and the figures must be considered as giving only rough indications of the true mean densities in these areas.

Areas selected for this sampling were productive commercial fishing areas, fairly shallow and with gentle gradients.

Table 3 : Results of grid sampling at various cleared (c/a) and uncleared(u/c) areas

DATE	AREA	AREA SAMPLED (m ²)	No m ⁻²	g m ⁻²	DEPTH	REMARKS
6.75	Charara u/c	2	42	261	3,2	Mostly <u>C.mossambicensis</u> (young)
3.76	Sanyati West c/a	1	31	300	3,2	<u>C.mossambicensis</u>
3.76	Sengwa East u/c	1	31	500	4,1	<u>C.mossambicensis</u>
1.77	Gache Gache c/a	1	49	1 175	3,0	High mass due to <u>A.wahlbergi</u> . Also <u>C.mossambicensis</u> and <u>M. dubia</u>
9.77	Lakeside c/a	1	52	335	4,9	<u>C.mossambicensis</u> , mainly small

4. Population Structures

a.) Caelatura mossambicensis

(i) Sanyati East cleared area

As mentioned under Methods, sampling in the Sanyati East cleared area in 1977 involved transect grid sampling, dive sampling, (transect), Petersen grab sampling and, in October 1978, all these methods as well as using a mollusc scoop. The object was to obtain as comprehensive a picture as possible of the mussel population structures, including sub-adult recruits, and hence data derived from all these methods have been combined. The population structures as at February/March 1977 and October 1978 are shown in Fig. 21 .

The histograms clearly show that the population is essentially an adult one with the greatest proportion comprised of mussels over 30 mm in length, and with very few sub-adults (below 22 mm - see PART TWO - REPRODUCTION) and juveniles (post glochidial stages) present. The sampling methods successfully yielded small C. africana (below 10 mm) and hence would also have yielded small mussels in the cleared area if these had been present. The only locality where a number of small mussels (18) were found using the scoop was at 4 m - 5 m depth in the western tree line, off Dandawa Village, in October 1978. Their length frequencies are shown as an inset in Fig. 21b. This find was of interest in that although 3 m² were sampled

only the shells of adult C. mossambicensis and C. africana, and no live specimens, were recorded. The possible significance of this is discussed later. (Other Causes Of Mortality, and Discussion).

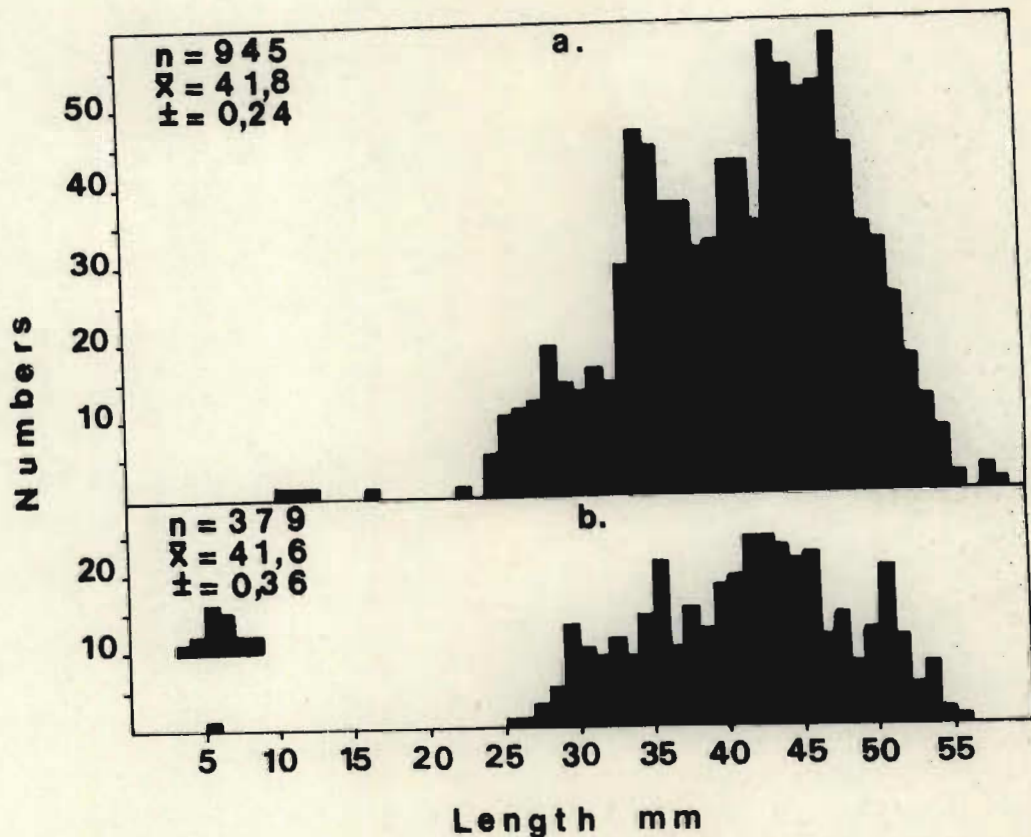


Figure 21: Population structures of C. mossambicensis for Feb/Mar 1977 (a), and October 1978 (b), in the Sanyati East c/a as determined by several different sampling methods. Inset shows juveniles recorded in the adjacent tree-line using a scoop. (\pm indicates S.E.)

In both sample populations shown in Fig. 21 the mean length was close to 41 mm and standard errors and confidence limits show these means are not significantly different at the 95% level. The largest specimen recorded was 58,6 mm, although 55mm - 56 mm appeared to be the 'average' maximum length of the population. Modal peaks are present in both populations, indicating the possible

presence of strong year classes.

(ii) Different depths, Sanyati East cleared area

Length frequencies of C. mossambicensis collected during dive sampling and grid sampling at different depth zones are shown in Fig. 22.

The figures show that differences do exist, with mean lengths of the samples increasing with increasing depth.

The means of the samples from the two different depth zones were found to be significantly different at the 95% level of confidence. Larger numbers of smaller mussels were recorded in the shallower zone than in the deeper zone.

(iii) Different areas in the Sanyati Basin

Length frequency histograms were compiled from the dive sampling done in different areas of the basin in 1976/1977, shown in Fig. 23.

In all cases the basic structures are similar, showing populations negatively skewed to the left, with disproportionately high representation of adults (22 mm and over) compared with juveniles. The smallest mussel recorded was in the 15 mm class, and the largest in the 58 mm class.

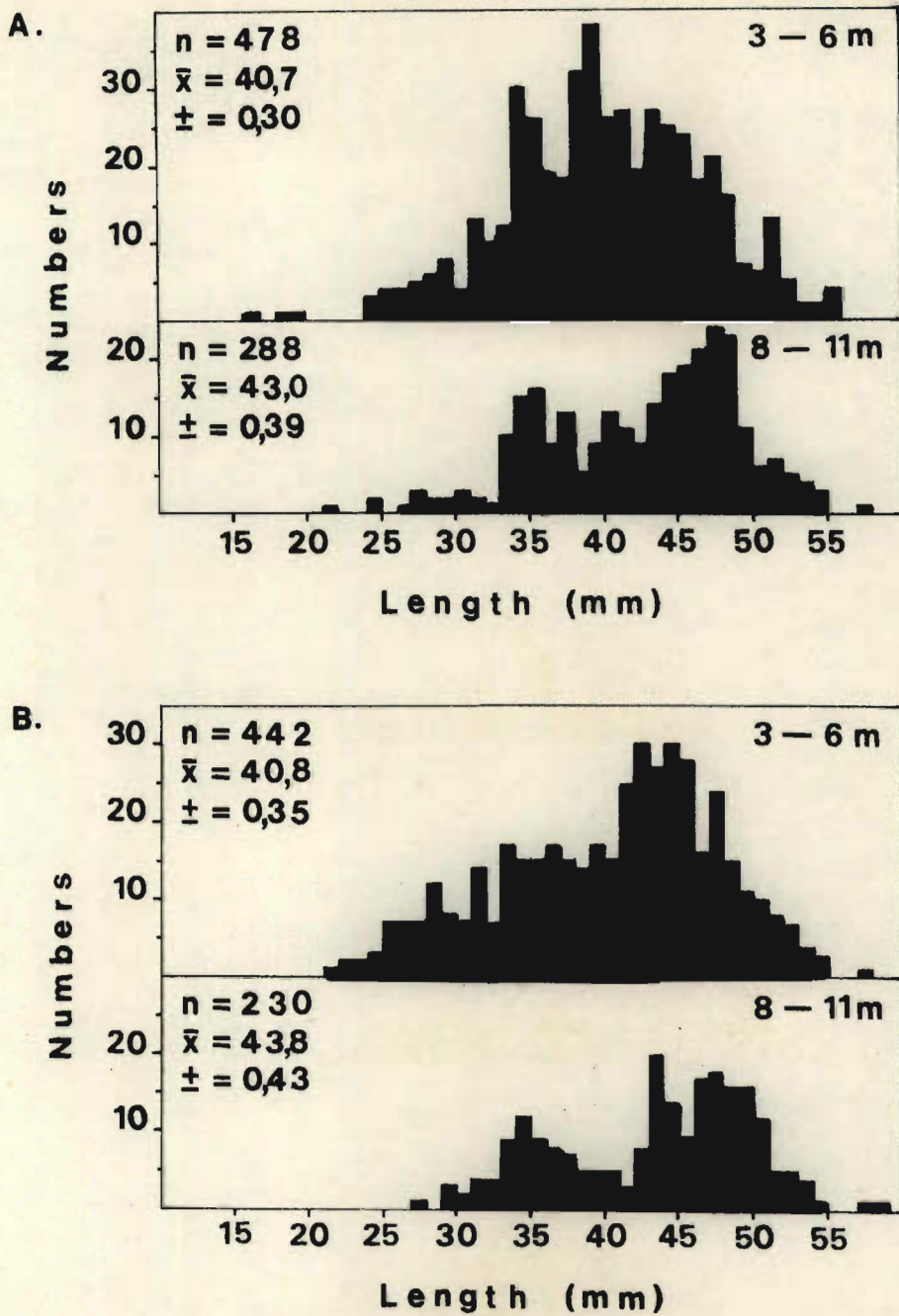


Figure 22: Length frequencies of sample populations of *C. mossambicensis* from different depth zones in the Sanyati East cleared area. (A: dive samples; B: grid samples)

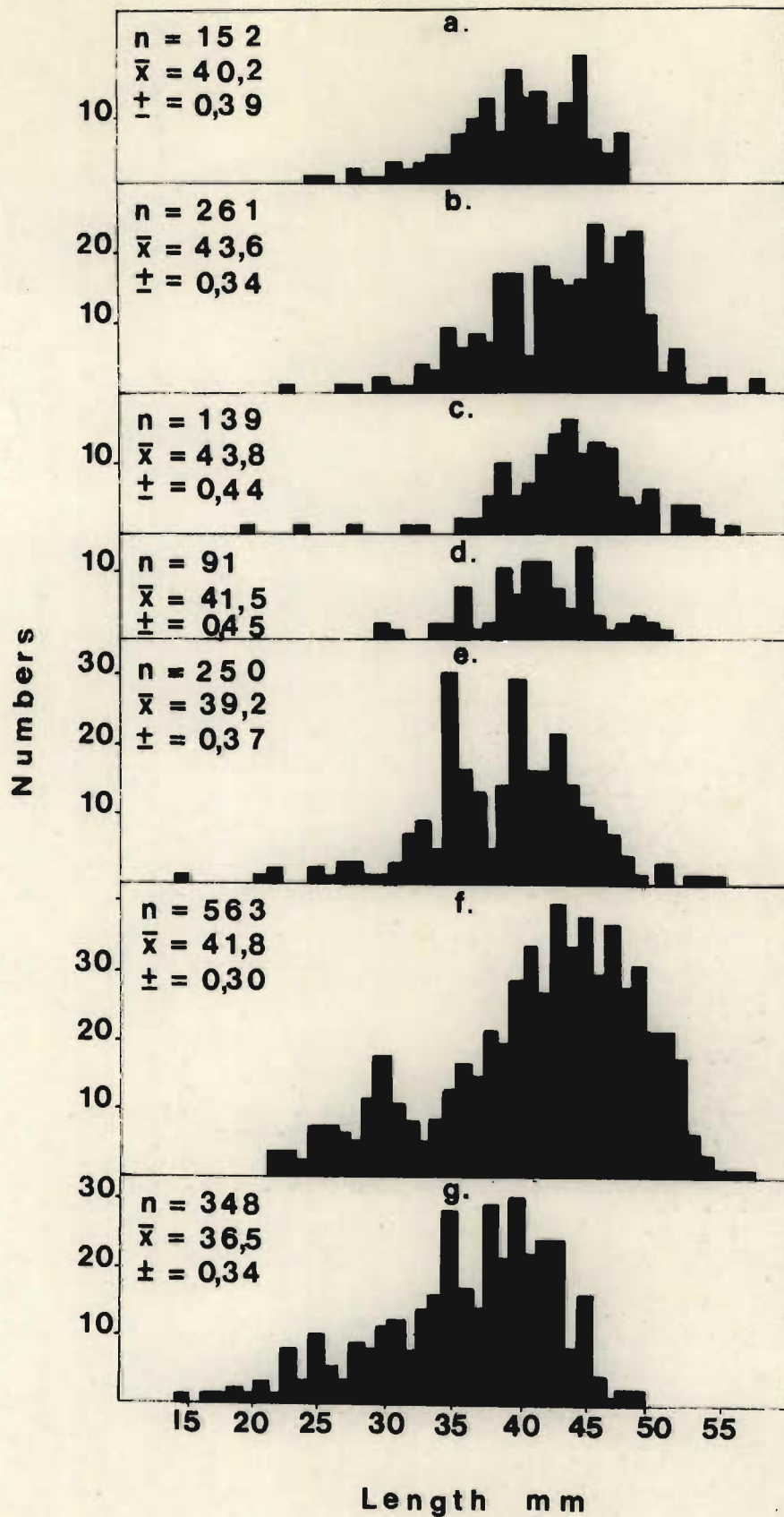


Figure 23: Length frequencies of dive sample populations of *C. mossambicensis* from various areas of the Sanyati Basin, 1976/1977. (a: Nyanyana; b: Charara; c: Naodza; d: Gache-Gache; e: Tsetse Island; f: Sanyati West; g: Islands)

Differences in the means of the sample population existed, and these were tested for significant difference at the 95% level of confidence, the null hypothesis being that the population means were the same, with differences arising solely due to chance. Not all the differences were tested, but sufficient to determine whether any differences were significant. Results of these tests are summarized in Table 4 .

Significant differences were found to exist between estuaries and the cleared areas, and between the island populations (Redcliffe, Long Island, Sampa Karuma) and other populations. Of the cleared areas , the Lakeside sample population mean differed significantly from the means of sample populations of the other cleared areas (Gache Gache, Sanyati East, and Sanyati West). Maximum size attained here was also smaller than from the other cleared areas. These three areas, with very similar mean lengths (41,5 mm, 41,7 mm and 41,8 respectively) showed no significant differences.

b.) Aspatharia wahlbergi

As with C. mossambicensis data collected using all sampling methods in the Sanyati East cleared area have been combined to depict the population structure shown in Fig. 24. While most of the data were collected in 1977, these were insufficient and dive sampling data collected in 1976 have been included to provide a clearer picture.

Table 4 : Results of significance tests comparing mean lengths of sample populations from different areas

TYPE OF AREA	AREA	MEANS (\pm S.E.)	RESULT
Cleared	Sanyati East & Sanyati West	41,7 (0,23) & 41,8 (0,30)	Not signif.
Cleared	Sanyati East & Gache-Gache	41,7 & 41,5 (0,45)	Not signif.
Cleared	Gache-Gache & Lakeside	41,5 & 40,2 (0,39)	Significant
Cleared & Estuary	Sanyati East & Charara	41,7 & 43,6 (0,34)	Significant
Uncleared & Cleared	Lakeside & Tsetse (West)	40,2 & 39,2 (0,37)	Not signif.
Uncleared & Islands	Tsetse (West) & Islands	39,2 & 36,5 (0,35)	Significant
Estuaries	Charara & Naodza	43,6 & 43,8 (0,44)	Not signif.

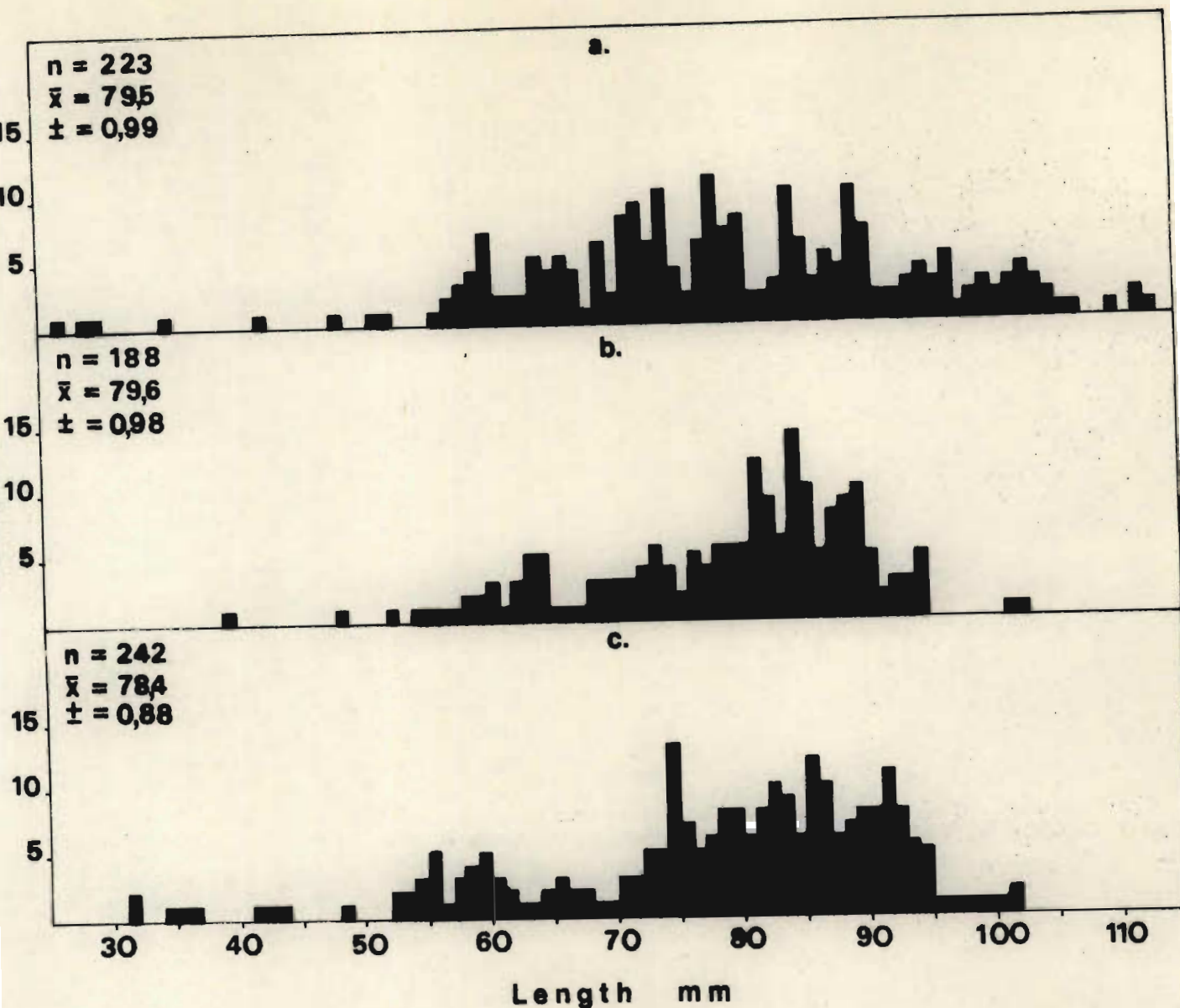


Figure 24: Sample populations of *A. wahlbergi* from various areas of the Sanyati Basin. (a: areas with strong river influence; b: Lakeside and Gache Gache cleared areas; c: Sanyati East cleared area)

Two other sample populations are also shown, one of mussels collected from the Lakeside and Gache Gache cleared areas representing two major cleared areas of the Sanyati Basin, (mainly from dive sampling done in 1976/1977), and another of mussels collected from cleared or uncleared areas with strong river influence, i.e. the Naodza cleared area, the Charara cleared area and uncleared areas and

mussels collected in the Lakeside cleared area from the mouths of two inflowing streams, the Nyanyana and Charara. These data were also collected mainly from dive sampling done in 1976/1977.

It seems from the histograms that the mussels from the river influenced areas reach the greatest maximum size. Here mussels over 100 mm in length were fairly common, whereas in the open water cleared areas, (i.e. areas more removed from river influence), mussels beyond this size were infrequent, the average maximum size per sample being about 95 mm.

Of particular interest is the disproportionate representation of larger or adult mussels (over 60 mm - see PART TWO) compared with juveniles and sub-adults, which are generally scarce in the samples. Since much smaller C. mossambicensis (mean size about 41 mm) were collected in abundance in the same areas as A. wahlbergi the adequacy of the sampling method cannot be questioned. Taking all three sample populations into account, mussels over 60 mm comprised 91% of the samples.

c.) Mutela dubia

This species was not common except in one or two localities and hence data collected in 1976/1977 from all sampling stations in the Sanyati Basin have been combined to show the sample population structure. (Fig. 25).

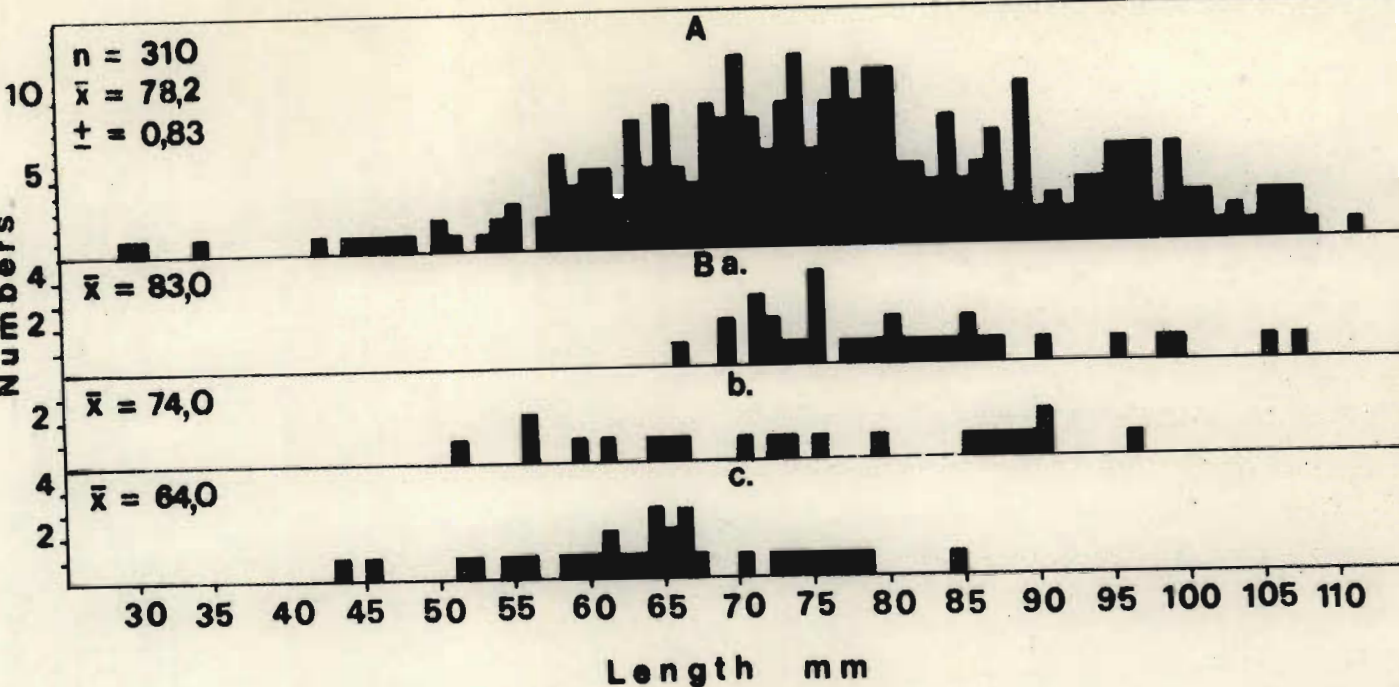


Figure 25: Sample population of *M. dubia* using combined data from various areas of the Sanyati Basin (A), and sample populations (B), from selected areas (Charara Estuary (a), Sanyati East (b) Islands (c)), showing differences in size range and mean size

As with the other two species it was obvious when sampling that differences in size of mussels existed in different areas, and this is also shown in Fig. 25.

The population is also essentially an adult population, with juveniles and sub-adults (below 55 mm) comprising only a small proportion of the total sample.

The samples from different areas - representing estuarine, island and shoreline populations - show that differences in size exist in different localities. Estuarine stations are river influenced, while islands are essentially open water stations. The Sanyati East Station represents a shoreline area, not under the direct influence of a river.

The largest specimens and the largest mean size were recorded from a river estuary station, while the smallest specimens and the smallest mean size were recorded from the island stations (Long Island and Sampa Karuma), separated from the mainland and streams or rivers by deep open water. Intermediate sizes were collected from the shoreline station. Since the mussels were collected over the same time period the shift to the right from the bottom (islands) to the top (Charara) does not represent growth.

5. Spatial Dispersion

a.) Cleared areas

Sampling was not conducted specifically to test for this parameter but nevertheless indications are available both from sampling results and observations. Three distinct types of distribution are generally recognized in sedentary biological populations - randomly distributed individuals, regularly distributed individuals and individuals grouped contagiously (i.e. in aggregations).

(i) Caelatura mossambicensis

The visual assessment of this species' spatial dispersion in the cleared areas is that they are aggregated. Observations suggest that they tend to occur in clumps, with areas between occupied by individual mussels or much smaller clumps.

Table 5: Counts of C. mossambicensis, A. wahlbergi and M. dubia from quadrats in the Sanyati East cleared area

QUADRAT	SAMPLE ONE			SAMPLE TWO		
	C.m.	A.w.	M.d.	C.m.	A.w.	M.d.
1	0	0	0	23	1	1
2	1	0	0	17	0	0
3	16	1	0	14	1	0
4	0	0	0	9	1	0
5	188	5	0	1	0	0
6	-	-	-	0	1	1
TOTAL	205	6	0	74	4	2
MEAN	41	1,2	-	12,3	0,63	0,33
VARIANCE	6 799	4,7	-	56,7	0,27	0,27
STD. DEV.	82,5	2,17	-	7,5	0,52	0,52

This suspected contagious tendency is shown in Table 5 , which records data taken from two samples of five and six quadrats respectively in the Sanyati East cleared area.

In both samples variance of the counts are considerably higher than the means, indicating a contagious distribution of the mussels (Elliot, 1971). The data were also tested for randomness of distribution, in which agreement with a Poisson series is the accepted test for randomness. In testing for agreement the variance to mean ration (χ^2) test was used where

$$\chi^2 = \frac{\sum (x - \bar{x})^2}{\bar{x}}$$

Agreement with a Poisson series is accepted at the 95% probability level ($P = 0,050$) if the χ^2 value lies between the appropriate 5% significance levels for $n - 1$ degrees of freedom.

In both samples the values of χ^2 obtained (663,3 and 23,0 respectively) led to rejection of agreement with the Poisson series at both the 95% and 99% probability levels, indicating that the dispersion of the population is certainly not random, and is probably contagious (where $s^2 > \bar{x}$). Since the samples were small it was not possible to test further for agreement with a Poisson series using the χ^2 test for goodness of fit.

Aggregation is also suggested by the frequency distribution of the number of mussels collected per dive,

shown for all species in Fig. 26.

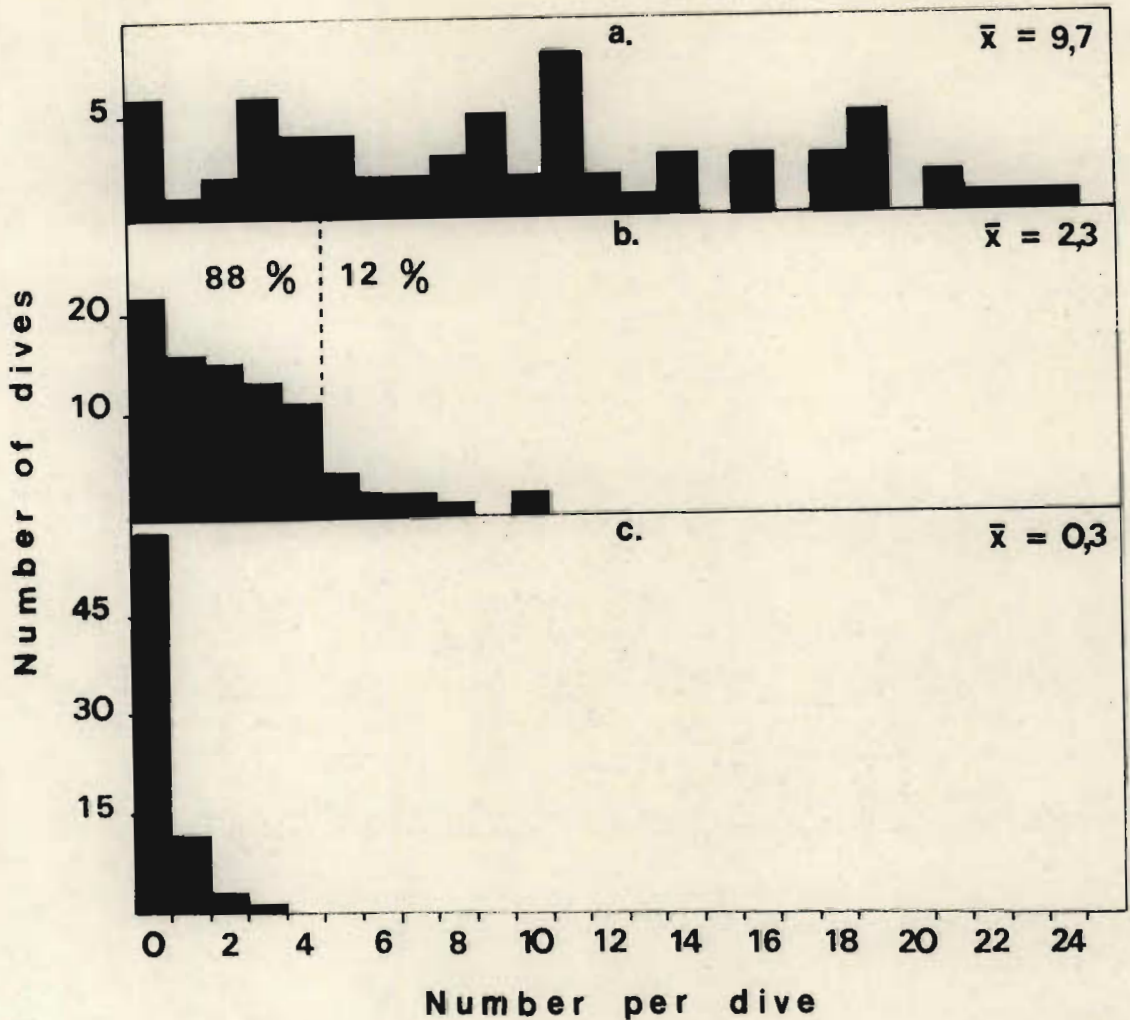


Figure 26: The frequency distribution of numbers collected per dive for *C. mossambicensis* (a), *A. wahlbergi* (b) and *M. dubia* (c). Data from cleared areas 1976/1977

The wide range of frequencies shown for *C. mossambicensis* (0 - 24; mean 9,7; standard deviation 6,7) is well representative of actual field experience, where one dive would yield none, or a few mussels, and the next 10 or more. Here again the variance of the counts ($s^2 = 44,5$) proved to be considerably greater than the mean ($\bar{x} = 9,7$) which also indicates aggregation. A typical example of this

situation was obtained in the Gache Gache cleared area, where two dives over soft silty substrate yielded 3,7 C. mossambicensis per minute, while the next two dives over a hard sandy substrate yielded 20,6 per minute.

(ii) Aspatharia wahlbergi

Visual assessment of this species' dispersion in the field was inconclusive because of the rather low numerical abundance.

The χ^2 test (variance to mean ratio) applied to the data in Table 5 gave conflicting results. In Sample One the χ^2 value (15,7) was above the value given for the 99% probability level, with the resultant rejection of agreement with a Poisson series and hence random distribution. In Sample Two the value of χ^2 (2,0) was well within the 5% significance levels of χ^2 , and agreement with the Poisson series and randomness could be accepted. Similarly, the variance of Sample One was higher than the mean ($4,7 > 1,2$) indicating aggregation, whereas in Sample Two the variance was less than the mean ($0,27 < 0,67$), indicating probable random distribution.

A more conclusive indication of dispersion is provided by dive sampling counts. Treatment of the dive sampling data from all cleared areas (Fig. 26) resulted in a frequency histogram positively skewed ($sk = 0,22$) and showing agreement with a negative binominal distribution ($P 0,05$) when the expected values were computed and compared

with the observed values in a χ^2 test for goodness of fit, where

$$\chi^2 = \frac{\sum (\text{Observed} - \text{expected})^2}{\text{expected}}$$

Variance of this distribution was higher than the mean (5,4 > 2,3). When tested for agreement with a Poisson series randomness was rejected at the 95% and 99% probability levels. A. wahlbergi would therefore appear to be contagiously dispersed, although it is doubtful whether this is as marked as C. mossambicensis, and at very low densities the species might be randomly dispersed.

(iii) Mutela dubia

The very low concentration of M. dubia in the cleared areas made it impossible to assess their dispersion visually. Table 5 shows the low numbers collected in the quadrats in the Sanyati East cleared area in which the variance to mean ratio test indicated the mussels were randomly distributed ($s^2 < \bar{x}$).

The data in Fig. 26 shows that the majority of dives resulted in no mussels being collected, whilst the largest number collected in any one dive was three. This would seem to indicate a rather random dispersion, but the variance of the data (0,37) proved to be greater than the mean (0,28), so possibly there is some degree of clumping. However the data are insufficient to draw any definite conclusion.

b.) Uncleared areas

(i) Caelatura mossambicensis

In the less productive areas of the lake the mussels are frequently found in greater concentration at the bases of objects, such as rocks and tree trunks, or underneath fallen branches or bark. In this respect their dispersion can be called aggregated, and this is well illustrated by samples taken from the Seiche Tower area of the Sanyati East grounds. Ten dives were made here with the following results:

DIVE NO.	AREA	NO. COLLECTED	NO. MIN ⁻¹
1 - 5	Open sand	3	0,65
6 - 10	Tower Base	61	11,50

The mussels were clearly concentrated around the concrete bases of the tower, and existed in comparatively low densities in the open areas away from the base. This is a situation fairly typical of many areas, particularly around the islands.

In the more productive areas the same applies, with concentrations of C. mossambicensis at the bases of objects, but with apparently similar concentrations in the open areas between objects. This is shown in Table 6. where six collecting dives of approximately one minute each were made amongst the trees off Dandawa (uncleared, Sanyati East).

The first three dives collected mussels from the bases of trees, while the next three collected mussels from open areas between the trees. Six further dives were then made at the same depth in the cleared area adjacent to the tree line to compare samples.

Table 6 shows a different situation from the Seiche Tower, with almost equal numbers being collected from both the bases and the open areas between the trees. In the adjacent cleared area a similar number of mussels was collected. Of interest here is that while the means of the two samples are obviously similar, the variances differ, indicating a possible difference in the degree of aggregation. A means of comparing the degree of aggregation between two samples is provided by David and Moore (1954) in Pielou (1969), who have suggested as a measure of aggregation

$$I = (V/M) - 1$$

where I is the index of clumping, V is the variance, and M is the mean of a sample.

In order to compare the degree of clumping evaluate

$$w = \frac{1}{2} \ln \frac{(V_1/M_1)}{V_2/M_2}$$

David and Moore state that if W lies outside the range of $-2,5/(n-1)$ and $2,5/(n-1)$ then I_1 and I_2 differ significantly at the 5% level.

Table 6: Samples of C. mossambicensis collected from uncleared and cleared substrates, Sanyati East

DIVE NO.	UNCLEARED NO. COLLECTED	CLEARED NO. COLLECTED
1	9*	19
2	25*	9
3	11*	11
4	21	11
5	12	18
6	9	19
TOTAL	87	87
MEAN	14,5	14,5
VARIANCE	46,3	21,5

*indicates samples from base of trees

Applying these formulae to the data in Table 6 I_1 and I_2 are 2,19 and 0,48 respectively, $W = -0,38$ and the range is $-0,5$ to $+0,5$. Since W lies within this range the conclusion is that the degree of aggregation is not significantly different at the 5% level.

(ii) Mutela dubia

This species was found to be more common in uncleared areas than cleared areas. This is shown by the catch per unit effort (numbers collected per dive) of 2,3; 0,9; and 1,6 from three uncleared areas - Charara Estuary, Tsetse Island West and Redcliffe and Antelope Islands - in comparison with the very low overall catch per unit effort of 0,28 per dive in the cleared areas. The overall catch per unit effort in terms of numbers per minute from uncleared areas was 1,1 mussels per minute, while from cleared areas it was 0,27 per minute. The variance of the data from uncleared areas was greater than the mean ($3,8 > 1,1$) suggesting an aggregated dispersion. Observations confirm that mussels were frequently located in small clumps under fallen branches or around the bases of rocks or trees. Probable reasons for these aggregations of both C. mossambicensis and M. dubia are suggested in PART TWO.

(iii) Aspatharia wahlbergi

This species showed no particular pattern of dispersion in the uncleared areas, and it is possible that their dispersion in these areas does not differ greatly, if at all,

from the situation in the cleared areas, i.e. a possible random distribution at low densities and possible aggregation at higher densities. For example, dive sampling in the Charara uncleared area resulted in a sample in which the variance was greater than the mean ($4,13 > 3,1$) indicating aggregation, whereas a similar sample in the Sanyati East uncleared area gave a sample in which the sample variance was less than the mean ($0,67 < 1,33$), indicating random dispersion. Concentrations of A. wahlbergi around the bases of trees or underneath objects is not a general feature of their dispersion.

6. Density - Cleared Versus Uncleared Areas

Both dive sampling and grid sampling have shown that the uncleared areas are just as prolific in mussels as the cleared areas. Reference to Table 3, for example, shows densities of 42 and 31 mussels m^{-2} , or 261 and 500 g m^{-2} respectively, for Charara and Sengwa East uncleared areas. These figures compare well with those obtained by grid sampling in the Sanyati East cleared area.

Similarly, Fig. 16 and Fig. 17 (the density maps) show that many of the high to medium-high density localities are in uncleared areas (e.g. Charara uncleared, Tsetse Island West, Sanyati East uncleared and Sanyati West uncleared). It has also been shown in a preceding sub-section that at least one species, M. dubia, has its highest densities in the uncleared areas.

7. Mortality

Of interest here was whether any significant form of mortality, other than natural mortality caused by old age, affected the population. A most likely cause was predation by other animals, and in the absence of known predators such as otters (Donnelly and Grobler, 1976) on the mussel grounds, a possible source was from the various fish species co-existing with the mussel population. While the study examining this aspect concentrated on one particular area it could be expected, by virtue of the fact that a wide variety of fish species was examined, to be indicative of the situation in the lake as a whole.

In addition to this study a record was kept of any other observations made, or data collected, pertinent to the subject of mortality, and these are presented in this sub-section.

a.) Predation by fish

The results of the predation study from the Lakeside stations, and other areas, are summarized in Table 7. The analysis shows that of the ten species examined, six had fed on bivalves, but only three in any significant degree, these being Haplochromis codringtoni, Synodontis zambezensis, and Clarias gariepinus. The combined results of other workers, in which nearly 10 000 fish representing 28 species were examined showed that only five species fed on bivalves : C. gariepinus, Distichodus schenga, H. codringtoni,

Hippopotamyrus discorynchus, S. zambezensis.

A breakdown of the bivalve species eaten by the three main predators in this study gave the following percentage results:-

MUSSEL SPECIES	<u>H.codringtoni</u> %	<u>S.zambezensis</u> %	<u>C.gariepinus</u> %
<u>C.africana</u> :	55,8	85,7	83,3
<u>C.mossambicensis</u> :	29,5	14,3	16,7
<u>A.wahlbergi</u> :	13,7	-	-
<u>M.dubia</u> :	1,0	-	-

This breakdown shows that the small clam , C. africana , was most frequently eaten by all three predators, in particular S. zambezensis and C. gariepinus .

H. codringtoni, a recognized mollusc feeder, was the only species that had taken more than two species. Similarly, the results of previous workers showed that C. africana, with one exception, was the only bivalve eaten by the five fish species mentioned earlier. The exception was H. discorynchus which had taken a few juvenile mussels, suspected of being A. wahlbergi, along with C. africana. (Kenmuir, 1970)

In this study only H. codringtoni crushed the bivalves eaten. C. mossambicensis and C. africana found in the stomachs of S. zambezensis had been swallowed whole, and in the case of H. codringtoni the bivalves were always small. In the Pongola River floodplain pans Corbicula forms the main dietary component of Clarias ngamensis while small species are also eaten by S. zambezensis (Heeg, pers. comm.).

Table 7: Results of stomach content analysis of ten benthic feeding fish species, March 1976 to June 1977

SPECIES	LAKESIDE		NYANYANA		OTHER AREAS		COMBINED	
	NO EXAM	% WITH BIVALVES	NO EXAM	% WITH BIVALVES	NO EXAM	% WITH BIVALVES	NO EXAM	% WITH BIVALVES
<u>Haplochromis codringtoni</u>	95	8,4	351	23,6	31	19,4	477	20,3
<u>Synodontis zambezensis</u>	39	2,6	71	8,5	45	13,3	155	8,4
<u>Clarias gariepinus</u>	123	4,8	175	4,0	2	0	300	4,3
<u>Hippopotamyrus discorhynchus</u>	64	0	181	0,6	21	0	266	0,4
<u>Eutropius depressirostris</u>	128	0	216	0,5	36	0	380	0,3
<u>Marcusenius macrolepidotus</u>	54	0	3	0	-	-	57	0
<u>Mormyrus longirostris</u>	-	0	56	0	1	0	57	0
<u>Mormyrops deliciosus</u>	15	0	-	-	-	-	15	0
<u>Heterobranchus longifilis</u>	1	100	1	0	2	0	4	-
<u>Distichodus schenqa</u>	1	0	-	-	-	-	1	-

b.) Mortality through other causes

Apart from mortality caused by fish predation, three other records of mortality amongst populations were noted at Lake Kariba.

In July 1975 a large number of C.mossambicensis shells were found washed up on the northern shoreline of Sengwa Point. No apparent reason for their presence could be established, particularly as the lake level was high and had been for about three months. A representative sample of approximately 140 shells were collected and measured for length. They were all of small size, the majority between 24 mm and 36 mm length.

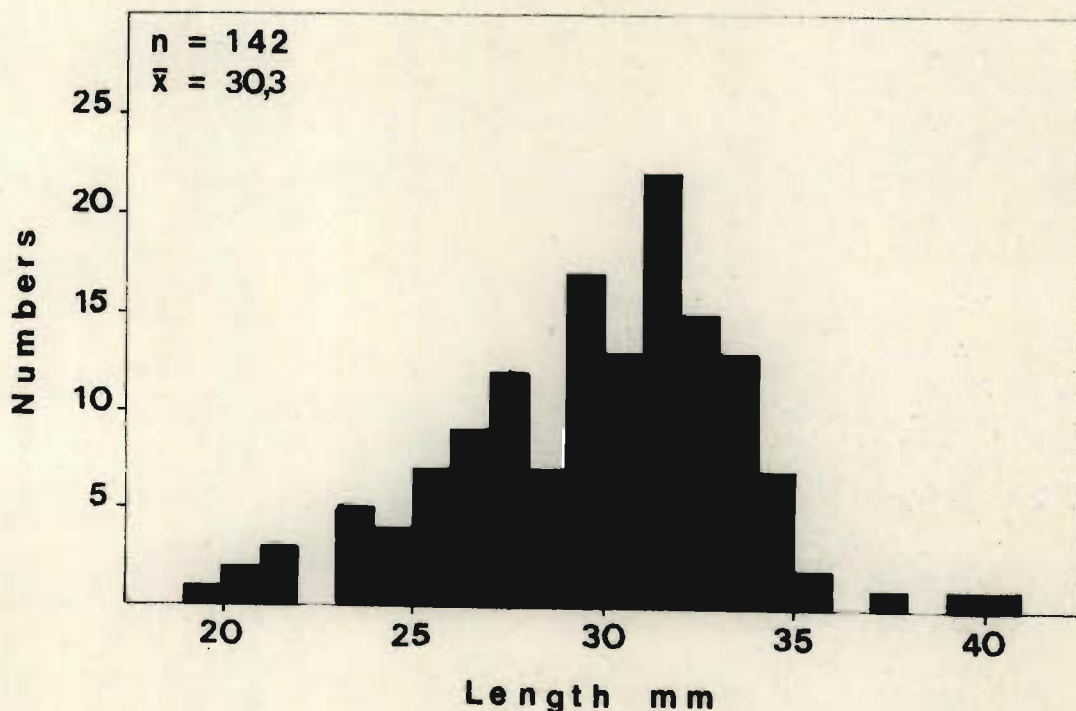


Figure 27: The length frequency of C.mossambicensis shells collected from Sengwa Point shoreline, July 1975

The reason for the mortality of this particular size class remained unresolved until a graph of past lake levels was studied, which showed that in the early part of 1975 lake level had dropped rapidly from 486,5 m.a.m.s.l. to almost 483,5 m.a.m.s.l. - a drop of nearly three metres. It would seem that this drop had stranded mussels, causing mortality, and a heavy wind blow with resultant wave action is likely to have washed the shells at a later date onto the grassy shoreline. Thus stranding due to a drop in lake level can be a cause of mortality amongst Lake Kariba mussels. This was also observed in February 1980, when widespread mortality was caused by a drop in Lake level. (French, 1980).

A second suspected cause of mortality is silt, either wave induced, but more probably from flooding rivers, settling on the substrate and burying the mussels. In October 1978 a 3 m² area amongst the trees in the Sanyati East fishing ground yielded a number of juvenile mussels (18, ranging in size from 4 mm to 9 mm). A number of empty shells of adult C. mossambicensis and C. africana were found, but no living material. Since an abundance of mussels exists on this Sanyati East fishing ground, the only logical explanation for a complete absence of adult bivalves here was that a heavy deposition of silt from the Sanyati River, during the preceding rainy season, had buried them (1977/1978 season), causing mortality. The juveniles found would thus represent early colonizers of the denuded substrate once silt deposition had stopped.

The above are examples of density independent

factors causing mortality in the population. A suspected example of density dependent mortality was found at the Seiche Tower base, where a dense concentration of C. mossambicensis exists in a small area ($\pm 9 \text{ m}^2$) around and between the concrete supporting boles of the tower. Several complete scoops of soil were removed from around the boles and both live mussels and shells were measured for length.

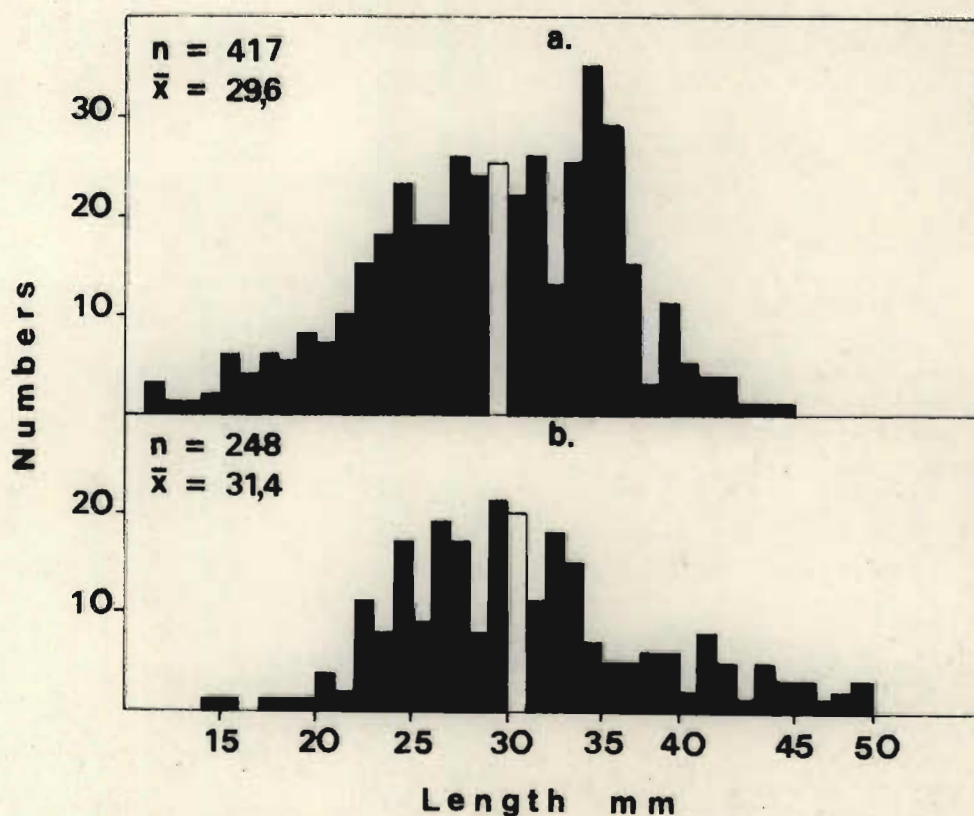


Figure 28 : Length frequencies of C. mossambicensis shells (a) and live specimens (b) from the Seiche Tower base, October 1978. Clear column indicates mean class

Three features of the samples merit comment :

- (i) the paucity of juvenile mussels (under 20 mm) in the live sample,
- (ii) the very much smaller mean size of the population (31,4 mm) when compared with other areas of the lake, and,
- (iii) the general similarity between the shell population and the live mussel population in terms of range, mean size and length frequency structure.

The shell histogram indicates mortality throughout the size spectrum, since in shape it corresponds approximately to that of the live population.

The Seiche Tower is several kilometres from the shoreline and from the mouth of the gorge, and it is neither subject to silt deposition (the substrate here is hard and sandy) nor to frequent exposure caused by lake level dropping (this particular population becomes exposed at a level of 482,5 m.a.m.s.l. and hence was exposed in late 1973, some five years earlier). The water here is generally clear. Mortality would therefore appear to be caused by some density dependent factor acting on individuals, regardless of size. It may be starvation at a time when nutrient levels and therefore food resources are low, or disease and / or parasitism, whose action would be facilitated by the close proximity of individuals to one another.

B. LAKE MCILWAIN

1. Species Composition

Species composition is shown in Fig. 29 and Fig. 30 . (Percent Numbers)

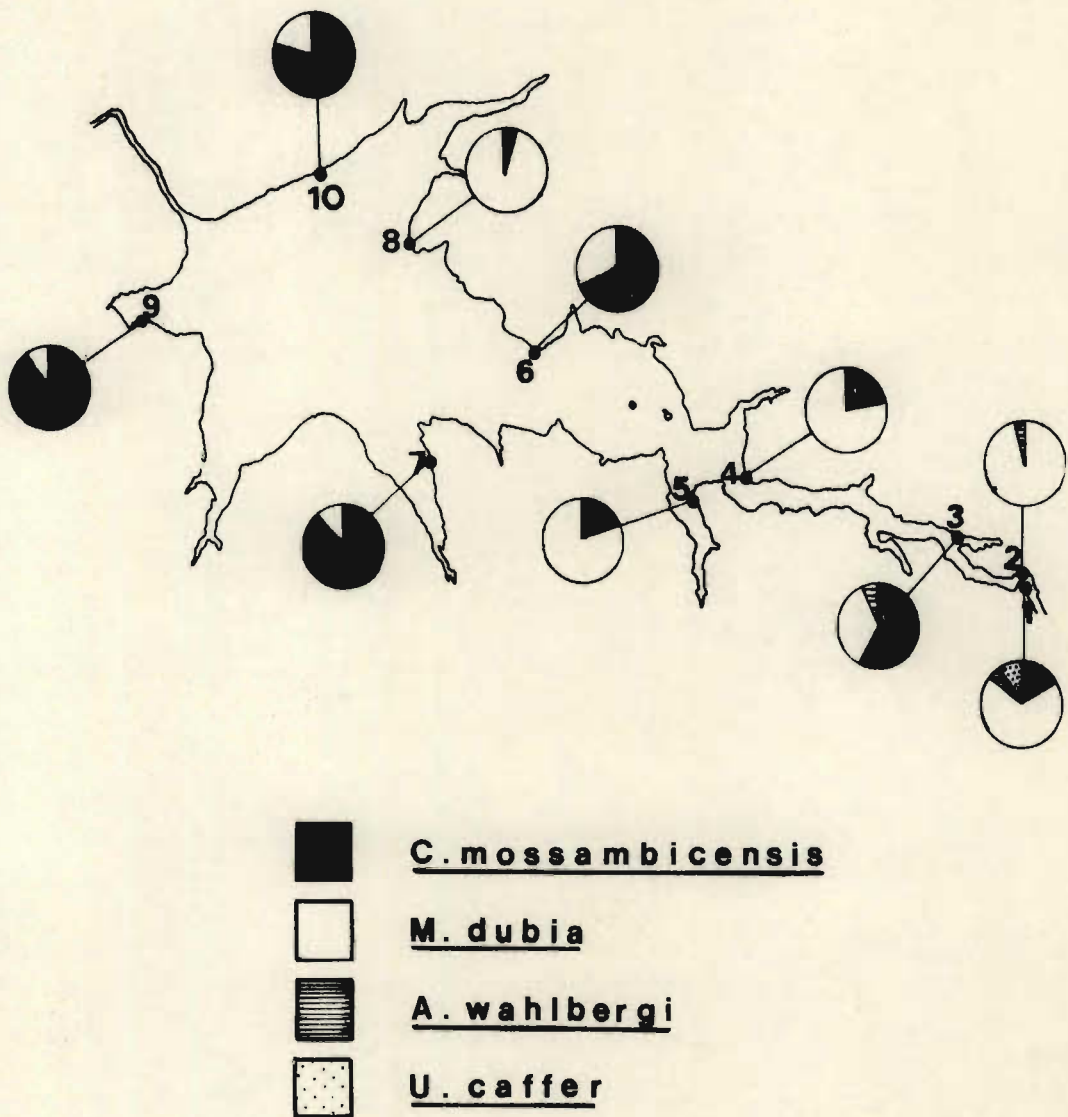


Figure 29: Species composition of the mussel fauna at various stations on Lake McIlwaine, July/August 1979. Level at time of sampling 0,93 m below spillway level

Both sampling periods showed that greatest species diversity occurred at the top end of the lake (river / lake interface) where four species were recorded : M. dubia, C. mossambicensis, Unio caffer and A. wahlbergi. The latter species occurred at only one other locality, Station 3, and was not recorded elsewhere while only a single U. caffer was recorded in the lake, near Pelican Point, after the sampling discussed here was completed.

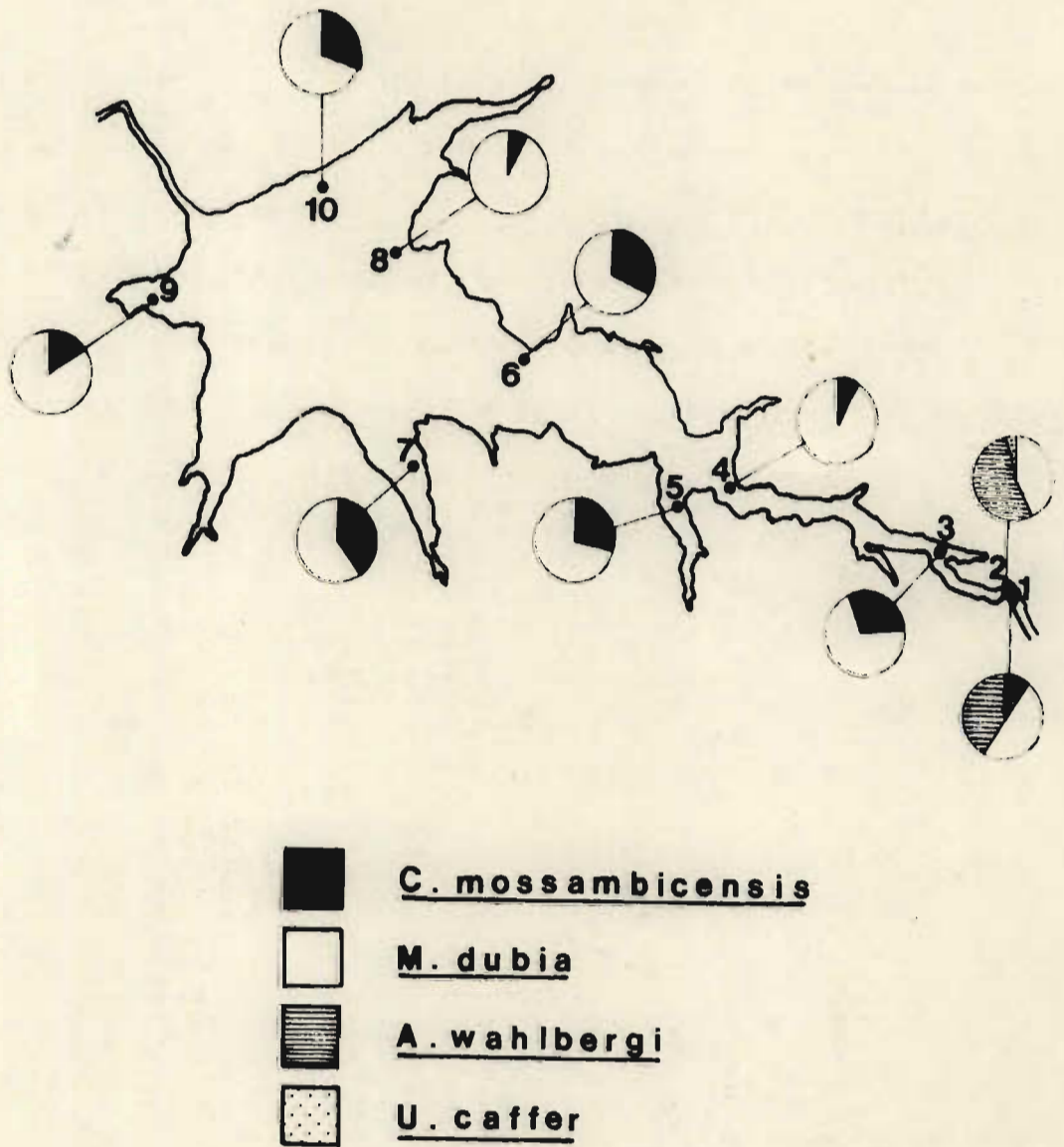


Figure 30: Species composition of the mussel fauna at various stations on Lake McIlwaine, October 1979. Level at time of sampling 2,1 m below spillway level

At all other stations in both July/August and October only two species were recorded, these being M. dubia and C. mossambicensis .

However, distinct differences in species composition are apparent when considering the two periods. In July/August C. mossambicensis dominated numerically at five out of eight lake stations. In October, when lake level had dropped a further metre, M. dubia dominated numerically at all eight lake stations. A second difference was the dominance of A. wahlbergi in the October sample from Station 1 and Station 2 (Upper lake), as opposed to dominance by M. dubia in July/August. An incidental feature of interest was that at Station 7 and Station 9, in July/August, numerous cracked shells and spoor indicated predation on M. dubia by water mongoose (Atilax paludinosus) or otter (Atilax capensis), or both. The proportion of this species might be under represented at these stations as a result.

2. Population Structures

The sample population structures of the two common species for the two sampling periods are shown in Figs. 31, 32, 33 and 34. In some cases, where data were scarce, combined length frequency histograms are presented.

The histograms clearly show that differences between the mean size exist at different stations, means being greatest in the upper lake stations, and significantly lower in the lake stations.

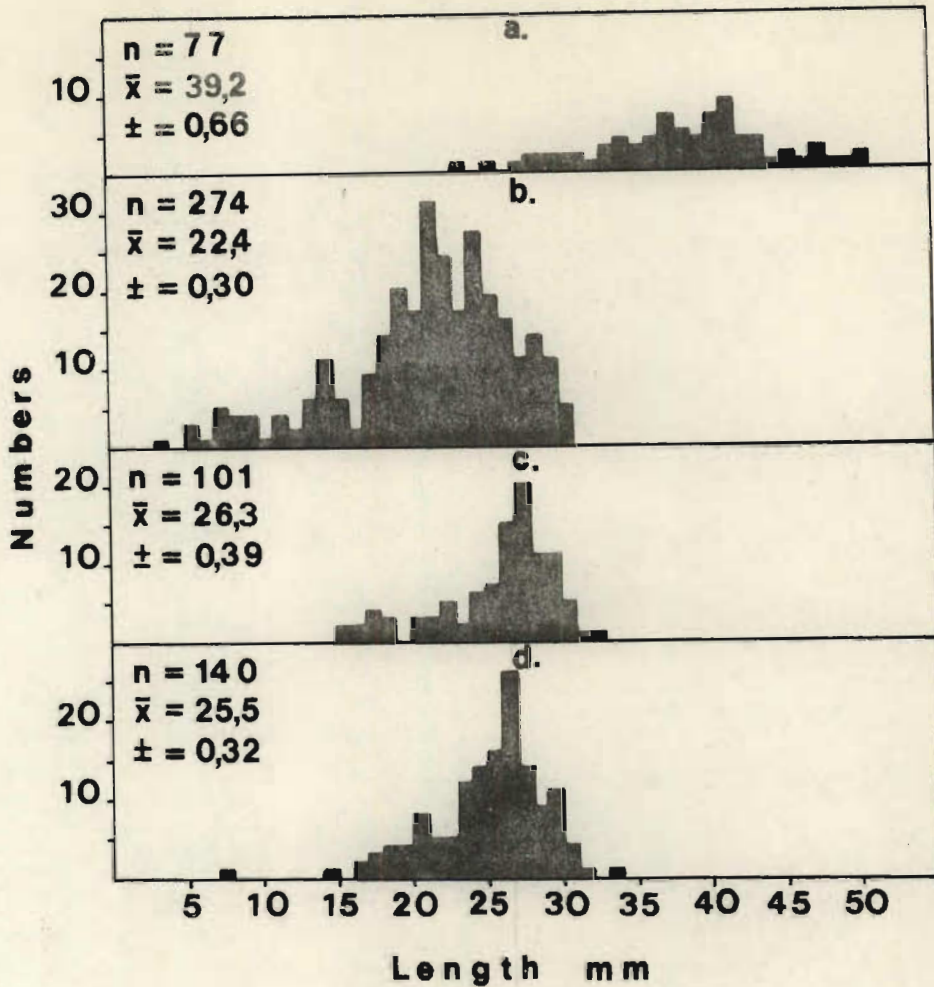


Figure 31: The sample population structure of stranded *C. mossambicensis* from Lake McIlwaine, July/August 1979. Upper Estuarine (a), Samaki and False Creek (b), Pelican Point (c), and Dassie Point, Lakeside, Tiger Bay, Crocodile Creek (d)

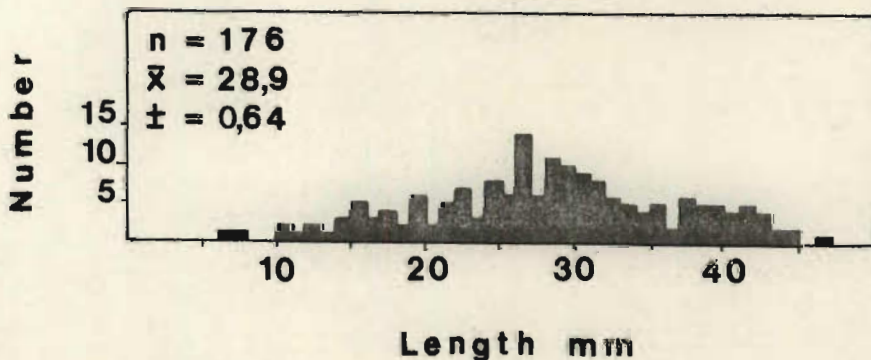


Figure 32: The sample population structure of stranded *C. mossambicensis* from Lake McIlwaine, October 1979

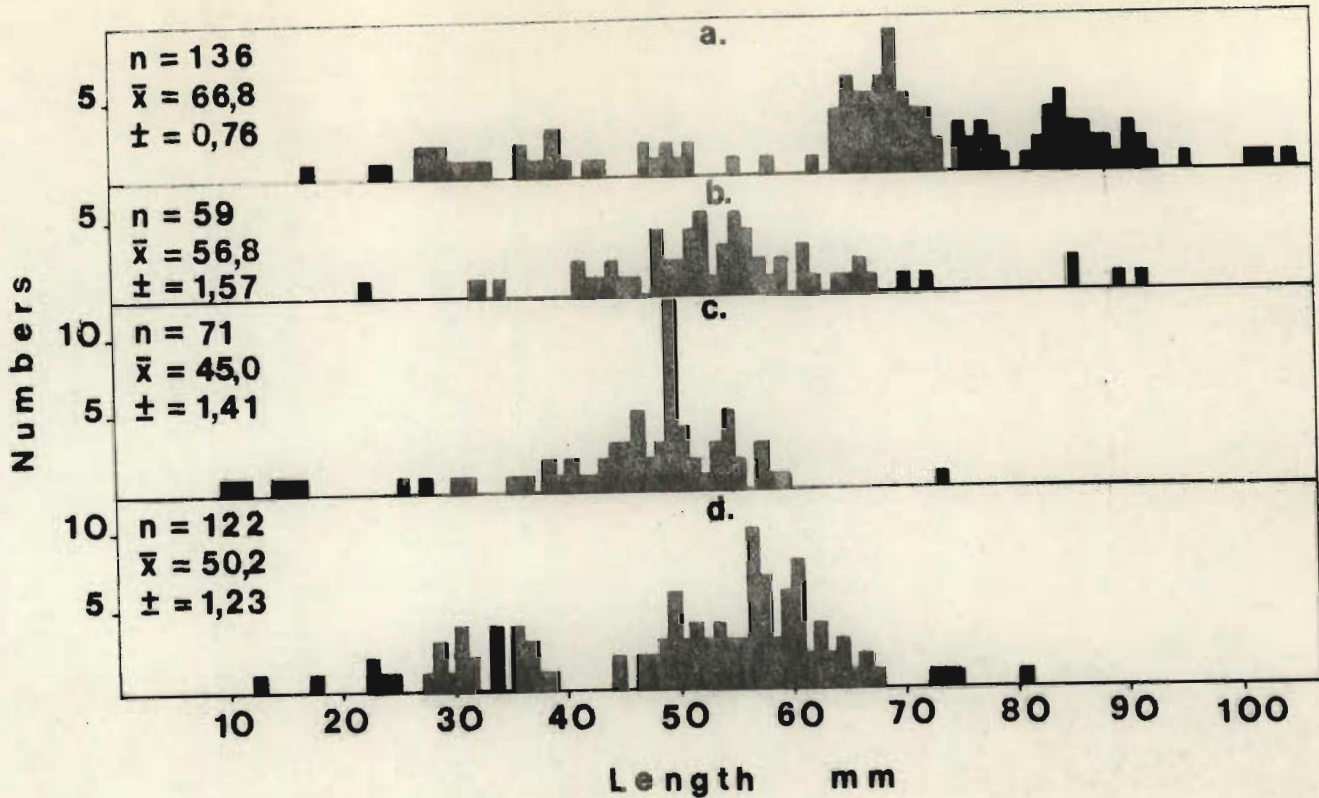


Figure 33: The sample population structure of stranded *M. dubia* from Lake McIlwaine July/August 1979. Stations are Upper Estuarine (a), Samaki and False Creek (b), Pelican Point (c), and Dassie Point, Lakeside, Tiger Bay, Crocodile Creek (d)

Marshall's results (1975) also showed greater mean sizes for both species from the upper lake stations. The generally small size of individuals collected in July/August can be explained by the fact that the substrates they were recorded from were exposed as recently as February 1977, and the higher areas of beach even more recently. The populations at time of sampling were thus between two and three years old. Greater mean lengths were recorded in October, when samples were collected at a lower contour, and clearly had been submerged for much longer before exposure. Similarly, Marshall (1975) collected larger mussels in samples taken when lake level had dropped 5,1 m below full supply level.

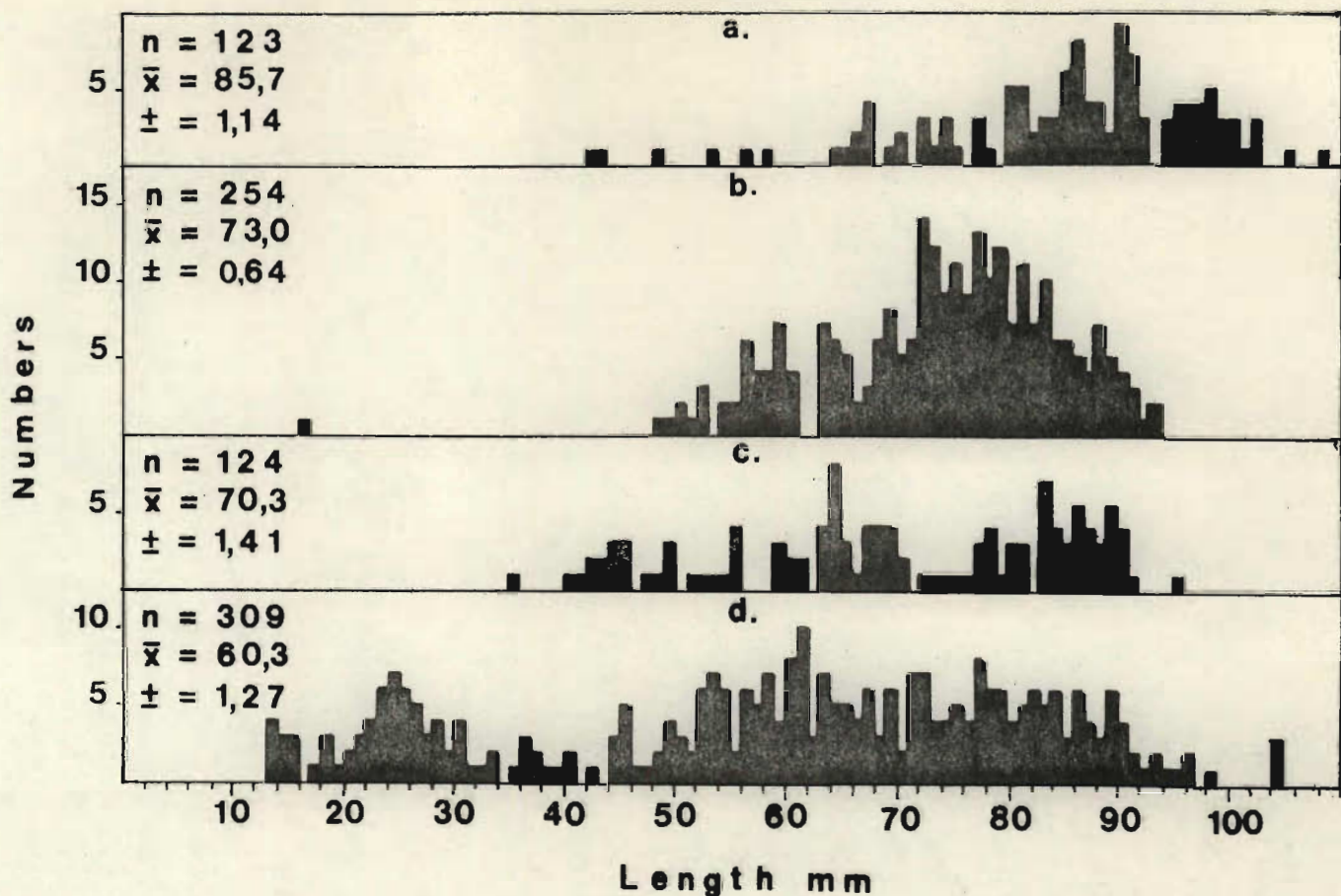


Figure 34: The sample population structure of stranded M. dubia from Lake McIlwaine October 1979. Stations are Upper Estuarine (a), Samaki and False Creek (b), Pelican Point (c), and Dassie Point, Lakeside, Tiger Bay, Crocodile Creek (d)

That deeper water supports larger individuals is also shown by a sample of M. dubia obtained from 2 m - 4 m depth off Pelican beach, between July 1978 and May 1979. These mussels measured 39 mm - 86 mm in length, with a mode at 79 mm, and a mean length of 72 mm.

The eight A. wahlbergi collected in July/August measured 57,2 mm - 84 mm with a mean length of 72,1 mm while the five U. caffer ranged in size from 36,5 mm - 81,0 mm with a mean length of 48,9 mm. In October the A.wahlbergi

collected ranged in size from 65 mm - 124 mm with a mean size of 104 mm, appreciably larger than the earlier sample. The four U. caffer collected in October ranged in size from 50 mm - 77,8 mm, with a mean length of 68,0 mm.

3. Absolute Densities

Mussel counts were made in quadrats at Stations 3, 4, 6, 7, 8, 9 and 10. Results of these counts are summarized in Table 8.

As can be seen, densities were very low, and at only one station in July/August (Crocodile Creek - Station 7), did numbers of C. mossambicensis rise above one per square metre. Mean density of this species was more than three times greater than the density of M. dubia at this time. In October the situation was reversed, and M. dubia was approximately four and a half times more common than C. mossambicensis. Marshall (1975) obtained mean values for C. mossambicensis and M. dubia of $0,09 \text{ m}^{-2}$ and 6 m^{-2} in 1973, when lake level was at a record 5,1 m below full supply level.

Two points of interest arise from Marshall's findings and the results of this study. The first is that the area Marshall sampled had probably never been exposed before, since the previous lowest drop was 3,9 m in 1968. The densities he recorded, therefore, probably represented optimal densities at that depth as these populations had 21 years in which to establish. If this is so, then densities of mussels in Lake McIlwaine as a whole are very much lower than densities in Lake Kariba.

Table 8: Densities (No m⁻²) of C. mossambicensis and M. dubia from various stations on Lake McIlwaine, July/August 1979, and October 1979

STATION	<u>Caelatura mossambicensis</u>		<u>Mutela dubia</u>		AREA
	July/Aug	Oct.	July/Aug	Oct.	
3	0,15	0,30	0,35	1,50	Mid/upper reaches
4	0,04	0,00	0,04	1,08	Samaki
6	0,42	0,15	0,19	0,32	Pelican Beach
7	2,00	0,44	0,28	0,82	Crocodile Creek
8	Nil	0,08	0,34	1,90	Dassie Point
9	0,80	0,02	0,08	0,50	Tiger Bay
10	0,04	0,07	0,04	0,06	Hunyani Hills
MEAN	0,50	0,14	0,19	0,88	
S.E.	0,25	0,06	0,05	0,23	

Note : M. dubia was usually more frequent than C. mossambicensis on mud substrates and vice-versa on sand substrates.

The second point of interest is the decreasing density of C. mossambicensis with increasing lake level drop, and conversely the increasing density of M. dubia at the greater lake level depth. The density of C. mossambicensis drops from 0,5 to 0,14 to 0,09 at depths of 0,9 m , 1,9 m and 5,1 m below full supply level. Conversely, M. dubia increases from 0,19 to 0,88 to 6 per square metre at these depths. This change in species composition with increasing depth is clearly shown in the next sub-section.

4. Depth Distribution

Results of the sampling done on Pelican Beach as water level receded is shown graphically in Fig. 35 and Fig. 36. Fig. 35 (a & b) shows a fluctuating but nevertheless gradually decreasing proportion of C. mossambicensis as lake level gradually dropped below full supply level (F.S.L., Fig. 35 d) with a converse increasing proportion of M. dubia. Accumulative percentages of these two species (c & e) shows clearly the gradually changing nature of the beach population of mussels over the period of time. When lake level had dropped approximately 1,6 m below full supply level, (indicated by dotted line), M. dubia started occurring more frequently, reflected as a sharp dip in the accumulative proportion slope. The mass proportion of C. mossambicensis dropped from 63% at the start of the survey in late June to only 8% by the end of October, while M. dubia increased from 37% to 92%. That these changes in proportion represent real changes in density of both species has been shown earlier (sub-section on Absolute densities), and is seen in Fig. 36.

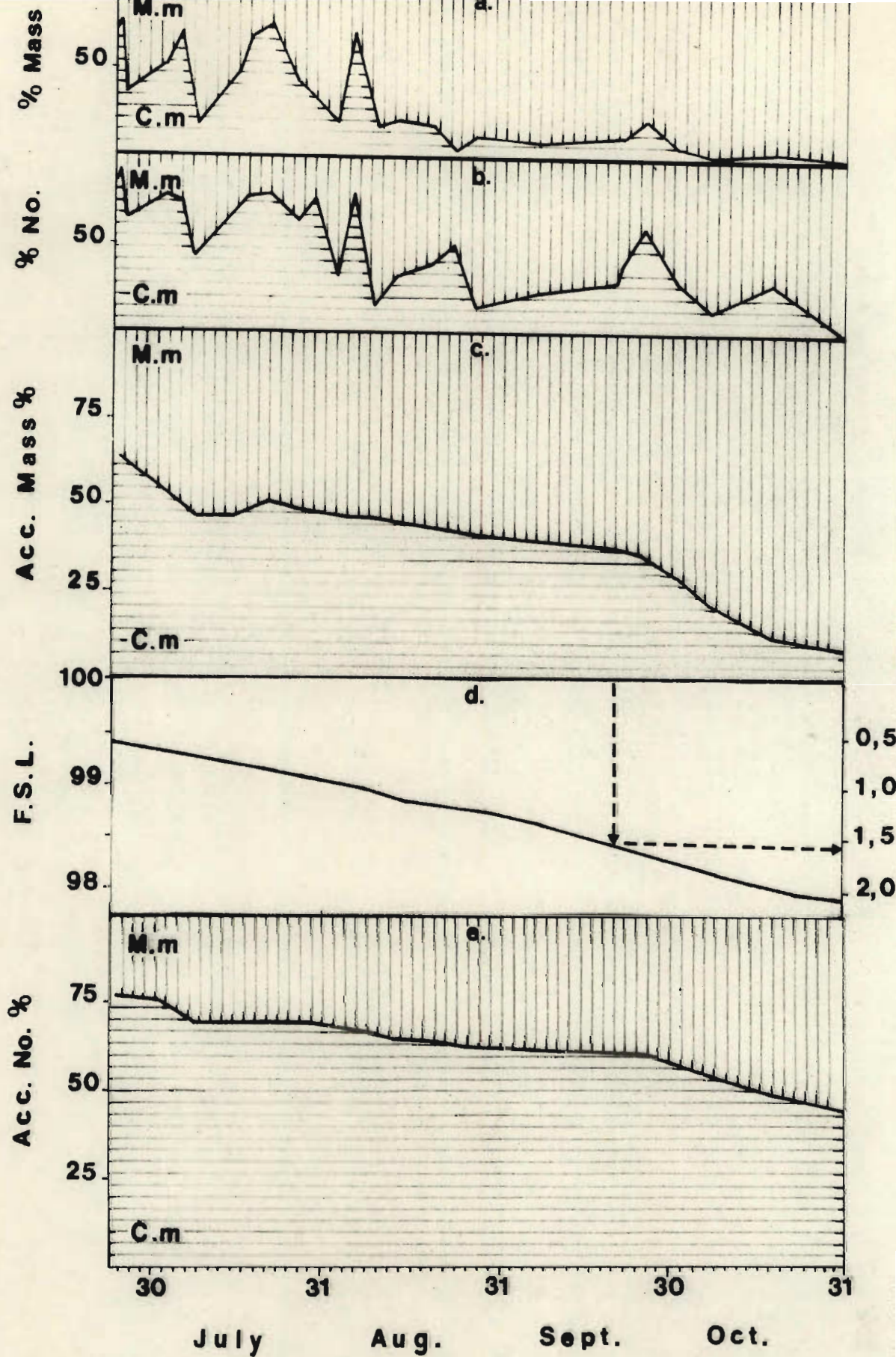


Figure 35: Showing the changing percentage composition of *C. mossambicensis* and *M. dubia* on Pelican Beach as water level receded, from June 1979 to October 1979

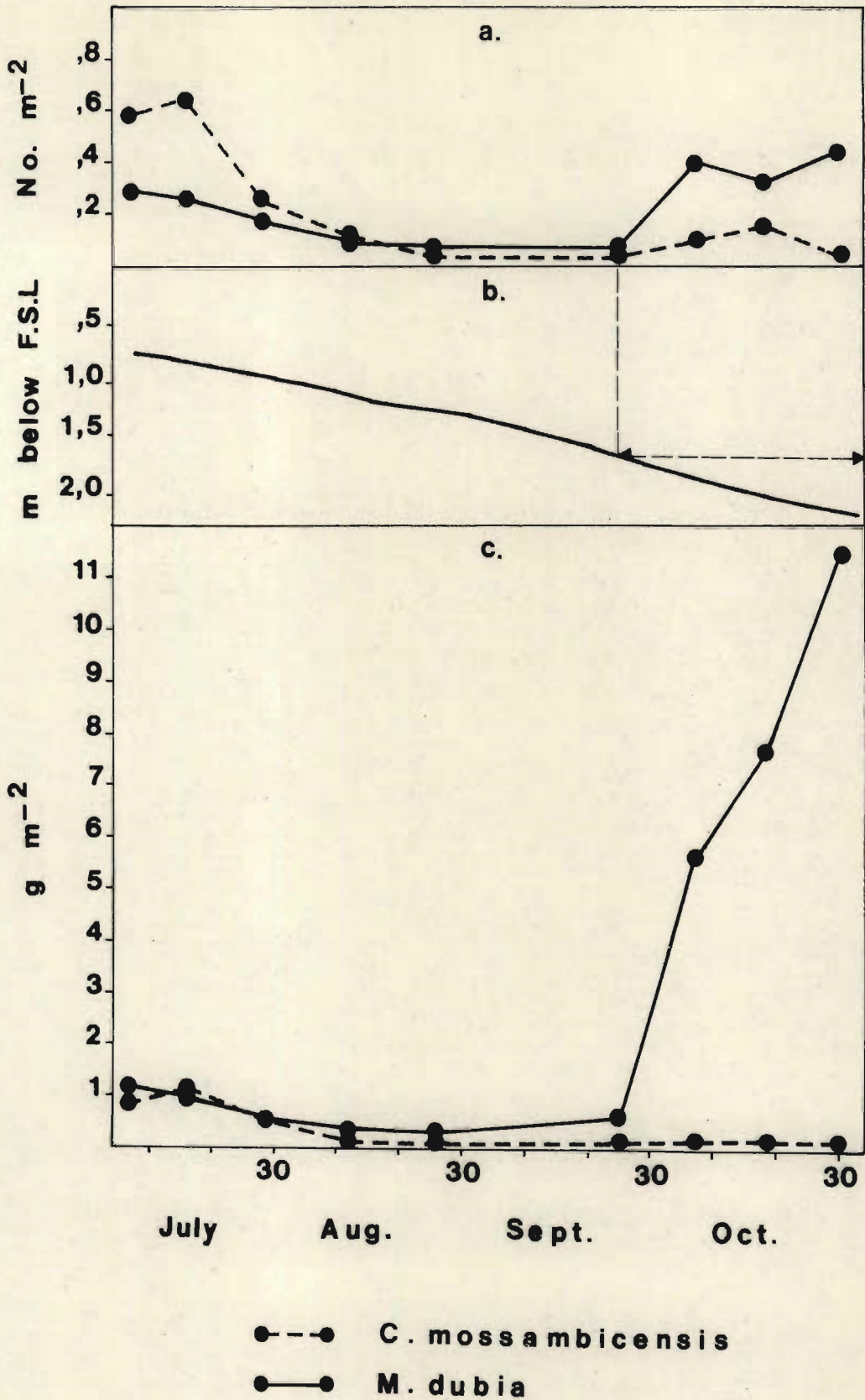


Figure 36: Showing changes in density of *C. mossambicensis* and *M. dubia* on Pelican Beach between June and October, 1979

It will be recalled that in July/August 1979 C. mossambicensis dominated, whereas when the lake had dropped a further metre by October 1979 M. dubia had become the more common species.

Fig. 36 (a) shows an overall decline of C. mossambicensis numerical density over the period, and an overall increase of M. dubia density. Fig. 36 (c) shows more clearly the density changes, with a very significant increase in M. dubia mass density taking place from approximately the 25th September when lake level was about 1,6 m below full supply level. Both species show a decrease in density from June/July, followed by increases in September giving a "trough" effect to the graphs. Thus there seems to be an intermediate zone of low density for both species between 1 m depth and 1,6 m depth below full supply level. The reason for this is not clear, as substrate was fairly uniform along the gradient, but it may be related to fish movements with cichlids moving from deeper to shallower water, and vice versa, at certain times of the day, as recorded by Caulton (1976) and Minshull (1978). If these fish are important hosts to the mussel larvae, then one could expect greater colonization of substrate where fish are either feeding or resting for prolonged periods, rather than areas which the fish are merely moving over.

5. Migration

Evidence of migration for three species was obtained in July and August 1979, when lake level had dropped from one to two metres below spillway level, and large numbers

of mussels had already been stranded. Observations on migration movements of C. mossambicensis, M. dubia and A. wahlbergi were made in shallow water, less than 60 cm depth, at Pelican Point Beach. The gradient of this beach was established as 1 in 38. In most cases the migration tracks led from shallow to deeper water.

a.) Caelatura mossambicensis

The clearly defined tracks of 14 mussels were measured for length, from the point where the track first became visible up to the mussel itself, with the following results:

LENGTH OF TRACK (cm) : 91; 92; 91; 152; 213; 107; 168; 137;
213; 122; 123; 152; 244; 152.
MEAN \pm S.E. : 147 cm \pm 13
PROPORTION MOVING
TOWARDS DEEPER WATER : 79%

These migrations had taken place in water less than 60 cm depth, beyond which no tracks were observed. This may suggest migrations are triggered when water reaches a certain depth. The time taken for these particular migrations is obviously not known, but taking into account the gradient of the beach and the rate of lake level drop at that time (approximately $0,85 \text{ cm day}^{-1}$), a mussel would need to move approximately 32 cm day^{-1} into deeper water to avoid ultimate stranding.

The average daily rate of migration is not known

but of several specimens whose positions were marked, one had moved 65 cm in 48 hours ($32,5 \text{ cm day}^{-1}$), and another 20 cm in 18 hours (27 cm day^{-1}). Others marked at various times either did not move, or if they did their tracks were obscured by wave action. Not all tracks moved directly towards deeper water. Many mussels had doubled back, or changed direction and moved parallel to the shore, or moved in seemingly aimless fashion. Stranded mussels usually moved a few centimetres through the substrate before coming to rest, and no evidence of burrowing was found.

b.) Mutela dubia

Eleven specimens found close to the waters edge in a few centimetres of water were position marked in the evening and their positions noted 18 hours later, with the following results :

DISTANCES MOVED (cm)	:	14; 18; 10; 27; 18; 9; 0; 13; 0; 0; 0.
MEAN OF ALL \pm S.E.	:	10 cm \pm 2,8
MEAN OF MIGRATORS \pm S.E.:		16 cm (27 cm day^{-1}) \pm 2,3
PROPORTION MIGRATED	:	64%
PROPORTION BURROWED	:	27%
PROPORTION HALF BURROWED	:	9%
PROPORTION MOVED OFFSHORE	:	57%
PROPORTION MOVED TOWARDS SHORE	:	43%

Of these eleven mussels only one was moving at a rate (27 cm in 18 hrs) sufficient to avoid being stranded. The substrate of this area is a rather uneven mixture of

hardish sand and clay, and rate of progress was undoubtedly dependent on the consistency of the substrate. Those that burrowed rather than moving on may have been in harder substrate. In an attempt to determine whether migrations took place mainly at night or during the day the positions of nine specimens were marked (this number purely arbitrary, dependent on the number seen migrating at the time) and positions noted each evening and morning over 63 hours, with the results shown in Table 9. Observations ceased when heavy wave action moved the marking sticks.

Several different patterns of behaviour are evident here. Most mussels moved only at night (Numbers 3; 4; 5; 6; 7; 8; = 67%), while one moved only during the day (Number 9), and two moved both nocturnally and by day (Numbers 1 and 2). Six mussels (Numbers 2; 3; 5; 6; 8; 9) moved and then remained stationary for from one to three half day periods before moving again. One mussel showed movement in each of three consecutive half day periods (Number 1), while another moved only once and remained stationary for the remainder of the period (Number 4). The mean was 127 ± 28 .

The observations do suggest that periods of migration are usually followed by periods of rest, and that distances of up to 173 cm are attainable in a half day period. (Number 3 moving in soft sand). While the data suggest movement takes place mainly at night this could be incorrect, as the observations started in the evening and all mussels marked, with the exception of Number 9, were already moving. They could represent a proportion of the population that are night

Table 9: Migration distances (cm) of M. dubia noted over day and night periods at Pelican Beach, August 1979

MUSSEL NO	1715-0715	0715-1715	1715-0800	0800-1715	1715-0815	DISTANCE IN 63 HRS
1	25	24	10	0	Disappeared	59
2	54	0	0	31	0	85
3	62	0	173	0	0	235
4	76	0	0	0	0	76
5	112	0	94	0	7	213
6	77	0	80	0	0	157
7	21	0	Disappeared	-	-	21
8	38	0	0	0	18	56
9	-	120	0	118	0	238

movers, and hence bias in selecting them for observation would have been introduced.

Mussel Numbers 1 - 3 and two others which subsequently disappeared moved 13; 19; 19; 19; and 11 cm respectively in the first hour of the 63 hour period. Speeds of 11 cm hr⁻¹ - 19 cm hr⁻¹ represent a theoretical potential ability to travel 132 cm - 228 cm overnight (12 hours). Obviously, from the distances actually travelled by Numbers 1 - 3, these theoretical potentials were certainly not realized. In fact, the distances travelled in the first hour represented 52%, 35% and 31% respectively of the actual distance travelled, or 16%, 24% and 27% of the theoretical potential distance. It is clear from this that the initial speeds observed were not sustained throughout the night. Of the five mussels, four travelled a greater distance in the first 30 minutes of travel than in the second:-

MUSSEL NO:	1st 30 mins (cm)	%	2nd 30 mins (cm)	%
1	11	58	8	42
2	7	64	4	36
3	6	46	7	54
4	13	68	6	32
5	12	63	7	37

Thus even the speeds recorded in the first hour were not sustained speeds, as 80% of the mussels exhibited decreased speed over the second half. These five mussels were

all in soft sand and the decrease was not due to a change in substrate consistency. The non-realization of the theoretical potential, as determined by the speeds actually recorded at time of observation (which themselves could be sub-maximum), could therefore be due to a gradually decreasing speed during the night, or movement with intervals of rest, or even a single short period of movement in which the total distance travelled takes place over a few hours only. Obviously a good deal of interesting research under more controlled conditions could be done on this aspect of their biology.

One other observation was a track which started at 11 cm depth and led for 270 cm straight into water 30 cm deep. An estimate based on the rate of water level drop at that time ($1,6 \text{ cm day}^{-1}$) assumed time taken to move 270 cm (2 days), indicates the mussel at its original locality would have been exposed in nine days, but by moving to deeper water time to exposure increased to 25 days. This mussel, therefore, had clearly improved its chances of survival.

c.) Aspatharia wahlbergi

In November 1978 several A.wahlbergi from Lake Kariba were placed in cages in approximately 1 m of water off Pelican Point Beach, pending removal for possible experimental purposes. Several escaped, and between July and September 1979 a few of these were recovered when receding lake level left them stranded on the beach. They were located 9,8 m; 13,8 m; 24 m and 30 m from the point where

they had originally been placed. Mean daily rates of movement over the period were 3,5 cm; 5,1 cm; 8,5 cm and 10,0 cm respectively.

Apart from indicating the ability of this species to migrate from shallow to deeper water, and that they do so, the mussels indicated a different response to stranding when compared with C. mossambicensis and M. dubia. Whereas the latter two species when stranded are normally found lying in a desiccated state above ground, A. wahlbergi were buried in the substrate, invisible to the inexperienced eye and located only by two small holes, made originally by the water currents from their siphons.

C. LABORATORY

Results of the exposure tests showed that both the C. mossambicensis and M. dubia died within six days from commencement of the experiment whereas at the end of the three month period the A. wahlbergi were still alive. These were placed in a bowl of water where they soon opened and started siphoning.

The results of the thermal tolerance experiment showed that the five C. mossambicensis tested were able to withstand a temperature of 42,2°C.

Salient features of their behaviour under the rapid temperature rise are shown on the following page :

TEMPERATURE °C	BEHAVIOUR
24 - 36	Behaviour apparently normal. Siphoning.
36 - 41	Contracting frequently and expelling water from siphons. Stress evident.
41 - 42,2	Two gaping ; appearance of death. Contractions in others ceased. Experiment ended.

Mortality appeared to start at 41,7°C, when one mussel suddenly gaped and remained open even when touched, followed shortly after by another at 42,2°C, exhibiting a similar appearance of death. At this point the experiment was stopped. The mussels were removed and placed in a bowl at room temperature. The next morning the "dead" mussels had recovered and the five were siphoning in a normal manner. Under the test conditions one can conclude that a state of disfunction was manifest at a temperature of approximately 41,5°C, but that the mussels were able to withstand a temperature of 42,2°C for a short period.

The Lake McIlwaine mussels (C. mossambicensis and M. dubia) exposed to the temperature range of 5°C - 34°C over a three day period all survived this treatment with no visible or apparent ill effects.

The response of the C. mossambicensis to decreasing levels of DO concentrations is shown graphically in Fig. 37 .

The test shows that mortality in Bowl 2 (not aerated, ambient temperature) started when DO concentrations dropped below 1 ppm. No mortality occurred in either of the control bowls (1 and 3), even though DO concentration had dropped to approximately 2,50 ppm in Bowl 3. (No aeration, 15°C). In this latter bowl the rate of utilization of DO was slower at the lower temperature than in the bowl at ambient temperature. The water in Bowl 1 (aerated) became saturated by the seventh day.

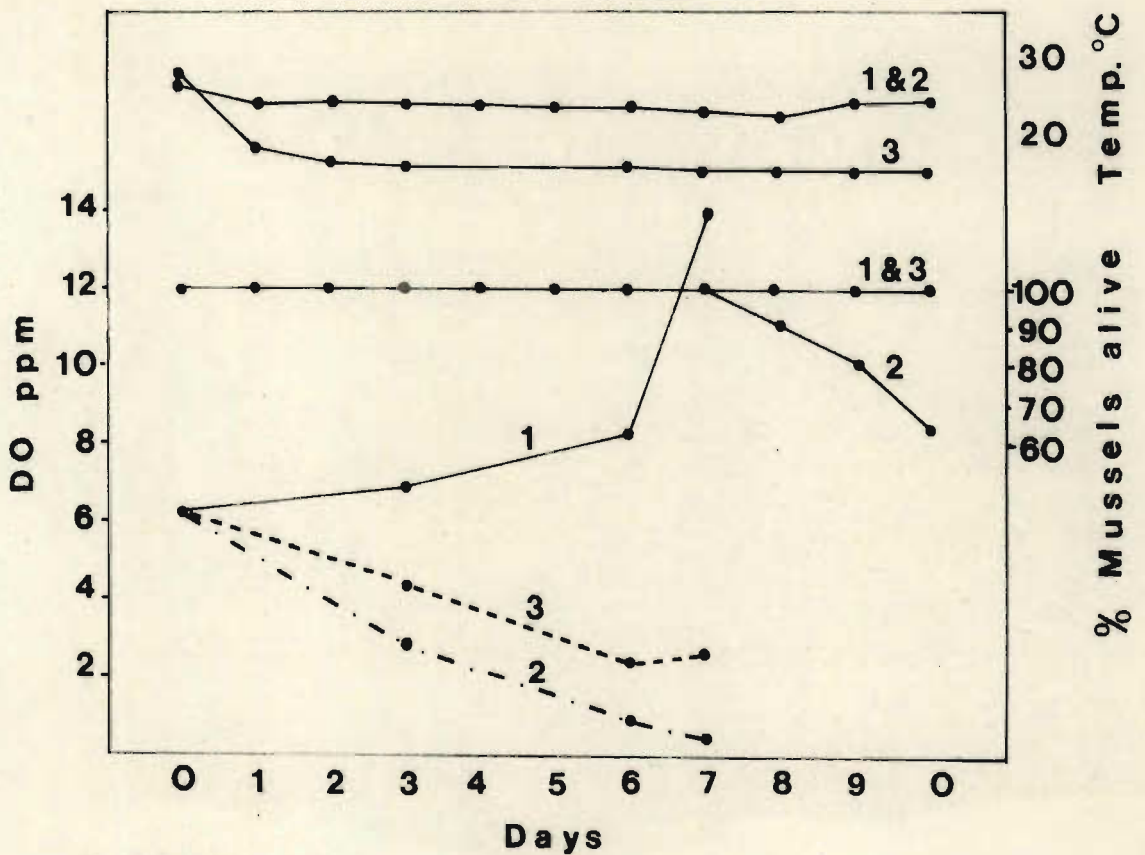


Figure 37: The relationship between decreasing levels of DO concentration and survival of *C. mossambicensis*. Top graph lines indicate temperature, middle graph line indicates mortality and bottom line indicates DO concentration in Bowls 1, 2 and 3

DISCUSSION

It is clear from this study that mussels are not only widespread in Lake Kariba but that many areas support thriving populations of a magnitude which suggests the possibility of commercial exploitation. The factors which influence, or appear to influence, their distribution and species composition, and also the size structure of the populations, will be discussed in this section, in an attempt to add to our understanding of their biology as a whole and to suggest lines of thought which might encourage future research. In this respect the sampling in Lake McIlwaine has proved advantageous, in that it has enabled comparisons to be made and in some cases has helped to explain aspects which, when viewed on their own in the context of a single lake, appear meaningless or inexplicable.

The first aspect considered is that of species composition in relation to distribution. Why are some areas heavily populated by one species and not by others? Since all three species are dependent on host fish for the successful completion of their life cycle, one possibility is that fish may play an important part in distribution patterns. A. wahlbergi appears to be associated with rivers, being recorded in Lake McIlwaine only in the upper riverine section of the lake, and in Lake Kariba in the vicinity of inflowing rivers. It is possible that the main host, perhaps only host, is a potamodromous fish. Obviously research into the question of host specificity could be productive. The distribution of M. dubia in Lake Kariba showed an interesting

characteristic in that its highest densities were amongst trees in uncleared areas. One would suspect that the presence of trees or similar submerged objects is necessary for a widespread distribution and high density of this species, and yet, in Lake McIlwaine, it is widely distributed and one of the commonest species throughout the whole lake, a water body generally devoid of submerged trees. Despite these contradictory situations the indications are that fish play an important part in these distribution patterns. Observations at Lake McIlwaine have indicated that the greenhead bream, S. macrochir is a main host species of the larvae of M. dubia. (See PART TWO - REPRODUCTION). This fish species is abundant and widespread in Lake McIlwaine (Marshall and Lockett, 1976) and presumably has played an important part in the distribution of M. dubia in the lake.

In Lake Kariba the greater concentration of M. dubia in the uncleared areas is probably related to the increased number of small fish species and juveniles of larger ones which act as hosts and inhabit these areas. That small fish are involved in the life cycle of both M. dubia and C. mossambicensis was indicated by two observations made in uncleared areas. The first was made at the base of a very large tree in the Charara Estuary, where an aggregation of M. dubia ringed the bole. Dwarf bream, (H. darlingi), inhabiting this area were seen to rub themselves vigorously on the sand, in the same manner that fish do in tanks when infected with larvae of M. dubia. Since these were the only fish observed it appeared they were probably the main host species, and responsible for the presence of

the mussels around the tree base.

A second observation involved the recovery of an aggregation of C. mossambicensis from the hollow bole of a tree, through a small hole some 10 cm above ground level, and big enough to admit only small fish. The fish inhabiting the bole and immediate surroundings were also dwarf bream and were probably responsible for the small colony of C. mossambicensis in the bole. There were many such examples, the dense concentration of C. mossambicensis around the base of the Seiche Tower being another example.

The obvious preference of small fish in Lake Kariba for areas offering various forms of cover is attributed to the presence of predators, in particular tigerfish (H. vittatus) in the lake (Kenmuir, 1977, 1978). Diving observations at Lake McIlwaine, off Pelican Point Beach, have shown that underwater forms of cover such as tree stumps and boulders are not inhabited by colonies of small fish as in Lake Kariba, even though H. darlingi and other small species are common in the Lake. (Marshall and Lockett, 1976). A thorough search for mussels in the diving area showed them to be sparsely and randomly distributed, and no aggregations occurred around the tree stumps or rocks as would have been the case at Lake Kariba. This observation was substantiated when lake level dropped, leaving such areas exposed and available for further examination. Fish predators in Lake McIlwaine are not common, and commercial and experimental fishing results show the population of tigerfish has declined in recent years.

It is apparent that a thorough knowledge of the host/larvae relationship in the field would assist in interpreting the distribution of mussel species in a water body. Undoubtedly other factors are also involved in these particular distributions, and all may act independently of one another or be inter-related. A species may be more tolerant of silt deposition, in which case dominance in river environments could be expected, and hence possible dependence on riverine fish species as larvae hosts.

With regard to their distribution in more general terms, one factor which has emerged from this study is the apparent tolerance of adults to differing environmental conditions. All three species were transported from Lake Kariba, an oligotrophic lake in a warm tropical climate, to Lake McIlwaine, highly eutrophic at a much higher altitude and with a cool climate, where they survived and bred normally, showing no apparent signs of discomfort from the translocation. The tests carried out on C. mossambicensis and M. dubia in which they were subjected to and survived extreme temperature ranges and low oxygen concentrations suggest that in the adult stage, at least, they are extremely hardy and tolerant of a wide variety of environmental conditions. Distribution therefore might not be influenced so much by the ability of adults to survive, but rather by the vulnerability of the young. Several attempts to rear post glochidial stages by infecting fish failed. (see PART TWO - REPRODUCTION), suggesting that these stages are extremely vulnerable. Similar failures are reported by Lefevre and Curtis (1912). Certainly, if one considers

the reproductive potential of the adults, and the actual sparsity of young in the field, mortality in the early stages must be very high, and one reason could be vulnerability of the young to environmental factors. In Lake Kariba the shallow, marginal waters to a depth of two metres was not productive, whereas deeper water supported substantial populations. Initially it was thought that vulnerability of mussels to annual drawdown and consequent exposure was the main, if not only, factor responsible for their absence from this zone. The situation in Lake McIlwaine has shown this view to be incorrect. Both M. dubia and C. mossambicensis are obviously capable of rapidly recolonizing and surviving in the first metre drawdown zone once water level rises. Similarly, Walley (pers. comm.) has recorded A. wahlbergi and C. mossambicensis in water only a few centimetres deep in pans at the Pongolo Flood Plain, which are subject to fluctuating water level, and in which stranded C. mossambicensis populations are subject to desiccation at low water level. Obviously the annual drawdown at Lake Kariba is not responsible for the general lack of mussels on the drawdown zone, and some other factor(s) must be involved. The tests on C. mossambicensis have shown the species to be resistant to high and low temperature conditions, such as might obtain in shallows, and to very low oxygen concentrations, which could occur in a stagnant pool left by receding water level. Thus the extreme environmental conditions that often prevail in shallow waters are not likely to be responsible for the relative scarcity of adult mussels in Lake Kariba's shallows.

The different situations in the two lakes suggests that a factor peculiar to Lake Kariba might be responsible. A tentative suggestion is that the larger size of Lake Kariba with vastly greater wind fetches results in silt re-circulation of a magnitude which stifles young mussels which may colonise this zone. Hard wind blows are fairly frequent over Lake Kariba, and silt re-circulation is often evident by discoloured water stretching out from the shorelines. In October 1978 a blow-up lasting several hours induced heavy seas, causing turbidity down to a depth of 7 m several hundred metres from the shoreline, where diving visibility was reduced to zero (pers. obs.). On Lake McIlwaine the generally compact sand and mud substrates with little silt and the shorter wind fetches do not result in re-circulation and substrate disturbance of the extent found in Lake Kariba, and the presence of mussels in the shallows suggests their resistance to this minor degree of disturbance. Another possibility is the presence of the grass P. repens on most of Lake Kariba's drawdown zones (certainly in the study area) acting in some unspecified manner detrimental to mussel development.

At the other end of the depth scale a combination of factors of which DO may be the most important, may be responsible for confining the mussel population to waters within approximately 11 m depth. Coche (1974) has shown that water in the lake as shallow as 10 m can, at times, have DO concentrations as low as 2 ppm. Obviously water not much deeper than 10 m at these times will have concentrations sufficiently low to cause mortality in mussels. The laboratory

tests showed that C. mossambicensis could survive 2 ppm DO but succumbed below this level. Imlay (1971) found that both adults and juveniles of several unspecified mussel species required a minimum 2,5 ppm of DO for survival at laboratory temperatures corresponding to summer field temperatures. All species examined by Imlay required 6 ppm for normal growth. Obviously in the natural environment one could expect a threshold for DO values below which important functions, such as growth and reproduction, will cease or be severely retarded. Related also to DO concentration would be fish movement, and hence mussel distribution. Obviously fish will not venture into water not attractive to them, and their role as hosts will be limited to the areas they inhabit. The shallower waters will obviously be of greater attraction to fish because of the abundance of food, oxygen and plant cover. Colonization of deeper waters may take place temporarily during winter when thermal and oxygen stratification breaks down and fish venture into deeper water, but these colonizers would be killed off when oxygen depletion again took place during summer. In Lake McIlwaine, for example, no benthic animals were found below 8 m in summer where 20% saturation values of oxygen were a limiting factor. (Marshall, 1978b) Other factors can also influence fish movement. Caulton (1975), for example, has shown that T. rendalli are incapable of entering water deeper than 7 m, while temperature preference may confine certain species to shallower water. Light penetration, limiting phytoplankton, periphyton and vascular plant growth, and hence reducing sources of food in the form of detritus and associated microbial flora (Heeg, pers. comm.) might be inhibitory to mussels in deeper water. Taking into

account relative light intensity data available for Lake Kariba (Coche, 1974) and DO at the 2 ppm level in relation to depth and their impact on living organisms, one could, without even sampling, predict the limits for existence of longer living benthic organisms such as mussels in the littoral zone to be somewhere between 10 m and 16 m. The actual depth recorded at Sanyati East cleared area, therefore, accords with such a prediction.

An aspect of interest relating to distribution, and demonstrating clearly that mussels in a water body are not homogenous with regard to size, was the difference in mean sizes encountered in different areas, in both Lake Kariba and Lake McIlwaine. These differences are probably related to water quality and related to this, food resources. Caulton (1970) showed that in terms of total dissolved solids, phosphate-phosphorous, and nitrate-nitrogen, the Lake Kariba estuarine waters were richer than either marginal areas or waters over areas of great depth, which includes stations adjacent to the steep sides of islands. Marginal areas were generally intermediate in nutrients between the other two type areas. If mean size was simply inversely related to density, the assumption being less competition for food, the densely populated estuarine areas should have smaller individuals than the less densely populated island areas. Since the reverse holds, it is probably correct to state that availability of food resources in a water body dictates relative mean size and range, other factors being equal. In this regard, the high densities in the Sanyati West cleared area are of interest. Could these densities be related to

nutrient enrichment of the water by the decomposition of the P. repens grass and animal faeces which takes place to a greater or lesser extent each year when the margins are flooded? The game park adjacent to this area carries a very large population of buffalo (over 3 000 head), hundreds of elephant, hippopotami and a variety of antelope which annually deposit large quantities of faeces on the grassy lake shore verges. Hippopotami, for example, are conservatively estimated as putting some seven tons of faeces per year per hippopotamus into the water (Heeg, pers. comm.), while McLachlan (1971) has shown that the nutrient status of water benefits considerably from decaying grass and faeces when the lake level rises. If this is true, it might not be coincidental that the highest density of C. mossambicensis in Lake McIlwaine in this study was recorded at Crocodile Creek, adjacent to the game park.



Plate 9 : Hippopotamus grazing on Panicum repens on the shoreline of the Yacht Club Harbour



Plate 10 : A bull elephant grazing on Panicum repens on the Matusadona shoreline

The suggestion above that nutrient levels might influence density and mean size, does not necessarily hold true for different water bodies. The sampling has shown that Kariba has very much higher densities than Lake McIlwaine, despite the latter's highly eutrophic status (Marshall, 1978b) and the former's more oligotrophic status. Similarly, Lake Kariba's mean population lengths for C. mossambicensis and M. dubia seem in general to be higher than Lake McIlwaine's. A greater nutrient status in two different water bodies would therefore appear not to be a guarantee of an associated increased abundance, or size of mussels. Other factors obviously play a part in dictating levels of density and growth. An important factor, for example, would be how the

nutrients are used. If aquatic macrophytes use them the resulting detritus and microbial fauna might be beneficial as food to mussels, whereas a dense bloom of non-edible blue-green algae, with a shading depressant effect on other flora and fauna, might be detrimental.

Differences in mean size were also noted in relation to depth. Individuals in the 1979 sample populations in Lake McIlwaine from approximately 1 m depth proved smaller than individuals taken by Marshall in samples in 1973 down to 5 m depth. This difference is most readily explained by the different lengths of time in which these two populations were able to grow, those in deeper water obviously having more time than the shallow water samples. The differences in size in the C. mossambicensis populations at different depths in the Sanyati East cleared area cannot be so easily explained, although some possible reasons can be advanced. The most likely reason is that the shallow waters, with the smaller mean sized population, have a higher turnover rate of individuals - possibly because of increased mortality through predation, siltation or other factors. An increased recruitment rate would thus tend to lower the mean size. Recruitment rate in the shallower areas would also be enhanced by the increased number of host fish here, compared with deeper water (pers. obs.). Another possibility is migration of older individuals to deeper water. In view of the migration noted in Lake McIlwaine this possibility cannot be discounted, and may take place when lake levels start dropping. However, no evidence of this was noted during the study period on Lake Kariba.

The predation study undertaken in Lake Kariba revealed an extremely low degree of predation on the mussels. Where predation on bivalves did take place, this was mostly on the small clam, C. africana, and even this was of a fairly insignificant nature in comparison with the sort of predation that Mitchell (1976) has shown to take place on other invertebrates such as the shrimp, Caradina nilotica, or the mayfly nymph, Povilla sp. . Lake Kariba has no real mussel-feeding fish capable of fracturing hard shells in the manner that the catfish Clarias ngamensis does in the Pongola pans where it feeds extensively on C. africana. (Heeg, and Kok, pers. comm.). Similarly , in Lake McIlwaine, only Sphaerium have been found in fish stomachs (Marshall, 1975) despite the obvious abundance of larger species. The absence of species adapted to taking advantage of this abundant food source is surprising , but one must bear in mind that both Lake Kariba and Lake McIlwaine are new ecosystems where niche occupation by mussels has proceeded rapidly in the absence of a predator system not wholly adapted to taking advantage of such an expanding food source.

Turning from the subject of distribution and density and the factors which appear to influence this, the structure of the populations merits comment in view of the general paucity of juveniles in the samples, in particular from Lake Kariba. At Lake Kariba the length frequency histograms of all three species from all areas and depths show a fairly characteristic paucity or even total lack of juveniles. Various authors have commented on the lack of young in field samples. Hunter, in Wilbur and Yonge (1964)

writes :

"Even in the common species of Anodonta and Unio young post glochidial bivalves have rarely been found and practically nothing is known about the development, growth or ecology of newly metamorphosed freshwater mussels".

Similarly, Lefevre and Curtis (1912) comment on the same problems, while Marshall (1975) mentions an almost identical situation to Lake Kariba in Lake McIlwaine, where the smallest M. dubia found was 30 mm in length. Quite probably the recruitment rate in a stable long lived population such as appears to be the case in Lake Kariba is very low. Krebs (1972) maintains that in populations at high densities, reproductive rates decline in some manner and stable or declining populations tend to have fewer young organisms. While the Lake Kariba populations certainly do have young mussels, this clearly cannot be attributed to a depressed reproductive rate since this has been shown to be high in two species, C. mossambicensis and M. dubia, in Lake Kariba. (See PART TWO - REPRODUCTION). It seems possible that adults in some way are capable of depressing the number of young post glochidia from colonizing established beds. In a situation where there is a rapid turnover of adults, which would arise if cropping took place, the number of young mussels might increase. It may not be coincidental that the only locality in Sanyati East where a concentration of juveniles was recorded was an area in the Dandawa treeline, where no adults were found. This could well represent a situation where an absence of adults (presumed killed by silt several months

before) resulted in increased recruitment and rapid recolonization. The density here (6 m^{-2}) represented approximately one third the mean density for the area ($21,3 \text{ m}^{-2}$ - see Table 2) and appeared to have been achieved in about six or seven months. If this is the case extrapolation of this recolonization rate would mean a return to normal numerical density in one and a half to two years (Provided sufficient adults are in the vicinity to infect host fish).

Further support for the idea that young are far more common in a developing population as opposed to a stable population is provided by the sampling in Lake McIlwaine. A comparison of the length frequency data obtained in July/August 1979 (this study) with that obtained by Marshall in 1973 shows a far greater number of juveniles recorded in 1979. The population sampled in 1973, when lake level had dropped to a record low level, probably represented a fairly stable population, with little recruitment, whereas in 1979 the samples represented a developing population recolonizing an area which had been exposed, and the previous population killed, as recently as 1977.

These indications of successful recolonization of hitherto denuded areas are interesting in that field observations and laboratory tests show that neither C. mossambicensis nor M. dubia can survive stranding caused by falling lake level. Exposure has a devastating effect on their populations, causing 100% mortality on all mussels exposed. Those that are not eaten by otters, mongoose or open-billed storks (Marshall, 1975) soon die from desiccation.

This is unlikely to be the case with A. wahlbergi, however, since this species obviously has the ability to withstand several months of exposure, and in fact Beadle (1974) describes a species from Malawi capable of living out of water for two years, and reviving within half an hour of being placed in water. French (1980) has also recorded a very high proportion of live A. wahlbergi stranded on Lake Kariba shorelines in February 1980, while very few C. mossambicensis and M. dubia were alive. Limited observations at Lake McIlwaine, involving the escaped A. wahlbergi from a wire cage, suggest that the onset of stranding causes the mussels to burrow into the sand or mud, which action undoubtedly assists in the ability to resist desiccation. The other two species take no such evasive action, and are usually found on top of the substrate or vainly trying to plough through it. Their intolerance to stranding suggests that populations could be completely eradicated in the event of water level dropping in a water body. This is unlikely ever to be the case, however, because of a behavioural mechanism in the form of migration which exists to ensure that a nucleus of the population will survive to recolonize once water level rises again. The migrations of mussels into deeper water observed at Lake McIlwaine almost certainly ensures the survival of the species in the face of adverse conditions. The significance of tolerance or intolerance to desiccation is examined further in the final discussion, where the development and nature of the mussel fauna in Lake Kariba and Lake McIlwaine, with particular reference to the influence of ecological principles on these parameters, is discussed. Aspects of the reproduction of the three species will be considered after the Summary.

SUMMARY

A number of different aspects have been covered in this section and to re-orientate the reader the more significant features of the study are summarized below.

A. LAKE KARIBA

1. The Lake Kariba bivalve stocks in the study area comprise three mussel species (C. mossambicensis, A. wahlbergi and M. dubia) and one clam species (C. africana).
2. Of the mussel stock - C. mossambicensis is the most widespread and important species, followed in terms of importance by A. wahlbergi and M. dubia. The latter species was important in some estuarine stations and was more common in uncleared than cleared areas.
3. Cleared areas, uncleared areas adjacent to them and certain river estuaries supported the most abundant stocks of mussels. Isolated islands and steep rocky areas had comparatively poor stocks.
4. In the Sanyati East cleared area mussel stocks extended down to 11 m +, but greatest densities occurred between 3 m and 9 m. From 0 m - 3 m few mussels were found. This situation probably exists in other similar mussel grounds.
5. Overall densities in this cleared area amounted to 29 mussels m^{-2} and 378 g m^{-2} . In the most productive depth zones densities rose to over 60 mussels m^{-2} and over 700 g m^{-2} .

6. Sampling in various other mussel localities of the lake showed densities between 31 and 52 mussels m^{-2} , and biomass densities of 261 to 1 175 $g m^{-2}$.
7. Populations of all three species comprised mainly adults with very few juveniles present, indicating populations in a probable stable state.
8. In the Sanyati East cleared area populations of C. mossambicensis had a smaller mean size in shallower water than populations in deeper water.
9. Populations of C. mossambicensis and M. dubia showed differences in mean size according to area, this being greatest in river estuaries and smallest from island littorals. Similarly, the largest A. wahlbergi were found in river estuaries.
10. Sampling indicated the C. mossambicensis population is comprised of aggregations of individuals. M. dubia appeared to be aggregated in uncleared areas, while the position in cleared areas was less clear. No clear trend emerged for A. wahlbergi.
11. Predation on bivalves by fish in the Lakeside area was minimal, and was concentrated on C. africana. Only three species of fish (H. codringtoni, S. zambesensis and C. gariepinus) utilized bivalves as a small fraction of their diet.
12. Mortality of the shallower littoral populations of bivalves is occasionally caused by lake level drop. Another suspected cause of mortality is silt deposition, caused by flooding rivers, or resuspension of silt in shallow littoral areas, caused by wind and wave action.
13. Preliminary tests showed C. mossambicensis to be hardy

and tolerant of a wide range of conditions, capable of withstanding high water temperatures (40°C), low water temperatures (5°C), extreme temperature ranges (5°C - 34°C) over 24 hours, low oxygen concentrations (2 ppm), and survival when translocated to a different water body at a different altitude.

14. Both C. mossambicensis and M. dubia are incapable of surviving in air for more than a few days, whereas A. wahlbergi was shown, under laboratory conditions, to survive a period of three months without succumbing.

B. LAKE MCILWAIN

1. Lake McIlwaine is essentially a two species lake. There are six bivalve species but of these only C. mossambicensis and M. dubia are widespread and common throughout the lake and comprise the bulk of the population.
2. Species present in Lake McIlwaine are the two mentioned above, plus A. wahlbergi, U. (cafferia) caffer, C. africana, and one Sphaerium species (Marshall, 1975).
3. A. wahlbergi was only recorded in the uppermost riverine reaches of the lake and has not invaded the lake proper. Only one specimen of U. caffer was recorded in the lake proper, whereas several were found in the uppermost riverine reaches. The uppermost section therefore has the greatest diversity of species.
4. Mean densities of C. mossambicensis and M. dubia throughout the lake in the drawdown zone in July/August were 0,5 mussels m⁻² and 0,19 mussels m⁻² respectively, and 0,14 mussels m⁻² and 0,88 mussels m⁻² in October.
5. M. dubia appeared to be more common than C. mossambicensis

on mud substrates, whereas C. mossambicensis appeared to prefer sandy substrates.

6. Following falling water level from June 1979 to October 1979, C. mossambicensis numerical dominance gave way to numerical dominance and complete biomass dominance by M. dubia.
7. This and previous sampling, (1975), indicates that M. dubia is the more common mussel species in deeper water, whereas C. mossambicensis in this study was the more common species in the extreme shallows.
8. Sample populations of C. mossambicensis and M. dubia from the drawdown zone in the lake proper in July/August 1979 had mean lengths of from 22 mm - 26 mm and 45 mm - 57 mm respectively. Because of lake drop in 1977 and consequent exposure these populations are estimated to be between two and three years old. Mean lengths for these species in October 1979 were 28,9 mm and 45 mm - 67 mm respectively.
9. The largest mussels, and consequently largest population mean lengths were found in the uppermost riverine reaches of the lake, in accordance with earlier sampling, (Marshall, 1975).
10. Falling lake level triggered off migratory responses in M. dubia and C. mossambicensis towards deeper water. Such responses would ensure survival of the species, since a remnant of the population would thus avoid stranding and would provide breeding stock for recolonization of the shallows when the lake level rose again.
11. Predation on M. dubia by water mongoose and / or otter was indirectly noted.

PART TWO - REPRODUCTION

REPRODUCTIVE CHARACTERISTICS OF THE STOCK

INTRODUCTION

Having described the stock, a second requirement in the management of a fisheries resource is to describe, as adequately as possible, the reproductive characteristics of the stock. While yields to a fishery are dictated by population parameters such as standing crop or production rates, the nature of the ultimate crop will be dictated by the breeding biology of the species involved, e.g. breeding size will determine cropping size minima.

With such requirements in mind, and aware of the paucity of information on the breeding biology of African freshwater bivalves, a program was planned to investigate the most important aspects of their reproduction. These were:-

- (a) The structure of the breeding population
- (b) Seasonal breeding activity
- (c) Frequency of spawning
- (d) Fecundity
- (e) The Parasitic stages

While these investigations were aimed mainly at the Kariba stock, some comparative work was also undertaken at Lake McIlwaine, in the hope that this would shed further

light on this aspect of their biology.

A preliminary review of the literature revealed a lack of information on the reproductive habits of the species concerned. While great progress has been made in recent years on European and North American inland bivalves, the anatomy and reproductive habits of mussels of the Ethiopian, Oriental and Australasian regions remains virtually unknown. Presumably the greater number of more urgent tasks and the limited number of qualified personnel in the so-called Third World has relegated such academic spheres of interest to backwaters, where they will remain until they become of more practical importance. Thus, while there was a good deal of Northern hemisphere literature to draw on, including the early and pioneering work of Lefevre and Curtis (1912), the only source of substance on African breeding was Fryer's work (1959, 1961) on Mutela bourquignati (Ancey) Bourquignat. Nothing further on this genus could be located, while nothing substantial could be found on either Caelatura or Aspatharia other than brief mentions in Heard and Guckert (1970), Heard and Vail (1976), and Appleton (1979). Yonge (1962) has published on the Etheriidae (freshwater oysters). Africa still remains very much a "dark continent" with regard to the subject of freshwater bivalve biology.

Against this background Fryer's work can be considered an important contribution, in that at the time it appeared nothing was known of the life history of this important African family, the Mutelidae, and Fryer's well documented and illustrated 1961 report not only rectified

this situation but also gave impetus to the school of thought which demanded that classification of bivalves take account, amongst other criteria, of larval forms. Could the alleged Mutelids of Australia really be mutelids, for example, when their larvae are glochidia, and totally unlike forms described by Fryer, or by Parodiz and Bonetto (1963), who studied South American species ?

In contrast to the African situation (and doubtless South American as well) considerable information on the breeding biology of freshwater mussels is accumulating in the Northern hemisphere, particularly in Europe and North America. The realization that classification on shell structure alone is unsatisfactory, while classification based on soft part anatomy and larval structure offers useful possibilities, has boosted research into these fields, with resultant benefit for reproductive biology (See, for example, Heard and Guckert, 1970; Heard, 1975). Studies on larval structures to establish criteria for classification have been honed to a sophisticated degree by the use of the scanning electron microscope (Giusti, 1973; Giusti et al, 1975), while advanced microscopy, microphotography and histological techniques have thrown considerable light on sexuality and seasonal activity of gonads. The studies by Heard (1965), Meier-Brook (1970), Holland and Chew (1974), Clark, Nybakken and Laurence (1975), Heard (1975), Seed (1975), Mackie, Qadri and Clarke (1976a & b) and Giorgi and De Martini (1977) are but a few of many on this subject. In addition, if one considers the contributions of authors

dating back several decades (Ortmann's contributions - 1909, 1910, for example) or even into the last century, it can be appreciated that much information has accumulated on Northern hemisphere freshwater bivalves.

The lack of information on African bivalves is thus considerably emphasized, and even basic details on such aspects as breeding seasons are not known. The findings presented here should therefore provide a foundation upon which further research can be built. Limitations on both time and facilities precluded more detailed studies being made, and consequently many gaps still remain to be filled. Possibilities for further research are thus suggested in the final discussion.

MATERIALS AND METHODS

1. Structure Of The Breeding Population, and Seasonal Breeding Activity

In studies concentrating solely on reproduction it is customary to examine sexual composition and seasonal breeding activity by means of histological techniques which are often long and elaborate. Such procedures allow detailed analyses of seasonal gonad activity and also allow sexual composition of the population to be determined. Unfortunately neither time nor facilities at Lake Kariba allowed this, and a much simpler approach was developed which nevertheless allowed an assessment to be

made of both the structure of the breeding populations and seasonal breeding activity. Monthly samples of the three species were collected and opened in the laboratory, and the demibranchs examined for eggs or larvae (or transitional stages). Those possessing either were designated "gravid". A small slit was then made in the gonad and the white extrusion was examined under the microscope for the presence of eggs. Mussels containing gonadal eggs and / or eggs or larvae in the gills were designated "active". This term thus covered those mussels which perhaps did not have genital products in their gills at the time of examination, but had eggs in the gonads.

The proportion of gravid individuals was then plotted on a monthly basis over a period of 16 months to show seasonal breeding trends. Length frequency histograms of all mussels examined were constructed, and the length frequencies of gravid and active mussels superimposed on these. Obviously those with eggs, either in their gills or gonads, or larvae in the gills, were considered to be the females of the population.

2. Frequency Of Spawning

Monthly sampling analysis indicates the seasonal nature of breeding, but does not indicate the frequency of spawning by individuals in a single year, as was also observed by Heard (1975). This aspect of reproduction has been ignored by many workers. During monthly analysis for genital products it was noted that mussels could be prised

open slightly, the marsupia examined for eggs or larvae (or transitional stages), a small sample of these removed from one of the ovisacs and examined under the microscope, and the mussels returned to the water. This meant that individual mussels could be examined periodically for sexual activity. Samples of C. mossambicensis and M. dubia were examined in this way and those with marsupial contents were retained in containers in the lake, where they could periodically be removed, re-examined, and then returned to the lake. At the time of this research A. wahlbergi were not breeding and hence were not included in the study.

3. Fecundity

Heard (1975) mentions that European species of Anodonta can carry as many as 3 000 000 incubating young. Since the fecundity of African Unionidae appears to be completely unknown, this aspect was investigated in C. mossambicensis, the most common and important species in Lake Kariba.

In fish the normal approach in determining fecundity is to remove the eggs entirely from the gonadal sacs and extrapolate total egg numbers by subsampling, using area, mass, or volume to describe sub-samples. Examination of the marsupial demibranchs of C. mossambicensis showed the species to be tetragenous (i.e. incubating eggs in all four demibranchs) and incubating the eggs within numerous brood or ovisacs (i.e. water tubes used as marsupia) separated from each other by interlamellar septa, as shown in Fig. 38.

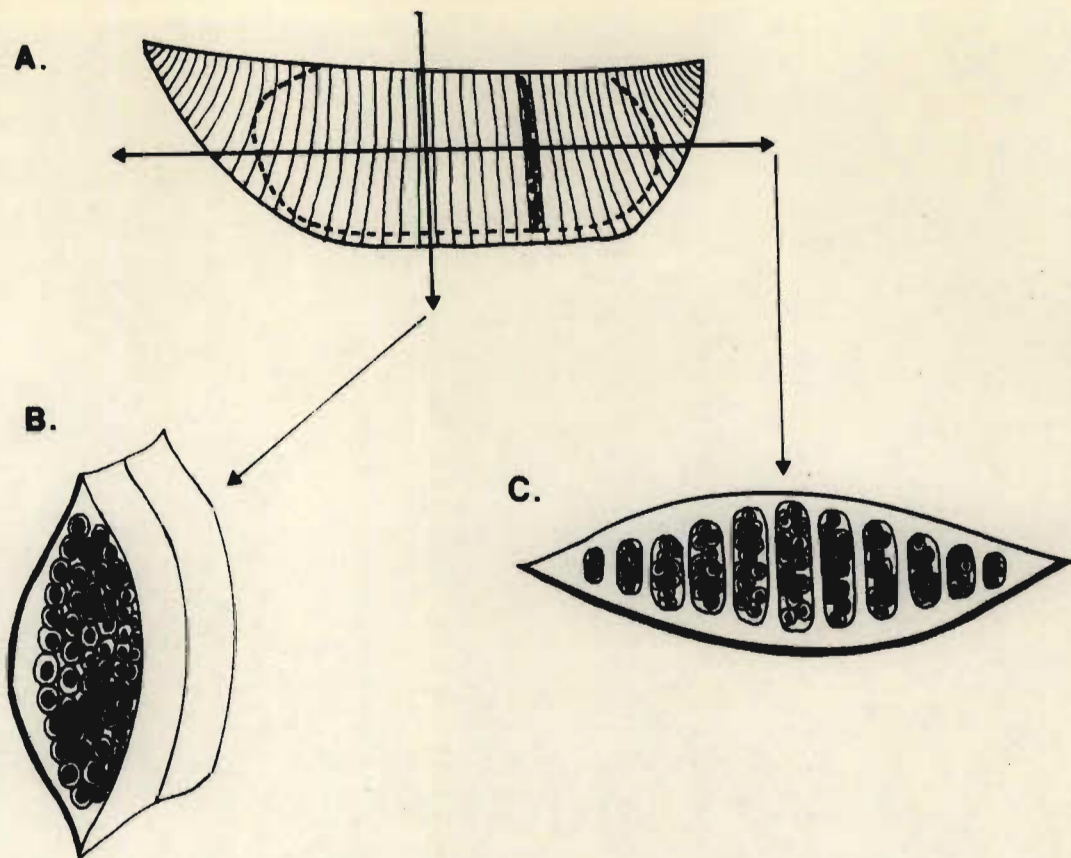


Figure 38 : The marsupial demibranch (A) of C. mossambicensis, with lateral (B) and longitudinal (C) cross-sections to show the arrangement of the eggs in the ovisacs. Normal outline of the brood (dotted line) is shown in A

The small size of the eggs and difficulty experienced in extracting them from the mass of tissue without crushing them led to a different approach being adopted. During routine collecting of mussel samples it was noted that when large numbers of C. mossambicensis were confined in a container (a basin or bucket) they prematurely extruded egg masses in a slipper shaped agglutinated form, presumably as a result of stress arising from low oxygen tensions in the water (Fig. 39). Each conglutinate represents the total egg mass from a single ovisac, described by Sterki (1898) as "placentae" and by Ortmann (1911) as "placentulae". They comprise two and in some cases three distinct sheets of eggs and a sheet in turn is comprised of a double layer of eggs (Fig. 39)

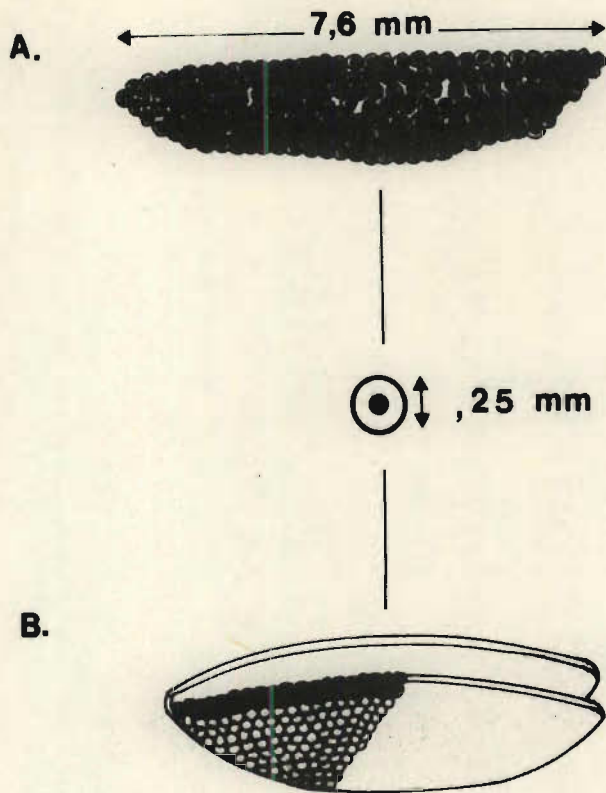


Figure 39: The typical appearance of an egg mass (A), viewed from the top, and (B), viewed from the side showing two sheets of eggs.

The method adopted was to count the number of ovisacs in a single gill, determine the mean length of the ovisacs, and then calculate the number of eggs in that particular gill by multiplying the number of ovisacs by the mean number of eggs found in an ovisac of that particular mean length. The latter was determined by collecting a large number of whole and undamaged conglutinates, measuring their length, counting the eggs in them, plotting number of eggs against length and fitting a regression to the scatter (Fig. 50). From the

graph it was possible to estimate the approximate number of eggs in a conglutinate, and hence ovisac of any given length.

The mean lengths of ovisacs were determined by carefully removing each marsupial demibranch (four in all), placing these flat on millimetre square graph paper over a bottom-illuminated drawing table, and carefully outlining the silhouette of the brood mass of each gill on to the graph paper. The number of squares enclosed by the outline was then used to determine mean length of the ovisacs which collectively made up the brood mass in the demibranch. The gills were then cut in half longitudinally and the number of ovisacs counted. The approximate number of eggs in each gill could then be estimated as described above, by multiplying the number of ovisacs by the number of eggs associated with the mean length of the ovisacs as determined from the graph.

Fecundity of a number of mussels of different sizes was thus calculated, and graphs were drawn to show the relationships between mussel length and fecundity, between fecundity and the number of ovisacs possessed, and between mussel length and number of ovisacs.

4. The Parasitic Stages

The investigation of the parasitic stages of freshwater bivalves could comprise a complete study in

itself, and as part of a much wider program objectives had to be restricted. The life cycle of Unionids is well known. Eggs metamorphose into glochidia larvae in brood chambers in the gills, these are expelled into the surrounding water where they become attached to the fins of fish or are drawn on to the gill filaments. Here they become encysted and develop from a larval form into a post-glochidial juvenile, which drops off the fish and develops into an adult.

The life cycle of a Mutela species has been described by Fryer (1961) and proved similar to the Unionid pattern in that eggs and larvae were brooded in the gills prior to expulsion into the surrounding water. These larvae infected a Barbus species, developed into juvenile mussels at the end of stalks, and then dropped off the host. Differences existed in the form of the larvae, mode and place of infection, and subsequent development of the larva, which gives rise to a stalk at the distal end of which a young mussel forms. Since no further work appears to have been done of Mutela, it was not known if the Kariba species would have a similar life cycle. The parasitic stage of Aspatharia was not known, although as a member of the Mutelidae it was expected to brood infective larvae and infect fish in a similar manner to Fryer's M. bourguignati. Basic objectives of the study were (a) to determine as much of the life cycle of A. wahlbergi as possible, (b) to determine whether M. dubia had a similar life cycle to M. bourguignati and (c) to determine whether a sub-tropical Unionid such as C. Mossambicensis possessed a similar life cycle to its temperate zone relatives in the Northern

hemisphere.

In order to induce parasitism of the larvae on fish hosts, and thereafter follow development, various species of fish were exposed to infection in bowls of aerated water in which larvae, removed from the gills of gravid mussels, were circulating. After periods varying from 15 minutes to an hour, the fish were removed and kept singly or in groups in other bowls, depending on size and species. Thereafter individual fish were removed at intervals and the progress of the infection, if any, was examined under the microscope and recorded. Lefevre and Curtis (1912) employed similar methods with success.

In addition, a large petri dish was placed at the bottom of each bowl in order to collect any juvenile mussels which might drop off the fish. Aerators were used to provide a constant supply of oxygen to the water. The fish were not fed prior to and during the experiments so that faecal matter and food would not accumulate in the petri dishes to the possible detriment of juvenile larvae. The dishes were covered with mesh to prevent possible predation on the juvenile mussels.

Wild fish, from the Seiche Tower, where a dense concentration of C. mossambicensis existed, were examined for infective glochidia. Diving observations had shown that two cichlids, Haplochromis darlingi and Tilapia rendalli were common and likely to be hosts to the larvae and several of these were caught and examined. Other

species from the Lakeside area, where all three mussel species occurred, were examined for infections by mussel larvae.

RESULTS

1. Structure Of The Breeding Population

At the outset it should be mentioned that gonadal studies of bivalves have shown that it is not possible to positively identify male and female sexes without sectioning and microscopic examination of the gonad (Wilbur and Yonge, 1964). The reason is that while the vast majority of species (as many as 96% according to Coe, 1943) are dioecious (i.e. gonachoristic, or having separate sexes), many species have a proportion within the population that are hermaphrodite (monoecious). According to Wilbur and Yonge (1964) and also Pelseneer (1895) most hermaphroditism occurs amongst bivalves which incubate their young in the mantle cavity or gill, rather than those which broadcast their eggs, and also occurs more commonly among freshwater molluscs than marine molluscs (Purchon, 1951, Fretter and Graham, 1964). Thus a bivalve emitting sperm or eggs may not necessarily be a true male or female, as there may be immature gametes of the opposite sex in the gonad. In a study of eight species of Anodonta, Heard (1975) was able to show that considerable variations in sexual conditions existed. He found that three species were uniformly dioecious, four species contained at least one kind of hermaphrodite (predominantly male, or female)

in addition to the normal males and females, and one species had no true males, only female hermaphrodites and females.

Despite these inevitable exceptions to the rule, most bivalves are genuinely dioecious (Wilbur and Yonge, 1964; van der Schalie, 1966, 1969) and it is possible to determine the approximate sexual structure of the population by examining the gonads for eggs and the gills for eggs or larvae. These are assumed to be females, while those without such sex products are assumed to be males, (H. and A. van der Schalie, 1963) and hence an approximate sex ratio can be established. In addition, the size at which females start incubating eggs can be determined, (i.e. size at maturity) and size at which this ceases - senility or post-reproductive phase can be established.

a) Caelatura mossambicensis

With an abundance of material for this species from Lake Kariba it was possible to prepare length frequency histograms showing active mussels from estuarine, marginal and island populations (Fig. 40(A).) In addition a length frequency histogram depicting the distribution of gravid individuals from all localities is shown in Fig.40(B)

Three main points of interest arise from these graphs. The first is size at which breeding commences. The smallest gravid mussel encountered was 23,0 mm and one can assume that this is the approximate size and age of commencement of breeding. A mussel of this size is approximately one year old (see PART THREE).

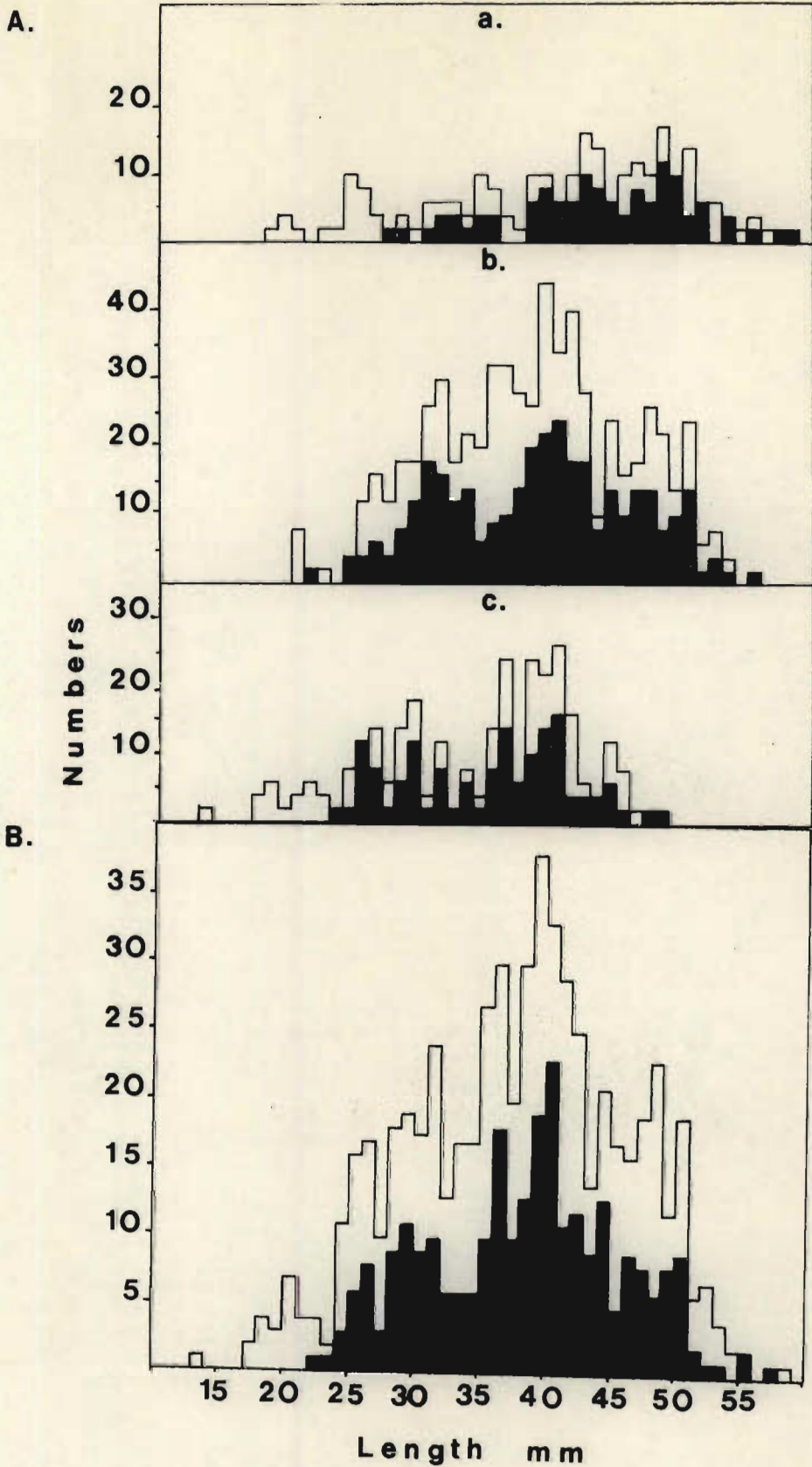


Figure 40: Length frequencies of *C. mossambicensis* from estuarine (a) marginal (b) and island populations (c) Lake Kariba in 1976/1977 showing active (female) component shaded. (Active = eggs in gonads and/or eggs or larvae in gills.) Figure B shows all mussels examined with shaded area representing gravid mussels (gravid = eggs or larvae in gills)

In Lake McIlwaine a similarly constructed histogram of mussels collected in the shallows when lake level was dropping (July 1979 to November 1979) shows the smallest gravid mussel collected was 21,4 mm in length. (Fig. 41). Since the growth rate of C. mossambicensis in Lake McIlwaine is suspected of being slower than that in Lake Kariba, size may be the criterion in determining the onset of maturity and not age. In Lake McIlwaine therefore breeding amongst the females would appear to start at a later age than in Lake Kariba.

The second point of interest is that the largest mussels in the Lake Kariba samples included gravid individuals. Breeding amongst the females therefore seems to continue until death, without a post-reproductive or senility phase occurring.

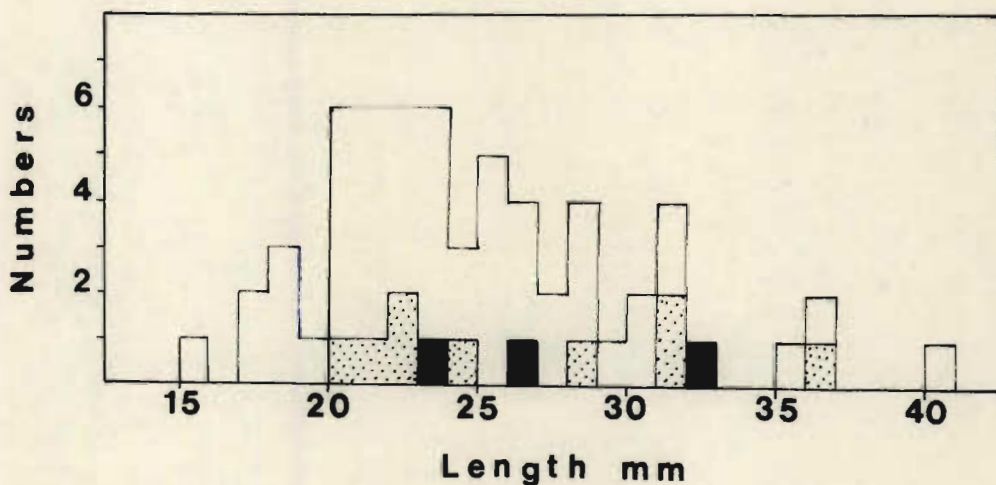


Figure 41: Length frequencies of all C. mossambicensis examined from Lake McIlwaine. Stippled and shaded areas represent active and gravid mussels respectively

A similar situation in which even the oldest animals of eight Anodonta species displayed active gametogenesis, and most of the oldest females and female hermaphrodites were gravid, was recorded by Heard (1975). This has also been mentioned by Stansbery (1967) and shown to occur in the freshwater bivalve Musculium seuris (Mackie et al, 1976a) and might well be a feature common to all bivalves.

The third point of interest is the sex ratio in the samples. In Fig.40(B) gravid mussels (i.e. with eggs/larvae in gills) comprised 48% of the total sample, excluding mussels below 23 mm, which are regarded as immature. The percentage of active mussels (i.e. with eggs in gonads and/or larvae in gills) was 53% in the combined estuarine, marginal and island samples, considering only mussels 22 mm and above (the smallest active mussel found was in the 22 mm class). If one assumes that non active mussels are males, and active mussels are females, the ratio of female to male is therefore 1,13 : 1 (53%:47%). If a very small proportion of the so-called females are in fact hermaphrodites then the true ratio of females to males would be closer to parity. Whatever the case the sex ratio of C. mossambicensis in Lake Kariba appears to be approximately one to one, a finding which accords with some figures given by Wilbur and Yonge (1964) for various bivalve species. Appleton (1979), examining the gills found a ratio of 1,4 : 1 for C. kunenensis from the Kunene River.

A breakdown of the sample into size classes to

determine the relative proportions of gravidity in each size class is shown graphically in Fig. 42.

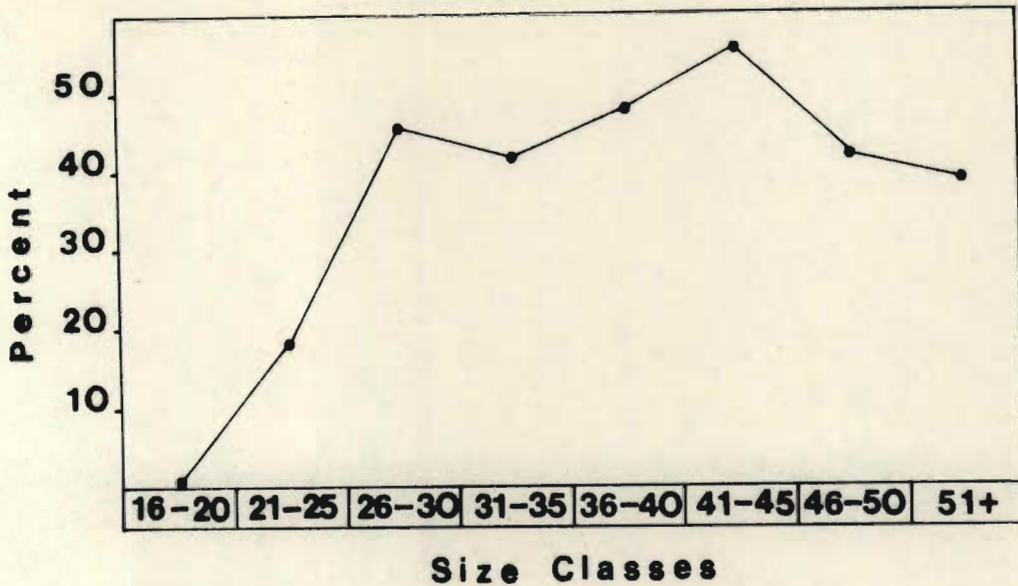


Figure 42 : Percentage of gravid individuals in different size classes of C. mossambicensis from Lake Kariba

The 21 mm - 25 mm class had the lowest proportion, while the 41 mm - 45 mm class had the highest proportion. The graph confirms that breeding takes place through to the largest sizes, with no decline to zero, which would occur if a senility phase existed. In general, there was a fairly constant level of gravidity for all groups between 26 mm and 51 mm.

b.) Aspatharia wahlbergi

A length frequency histogram showing gravid and active mussels in the sample population is shown in Fig. 43. Few gravid mussels were found and hence gravid and active have been combined in one graph.

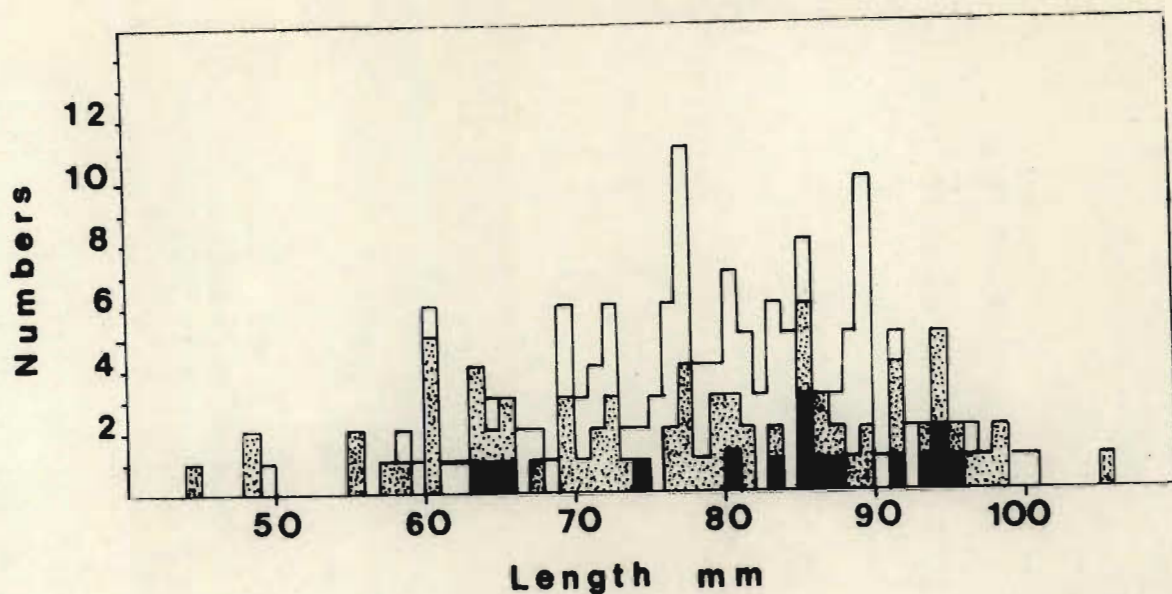


Figure 43 : Length frequencies of all A. wahlbergi examined from Lake Kariba in 1976/1977 showing active component (dotted), and gravid component (shaded)

As with C. mossambicensis, the points of interest relate to size at first spawning, size when spawning ceases, and the sex ratio. Gravid mussels were scarce because the species breeds seasonally in Lake Kariba (see next section) and for much of the year this category of activity was absent from the samples. The available data suggests that brooding of eggs commence between 60 mm and 65 mm, and gonadal eggs were first noted at 49 mm. Fifteen of the mussels below 64 mm were examined during the breeding season, and since none were brooding eggs or larvae, spawning activity can be considered to start at approximately 64 mm, when the mussel is from two to three years old.

The largest gravid mussel was found in the 96 mm class, which coincides with the "average" largest size for specimens from the cleared areas, although being somewhat smaller than lengths encountered in the estuarine areas. Most of the mussels above 96 mm in the sample were taken from the Charara Estuary during the non-breeding season, while the large gravid mussels were collected from Sanyati Basin cleared areas during the breeding season. Gravidity was found in A. wahlbergi up to 110 mm in specimens from the upper reaches of Lake McIlwaine in October, 1979.

A. wahlbergi females obviously breed for the duration of their lifespan, with no period of senility.

Concerning the sexual composition, active mussels comprised 49,4% of the sample, which gives a sex ratio of 1:1 if one assumes these to be the females and the remainder the males.

c.) Mutela dubia

Length frequency histograms showing active and gravid mussels are shown in Fig. 44 and Fig. 45.

Brooding of eggs or larvae appears to start at a length of about 52 mm, or an age of one to two years. This is an approximate length, as clearly more mussels under this length would need to be examined to determine the lower breeding age with certainty. In the sample from Lake McIlwaine, only three mussels under 50 mm (44,0 mm, 48,0 mm and 49,5 mm) were gravid.

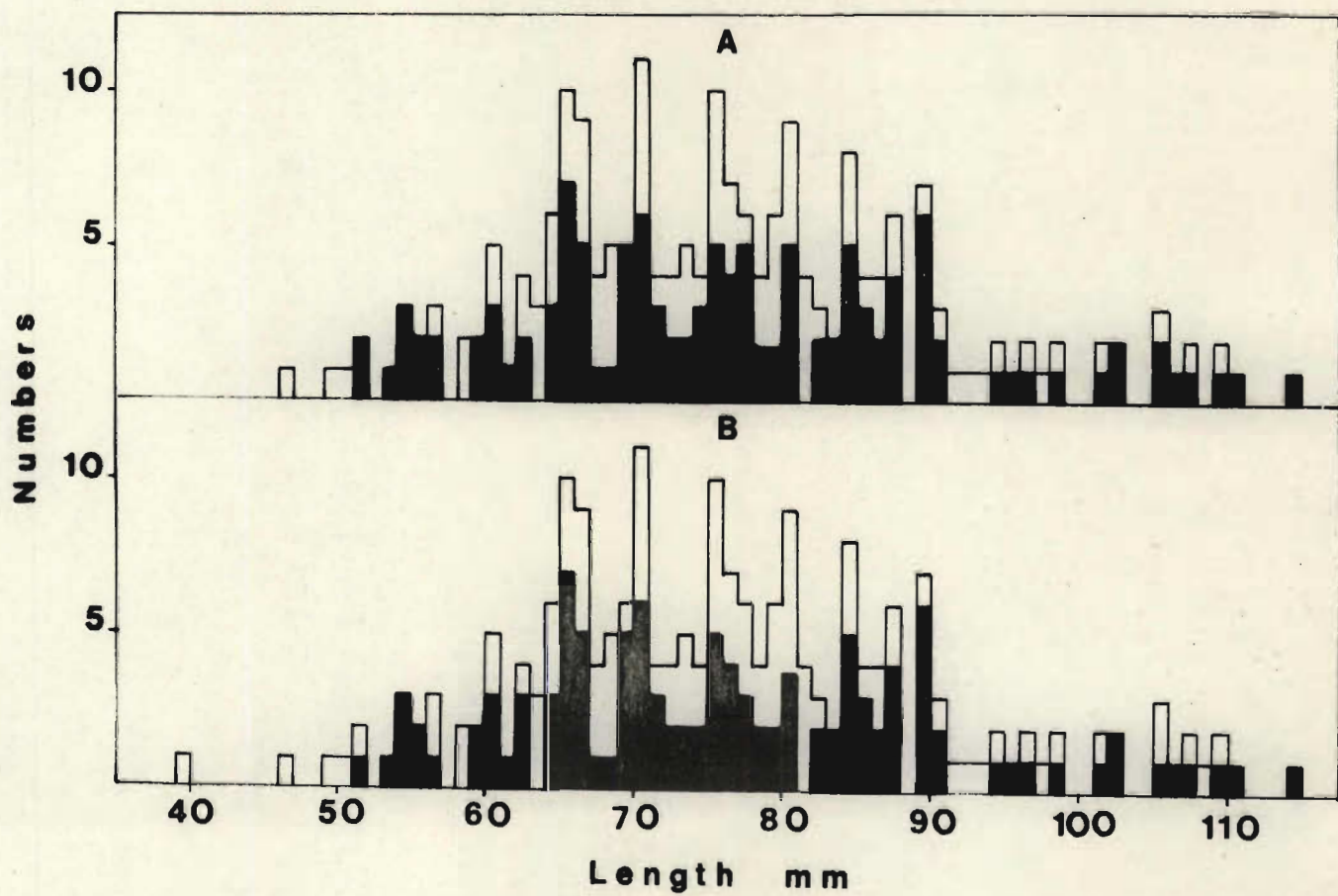


Figure 44: Length frequencies of all *M.dubia* examined from Lake Kariba in 1976/1977 showing (A) the active component (shaded) and (B) the gravid component (shaded)

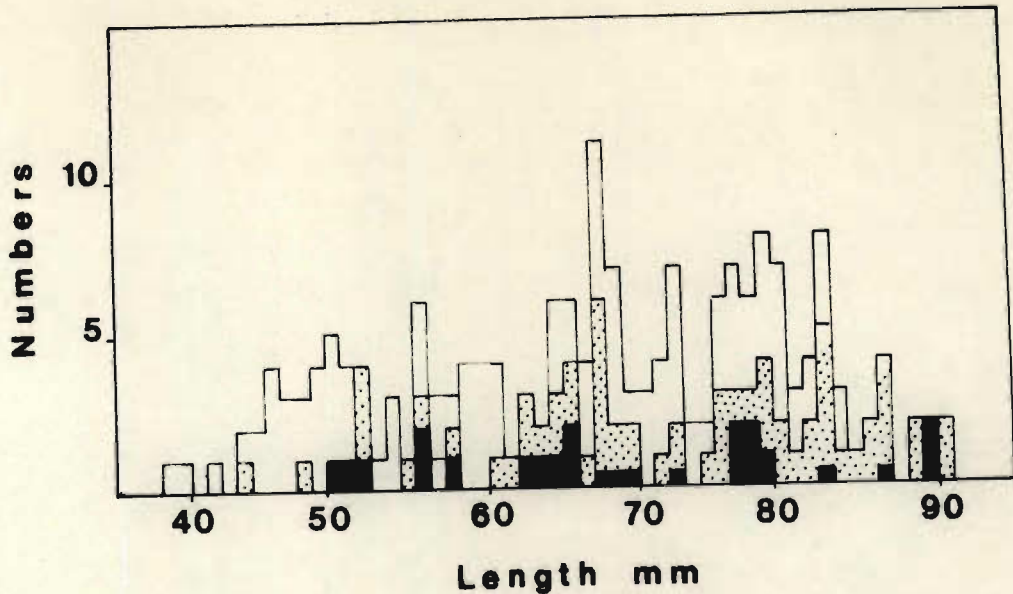


Figure 45: Length frequencies of all M. dubia examined from Lake McIlwaine in 1978/1979, showing gravid component shaded and dotted (shaded = only larvae in gills)

Size at sexual maturity in Lake McIlwaine appears to be somewhere between 44 mm and 50 mm, although 52 mm seems to be the average length at which breeding starts. The McIlwaine data again suggests that size of the individual is the criterion which determines the onset of breeding, and not age, as growth rate in Lake McIlwaine is suspected of being slower than in Lake Kariba.

Female breeding obviously continues for the duration of a life of the individual, as both Fig. 44 and Fig. 45 show gravid mussels amongst the largest individuals found.

Sex ratios, again on the assumption that

active mussels are females and the remainder are males, indicates an approximate one to one ratio of females to males. In Fig 44 (A) active mussels comprised 57% of the sample population (1,3:1), while in (B) gravid mussels comprised 51,1% of the sample population. If a proportion of the active mussels are hermaphrodites the ratio of true females to true males would then be closer to parity, and the proportion of gravid mussels (51%) might be a more accurate reflection of the true ratio.

In Lake McIlwaine interest centred mainly on the seasonal aspect of breeding, and while all gills were examined not all gonads were. However, one sample of 40 mussels, collected from shallow water in July, 1979, gave a proportion of 55% for active mussels, or a ratio for females to males of 1,2 : 1 close to the figure obtained in Lake Kariba.

The general sex ratio for all three mussel species was 1:1. Only more detailed gonad examination could determine if a small proportion are hermaphrodites. This seems likely, as some mussels extruded only minute quantities of eggs from the gonad, but were nevertheless considered females.

2. Seasonal Breeding Activity.

In temperate climates work on annual breeding cycles of freshwater bivalves has shown that the majority of the species examined are seasonal breeders. Species

are often termed long term breeders (bradytictic) or short term breeders (tachytictic) depending on whether they carry glochidia for long periods, usually over winter, or release them when they are developed. While there is considerable variation in brooding period and time of discharge amongst glochidia-bearing bivalves (See, for example, Lefevre and Curtis, 1912; van der Schalie, 1963; Negus, 1966; Heard, 1975; Giusti et al, 1975) a common feature is the presence of one or two distinct breeding seasons, terminating in discharge of glochidia at some period during the year. Giusti et al (1975), for example, showed that in Anodonta cygnea the demibranchs started carrying eggs in October and from November to March fully developed glochidia were shed as evidenced by the large numbers of glochidia infestations on fish at this time.* Similarly, Castagnolo (1978) has shown that Unio elongatulus ejects glochidia throughout summer and A. cygnea throughout winter, in the Po River, Italy. Here the two species have distinct spawning seasons, out of phase with one another.

Kariba, lying at a low altitude in a hot valley, with sub-tropical climate, obviously offers a more consistent and equable environment than that which pertains in Northern latitudes, and seasonal breeding patterns were expected to differ from those in temperate climates.

* Giusti et al (1975) considers that many of the so called Spring spawners (Bradytictic spawners) have in fact been shedding glochidia all winter, and obviously the whole question of mussels "carrying over" the brood until some favourable spawning time needs closer examination.

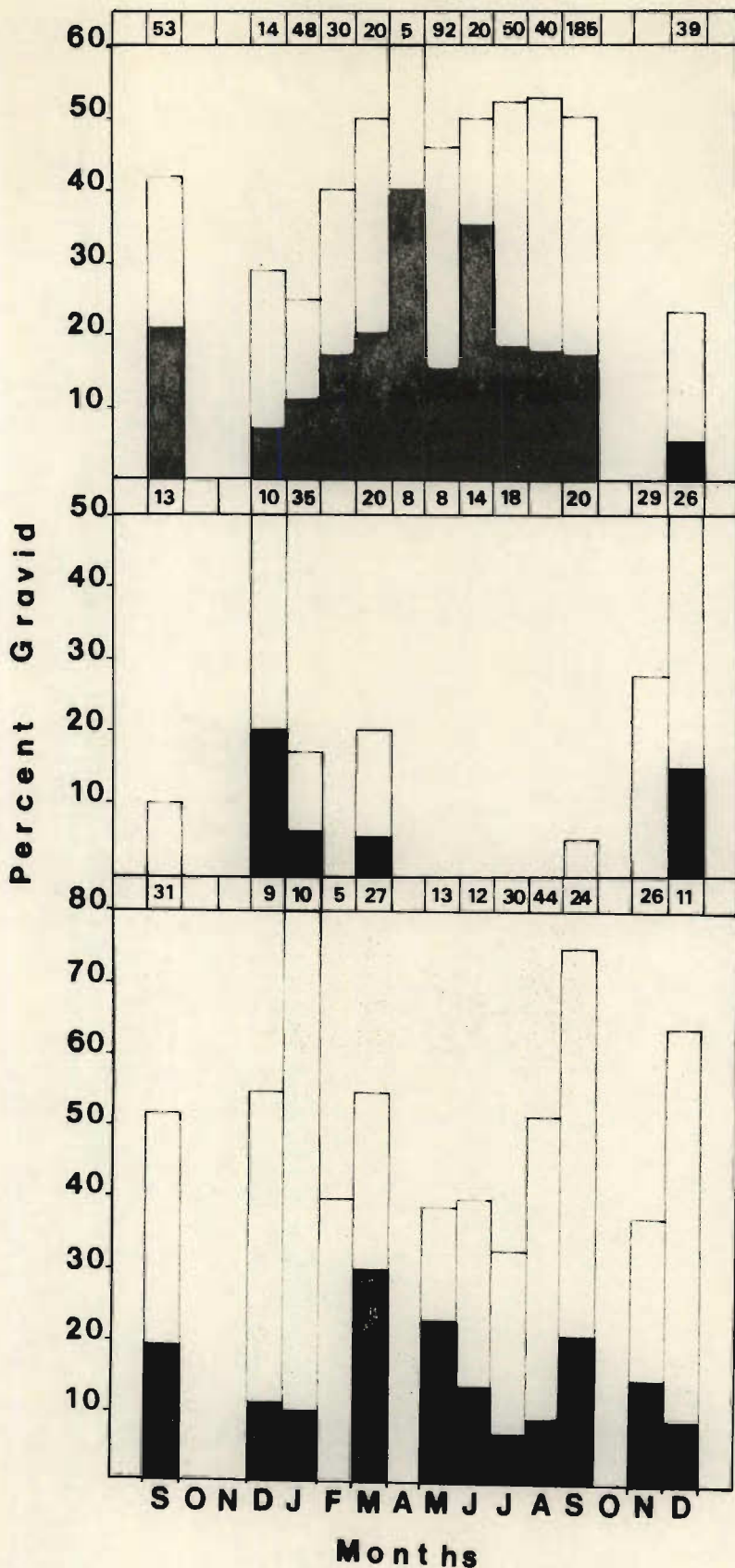


Figure 46: Seasonal breeding activity in Lake Kariba in 1976/1977 shown by the percentage of gravid mussels in the samples of *C. mossambicensis* (a) *A. wahlbergi* (b) and *M. dubia* (c). The shaded portion represents the proportion carrying larvae only.

As previously mentioned, detailed histological examination of gonads was not possible and determination of seasonal breeding activity was made on the basis of monthly analysis of the gills for eggs and/or larvae. The assumption was made that because of the year round favourable temperature conditions, larvae are not carried for long periods but are shed by the females once they have reached full development, and hence the presence of larvae in the gills is indicative of breeding at that particular time. This assumption was fully justified by the findings of the study to determine frequency of spawning of individuals, described in the following section.

a.) Caelatura mossambicensis

Reference to Fig. 46 shows that this species carried eggs and larvae in gills throughout the year. While no absolutely clear pattern emerged there appeared to be a gradual increase in the number of gravid animals from the beginning of the year until March/April when the number levelled off. The proportion carrying larvae also increased from the beginning of the year, being highest in April and June, and then levelling off until September. These samples were collected from different areas of the Sanyati Basin, which may explain the lack of a completely clear pattern if slight locality differences do exist. Monthly sampling from a single locality would probably provide a clearer picture. The glochidia were in varying degrees of development, but samples of fully developed larvae, freed from the egg membrane and showing "clapping" movement

(i.e. the two valves opening and closing) were recorded throughout the year. Infected fish were recovered from the field in August 1977, and laboratory infections were induced in March, July and September. On the evidence of gravidity the species appears to breed throughout the year, with possible increased activity through the winter months. In Lake McIlwaine mussels were examined in early May, July, September, October and November and gravid mussels were present at all times.

b.) Aspatharia wahlbergi

Gravid mussels were recorded only during the summer months of September to March, and animals with larvae only from December to March. From April to July no sign of incubation of either eggs or larvae was noted. This species is obviously a seasonal breeder, as opposed to the continuous nature of the breeding of C. mossambicensis. It is interesting to note that two out of four A. wahlbergi brought from Kariba in October 1978 and placed in a shallow pond at McIlwaine were brooding larvae on 6th April, 1979; thus there may be a different breeding cycle at McIlwaine. Gravid specimens (eggs and larvae) were recorded in the upper reaches of the lake in October 1979.

c.) Mutela dubia

Like C. mossambicensis, gravid animals were recorded throughout the year, and larvae were present with one exception (the small February sample) in all samples.

While a pattern of increased or decreased activity is not clear, there could be a decrease in gravidity through the middle of the year, as opposed to the possible increase shown by C. mossambicensis at this time. The two species may be out of phase with one another, but this needs clarification through detailed gonad analysis. Infected fish were recovered from the field in June, 1977, while fish in the laboratory were successfully infected in June, July, August and September (and at Lake McIlwaine in July 1978 and January 1979). Fully developed larvae, free from the egg membrane and showing both ciliary and muscular movements, were noted throughout the year. Fryer (1961) mentions that M. bourguignati in Lake Victoria breed throughout the year.

In Lake McIlwaine no gravid mussels were recorded from the winter sample in May, 1979. Unfortunately no collecting was done between January and May because of convalescence and hence there is a gap here. The species appears to breed for most of the year in Lake McIlwaine, with an indication of cessation in winter. The largest proportions of gravid mussels were recorded in January and September which suggests a possible breeding peak during the summer months. A similar pattern can be detected in Lake Kariba. The higher proportion of gravid mussels in July 1979 compared with July 1978 in Lake McIlwaine is of possible significance. While the samples up to July 1978 were collected by diving in water from 2m - 4 m depth, the July 1979 and subsequent samples were collected

from water less than 50 cm depth, when lake level was falling and exposing the mussels for easy collection. These mussels were thus subject to a fluctuating daily temperature regime rather than the more constant temperature that would be experienced in the deeper water. Possibly daily warming of the water after cold night temperatures triggers off increased breeding activity. This in itself could be a type of survival mechanism, an attempt at ensuring perpetuation of the species through increased breeding activity in the face of adverse circumstances. However, this is mere speculation.

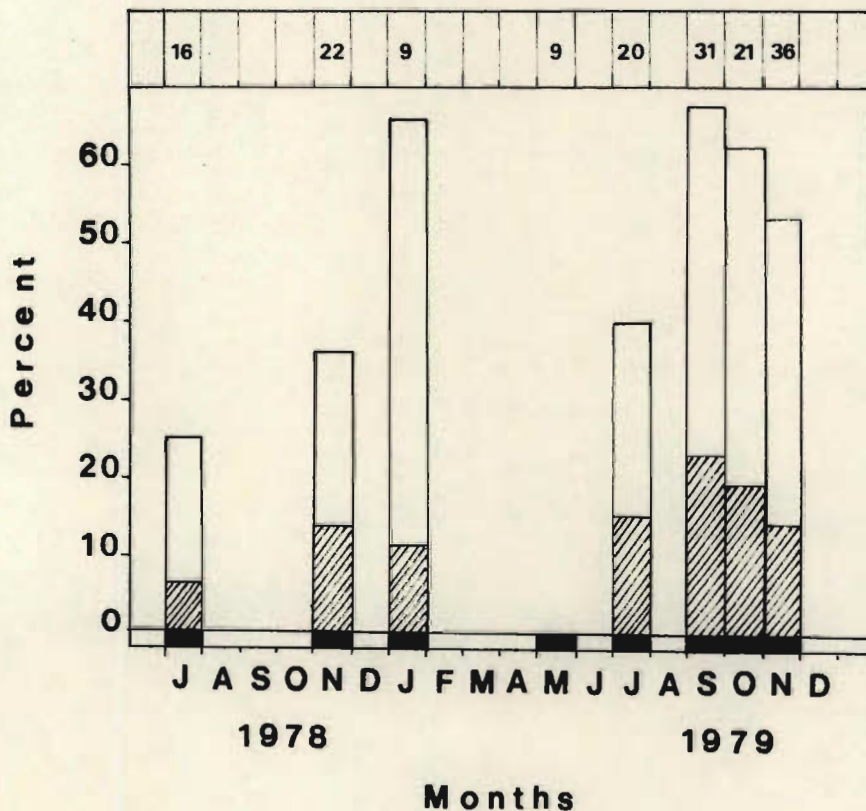


Figure 47: Seasonal breeding activity in Lake McIlwaine in 1978/1979 shown by the percentage proportion of gravid *M. dubia* in samples from Pelican Point. The shaded portion represents the proportion carrying larvae only

3. Frequency Of Spawning

As mentioned earlier, the presence of mature larvae in the gills of C. mossambicensis and M. dubia throughout the year indicated year round breeding, but did not elucidate the spawning frequency of individuals. A situation of all year breeding as indicated by the presence of breeding elements in monthly samples is either a manifestation of phased spawning, in which individuals spawn only once, but out of phase with other individuals to give spawning coverage to the whole year, or a manifestation of repeated spawning by individuals throughout the year, again giving spawning coverage all through the year. In view of the equable environmental conditions pertaining in the lake it seemed unlikely that spawning would be restricted, and successive or repeated spawning was suspected. Results of the study to determine this are presented below.

a.) Caelatura mossambicensis

Eight mussels were examined initially, but three subsequently died, so that five were examined for eggs or larvae over the total period of study (127 days). The results of this study are summarized in Table 10 .

The Table shows that all mussels examined, with the exception of one, produced more than one brood of eggs over the 127 day period. The early death of Mussels No. 1 and 2 could not be attributed to anything in particular, except possibly stress from handling.

Table 10: Results of periodic examination of the gills of several C. mossambicensis for eggs and larvae over a 127 day period

MUSSEL NO	21/7	28/7	9 / 8	22/8	2 / 9	12/9	22/9	7/10	18/10	28/10	7/11	25/11
1	Eggs	Larvae	Eggs	Dead	-	-	-	-	-	-	-	-
2	Eggs	Empty	Eggs	Dead	-	-	-	-	-	-	-	-
3	Empty	Empty	Eggs	Eggs	Empty	Eggs	Empty	Empty	Empty	Empty	Empty	Empty
4	Larvae	Eggs	Larvae	Eggs	Empty	Empty	Empty	Empty	Empty	Empty	Empty	Empty
5	Larvae	Eggs	Larvae	Larvae	Eggs	Larvae	Dead	-	-	-	-	-
6	Larvae	Eggs	Larvae	Larvae	Eggs	Larvae	Eggs	Eggs	Empty	Empty	Empty	Empty
7	Eggs	Larvae	Eggs	Eggs	Larvae	Eggs	Empty	Eggs	Larvae	Empty	Empty	Empty
8	Empty	Empty	Empty	Empty	Empty	Empty	Empty	Empty	Empty	Empty	Empty	Empty

These results can be further summarized for clarification:

MUSSEL NO.	REMARKS
1 & 2	Two broods within 19 days. Died
3	Two definite broods, probably three over 127 days.
4	Three definite broods over 127 days.
5	Three definite broods within 53 days. Died.
6	Four definite broods, possibly five, over 127 days.
7	Four definite broods over 127 days.
8	No eggs produced. Possibly a male.

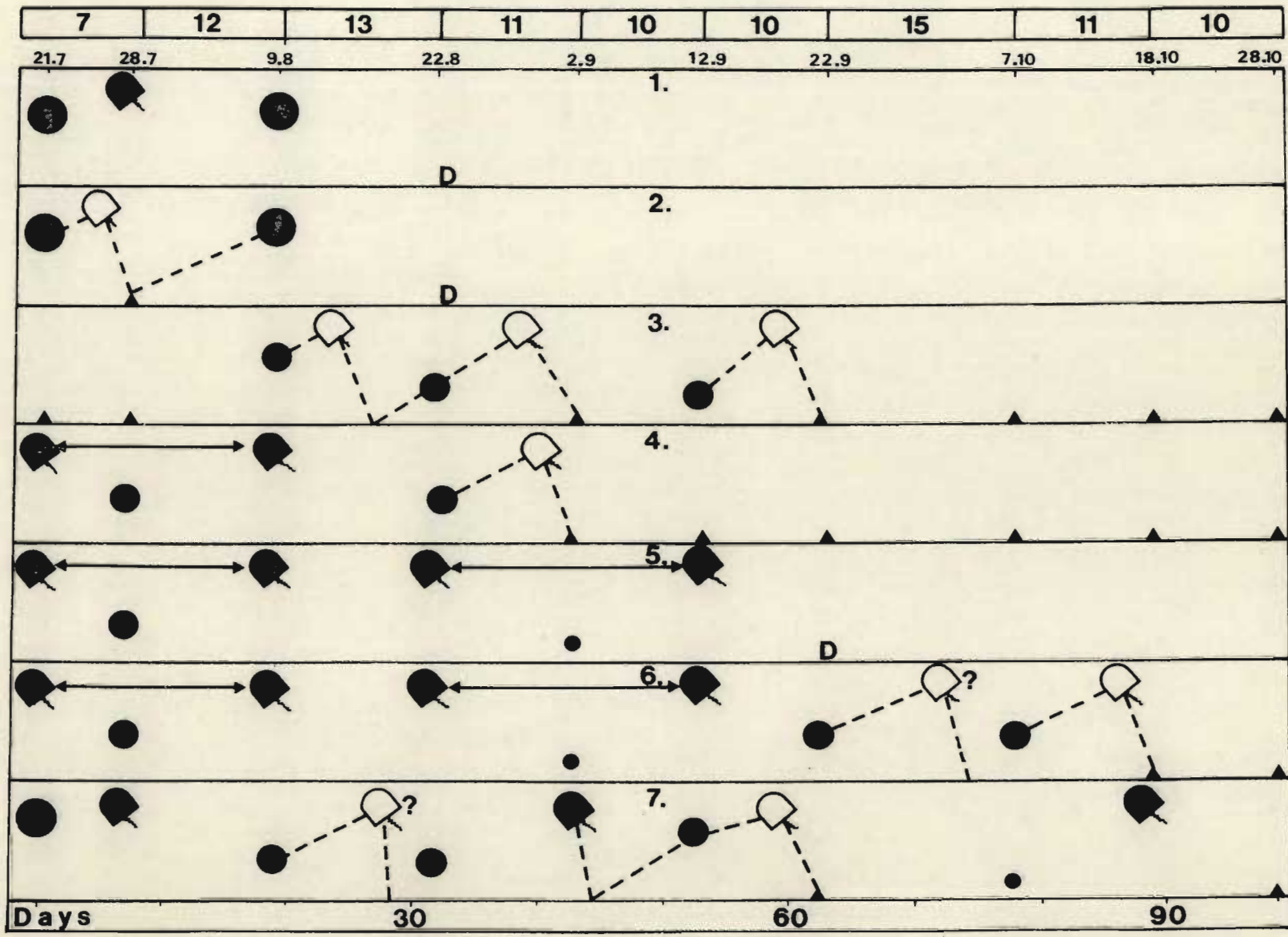
With reference to Fig. 48 , Mussel No. 1, the period of time between successive broods of eggs, with a larval brood recorded in the interim, was 19 days (21st July to 9th August).

In Mussel No. 2, the period between successive broods of eggs, with empty gills recorded in the interim period was also 19 days (21st July to 9th August).

In Mussel No. 3, the time between successive broods of eggs, with empty gills recorded in the interim, was 21 days (22nd August to 12th September). The eggs recorded on the 9th August were larger and more developed than those on the 22nd August, and were obviously a different brood.

In Mussel No.4, the time between successive broods of larvae, with eggs in the interim, and eggs recorded again after the second brood of larvae, was 19 days (21st July to 9th August).

Figure 48: Results of the examination over a period of 127 days of the gills of seven C. mossambicensis for eggs or larvae. The D-shaped figures represent glochidia, either actually recorded (shaded), or hypothetical (open). Circles represent eggs recorded on that date, while shaded triangles indicate the gills were empty when examined. The vertical position of the eggs indicates the size of the eggs, those nearest the base line being the smallest. The "D" means mussels found dead. Dates of examination are shown at the top of the diagram, and above this the figures show the period in days, between each examination. The horizontal two-headed arrow indicates larvae are definitely different broods.



Mussels No. 5 and 6 had identical gill conditions from 21st July to 12th September (53 days). During this period three different broods of larvae were recorded, and two different broods of eggs. The period of time between successive broods of larvae on the 21st July and 9th August, with eggs in the interim, was 19 days. However, larvae were also present on the 22nd August, and since it is not known if this was the same brood as that of the 9th August, the time period could be 32 days (21st July to 22nd August). In view of the intervals mentioned above it seems unlikely that these were two different broods, as the period between them was only 13 days (9th August to 22nd August). The larval broods of 9th August and 22nd August were separated from another larval brood on the 12th September by a brood of eggs, giving intervals of either 34 days (9th August to 12th September), or 21 days (22nd August to 12th September), dependent on whether the broods of the 9th August and the 22nd August were the same or two different broods.

In Mussel No. 6, the period of time between successive broods of eggs, with larvae in the interim, was 20 days (2nd September to 22nd September). However, eggs of similar size to those of 22nd September were also present on the 7th October, and if these were still the same brood the period would then be 35 days (2nd September to 7th October). If the egg broods of 22nd September and 7th October were different broods the interval between them was 15 days.

In Mussel No. 7, the period of time between successive broods of eggs, with larvae in the interim was

19 days (21st July to 9th August). The eggs recorded on 22nd August were smaller than the preceding brood, and were obviously a different brood. The period of time between another successive brood of eggs, with larvae in the interim, was approximately 20 days (22nd August to 12th September). This particular mussel produced three recorded broods and a hypothetical brood of larvae in 89 days (21st July to 18th October) suggesting periods between successive broods of approximately 23 days.

Obviously exact time cycles cannot be established on the basis of these results, but it seems probable that the normal period of time for eggs to pass into the ovisacs, develop into mature larvae, and then be expelled, is probably in the region of between three and five weeks. Thus it is theoretically possible for a female to produce ten broods a year. Whether or not this happens in the wild state is not known, but seems unlikely as indicated by many successive empty brood pouches.

Also of interest was the greater degree of activity shown by the mussels in the first half of the study period, in the colder months, than in the warmer second half. The decline however may have been due to stress from handling.

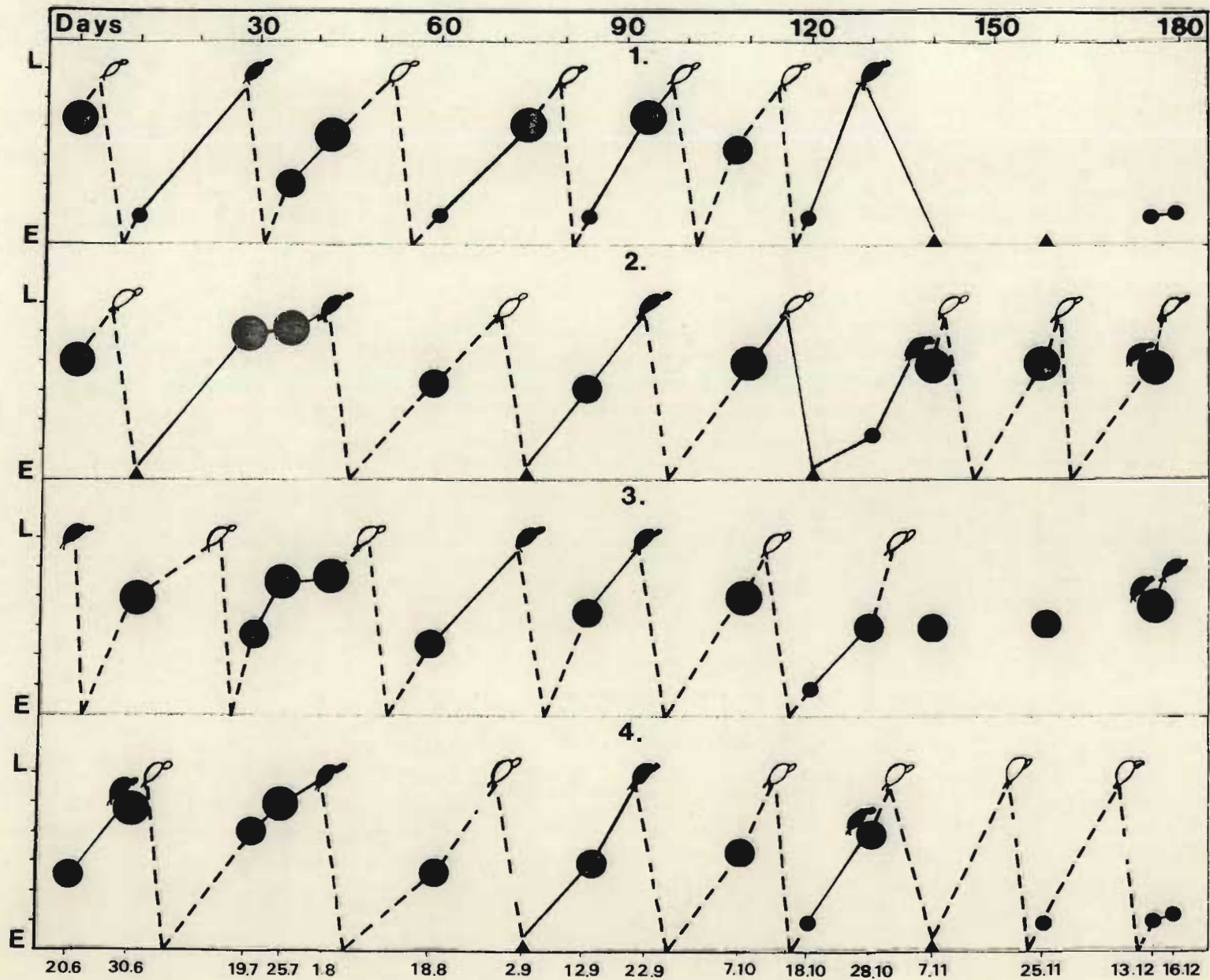
b.) Mutela dubia

Results of the periodic examination of four mussels for genital products are summarized in Table 11 and shown graphically in Fig. 49.

Table 11: Results of periodic examination of the gills of four M.dubia for eggs or larvae over a 179 day period

MUSSEL NO	1		2		3		4	
DATE	GILLS CONTAIN	DIAMETER OF EGGS μ	GILLS CONTAIN	DIAMETER OF EGGS μ	GILLS CONTAIN	DIAMETER OF EGGS μ	GILLS CONTAIN	DIAMETER OF EGGS μ
20/6	Eggs	209	Eggs	209	Larvae	-	Eggs	186 - 197
30/6	Eggs	151 - 174	-	-	Eggs	203 - 215	Eggs/Larv	209 - 221
19/7	Larvae	-	Eggs	209 - 230	Eggs	186 - 207	Eggs	197 - 221
25/7	Eggs	169 - 186	Eggs	209 - 215	Eggs	198 - 221	Eggs	209 - 221
1/8	Eggs	198 - 209	Larvae	-	Eggs	203 - 215	Larvae	-
18/8	Eggs	174 - 180	Eggs	192 - 203	Eggs	192 - 203	Eggs	180 - 203
2/9	Eggs	203 - 215	-	-	Larvae	-	Empty	-
12/9	Eggs	174 - 180	Eggs	198 - 203	Eggs	197 - 209	Eggs	186 - 203
22/9	Eggs	209 - 215	Larvae	-	Larvae	-	Larvae	-
7/10	Eggs	198 - 209	Eggs	198 - 209	Eggs	209	Eggs	197 - 209
18/10	Eggs	162 - 174	-	-	Eggs	174	Eggs	162 - 174
28/10	Larvae	-	Eggs	174 - 186	Eggs	186 - 197	Eggs/Larv	209
7/11	-	-	Eggs/Larv	209	Eggs	186 - 197	Empty	-
25/11	-	-	Eggs	198	Eggs	197 - 209	Eggs	174
13/12	Eggs	174 - 186	Eggs/Larv	209	Eggs/Larv	197 - 209	Eggs	174 - 186
16/12	Eggs	-	-	-	Larvae	-	Eggs	-

Figure 49: Results of the examination of the gills of four M.dubia for eggs or larvae at varying intervals of time over a 179-day period. Eggs and their size (diameter) are indicated by the size of the black circles, and also by the position of the circle in relation to the scale at the left hand side of the figures (E to L). Actual egg sizes are shown in Table 11. Gills empty are indicated by black triangles on base-line E while actual larvae recorded are indicated by black figures at top of scale (L for larvae.) Probable larvae are indicated by open figures. Unbroken lines connect actual recordings of events, while broken lines trace theoretical series of events



The results show that during the 179 day period Mussel No. 1 produced at least eight broods; Mussel No. 2 produced at least seven broods, possibly eight; Mussel No. 3 produced at least seven, possibly more; and Mussel No. 4 produced at least seven, possibly eight.

Thus a minimum of 29 broods were produced by the four females over the period, which encompassed both winter and summer seasons. On the basis of an average of seven or eight broods over the period the mean interval between broods was 22 or 26 days.

The results suggest that the period between successive broods may be longer in winter than in summer. Considering Mussel No. 4, early stage larvae were present on 30th June and larvae on 1st August, with eggs recorded in the interim. Assuming these to be successive broods, the interval was 32 days. In early summer, larval broods were recorded on 22nd September and 28th October (36 days), with a probable brood in between (Fig. 49), giving a speculative summer interval of approximately 18 to 20 days, allowing a few days extra for the early stage brood of 28th October to reach full development. Mussel No. 3 had an interval of 20 days between the successive broods of 2nd September and 22nd September. Mussel No. 2 had larval broods on 22nd September and 7th November (45 days), with a probable brood in between, giving an interval of approximately 22 days. Thus three to four and a half weeks seems to be the normal period for this species to produce successive broods, the actual length of time possibly dependent on the seasons.

In contrast to C. mossambicensis there was no clear-cut decrease in sexual activity as the study period extended from winter into summer.

4. Fecundity

This was determined for C. mossambicensis. As explained in the Methods section the first relationship established was that between the length of the egg packet and number of eggs comprising the packet from which it was possible to calculate the number of eggs contained by a gill if the mean length and number of brood chambers was known (Fig. 50).

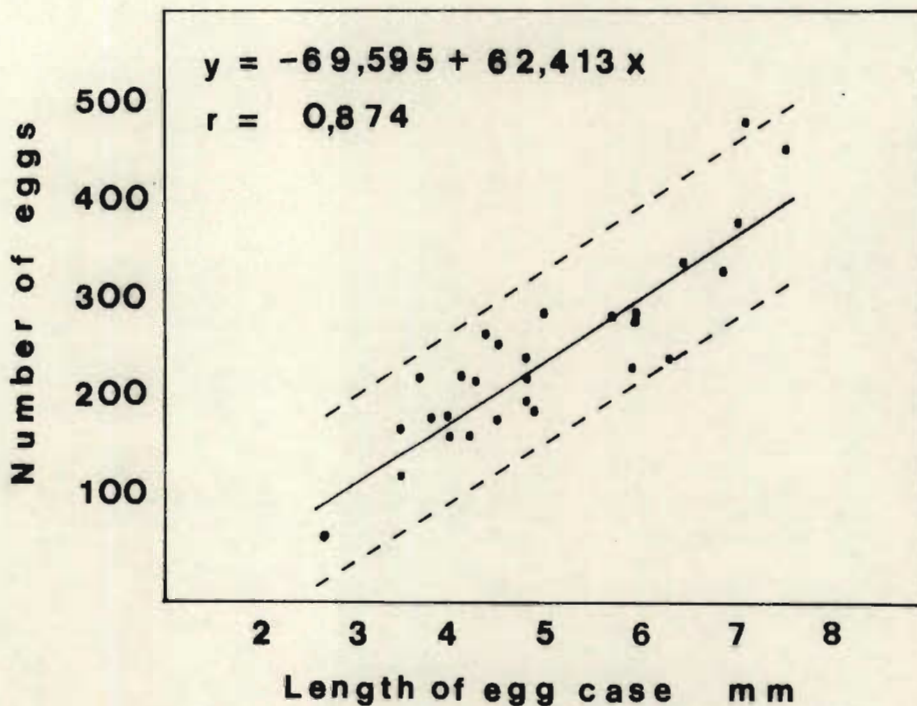


Figure 50: The relationship between length of egg packet of C. mossambicensis and number of eggs comprising the packet (95% confidence limits indicated by dotted line)

The validity of the method in determining fecundity therefore depends to a large extent on the degree of correlation existing in the relationship between length of egg packet and number of eggs contained by the packet. This relationship is shown in Fig. 50.

The correlation was high ($r = 0,874$) and the relationship was found to be highly significant ($P < 0,001$). The 95% confidence limits encompassed all the points of the scatter, with the exception of one. The relationship was considered sound and the estimation of fecundity proceeded from this point with the determination of the fecundity of eight mussels ranging in size from 28 mm to 51 mm.

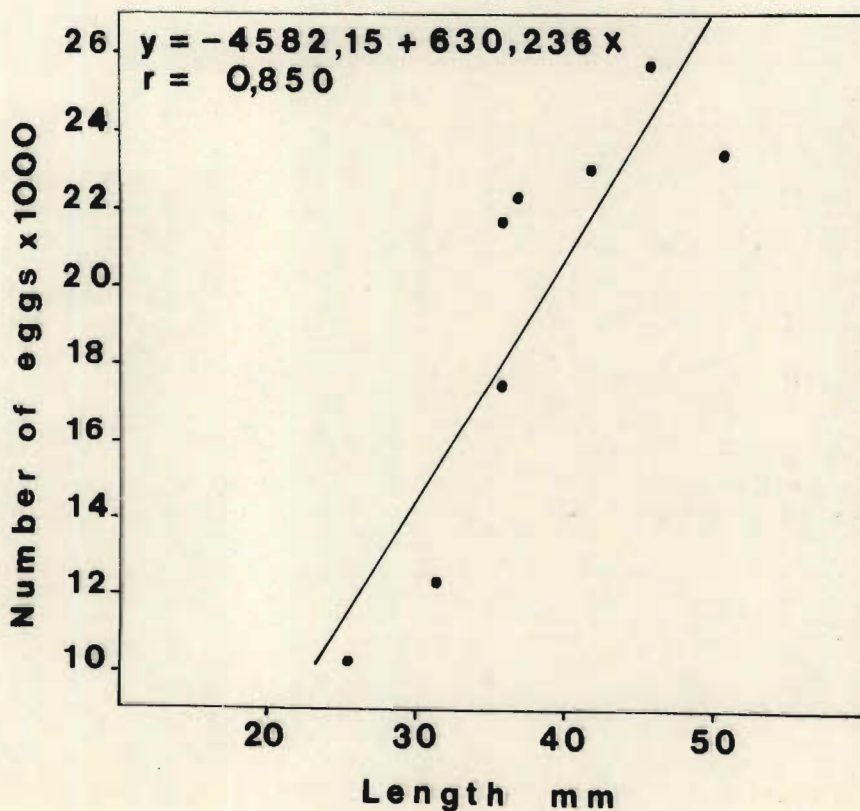


Figure 51: The relationship between length of C. mossambicensis and fecundity

Pennak (1953) states that fecundity in Unionids ranges from several thousand eggs in the smaller species to more than 3 million in some of the larger ones. Fecundity, as shown above, ranged from 10 000 eggs for an individual of less than 30 mm to almost 26 000 eggs for an individual of slightly over 45 mm. As could be expected a good correlation ($r = 0,850$) existed between length of mussel and number of eggs contained by the individual, with larger mussels having two to three times more eggs than the smaller ones. This correlation was found to be highly significant ($0,005 > P > 0,001$). Studies elsewhere indicate that an increase in breeding performance with an increase in size appears to be the norm in freshwater bivalves (Heard, 1965; Meier-Brook, 1970; Mackie et al 1976a) although there appears to be some variation amongst individuals of a given length, as has also been shown to occur in the marine red abalone, Haliotis refescens, (Giorgi and de Martini, 1977). The regression equation indicates a range of 10 000 - 30 000 eggs for a size range of 23 - 55 mm.

H. and A. van der Schalie (1963) report that in the freshwater mussel Actinonaias ellipsiformis the number of ovisacs increased with the size of the female, ranging from 9 to 25 per gill. Similarly in C.mossambicensis the number of ovisacs increased in relation to an increase in length of the mussel (Fig. 52)

While the correlation is highly significant ($r = 0,849$, $P < 0,001$) it is also evident that variation

amongst mussels of similar lengths exists.

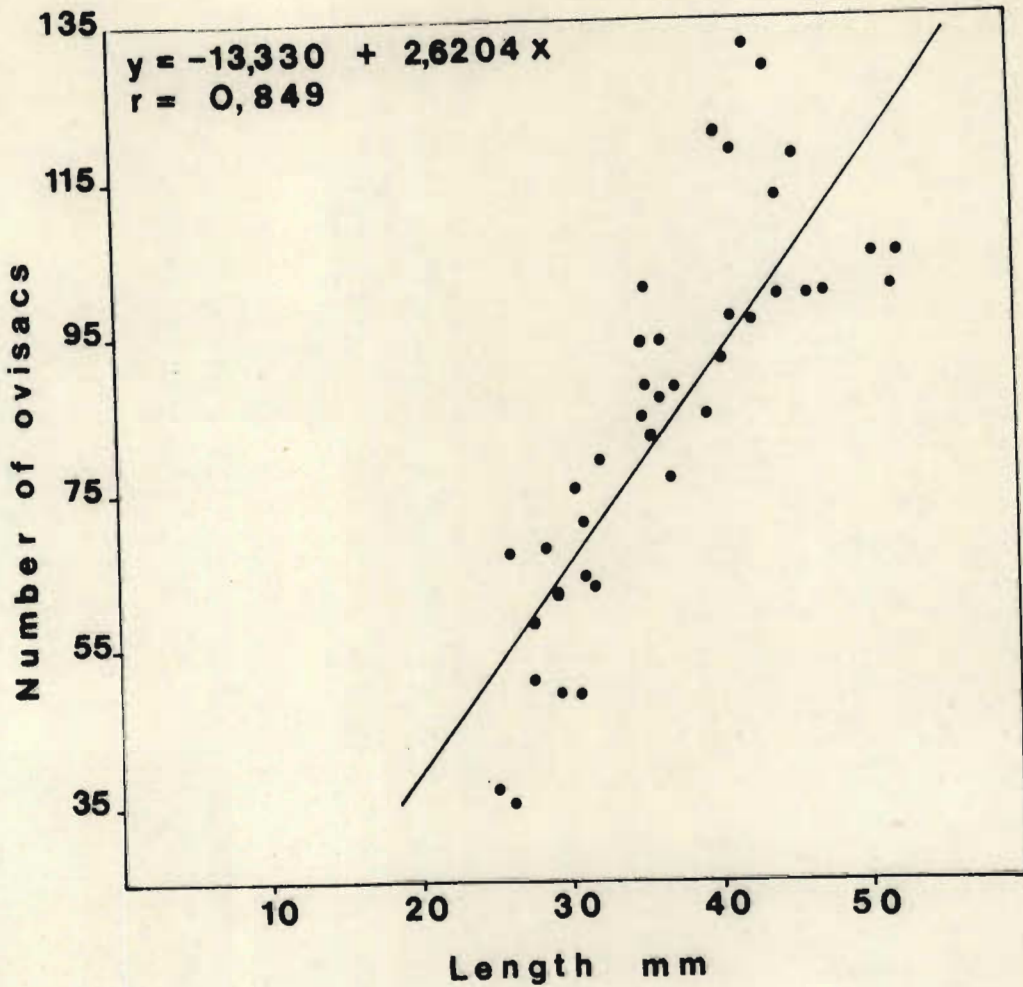


Figure 52: The relationship between the length of C. mossambicensis and the number of ovisacs possessed

The actual numbers recorded ranged from 35 for a mussel of 26 mm to 182 for a mussel of 43 mm. On the basis of number of ovisacs possessed, the implication is that fecundity amongst the larger mussels is three to four times higher than fecundity of the smallest mussels, assuming a positive correlation between number of ovisacs and fecundity. That such a relationship exists is shown in Fig. 53.

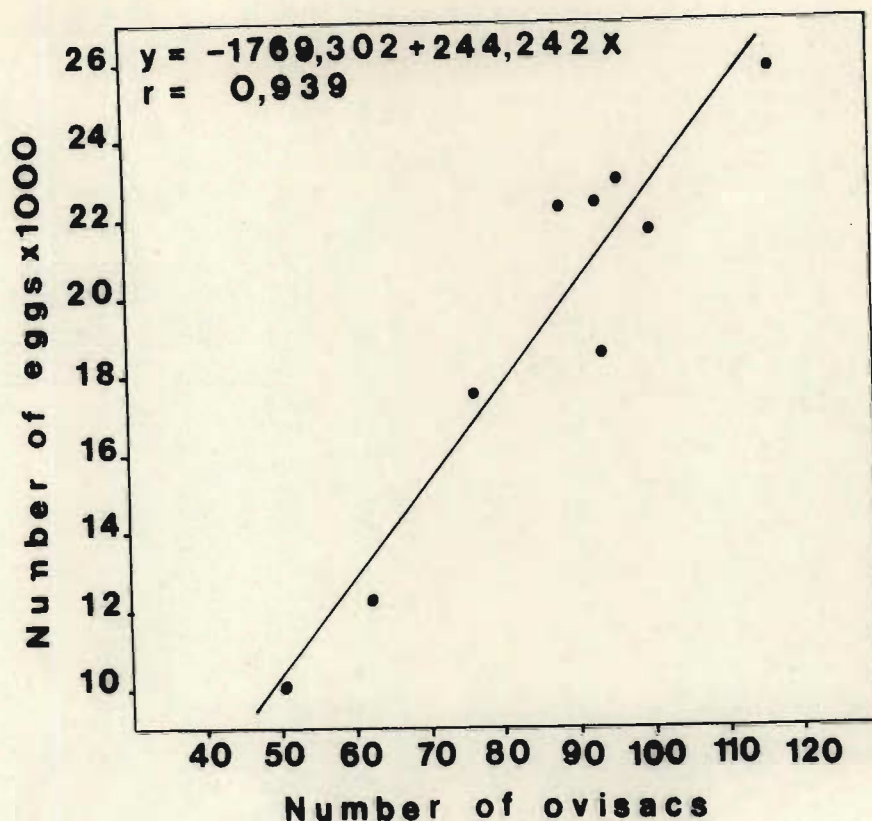


Figure 53: The relationship between the number of ovisacs possessed by C. mossambicensis and fecundity

Figure 53 shows that a highly significant correlation exists between the number of ovisacs possessed and fecundity. ($r = 0,939$; $P < 0,001$). The more ovisacs possessed, the greater the fecundity, with a certain amount of variation existing amongst individuals of similar length.

A few further features of the organisation of C. mossambicensis with regard to their ovisacs are worth mentioning. Of the four gills serving as marsupia, the inner gills almost always contain the largest number of

ovisacs, and hence also eggs. Out of 33 mussels ranging in size from 25,4 mm - 53 mm, 85% had more ovisacs in the inner gills than in the outer gills. Only 9% had more in the outer gills, while the remaining 6% had equal numbers in outer and inner gills. The percentage of ovisacs in the inner gills, of the total number possessed by the mussel, ranged from 77,8% - 41,9%, but the mean was 55,5% (SE = 1,113), and hence the mean percentage contained by the outer gills was 44,5%. This means that on average the inner gills contain 10% more ovisacs than the outer ones, and this situation occurs in some 85% of mussels.

There is also an indication that the smaller mussels contain a greater proportion of ovisacs in the inner gills than the larger mussels. Of the 33 mussels, 18 were under 40 mm in length and the mean percentage of ovisacs in the inner gill out of the total number possessed, was 58,01%. Of the remaining 15 mussels, over 40 mm, the mean percentage of ovisacs in the inner gills, out of the total possessed, was 52,5%. The difference between these means was found to be significant at the 95% level with a probability of between 0,02 to 0,01. Thus the proportion of ovisacs in the inner and outer gills more nearly approaches parity in the larger mussels than in the smaller. Of the larger mussels, 73,3% ($\frac{11}{15}$) contained more ovisacs in the inner gills than the outer gills, compared with 94,4% ($\frac{17}{18}$) for mussels under 40 mm.

With regard to left and right pairs of gills, there is no difference between the number of ovisacs

possessed. Of the 33 mussels examined, the mean proportions of ovisacs possessed by left and right pairs of gills were 50,2% and 49,8% respectively. These proportions were not significantly different at the 95% level of confidence.

5. The Parasitic Stages

An attempt was made in this study to infect fish with the larvae of the three species and follow progress of the developing larvae through to the point where the post-larval stage left the fish host (to begin its juvenile and adult life) i.e. the 'parasitic stage', an important part of the life cycle of the individual. The study proceeded on the assumption that all three species are parasitic in the larval stage, being members of the Unionid and Mutelid families, groups known for the parasitic larvae carried in modified gills (Purchon, 1977). Earlier studies had shown that the gills of these species carried larvae and it was reasonable to assume these were parasitic in accordance with the norm of their respective families.

a.) Caelatura mossambicensis

(i) The larvae

These are typical glochidial larvae, comprising two "D"-shaped and apparently hookless valves which periodically open and snap shut when infective. They measure 0,25 - 0,26 mm in length, 0,26 - 0,27 mm in

height, and some 0,08 mm in width.

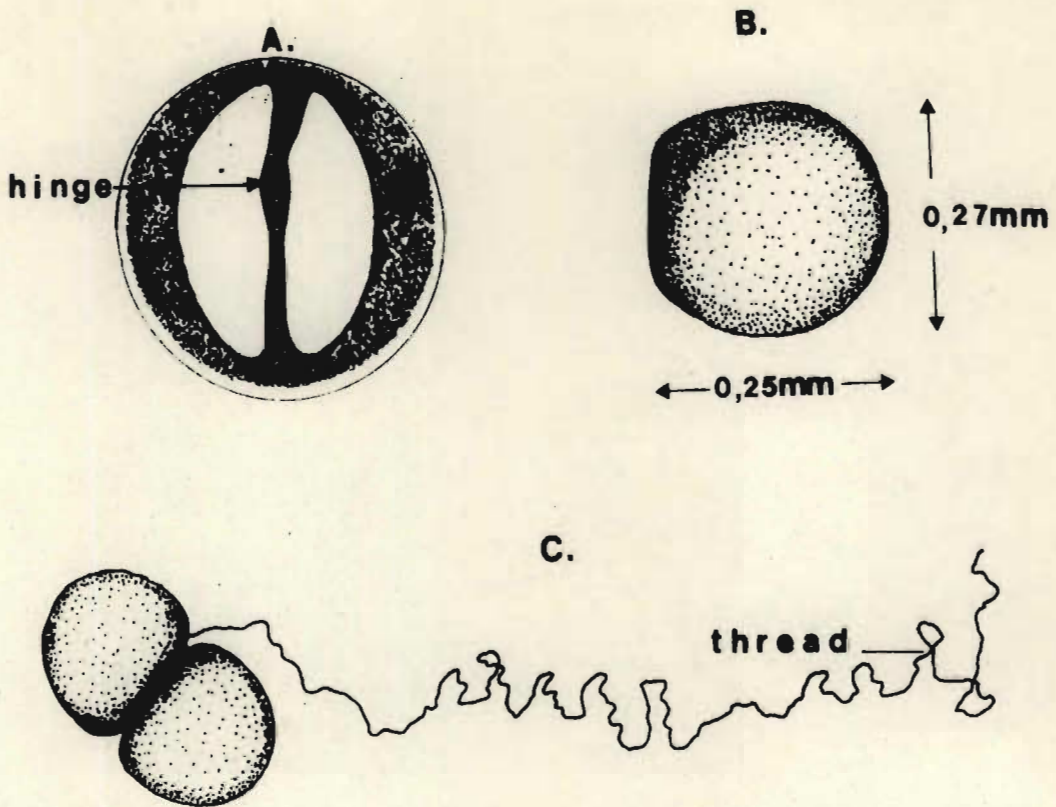


Figure 54: The larva of C. mossambicensis still in the egg membrane showing hinge (A) expelled and closed showing the dimensions (B) and open, showing the coiled thread (C)

Height is greater than length, a characteristic feature also of several species from the Oriental Region (Heard and Vail, 1976). The encapsulating egg membrane enclosing the larvae when it hatches measures $\pm 0,29$ mm in diameter. The larval dimensions given here are similar to those given by Appleton (1979) for the larvae of C. kunenensis, which measured 0,263 mm x 0,265 mm for length and height, and which also appeared to be hookless. Pennak (1953) gives the range of glochidial diameter for various species as 0,05 mm - 0,50 mm. The larvae of Unio caffer

are apparently smaller than those of C. mossambicensis and C. kunenensis, measuring 0,21 mm x 0,21 mm, and are sub-triangular in shape and hooked. (Heard and Vail, 1976). Ortmann (1918) gave dimensions for U. caffer of 0,23 mm - 0,25 mm x 0,20 mm - 0,21 mm high.

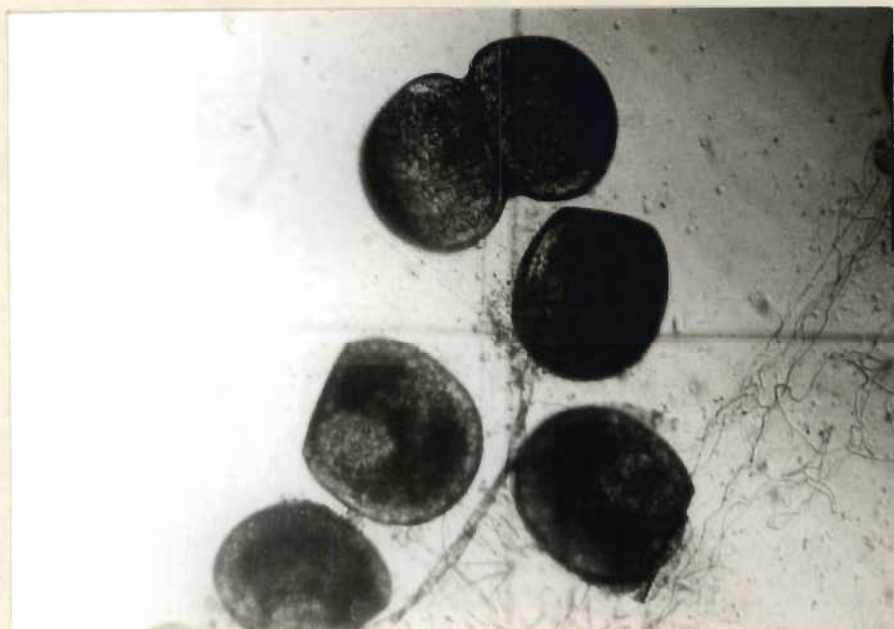


Plate 11 : Photo of D-shaped glochidia larvae of C. mossambicensis. Note the coiled thread to the right of the larvae

The larvae of C. mossambicensis each contain a long filamentous thread, and are expelled from the mussel in a sticky conglutinuous mass which becomes entangled on the fins and in the gills of fish, where encystment may take place.

(ii) The parasitic stage.

Despite the apparent lack of hooks (this needs confirmation) the larvae were able to attach themselves to the fins of a number of different fish species. Haplochromis darlingi, Pseudocrenilabris philander, Sarotherodon mortimeri and Tilapia mortimeri (cichlids) were all successfully infected in the laboratory. The most common fins for attachment were the dorsal and caudal fins, while the pectoral fin showed the lowest degree of infection.

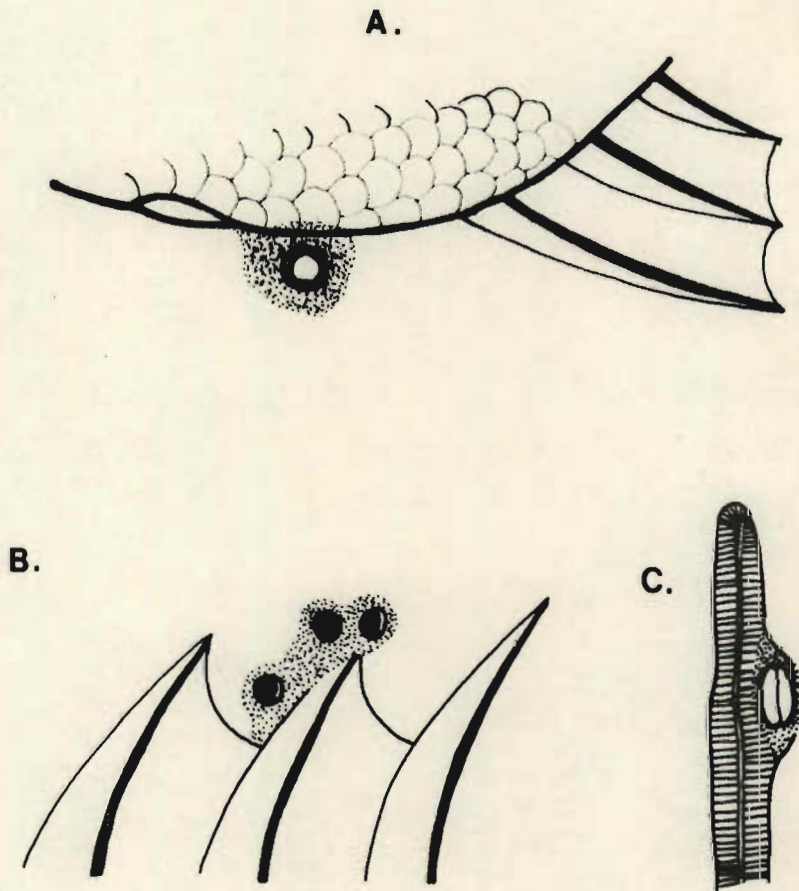


Figure 55: Various places of attachment of larvae on fish host (A): on body (B): on dorsal fin (C): on gill filament. Dotted areas indicates encystment of larvae by host epidermal cells

Of the four species, H. darlingi were the most heavily infected, probably because of their bottom dwelling habits, P. philander were least infected, and the other two were infected in equal degrees. While most of the attachments were on fins, in a few cases attachment to the body was observed.

An examination of four cichlid species from the lake - Haplochromis codringtoni, H. darlingi, S. mortimeri, and T. rendalli, - showed that all four had encysted larvae in their gill filaments, and in a few cases on their gill rakers as well. Of interest was the comparative degree of encystment found in the T. rendalli and H. darlingi from the base of the Seiche Tower, where they co-existed above a population of C. mossambicensis.

	NO. EXAMINED	SIZE RANGE (mm)	NO. ENCYSTED LARVAE	MEAN NO. FISH
<u>T. rendalli</u>	7	56-98	240	34,3
<u>H. darlingi</u>	3	65-119	8	2,7

Quite clearly the T. rendalli were far more heavily infected and are obviously a more suitable host for gill attachment of the larvae than H. darlingi.

The encystment process of a larva on a gill filament of a T. rendalli of 80 mm was observed under a microscope from the time the larva snapped shut on the epidermal cells of the filament to the time it was completely covered by the epidermal layer. Three stages of the

process, which took $3\frac{1}{2}$ hours, are shown below. The early encystment was photographed and is shown in Plate 12. Seshaiya (1969) reports that the hooked glochidial larva of Lamellidens corrianus completed the encystment process within half an hour.

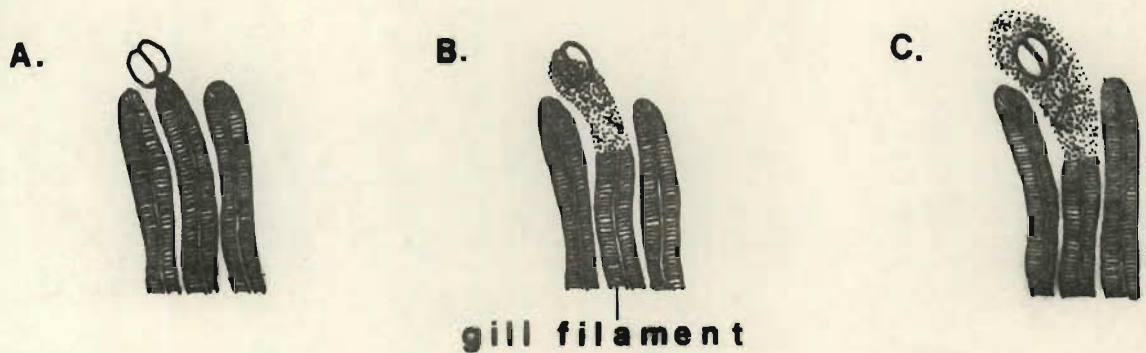


Figure 56 : Three stages in the encystment process of a glochidial larva on the gill filament of a T. rendalli. (A) : attachment; (B) : partial enclosure; (C) : complete enclosure. Healthy cells appear to disintegrate resulting in the enclosing "cyst" (dotted area)



Plate 12 : Encysted larva of C. mossambicensis at the tip of a gill filament of a T. rendalli

While apparently successful infections of these fish species took place in the laboratory, young post glochidial mussels were never found in the petri dishes, and encysted larvae in the gills and fins never appeared to develop further than their original form. In many cases encysted larvae on fins disappeared, presumably rubbed off by the fish or possibly sloughed off. According to various authors glochidial larvae will attach to a wide variety of hosts, including Urodeles, but are sloughed off by most before metamorphosis, while some hosts are also able to acquire immunity to further infections. (Arey 1932, Baer 1952). Seshaiya (1969), for example, records that fish of the genus Ophiocephalus could successfully serve as a host for six or seven infections, but further infections were unsuccessful and the glochidia dropped off without metamorphosis. Undoubtedly specific hosts are required by many species.

Obviously encystment on the fish does not necessarily mean successful metamorphosis. Lack of success in obtaining metamorphosis may have been due to a fault in technique, rather than an indication that the fish species were not suitable hosts. The very nature of the distribution of C. mossambicensis in Lake Kariba almost certainly suggests that cichlids are hosts, perhaps amongst others, of larvae. The findings of other workers (Lefevre and Curtis, 1912; Seshaiya 1969; Giusti et al 1975, Jubb 1976) suggests that at least some mussels are not host specific, but may utilize a variety of species. Confident determination of a species as a suitable host can however only be obtained when successful metamorphosis and dropping

off of the post-glochidial juvenile is observed.

b.) Aspatharia wahlbergi

(i) The larvae

Compared with those of both C. mossambicensis and M. dubia, the eggs and larvae brooded in the marsupia of A. wahlbergi are small

Eggs observed in the ovisacs ranged in size from 0,058 mm - 0,192 mm in diameter - considerably smaller than the eggs of C. mossambicensis, which have a diameter of 0,3 mm when the developing larva is ready to hatch from the membrane, and smaller than those of M. dubia which reach a diameter of 0,23 mm.

The free living larva is rather similar to that of M. dubia, and also to that of M. bourquignati described by Fryer (1961), but considerably smaller. Viewed from the top it has a superficial resemblance to a veliger larva, with two distinct ciliated lobes, rather like a velum, emerging from the anterior end of the body. The body itself is oval, some 0,12 mm - 0,13 mm long, and not quite as wide.

The side view showed a small hook extending downwards, at the posterior end of the larval shell. There may be more than one hook present. The long single tentacle found in the larvae of Mutela species was not noted, and in this respect A. wahlbergi larvae appear to

differ from the larvae of Mutela.

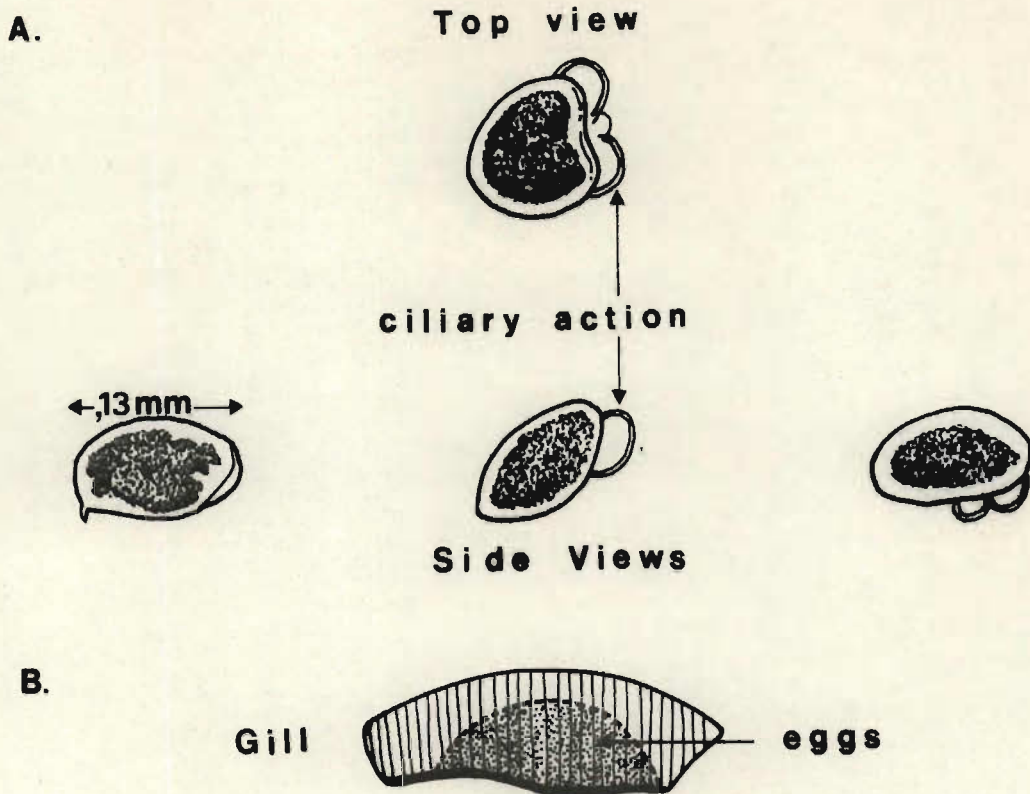


Figure 57: General appearance of the larva of A. wahlbergi (A), and showing the general area of the inner gill (B) occupied by the brood (Dotted)

Fryer (1961) noted that while the larvae of M. bourquignati also superficially resembled a veliger larva the differences were deep-seated, and he considered it unwise to press the homology too far. Since A. wahlbergi belongs to the family Mutelidae with larval cellular arrangement probably similar to the larva of Mutela, the same consideration doubtless applies here.

(ii) The parasitic stage

Three attempts were made to infect fish with the

larvae and follow development. Because of the seasonal nature of the breeding of A. wahlbergi this could only be attempted during the summer months, when larvae were available. The first two attempts certainly showed the larvae to be parasitic, as the fish introduced into the bowl with the larvae all died afterwards, heavily infected with small nodules erupting like mole hills from their bodies and fins. Investigation showed these to be epidermal encystments covering the place of attachment of the larva, which was indicated by a small black spot. The lesson learned was that the larvae appeared to be highly infective, and that over-infection could quickly result in the death of potential fish hosts. The fish killed in this manner were juvenile T. rendalli, adult P. philander and small Barbus. The third attempt involved placing adult A. wahlbergi in a tank in which several small Barbus had been installed. The A. wahlbergi were collected from the river/lake interface of Lake McIlwaine in October 1979, and placed in the 50 l fish tank in sand substrate, on 14th October. This was a preliminary trial to see if the mussels would shed their larvae, resulting in a lower degree of infection of the fish than was achieved when placing larvae in fish-occupied bowls. Signs of infection were noted the following day when the Barbus started twitching, as fish do when being infected by M. dubia larvae. By the third day three Barbus had died and on examination they were found to be covered (Head, body and fins) by the small nodules described above. The two remaining Barbus were removed from the tank and placed in a small eye-level observation tank. Reddish patches characterized sites of infection, and examination showed

this to be blood. Although fairly heavily infected these two Barbus survived, without any development of the nodules taking place, and by the 29th (15 days after initial infection) all signs of the nodules had disappeared. Further experimentation was not possible at this stage because of other commitments. However, the experiment had shown the method of infecting to be successful, and again showed the lethal effect on the hosts of over-infecting. The lack of development of the larvae on the hosts was disappointing, and suggests that they may be host specific or that development may be intracellular, rather than the conspicuous semi-extracellular manner of M. dubia. However, nothing was discernable, and no baby mussels were noted on the bottom of the small tank.

c.) Mutela dubia

(i) The larvae

These are incubated in the inner gills only and emerge from the egg membrane when this has a diameter of approximately 0,23 mm. The larva itself closely resembles that of M. bourquignati as described by Fryer (1961), consisting of an oval shield-shaped body from which two ciliated lobes protrude in a fashion similar to the larva of A. wahlbergi. These lobes can be withdrawn into the ventral concavity so as not to be visible, or extended to give the whole larva a terrapin-like appearance (Figure 58). At the posterior end, on the ventral side, is a smaller lobe, from which a number of

curved hooks extend downwards. The exact number of hooks was difficult to determine, but there appeared to be about five to seven. The main distinguishable features of the larva are shown in Fig. 58.

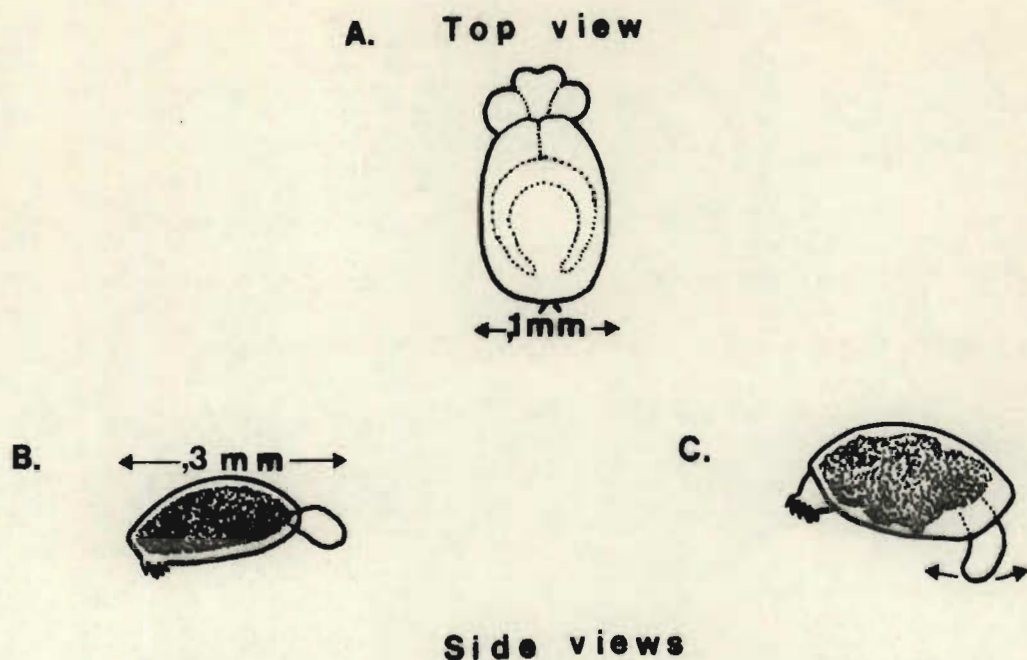


Figure 58: Side and top view of the larva of M. dubia (A & B) showing the main features and dimensions, and direction of extension and retraction movement of the frontal ciliated lobes (C). Note the terrapin - like appearance and hooked posterior lobe

The fully extended length of the larva is about 0,3 mm and the width 0,1 mm - 0,14 mm, i.e. as wide as the larvae of A. wahlbergi are long. The length of the shield or carapace is about 0,24 mm. Each larva possesses a long colourless and transparent tentacle, which can be seen in Plate 14. These tentacles can be distinguished inside the egg membrane when the larvae are about to hatch. Fryer (1961) noted the same peculiar structure in the larvae of

M. bourguignati and established that this appendage could be as much as 76 times longer than the larval body. With the aid of a camera lucida and planimeter he determined the length of one tentacle as 15,5 mm. While no accurate lengths could be determined in this study, one tentacle measured very crudely under the microscope was at least 10,5 mm long which confirms Fryer's observation of their length relative to the larva's length. Like those described by Fryer they tapered in diameter from the origin to the distal end.



Plate 13 : Side view of the terrapin - like larva of M. dubia, showing the ciliated lobes, and the curved hooks at the posterior end

Fryer was unable to ascertain the exact origin of this tentacle, but did observe that it arose somewhere in the vicinity of the ciliated lobes. One measurement

made in this study showed the diameter of the tentacle to be 0,035 mm at the broadest end. This accords with Fryer's observation that the tentacle has a diameter of more than 0,03 mm at its origin.



Plate 14 : Top view of the larva of M. dubia. Note the threads criss - crossing through the picture

(ii) The parasitic stage

Fully infective larvae are expelled from the adult through the exhalent siphon (Fryer, 1961; pers. obs.) in a brown sticky gelatinous mass which probably facilitates their adhesion to the substrate or aquatic plants, into which unsuspecting fish will swim. Observations show that these free - living larvae can remain alive and presumably infective for at least 48 hours. Fish in a tank in which

the larvae are circulating will periodically wriggle and twitch, and occasionally dart forward, or rub themselves on the sides or bottom of the tank. This behaviour was also noted in the field and must be related to the process of infection which appears to irritate the fish. Alternatively larger cichlid species will remain in a stationery position close to the bottom of the tank, moving only when they are presumably being infected. Such reactions were noted in glass aquaria containing Sarotherodon macrochir at Lake McIlwaine, in which no larvae had been placed. These fish had a few to several small patches of what appeared to be fungal infections on their bodies and fins, and investigation showed that these were the sites of M. dubia larval infections, in various stages of development. Water pumped directly from the extreme shallows of the lake (less than 30 cm depth) was being circulated through these aquaria, along with the larvae, which were the source of infections. Interesting points arising from this observation were (a) the origin of the larvae, showing that the extreme margins of the lake carried infective larvae, (b) the fact that the larvae survived the journey through the pipe into a reservoir and then through another pipe into the aquaria - showing them to be hardy, and (c) the fungal-type growths resulting from infection, which an unsuspecting observer would certainly not relate to the presence of M. dubia in the nearby lake. Such bushy growths were also noticed around larval infections on fish at Kariba - both naturally infected in the lake and artificially infected in the laboratory. Obviously the process of infection creates a small crack in the external defences of the fish allowing these small

localized growths to take place. A closer investigation of these bushy patches showed they were in fact stalked colonial ciliates, presumably of the Order Peritrichida, which has parasitic members. Fryer reports a similar phenomenon, and says that these "necklaces" are almost always present.

Research on Lake McIlwaine (PART ONE) has now shown M. dubia to occur in the extreme shallows of the lake, and to have a possible breeding peak in summer, which explains why larvae were pumped from the lake at this time.

Observations under the microscope show that infection is quick once a larva comes into contact with the fish. Attachment is made with the anterior end pressed into the fish, either on a fin or the body, so that the remaining portion of the body stands out like a small stalk (Fig. 59). Presumably initial attachment is made either with the aid of the sticky thread or the hooks, or both. Fryer maintains that the enclosure of the larvae by mucous produced by the host provides subsequent anchorage for the parasitic stage to develop. Within two days the stalk is considerably longer, and the larva is firmly attached to the host by means of two processes, somewhat resembling roots, which have grown forward into the host's tissue. Fryer has named these haustoria, whence his term haustorial larvae. It was noted that where infection had taken place on a fin the haustoria aligned themselves with a fin ray, as shown in Fig. 59. Where infection was on a scale, the scale material in the immediate vicinity of the haustoria

was eroded in a manner suggestive of acid corrosion. Both these observations are similarly reported by Fryer, who noted that these anterior outgrowths align themselves alongside some firm skeletal structure, and that the erosion is caused by digestive juices extruded from the haustoria. The subsequent development of the haustoria larvae proceeds along the lines already fully described in detail by Fryer for M. bourguignati. Fig.59 shows the time factor and general dimensions involved in the lengthening of the posterior stalk to the stage where the distal extremity gives rise to the young mussel (g to j), complete with shell valves and internal organs such as gills, alimentary canal and other viscera (k). The time factor and dimensions of the different stages given in the figure are based on a number of observations on different haustorial larvae, and therefore represent the general pattern of development from time of infection to complete development. Obviously it was not possible to periodically draw and measure a single developing larva on a fish without damaging or killing either the fish or the larva. Variation does occur, both in the length of the stalk and the length of the haustoria, and undoubtedly also in the length of time for full development. The total length of the mussel stalk and haustoria generally varied between 4 mm and 5 mm, although shorter stalks did occur. Fryer noted similar variation and provides a diagram of mussel, stalk and haustoria some 5,5 mm in total length.

The time of 21 days for full development given in Fig.59 was derived from successful metamorphosis of two

haustorial larvae on a southern mouth brooder, P.philander, at Kariba in September 1977 when aquarium water temperatures were 25°C - 28°C. One fully developed mussel dropped off on the night of the 20th day and another the next day. Prior to this an infection initiated in late winter (July), when the aquarium water was several degrees cooler (20°C - 23°C), had reached a much less mature stage of development after 21 days. This larva was excised and photographed to show the typical nature of the haustorial larva (Plate 15). Fryer quotes a development time of 25 days for M.bourquignati at a water temperature of 24°C - 25°C. Duration of metamorphosis could well be dependent on water temperature.

Prior to the young mussel dropping off the stalk it is fairly active, with the foot being extended and retracted periodically, and the shell valves opening and closing. These movements are undoubtedly to facilitate the break of the mussel from the stalk. Fryer notes similar muscular movement and also observed the tip of the foot being inserted into the open end of the stalk and used as a lever to force stalk and animal apart.

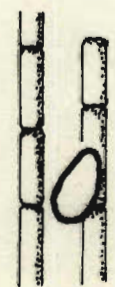
At the time of dropping off the mussel measures about 1,4 mm, although this might vary. Fryer gives lengths of about 1,3 mm to 1,4 mm for M. bourquignati. Of interest is that the small mussel has a means whereby it can attach itself to the substrate, presumably a sticky thread of some sort. This can easily be demonstrated by placing the young mussel in a petri-dish, covered by a thin film of water and tilting the dish so the water swirls to

and fro. The small mussel will stay in one place, anchored securely to the bottom. According to Fryer the means of attachment is by a byssus thread, consisting of a single coiled hyaline filament 0,007 to 0,008 mm in diameter and usually larger than the animal. While such a structure might not be too important in a static lake, it obviously would serve a valuable function in a river, where even a gentle current could carry the mussel away were it not securely attached to the substrate. In shallow water in a lake the thread would prevent the young mussel from being washed up on to the beach by wave action.* The young mussel is in an advanced stage of development when it drops off, and organs observed through the transparent shell valves were the active foot, ctenidia and general visceral mass in which no single feature could be identified. (Fig. 59). According to Fryer the still attached mussel of M. bourquignati commences collecting suspended matter by means of currents set up by the ctenidial cilia, and to all intents and purposes is a young bivalve, capable of surviving as an independent feeder even if prematurely detached from the stalk and supplied with particulate food.

* Although no byssus threads were ever noticed on mussels collected from either Lake Kariba or Lake McIlwaine despite the large number examined, a mussel of 37 mm collected from a large pool above a weir on the Hunyani River, in May 1980, had a single elastic thread, several centimetres long, extending from within the shell to the substrate. It could not be definitely determined if this was a byssus thread, but in view of the riverine habitat, with mussels periodically being subjected to strong currents, it may well have been.

Figure 59: Various stages in the development of the haustorial larva of M.dubia. (a) attachment of larva to host between two fin rays (b)-(e) growth of stalk and showing haustorial larva firmly anchored beneath a fin ray (f)-(h) developing mussel at end of stalk, with valves open and foot protruding, (i) appearance of haustorial larva attached, (j) dimensions of whole organism and (k) the fully formed mussel detached from the stalk

a. Infection



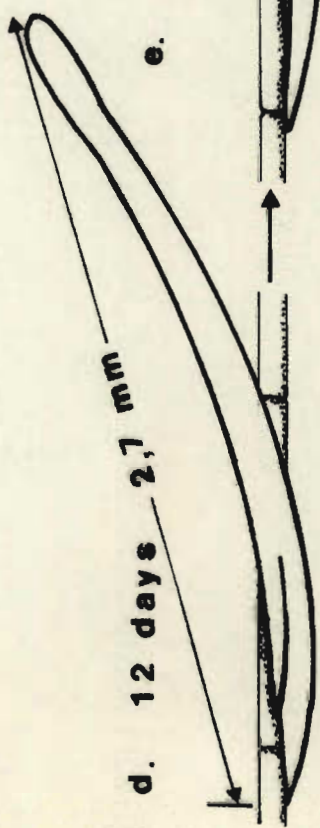
b. 2 days



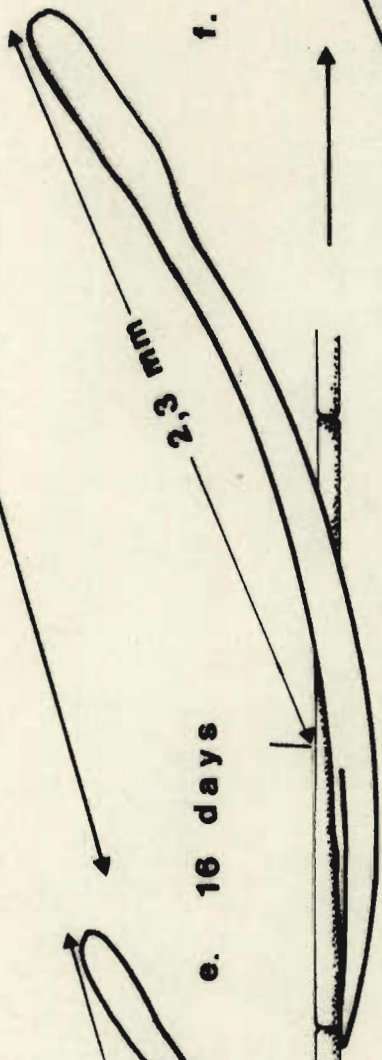
c. 4 days



d. 12 days 2.7 mm



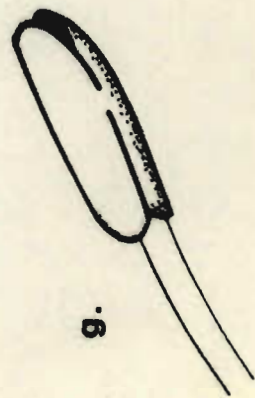
e. 16 days



f. 19 days



21 days



i.



j.



k.

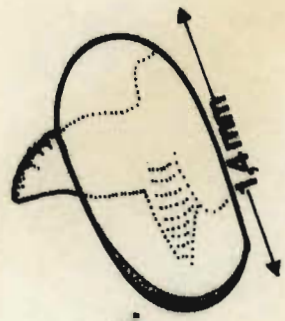




Plate 15 : Photograph of excised haustorial larva after 21 days development

(iii) The fish hosts

Fryer found that the cyprinid fish, Barbus altianalis radcliffi, was the fish host of the parasitic stage of M. bourquignati in the Victoria Nile and Lake Victoria. He did not record any other species of fish acting as hosts to the parasitic larvae. During this study the following fish species (cichlids) were successfully infected in the laboratory with larvae which developed into haustorial larvae - Pseudocrenilabrus philander, Haplochromis darlingi and Tilapia rendalli. In addition, well developed haustorial larvae where the distal mussel was either well formed or forming were found on the following species in Lake Kariba - Haplochromis codringtoni (cichlid), Sarotherodon mortimeri (cichlid) and Hippopotamyrus discorhyncus (mormyrid). At Lake McIlwaine, Sarotherodon macrochir was successfully infected to complete development in the laboratory. Other species infected by the larvae, but in which further development was not seen or did not take place were Barbus fasciolatus, Barbus trimaculatus (both cyprinids), Eutropius depressirostris and Synodontis zambezensis (unscaled members of the catfish family.)

It is apparent from this that the larvae are not host specific, and a variety of different species can act as hosts. Some species may, however, be more suitable as hosts than others. An example of this was shown at Lake McIlwaine, where, as already described, the aquaria were unwittingly inoculated with larvae from the lake. All

species in the aquaria at this time - juvenile T.rendalli, S.macrochir, H. codringtoni and Labeo altivelis (a cyprinid) showed the normal indications of irritation when in contact with the larvae, twitching and rubbing themselves on the sides or bottom. However, of the four species, haustorial larvae were seen only on the S. macrochir. In two aquaria where T. rendalli and S. macrochir were mixed and hence were subjected to the same degree of infection between 50 and 60 infections were noted on eight S.macrochir and none on four T. rendalli, when visually examined through the sides of the aquaria. The L. altivelis were particularly vigorous in rubbing themselves on the sides or bottom, whereas S.macrochir twitched or darted forward, and then would settle in a stationary position close to the bottom, where they provided a stationary target for larvae.

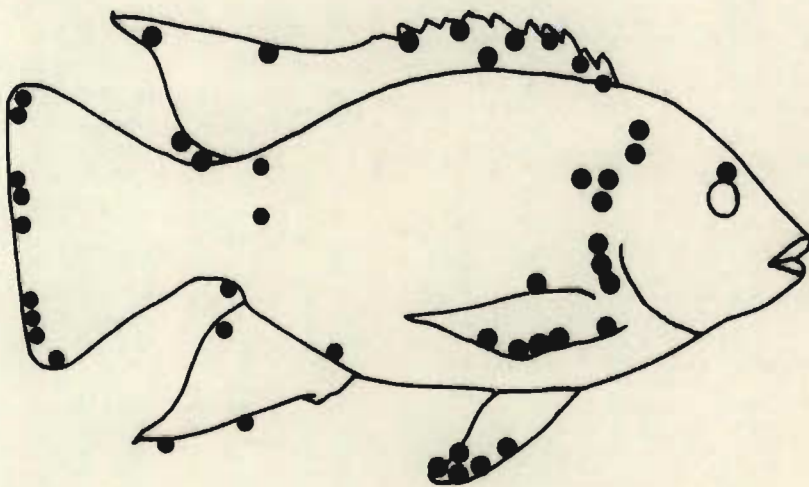


Figure 60: Showing the sites of M.dubia larval infections on a juvenile S.mortimeri infected in the laboratory.

Observations on fish from the field show that the larvae take root either on the host's fins or scales.

A green bream (H. codringtoni) from Lake Kariba had two well developed haustoria, one situated on the dorsal fin and the second, almost ready to drop off as a young mussel, on a scale on the side of the body. A typical pattern of laboratory infection is shown in Fig. 60 on a 6 cm S. mortimeri where infections were mainly on the fins, but also on scales on the body and on the unscaled head region. Not all of these infections develop into full haustorial larvae, and many are either successfully rubbed off by the fish or drop off as a result of the fins degenerating along the margins due to these infections. This may be caused by the direct action of the larvae themselves, or as a secondary effect due to bacterial infection, as suggested by Fryer (1961). Heavily infected fish become extremely unsightly with tattered fins (particularly the caudal) and bush patches on body and fins, where colonial ciliates have colonized the wound region of an established haustorial larva. It is best therefore, in experimental work, to try and obtain only a light infection of the fish. The larvae most likely to develop successfully are those which obtain a secure situation on the host adjacent to a sturdy fin ray, or on a scale, particularly in a locality where they are unable to be rubbed off.

This study has shown the parasitic cycle to be similar to that described by Fryer for M. bourquignati. Many of his findings paralleled those described here, and there were no apparent differences where comparisons of various aspects could be made. Fryer (1961) stated that other mutelids would certainly be found to have a

similar larval development to that of the species he studied. This study has confirmed his suggestion and it now remains to be seen if it holds true for other Mutela species.

DISCUSSION

The generally high biomass of bivalves encountered in Kariba and described in the first part of this thesis can now be viewed against the background of their breeding habits.

It is clear from this study that the reproductive potential of the bivalves studied is extremely high, with a number of factors in their favour. The populations are comprised of an approximately equal proportion of males and females, ensuring that successful fertilization takes place. Breeding of two of the three species apparently takes place throughout the year, with no seasonal cessation of activity, and individuals of the two species almost certainly breed several times a year. Breeding starts at an early age, and continues for the duration of the life of an individual. Fecundity is high, and the littoral zone occupied by the mussels has an abundance and diversity of fish life (Mitchell, 1976) to serve as hosts for the larval parasites. Climatically, the warm temperatures favour rapid development and metamorphosis of the various stages (egg to larvae, for example), thus hastening the development

from one stage to the next and doubtless resulting in a continual flow of recruits to the adult ranks. Against this background it is hardly surprising that Kariba enjoys the high biomass of mussels that it does.

Secondly, the breeding biology can generally be considered to favour commercial exploitation, since the high reproductive potential and continuous breeding cycle suggests that a minimum of restrictions need be imposed .

While the general pattern of mussel reproduction in Kariba is now understood there are a number of fields which require further elucidation. There are the obvious gaps, in such aspects as fecundity of M.dubia and A.wahlbergi and the metamorphosis of glochidial larvae, but priority needs are those where further investigation will not only resolve questions only partly answered in this study, but also throw light on other aspects of their biology, or at least suggest useful lines of thought.

One of the areas where useful research can be done is the question of host/parasite specificity, or suitability, since this should help to explain distribution of the species, not only in a single body of water, but geographically as well. This subject is also becoming important in unravelling past fish distributions, inferred from the presence of mussels, or mussel remains, in sediments. (Jubb, pers.comm., and 1976; Appleton 1979) Obviously a sound knowledge of host/parasite relationships

can assist greatly in interpreting distribution patterns. The discovery at Lake McIlwaine that S. macrochir are more prone to infection than other fish species probably explains why M. dubia is common and widespread in Lake McIlwaine, where S. macrochir is a widespread and abundant species. Marshall (pers. comm.) has even suggested that M. dubia may have been introduced to this lake with the introduced S. macrochir. This species' habit of shoaling in extremely shallow water with T. rendalli, (Minshull, 1978) probably explains the presence of both C. mossambicensis and M. dubia in the shallows of Lake McIlwaine. The infection of cichlid species in Lake Kariba by the glochidia of C. mossambicensis undoubtedly explains this species wide-spread and common distribution pattern, and in particular its invariable presence around objects where small bream live and find protection against predators. Conversely, why are A. wahlbergi restricted in their distribution in both Lake Kariba and Lake McIlwaine, apparently favouring riverine environments? Could the host or hosts be riverine-type fish - Barbus species for example? While the species studied here might not be host specific, it is obvious that some fish species will be more suitable hosts than others, and these might be mainly responsible for distribution patterns. Thick scaled species might be more easily infected than thin-scaled ones, for example, or bottom dwellers more so than midwater species. Even if it was established that host specificity or suitability was not manifest, the finding would then usefully channel thoughts to other reasons for distribution patterns observed in rivers and lakes. A useful corollary would be the application of

such knowledge in the field of freshwater mussel culture, or for the purposes of introducing mussels to water bodies for one purpose or another. This latter aspect is receiving consideration in South Africa (Seaman, pers. comm.)

Another field of interest is the effect of temperature on development times of the various stages of larval growth. This again has implications in both management and academic spheres. In this study there were clear indications that metamorphic events speeded up at higher temperatures. This suggests that the rate of breeding, and hence chances of successful infection, could be very much higher in a warm climate than in a colder one, as the turnover of stages would be greater. Here again questions arise - could this be a contributory reason for the generally higher densities of Kariba when compared with McIlwaine? If C. mossambicensis and M. dubia females produce more broods per year at Kariba than McIlwaine, because of shorter interval between broods as a result of higher temperatures, the rate of infection should be very much higher as well. Lefevre and Curtis (1912) and Seshaiya (1969) provide examples of the speeding up effect of temperatures on development times of glochidial larvae on their hosts. This aspect would be particularly important in an impoundment where the fish species present were not entirely suitable as hosts and infection rate was low, or where breeding occurs over a few months only (A. wahlbergi), and it would be advantageous to produce as many broods as possible (if the species is a successive brooder). Conversely, cooler temperatures may also be important. It is well known that

marine bivalves can be induced to spawn by raising the temperature of the water by a few degrees (Loosanoff and Davis, 1963). By the same token, is it possible that a species could be induced to spawn by lowering the temperature of the water by a few degrees? The influx into Kariba of cooler river and rain water as a result of the seasonal rains might well be an inducement to spawn in the case of A. wahlbergi. If this were the case it could explain the association of A. wahlbergi with rivers and riverine areas. Whatever the case, the temperature environment is undoubtedly important in influencing the breeding pattern of individual species, and a better understanding of this would assist in the interpreting of general distributions, densities and composition on a geographical scale. Again an important corollary to the acquisition of such knowledge on the relationship of temperature to breeding would be its application to freshwater mussel culture endeavours, if and when these take place. Fuziwara (1978), for example, has shown that year round spawning of Corbicula leana can be induced if winter temperatures are maintained above 19°C.

Another field which warrants research is the immediate fate of larvae expelled from the parent. How long do they remain infective, and in what kind of environment are they most infective? Answers to such questions again have both management and academic interest and implication. Would the expelled larvae be more successful amongst plant life, where fish could brush against them, than in a barren environment where they would settle to the ground and possibly reduce their chances of contact? If this is the

case it might be a partial explanation why Lake McIlwaine has lower densities of mussels than Lake Kariba, which generally has an abundance of submerged plant life in comparison with the dearth in Lake McIlwaine. Would larvae be more infective on shallow barren substrates where they were subject to wave action and stirring up than deeper substrates and static water? How does temperature affect the larvae? Do they live longer and hence remain infective longer in colder water, where metabolic processes are slowed down? If so, this might partially offset the disadvantages of colder temperatures slowing down the metamorphic stages, as mentioned earlier.

It is obvious that this field is rich in research possibilities, a few of which have been mentioned here. Biological abstracts abound in summaries describing studies on obscure physiological and biochemical aspects of bivalves, while many basic and yet necessary fields of research, the elucidation of which will contribute greatly towards a better understanding of bivalve ecology, are largely ignored. The result is a rapidly accumulating pool of knowledge, much of dubious importance, and little of real value. Appleton (1979) has rightly pointed out that despite the considerable importance of bivalves in benthic communities where they frequently dominate in terms of biomass, virually nothing is known of the ecology of the African species.

SUMMARY

Caelatura mossambicensis

1. This species incubates glochidial larvae in all four demibranchs.
2. The smallest specimens found incubating larvae were 23,0 mm in Lake Kariba and 21,4 mm in Lake McIlwaine. This size range signals the onset of maturity.
3. There is no period of senility, as even the largest specimens brood eggs and larvae.
4. Breeding appears to take place all year in Lake Kariba, as mature larvae were found in the gills throughout the year. This appears to be the case in Lake McIlwaine
5. Females can produce successive broods of larvae at intervals of from three to five weeks. Several broods are probably produced per female per year.
6. The sex ratio in both lakes was approximately 1:1.
7. Observed fecundity at Kariba ranged from approximately 10 000 eggs for a specimen of less than 30 mm to 26 000 eggs for an individual of slightly over 45 mm
8. Positive and significant correlations were noted between length and fecundity, length and number of ovisacs possessed, and between fecundity and number of ovisacs possessed. Breeding capacity thus increased with an increase in size.
9. The inner gills almost always carry more ovisacs and hence eggs than the outer gills, and this is more marked in the younger mussels than the older mussels.

10. The eggs hatch into D-shaped larvae measuring 0,25 - 0,26 mm in length, 0,26 - 0,27 mm in height, and approximately 0,08 mm wide.
11. Encystment of the larvae was noted in several species of cichlids in Lake Kariba, although metamorphosis was not observed.

Aspatharia wahlbergi

1. This species incubates eggs and larvae in the two inner demibranchs only.
2. The smallest specimen found incubating larvae in Kariba measured 64,0 mm.
3. There is no period of senility and females breed for the duration of their lives.
4. Brooding takes place in Kariba in summer only, from September to March. No incubating females were recorded between April and July.
5. The sex ratio in Kariba was 1:1.
6. The larvae are smaller than those of M.dubia, which they resemble, being some 0,12 - 0,13 mm long. They are almost as wide and have two ciliated lobes anteriorly, and a hook or hooks ventro-posteriorly.
7. The larvae are parasitic on fish. Heavy infection of the host causes death, whereas fish more lightly infected survive.

Mutela dubia.

1. This species incubates eggs and larvae in the two inner

demibranchs only.

2. The smallest specimens found incubating eggs were 51,9 mm in Lake Kariba and 44,0 mm in Lake McIlwaine.
3. There is no period of senility, as even the largest specimens brood eggs and larvae.
4. Mature larvae were recorded in gills throughout the year in Lake Kariba and hence breeding appears to take place all year. Breeding appeared to cease at McIlwaine in winter only.
5. Females in Kariba can produce successive broods of larvae at intervals of 18 - 32 days. The length of the interval appears to depend on the season, being shorter in summer and longer in winter. Several broods are probably produced per female per year.
6. The sex ratio in Lake Kariba was approximately 1:1.
7. The larvae are approximately 0,3 mm in length, oval-shaped with two frontal ciliated lobes, a long tentacle many times the length of the larva, and with ventro-posterior hooks. The whole organism resembles a terrapin from the side and top view.
8. The larva attaches itself to a fish and develops into an haustorial larva, comprised of two haustoria or roots which grow into the host's tissues, and an exterior stalk which develops a small mussel at its distal end. The whole organism can reach 5 mm in length.
9. This mussel develops adult organs and drops off the stalk after about three weeks development at a length of approximately 1,4 mm.
10. The larvae can infect a variety of fish species, and

are not host specific, although some fish species appear to be more suitable as hosts than others.

11. The developmental history was similar to that described by Fryer for M. bourquignati.

PART THREE

STANDING CROP AND PRODUCTION

INTRODUCTION

This section incorporates the studies on linear dimensions and length - mass relationships, determinations on gross biochemical composition and energy content, and computations on age and growth. These various results have then been utilized in combination with population parameter studies (PART ONE), and reproduction studies (PART TWO), to determine the age composition of the stock, age at maturity, standing crops in terms of tissue and energy values, and production rates in terms of tissue and energy values in the Sanyati East cleared area.

A. LINEAR DIMENSIONS AND LENGTH - MASS RELATIONSHIPS

MATERIALS AND METHODS

Such statistical relationships are important in allowing estimates of one value to be predicted from given values of another character and are essential background data in population dynamic studies. They may also serve a more practical function from a commercial point of view (see Haynes, 1966; Haynes and McMullen, 1970), or be of value to taxonomists seeking to compare dimensions of material from different systems or different areas in the same system (Cvancara, 1963; Ortmann, 1920; Heard and Vail, 1976; Appleton,

1979). The dimensions of a fragment may also be utilized to determine other dimensions of the former whole animal.

The following relationships were determined:

- a.) total length against height and width,
- b.) width against height, and
- c.) total length against total wet mass, wet viscera mass, dry viscera mass and shell mass.

Descriptions of the dimensions used are :

Total length : The maximum antero-posterior dimensions of the shell.

Height : The maximum dorso-ventral dimension of the shell measured at right angles to the length.

Width : The maximum transverse dimension of the shell with both valves in the normal closed position.

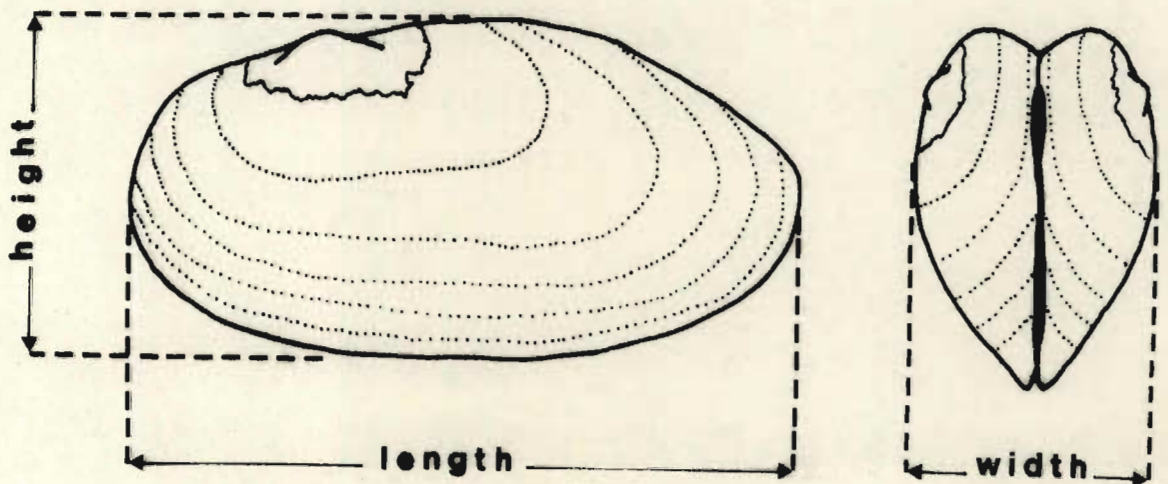


Figure 61: Diagrammatic representation of a mussel showing height, length, and width dimensions

Total wet mass : Surface water removed, and the total shelled mussel weighed.

Wet viscera mass: Total body mass removed from the shell, placed briefly between two absorbent pieces of tissue paper to remove surface water, and then weighed.

Dry viscera mass: The shell free total body mass oven dried to constant mass at 100°C. Some workers prefer lower drying temperatures (60°C - 70°C) as volatiles are less likely to be driven off. However Winberg (1971) states that mass obtained at higher temperatures (100°C - 105°C) differs little from that obtained at lower temperatures. The higher temperature was preferred in this study because the viscera of the very large mussels took very much longer to dry at 70°C than at 100°C.

Shell mass : Shells air dried for one to two hours to allow surface water to dissipate, and then weighed.

Linear measurements were made to one decimal place using vernier calipers, while mass was determined in grams on a dialogram scale to two decimal places. Mussels under 10 mm in length were weighed on an electronic balance to four decimal places.

For the linear relationships, regression equations were calculated using the methods of least squares, and product - moment correlation co-efficients were calculated for each relationship. In the curvilinear length - mass relationships the data were transformed to logarithms and log - length plotted against log - mass.

Regression lines were fitted according to the equation :

$$\log y = \log a + b \log x$$

which gives $y = ax^b$ as the non linear equation, where b defines the gradient and a the point at which the regression line crosses the y axis. Correlation co-efficients were then determined using the log values instead of the original x and y data.

RESULTS

1. Viscera, Shell And Water Proportions

The percentage composition of the three species in terms of viscera, shell and loose water mass is shown in Table 12. The variation in sample numbers resulted from the difficulty in obtaining some size classes.

In general, the flesh (viscera) mass of the whole animal comprised approximately one third of the total mass, 28,8% - 34,9% , for all size classes. In two of the species, (C. mossambicensis and A. wahlbergi), the shell mass proportion was greater than the viscera mass proportion, comprising approximately 40% of the total mass. Only in M. dubia with a thinner, lighter shell, did the shell mass proportion consistently comprise less in all size classes than the flesh mass proportion. In two species, (A. wahlbergi and M. dubia), shell mass proportions were fairly consistent for all size ranges.

Table 12: The viscera, shell and loose-water composition of C.mossambicensis, A.wahlbergi and M. dubia from Lake Kariba

SPECIES	SIZE CLASS	NO	% VISCERA ± S.E.	% SHELL ± S.E.	% LOOSE WATER
<u>C.m.</u>	10 - 19	7	28,9	21,0	50,1
	20 - 29	10	34,9	23,0	42,1
	30 - 39	10	36,7	31,1	32,2
	40 - 49	10	39,0	31,4	29,6
	50 - 55	10	40,2	36,0	23,8
MEAN	10 - 55	47	28,8 ± 1,0	36,4 ± 0,74	34,9 ± 1,6
	30 - 55	30	33,1 ± 0,76	38,9 ± 0,57	28,0 ± 1,2
<u>A.w.</u>	50 - 69	3	35,7	39,0	25,3
	70 - 79	10	33,6	40,5	26,0
	80 - 89	10	34,4	41,2	24,4
	90 - 99	10	36,1	39,9	24,0
MEAN	50 - 99	33	34,9 ± 0,64	40,4 ± 0,50	24,7 ± 0,78
<u>M.d.</u>	55 - 69	6	37,9	27,5	34,7
	70 - 79	10	32,9	31,3	36,0
	80 - 89	10	32,1	31,9	36,1
	90 - 99	10	34,5	33,0	32,5
	100 - 105	5	38,1	31,7	30,2
MEAN	55 - 105	41	34,4 ± 0,59	31,3 ± 0,38	34,3 ± 0,57

However, in C. mossambicensis the proportion increased from 28,9% - 40,2% from the smallest size class to the largest. Viscera mass proportion also increased from 21,0% - 36,0% whereas in A. wahlbergi the proportion of viscera mass was fairly consistent for all size classes. In M. dubia, viscera mass appeared to increase with increasing size. The loose water component was lowest in A. wahlbergi (24,7%) and highest in C. mossambicensis and M. dubia (34,9% and 34,3% respectively).

In very general terms, the total mass of the mussel removed from the water is comprised of one third flesh, one third shell, and one third loose water.

2. Linear Relationships

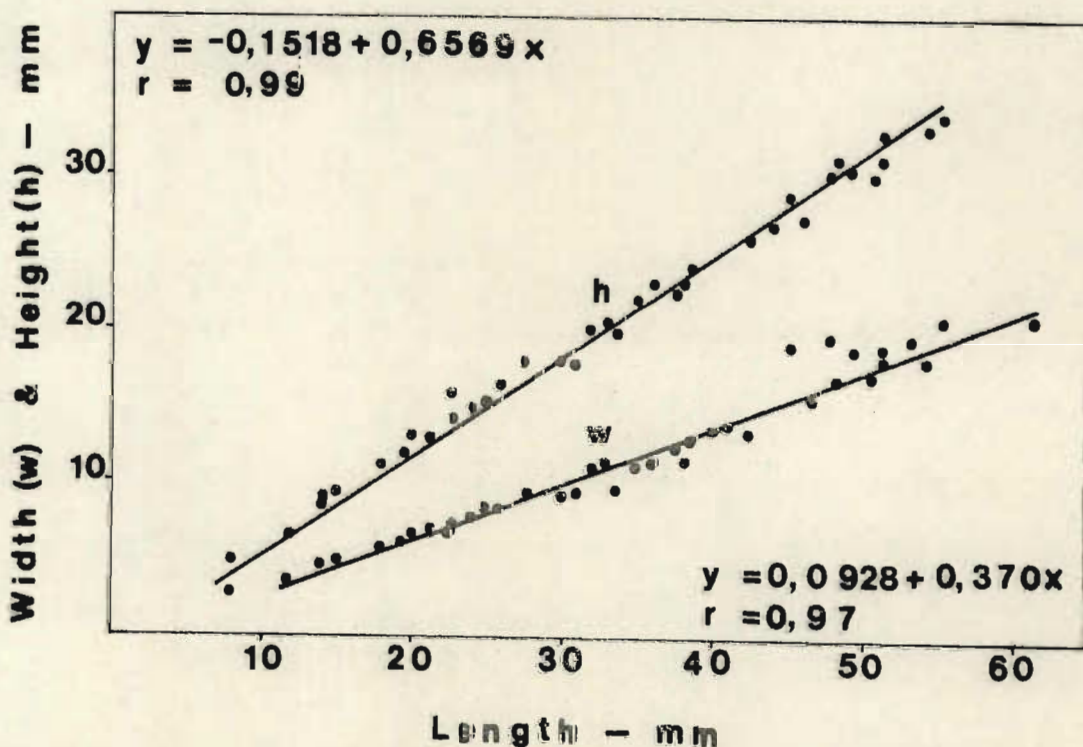


Figure 62 : Length - height and length - width relationships of C. mossambicensis

Relationships for the various linear dimensions are shown in Figs. 62, 63, 64, and 65. The regression equations and correlation co-efficients are included on the graphs, and are applicable to the relationship as a whole from the smallest to the largest of the mussels examined.

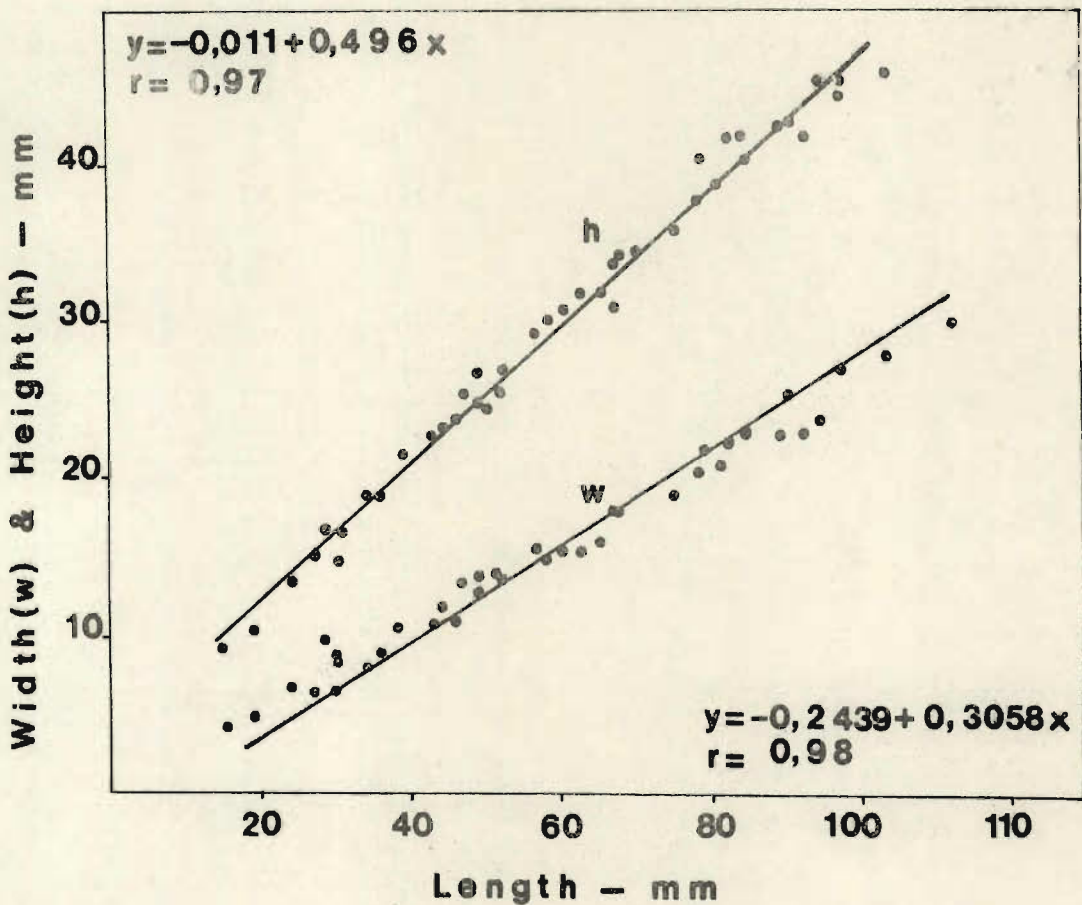


Figure 63: Length - height and length - width relationships of A. wahlbergi

The regression lines fitted allow a visual assessment of the closeness of fit of the line, and indicate whether or not there is some deviation from the relationship as described by the equation.

In all cases, clear relationships were found, as shown by the significantly high correlation co-efficients,

showing that growth in one direction is proportional to growth in another direction, and the relationship holds true throughout the life of the individual.

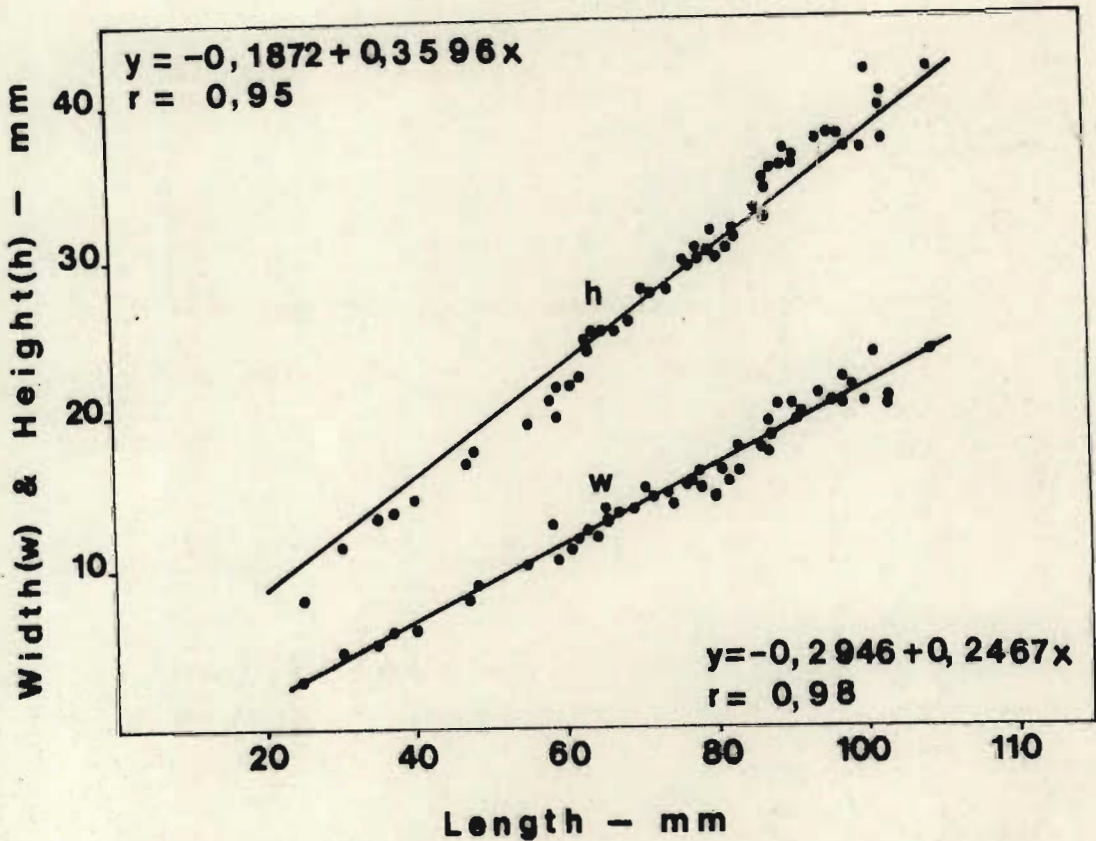


Figure 64: Length - height and length - width relationships of M. dubia

There are obviously slight differences in some relationships at various stages of the lives of individuals, evident in the regression of length against height for M. dubia, for example, where the points lie below the line up to a length of 60 mm. Since the regressions were intended to provide data representing the population spectrum as a whole, no separations according to sex or area were attempted, which doubtless accounts for the fairly broad scatter obtained for most of the relationships.

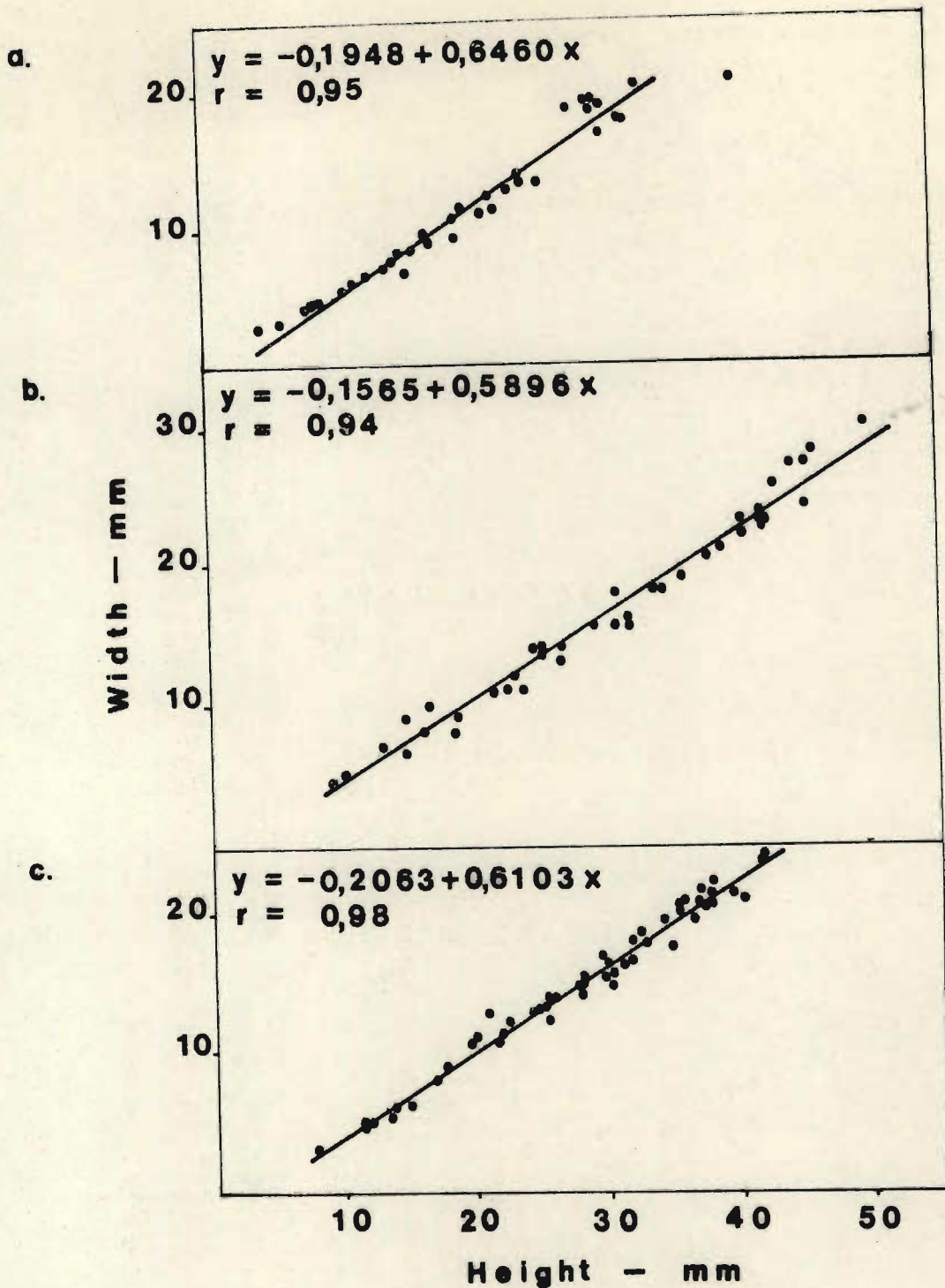


Figure 65 : Height - width relationships of *C. mossambicensis* (a) *A. wahlbergi* (b) and *M. dubia* (c)

Apart from individual variation, it is also known that shape can vary according to environment (Pennak, 1953; Sutcliffe and Durant, 1977; Appleton, 1979), and also according to sex (Heard, 1975). Different environments in

Lake Kariba would be represented by estuarine and open shoreline, for example, while sexual differences might well occur, as they have been shown to occur in Anodonta species in North America (Heard, 1975). Sexual differences in size could only be shown by statistical testing, using the t test for correlated mean sizes (Snedecor, 1956) as used by Heard, who based size on the index width / total length x 100.

3. Length - Mass Relationships

The relationships of length - mass (total, wet tissue, dry tissue and shell) are shown in Figs. 66, 67, 68 and 69.

Only in C. mossambicensis did the scatter depart sufficiently from a straight line to warrant calculating more than one regression equation for a single relationship. Thus for length - total mass three regression equations were derived; two for length - dry tissue mass, although one could have sufficed with loss of a small degree of accuracy in calculations. Two equations were derived for length - shell mass. The other two species exhibited a sufficiently consistent relationship throughout the length range to calculate only one equation for each relationship. In order to simplify the calculations, which involved log values, length values were computed in centimetres rather than millimetres. Log mass values are plotted against log millimetre values in the graphs to maintain consistency of presentation.

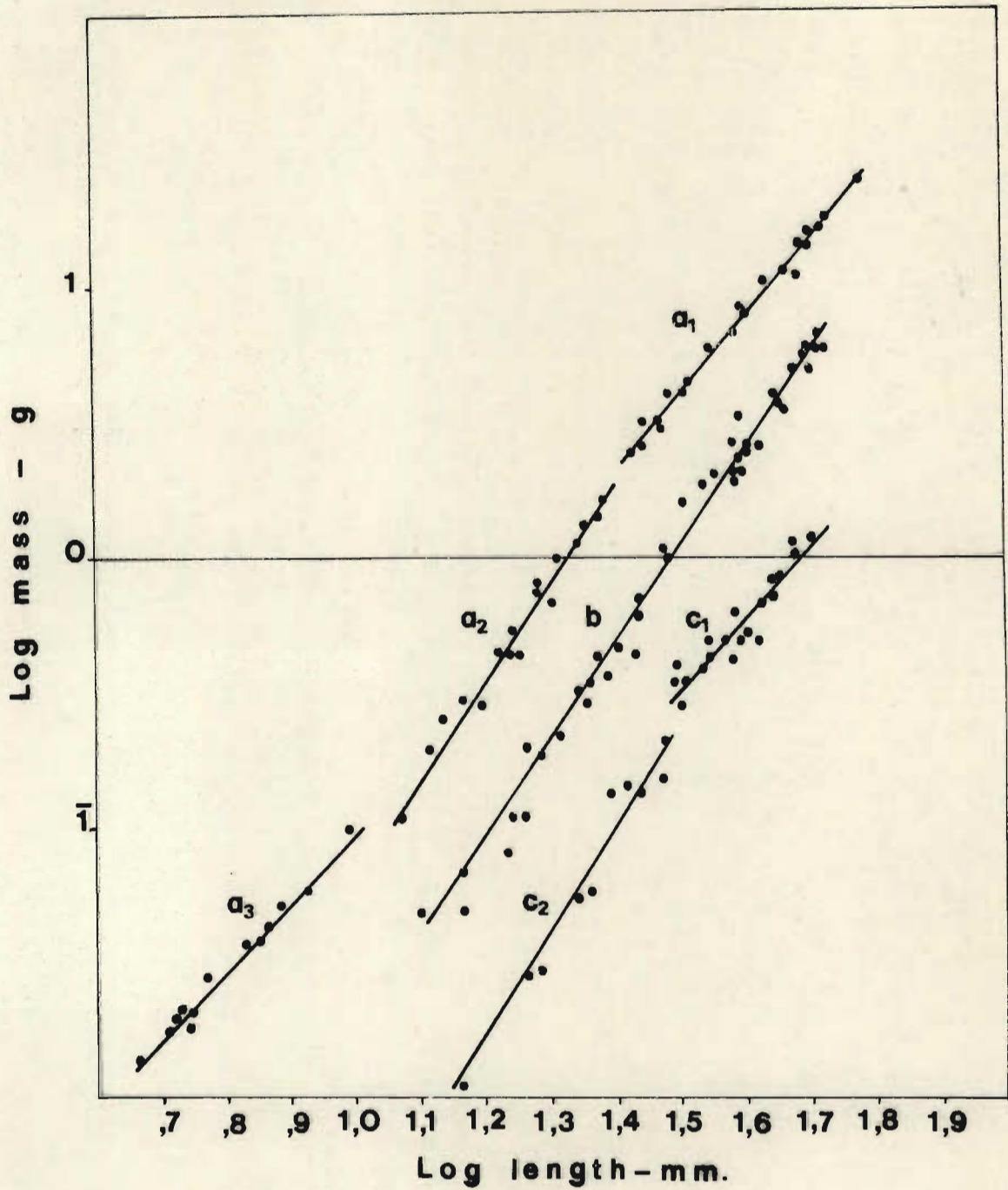


Figure 66: Length - mass relationships of *C. mossambicensis* : total mass (a), viscera mass (b), dry mass (c)

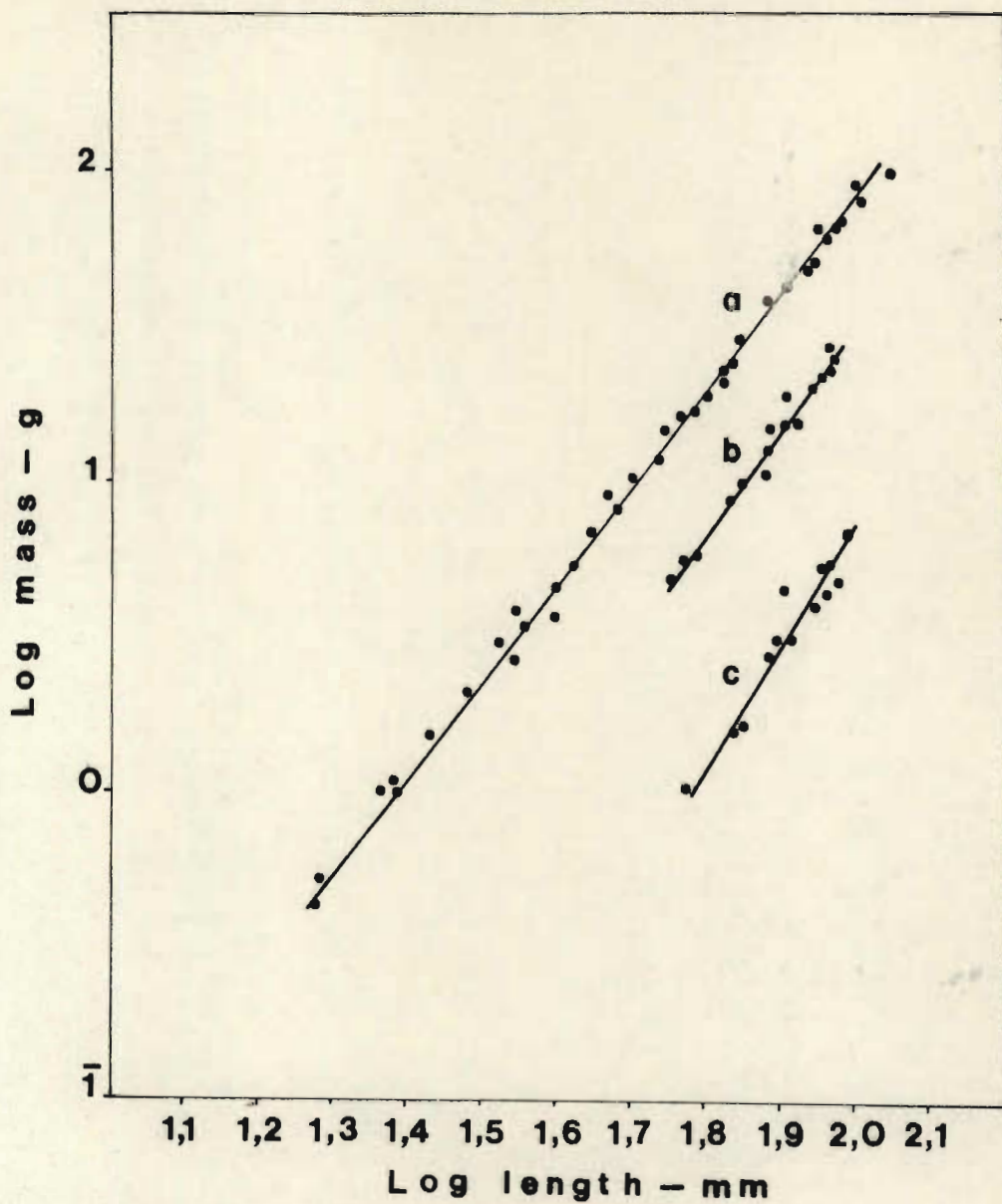


Figure 67: Length - mass relationships of A. wahlbergi : total mass (a) viscera mass (b) dry mass (c)

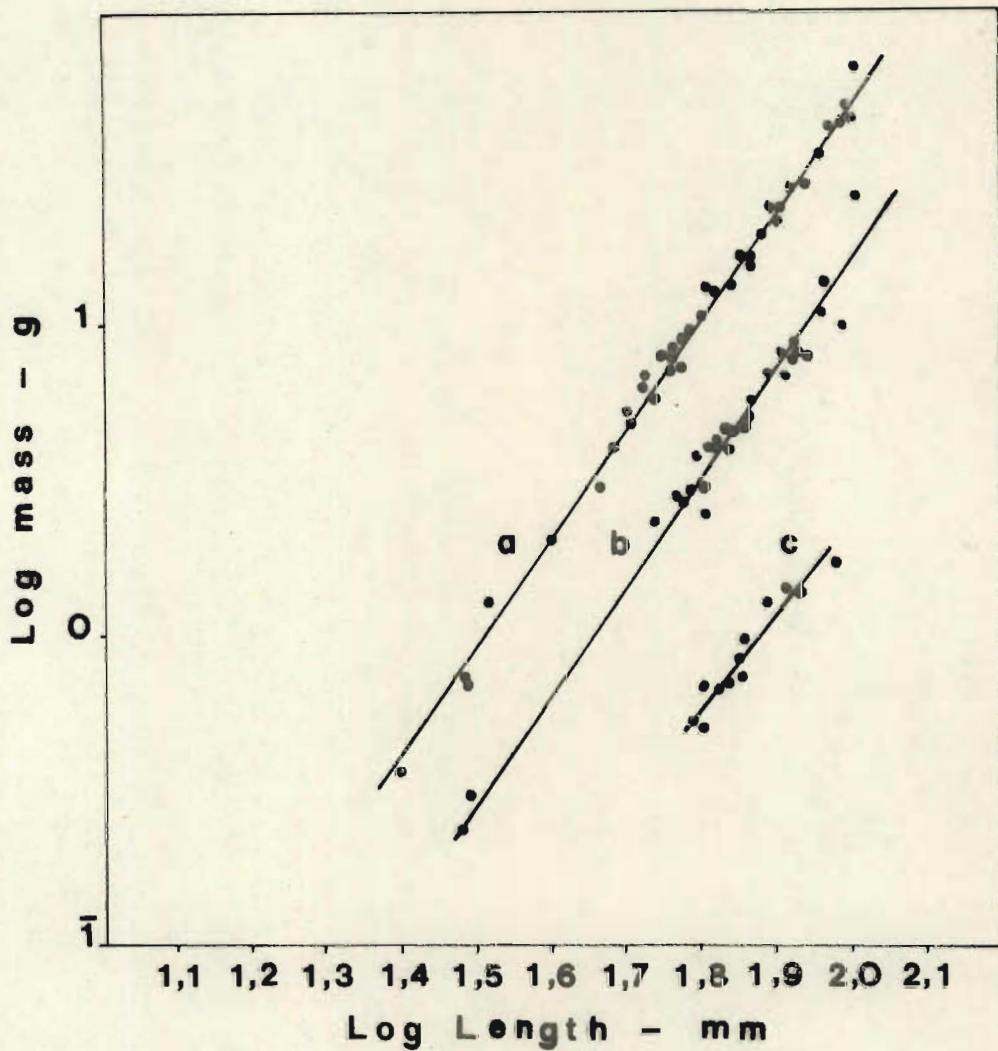


Figure 68: Length - mass relationships of M. dubia: total mass (a), viscera mass (b) and dry mass (c)

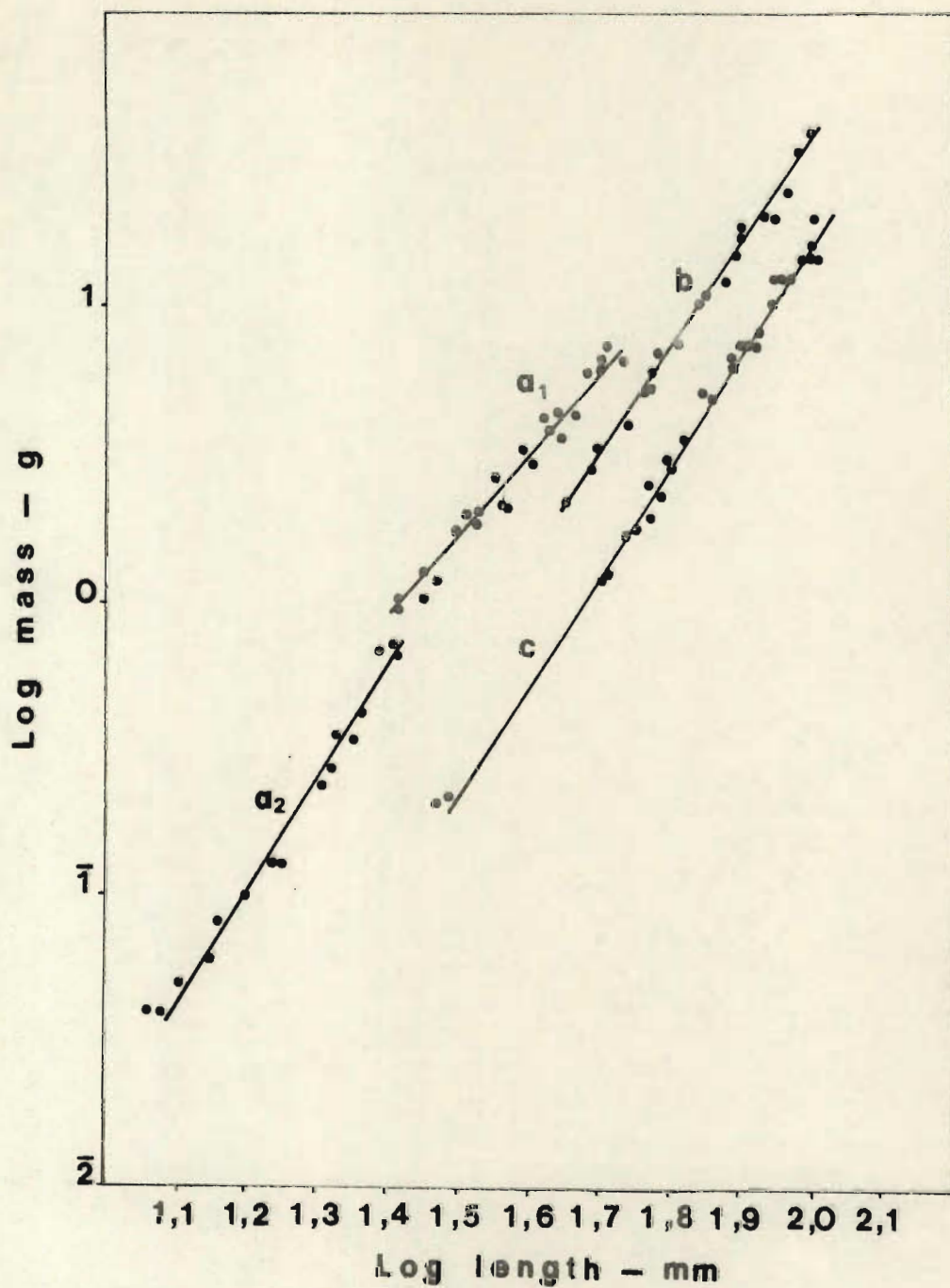


Figure 69: Length - mass relationships (shell):
C. mossambicensis (a), A. wahlbergi
 (b), M. dubia (c)

The regression equations and correlation coefficients for each relationship for each species are given below:

a.) Caelatura mossambicensis (Fig.66 and Fig. 69).

Total mass :	(a ₁)	$\log y = -0,8334 + 2,8352 \log x; r = 0,987$
	(a ₂)	$\log y = -1,2200 + 3,6102 \log x; r = 0,991$
	(a ₃)	$\log y = -3,5483 + 2,5088 \log x; r = 0,991$
Wet tissue mass :	(b)	$\log y = -1,7645 + 3,5750 \log x; r = 0,995$
Dry tissue mass :	(c ₁)	$\log y = -1,8158 + 2,6293 \log x; r = 0,980$
	(c ₂)	$\log y = -2,5145 + 3,7872 \log x; r = 0,983$
Dry shell mass :	(a ₁)	$\log y = -1,1242 + 2,6861 \log x; r = 0,970$
	(a ₂)	$\log y = -1,7899 + 3,9503 \log x; r = 0,987$

b.) Aspatharia wahlberqi (Fig. 67 and Fig. 69)

Total mass :	(a)	$\log y = -1,2086 + 3,1256 \log x; r = 0,998$
Wet tissue mass :	(b)	$\log y = -1,7742 + 3,2508 \log x; r = 0,983$
Dry tissue mass :	(c)	$\log y = -3,0474 + 3,9032 \log x; r = 0,971$
Dry shell mass :	(b)	$\log y = -1,9951 + 3,5601 \log x; r = 0,995$

c.) Mutela dubia (Fig. 68 and Fig. 69)

Total mass	(a)	$\log y = -1,7602 + 3,4613 \log x; r = 0,996$
Wet tissue mass :	(b)	$\log y = -2,205 + 3,4099 \log x; r = 0,975$
Dry tissue mass :	(c)	$\log y = -2,4709 + 2,8219 \log x; r = 0,964$
Dry shell mass :	(c)	$\log y = -2,5185 + 3,7263 \log x; r = 0,994$

It is interesting to note that the above length -

mass equations could not be used indiscriminately to determine mass from known length for Lake McIlwaine mussels. The latter are considerably heavier, length for length, than their counterparts in Lake Kariba. An easy means of comparing length - mass relationships of mussels from different sources, without having to construct further graphs, is to fit the equation:

$$y = K x^3$$

to the data and compare results. (Where y = mass, x = length, and K = co-efficient characteristic of each population.) The value of K is determined for each population by measuring and weighing about 10 individuals and calculating the mean y/x^3 . The higher the value, the heavier the individuals in that particular sample in relation to the other sample.

Thus for 10 C. mossambicensis from Lake McIlwaine and 10 from Lake Kariba, (between 11,5 mm and 30,0 mm), K values of $0,1353 \pm 0,002$ and $0,0934 \pm 0,005$ were obtained, indicating the Lake McIlwaine mussels are considerably heavier than the Lake Kariba mussels. Similarly, two samples of 10 M. dubia each, between 61 mm and 69 mm, gave K values of $0,0502 \pm 0,0010$ and $0,0429 \pm 0,0012$ for Lake McIlwaine and Lake Kariba respectively, while another two samples of 10 A. wahlbergi each, between 74 mm and 87 mm, gave K values of $0,0590 \pm 0,0017$ and $0,0448 \pm 0,0017$ for Lake McIlwaine and Lake Kariba respectively.

B. BIOCHEMICAL COMPOSITION AND CALORIFIC VALUES

In this study the aim was to establish a basic background knowledge of the biochemical make-up of mussels with regard to water, fat, protein and ash content, and also calorific content. In addition, with a view to their possible importance as a food source for either humans or livestock, the amino acid composition of the protein content was determined, while the ash content of one species was analysed. It is stressed here that these determinations were intended only to provide a broad indication of their gross biochemical composition, and hence general nutritional value as a food source. Ansell (1974), and recently workers in Rhodesia, (Caulton, 1976; Cochrane, 1978) have shown that considerable seasonal variation in various biochemical components occurs (e.g. lipids, protein) amongst both bivalves and fish, and it is obvious that true mean values can only be obtained by analysis on a monthly basis over an entire year. The samples for analysis were collected from Lake Kariba in October 1978, a period of low productivity when both protein and lipid values in sardines (Limnothrissa miodon) are at their lowest (Cochrane, 1978) and growth in mussels has slowed down (pers. obs.). Obviously this factor should be taken into account when considering these results.

MATERIALS AND METHODS

Ten to twenty mussels of each species were collected from the Sanyati East cleared area in October 1978, the shells removed and the flesh mass of each mussel

weighed, oven dried and then reweighed to determine water loss and dry tissue mass. The dry tissue of each species was then crushed and homogenized in a pestle and mortar to a fine powder, and sub-samples of this used for the calorific and biochemical analyses. In addition, samples of C. mossambicensis of different size groups were collected (10 in each sample) and wet and dry viscera mass of each group determined collectively, to determine if group differences in water content existed. Methods used for each analysis are outlined below.

1. Water Content

This was calculated from the difference between wet and dry mass, expressed as a percentage of the total wet mass. The method of obtaining dry mass has already been described.

2. Fat Content

A soxhlet continuous extraction apparatus was used to determine fat content. Four sub-samples of each species of approximately 2 g, weighed to four decimal places, were subjected to hexane extraction for four to five hours. The fat content in the extraction flask was then weighed, once the solvent had been driven off by heating over low heat in an oven at 60°C, and the fat content expressed as a percentage of wet and dry mass. The resultant figures give reasonably accurate but nevertheless approximate estimation of the true fat content, as different solvents are known to

give slightly different results, particularly where low fat values exist (Brown, 1957).

3. Ash Content

The de-fatted samples of each species were weighed to four decimal places and ashed in a muffle furnace at 450°C- 550°C. The resulting ash was weighed and the percentage ash content of each sample determined.

Some additional values for M. dubia and A. wahlbergi were obtained by weighing the ash remaining in the crucible after combusting samples in a bomb calorimeter and calculating this as a percentage of the original sample before combustion. Ash values obtained in this way are usually underestimates as the high temperatures of burning decompose some mineral salts, with a reduction in the mass of residue.

The ash residue remaining after A. wahlbergi had been combusted formed a high proportion of the total sample, and was welded or fused by the heat into slag-like pellets. These were collected and submitted to the Inorganic Section of the Chemistry Department of the University of Zimbabwe for analysis.

4. Protein Content

Laboratory facilities were on loan from the Ministry of Agriculture at a busy time, and hence values were

determined only for two species - C. mossambicensis and M. dubia - the main species of Lake Kariba and Lake McIlwaine.

Two methods were used. The first was the Kjeldahl method for crude protein analysis, which determines as ammonia the total nitrogen (except nitrate) content of the sample. The figure obtained is multiplied by 6,25 since the nitrogen content in various proteins varies between 13% and 19%, and the co-efficient 6,25 is related to a mean value of 16% ($\frac{100}{16}$). The protein thus determined is known as "crude" protein, because it is obviously an approximate estimation. Four sub-samples of each of the two species were analysed. Source of the method was "Official Methods of Analysis of the Association of Official Agricultural Chemists", 1960, 2.036.

The second method involved determining protein nitrogen by microkjeldahl and direct nesslerization technique (Johnson, 1941) and determining nitrogen content against a blank on a standardized spectrophotometer. The method is essentially for very small samples, and required the initial sample of 1 ml to contain 10 - 60 microgram N. Since the sample to be analysed was in solid powder form (0,5 g) this first had to be digested in concentrated H_2SO_4 to form a solution, and then diluted considerably to give 1 ml nitrogen content in the range of 10 - 60 micrograms N. The analysis then proceeded according to the method outlined. This method was used as a check on the Kjeldahl method, and a sample of C. mossambicensis was analysed to compare results.

5. Amino Acid Content

This was determined by the Department of Research and Specialist Services, using a Beckman Model 118 amino acid analyser.

6. Calorific Content

Calorific values in kJ g^{-1} ash free dry mass were determined at the University of Zimbabwe, using a Gallenkamp ballistic bomb calorimeter, calibrated with Benzoic acid. Five or six replicates of each sample were combusted. In addition to the samples of adult specimens of the three species from Lake Kariba, a sample of adult M. dubia from Lake McIlwaine, collected in May 1979 was combusted, and a sample of juvenile A. wahlbergi from Lake Kariba.

RESULTS

The results of water, fat, ash and protein analyses have been combined and are presented in Table 13 .

1. Water Content

The mean proportions of water in the three species were remarkably similar although the standard errors differed slightly. The water content of five different size groups of C. mossambicensis in the range 30 mm - 50 mm ranged from 79,3% - 81,8%, with a mean also of 80,7% (S.E. 0,56). The range recorded , 79% - 82%, accords with figures quoted by

Table 13: The gross biochemical composition of body tissue of the three species from Lake Kariba (\pm S.E.)

	DRY TISSUE			
	% Water	% Fat	% Ash	% Protein
<u>Caelatura mossambicensis</u>	80,7 \pm 0,72	5,7 \pm 0,35	11,7	47,0 \pm 0,90
<u>Aspatharia wahlbergi</u>	80,6 \pm 0,51	7,0 \pm 1,25	23,3	-
<u>Mutela dubia</u>	80,8 \pm 0,32	6,6 \pm 0,96	9,4	44,6 \pm 0,64

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Vinogradov (1953) who states that on average 75% - 85% water is present in the soft parts of mollusca, the largest amount occurring in bivalves. Ansell (1974) records values of 83% - 88% for marine mussels (Lima hians), while Griffiths (1905) quotes a figure of 81,1% for the European freshwater mussel, Anodonta. Water content is one component that can vary inversely in relation to tissue fat content (Caulton, 1976).

2. Fat Content

The fat content of dry mass of the three species ranged from 5,7% in C. mossambicensis to 7,0% in A. wahlbergi or from 1,14% - 1,4% of wet mass. These rather low fat values are not surprising if one considers that (i) the animals are essentially sedentary and do not require energy reserves for migrations, and (ii) are living in a year round favourable environment not subject to any great extremes and hence not requiring large food reserves to tide them over lean periods. Ansell (1974) recorded similar fat values (4,9% - 8,23%) and also showed that both sexual and seasonal differences in fat content existed, with females having more fat than males, and values reaching a peak prior to spawning. Fluctuating fat values are also common to fish, shown by Cochrane (1978) to occur in the sardine, L. miodon in Lake Kariba, and by Caulton (1976) in the cichlid, T. rendalli in Lake McIlwaine. Thus one could expect similar fluctuations amongst the bivalve population, with fat content probably rising at more productive times of the year. Determinations over a year involving equal proportions of males and females would be needed to

establish a true mean fat value for each species. Different solvents are known to give different results, particularly in animals of low fat value (Brown, 1957) and an even truer mean could be obtained using two or three different solvents for the determinations.

3. Ash Content

Ash values were determined as 9,7% to 23,3% of dry mass, being highest in A. wahlbergi. That 23,3% is not the upper limit for this species is shown by the ash value of 29,7% obtained after burning a sample in the bomb calorimeter - indicating that values could exceed 30%. The results here accord fairly closely with some figures given by Winberg (1971) for freshwater molluscs, 11,3% - 30,3%, in which two Unionids (Unio pictorum and Unio tumidus) had mean values of 12,8% and 15,8% respectively, with standard deviations of 5,9 and 4,8. The value of 11,7% given here for C. mossambicensis falls within this range. An ash value of 7,6% was obtained for M. dubia after burning in the bomb calorimeter - somewhat lower than the muffle furnace figure. Ansell (1974) gives values of 13% - 24% for L. hians, with indications of seasonal fluctuation, while Vinogradov (1953) gives values of 5% - 12% for various marine bivalves, and states that the amount of ash in mature Mollusca is about 8% - 10% on average. According to Winberg, (1971) the ash content of a species may vary considerably, apparently depending on its physiological state and ecological conditions. Results of the ash residue from the two samples of A. wahlbergi are presented in Table 14.

Table 14: The chemical composition of the mineral fraction of A. wahlbergi after combustion in a bomb calorimeter

COMPOUND	SAMPLE 1 (ex LAKE KARIBA)	SAMPLE 2 (ex LAKE MCILWAIN)
SiO ₂	0,57	1,33
Al ₂ O ₃	0,03	0,36
Fe ₂ O ₃	0,81	0,97
CaO	44,31	44,12
MgO	0,87	0,78
Na ₂ O	0,42	0,25
K ₂ O	0,24	0,18
P ₂ O ₅	40,43	39,40
MnO ₂	12,63	12,87
NiO	28ppm	32ppm
CuO	30ppm	14ppm
TOTAL	100,21	100,26

The metallic slag - like appearance of the ash residue is probably due in part to the manganese fraction, which accounts for a fairly high proportion of the total composition in both samples.

4. Protein Content

Crude protein values for C. mossambicensis and M. dubia determined by the Kjeldahl method gave values of 44,6% and 47% of dry mass respectively (8,9% and 9,4% of wet mass). Ansell (1974) obtained seasonal protein values for dry mass ranging from 47% - 69%, while according to Lee and Pepper (1956) figures for the protein content of molluscs such as oysters are 44% - 48%. Borgstrom (1961) gives figures for wet mass of 8,6% - 12,6% for Ostrea edulis (approximately 43% - 63% of dry mass, assuming 80% water), 8,9% - 11% for Mytilus edulis (approximately 45% - 59% of dry mass), and 11,3% - 19,4% for Mytilus munahuensis (approximately 56% - 97% of dry mass). Carteni and Aloj (1934), quoted in Borgstrom, analysed eight different molluscs and found a protein range of 8,4% - 14% (approximately 42% - 70% of dry mass). Heeg, (pers. comm.) considered the values obtained here rather low in comparison with results he obtained on snails. As a result a sample of C. mossambicensis was analysed as a check using the microkjeldahl and direct nesslerization technique, which gave a value of 49,1%, only 4,5% higher. While the values obtained in this study are low in comparison with the generally accepted mean value of \pm 65% protein for fish, they do fall within the range for other molluscs,

quoted above, although generally at the lower end of the scale.

A possible explanation for the low values obtained is a seasonal one. Cochrane (1978), determining the gross chemical composition of sardines in Lake Kariba, on a monthly basis, showed that an 18% difference existed between the highest value of protein in March 1977, and the second lowest value in October 1976. Similarly, his lowest lipid value was recorded in October 1976, some 66% lower than the highest value recorded. The months preceding the rains are unproductive months when the sardine population in Lake Kariba is subject to a crash as a result of a plankton food shortage, and animals whose lives are inter-related with the plankton/detritus cycle could be similarly affected. The growth studies on Lake Kariba mussels show clearly that growth either slowed down or stopped completely from September to December, when food reserves were probably at an annual low. Thus there are good reasons for suspecting that protein values in mussels in October would be extremely low in comparison with more productive months of the year.

5. Amino Acid Content

Amino acids of the three species were determined as $g\ 16gN^{-1}$ and also as a percentage of the sample mass.

These results are presented in Table 15, and the percentages graphed in Fig. 70.

Table 15: Amino acid content of C. mossambicensis
A. wahlbergi and M. dubia

AMINO ACID	g 16gN ⁻¹			% of sample mass		
	C.m.	A.w.	M.d.	C.m.	A.w.	M.m.
LYSINE (Ly)	7,3	7,4	6,7	2,68	1,85	2,89
HISTIDINE (H)	1,7	2,1	1,5	0,64	0,54	0,68
AMMONIA (Am)	1,6	1,6	1,4	0,58	0,38	0,60
ARGININE (Ar)	6,2	6,8	6,4	2,26	1,72	2,76
ASPARTIC ACID (AA)	11,0	10,1	11,0	4,03	2,56	4,77
THREONINE (Th)	4,6	4,8	4,6	1,65	1,22	2,01
SERINE (S)	4,9	4,3	4,4	1,78	1,09	1,87
GLUTAMIC ACID (GA)	20,7	18,6	20,9	7,57	4,70	9,07
PROLINE (P)	3,9	4,2	3,6	1,44	1,05	1,57
GLYCINE (G)	6,3	6,4	6,6	2,32	1,62	2,88
ALANINE (Al)	4,9	6,0	5,7	1,81	1,51	2,50
CYSTINE (C)	+	+	+	+	+	+
VALINE (V)	5,0	5,4	4,9	1,82	1,36	2,16
METHIONINE (M)	1,4	2,0	1,9	0,52	0,50	0,81
ISOLEUCINE (I)	4,3	4,1	4,2	1,58	1,04	1,77
LEUCINE (L)	9,8	9,2	9,8	3,57	2,31	4,26
TYROSINE (T)	2,7	3,1	2,8	1,00	0,78	1,21
PHENYLALANINE (P)	3,7	4,1	3,8	1,36	1,01	1,64

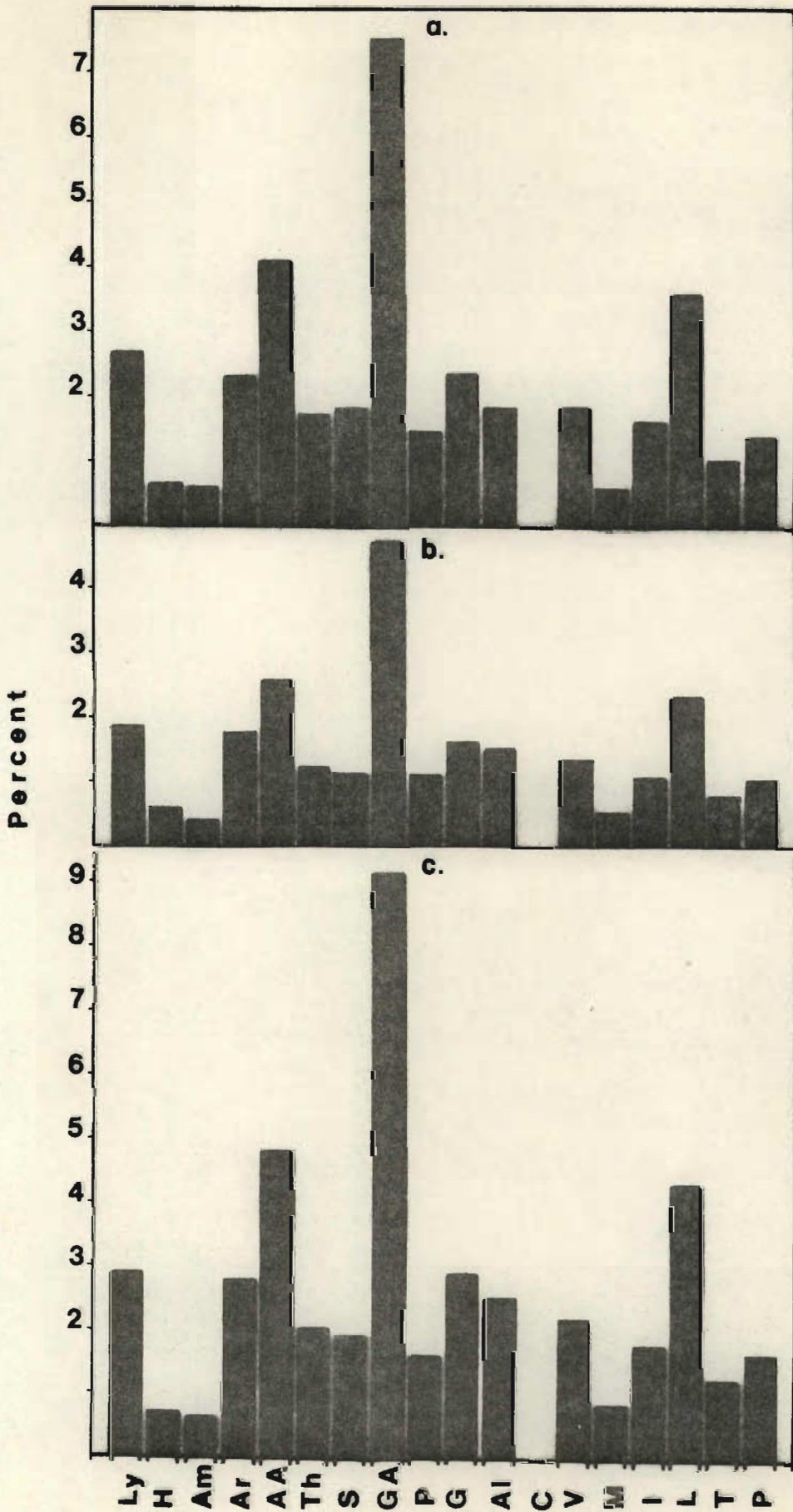


Figure 70: Percentage proportions of the amino acids of *C. mossambicensis* (a), *A. wahlbergi* (b) and *M. dubia* (c). See Table 15 for key

The results show the relative proportions of the 18 amino acids recorded and the basic similarity in structure, with glutamic acid, aspartic acid, leucine and lysine forming the four most important amino acids in all three species. Glycine and arginine come next in that order of importance in C. mossambicensis and M. dubia, and in reverse order in A. wahlbergi. Thus the three species share the same top six amino acids, and similarly they share the same bottom five - cystine, ammonia, methionine, histidine and tryosine - in similar but not in exactly the same order of importance. The remaining middle order seven amino acids are thus also shared, and in approximately the same order of importance with alanine, valine, threonine and serine forming the most important in this group, and isoleucine, proline and phenylalanine the lower three.

The analysis shows that of the 24 known naturally occurring amino acids, 18 occur in the three species, while of the 10 known essential amino acids (i.e. those incapable of being synthesized by the body, and hence being required in the human diet), nine were found in the mussels - these being arginine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, threonine and valine. The tenth essential amino acid is tryptophan - not recorded in the Lake Kariba mussels. From a nutritional point of view, therefore, the Lake Kariba mussels rate highly, and could be considered for use as a supplementary feed to certain domestic animals, and as a supplementary fish feed. Arginine, histidine, isoleucine, lysine, methionine, phenylalanine, threonine, tryptophan and valine are essential amino acid requirements

for the growth of chinook salmon (Mertz, 1972) and also for rainbow trout (Shanks, Gahimer and Halver, 1962), quoted in Halver (1972), and all of these, with the exception of tryptophan, occur in the mussels. Pigs and poultry, unlike ruminants, are unable to synthesize certain amino acids, and require these to be added to their diet. With the exception of tryptophan, dried mussel flesh would meet their requirements in this respect.

6. Calorific Content

Results of the bomb calorimetry are summarized in Table 16 .

The mean value of the 16 replicates of the adult Lake Kariba samples was $23,442 \pm 0,700 \text{ kJ g}^{-1}$, and for all 21 adult replicates including the Lake McIlwaine sample $23,525 \pm 0,544 \text{ kJ g}^{-1}$. Mean of all 27 replicates including the juvenile sample was $23,023 \pm 0,460 \text{ kJ g}^{-1}$.

According to Winberg (1971), quoting various authors, the calorific value of organic matter for most aquatic organisms approximates to $23,442 - 24,279 \text{ kJ g}^{-1}$ dry mass, with deviations from this caused by variation in the chemical composition of the organic material and to some extent by changes in the ecological conditions and physiological state of organisms. He suggests that the calorific value of various aquatic organisms lies within the limits of $23,400 \pm 3$ standard deviations, that is between 19,800 and 26,874 kJ g^{-1} , with a most probable value of $23,442 \text{ kJ g}^{-1}$.

Table 16: Calorific content of C. mossambicensis, A. wahlbergi and M. dubia (+ S.E.)

SPECIES	NO. REPLICATES	kJ g ⁻¹ (ash free)
<u>Caelatura mossambicensis</u>	5	24,697 ± 1,465
<u>Aspatharia wahlbergi</u> (adult)	6	21,349 ± 0,251
(juvenile)	6	20,930 ± 0,544
<u>Mutela dubia</u> (Kariba)	5	24,697 ± 1,088
(McIlwaine)	5	23,442 ± 0,293

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Slobodkin and Richman (1961) say that the majority of animals have a calorific content between 20,930 and 25,116 kJ g⁻¹. Cummins and Wuycheck (1971) give a mean value for aquatic molluscs of 22,981 kJ g⁻¹, and a grand mean for all aquatic invertebrates of 22,897 kJ g⁻¹. Winberg also maintains that any values below 20,930 kJ g⁻¹ organic matter should be treated as suspect, since very few organisms have such low values.

Ansell (1974) obtained a mean calorific content value of 4,2 for a whole years analysis by calculating calorific values in kcal g⁻¹ from the chemical composition of the mussels, and not direct calorimetry. The formula for this method (Winberg, 1971) is :

$$\frac{5,65 P + 4,10 C + 9,45 F}{100} \text{ kcal g}^{-1}$$

100

where P, C and F represent the percentage content of protein, carbohydrate and fat respectively. If applied to the Lake Kariba mussel according to their respective gross biochemical composition, values of 19,674 and 20,093 kJ g⁻¹ are obtained for C. mossambicensis and M. dubia respectively. According to Winberg, these values are suspect as they fall below 20,930 kJ g⁻¹. Ansell's extremely low value of 17,581 kJ g⁻¹ indicates this method may not be sufficiently accurate for bivalves. Obviously all the errors attendant in determining the various biochemical fractions are incorporated in the workings of the formula, and the

method at best can only provide a very rough estimation. Similarly, the method of obtaining calorific value according to the equation:

$$y = 0,0559 x$$

(Winberg, 1971), where y is the calorific value in kcal g^{-1} dry mass and x is the percentage organic matter present in the sample, could give suspect results.

If this formula is applied to A. wahlbergi with a high ash content, for example, (using 29% ash content for the calculation) a value of $16,618 \text{ kJ g}^{-1}$ dry mass is obtained.

Since the mean value of $23,442 \text{ kJ g}^{-1}$ dry mass obtained in this study for all three species agrees with the mean of many different organisms, and was determined using the most reliable method, i.e. by direct calorimetry, it was decided to use this figure in production calculations, which follow later. Winberg (1971) states that variations in calorific value due to differences in chemical composition need to be taken into account by hydrobiologists and the fact that many different kinds of organisms have an energy content of approximately $23,442 \text{ kJ g}^{-1}$ makes this a useful figure to use in calculations.

C. AGE AND GROWTH

One of the more important aspects in population dynamics is the construction of composite average growth curves for each species, enabling the standing crop and breeding sections to be given an age identity, and to serve as the basis for production calculations. In constructing these curves, regardless of the method, it is important to disregard the growth of extreme elements in the population, which may be either fast or slow, male or female, and concentrate on the average population growth from which representative estimates of production, or other parameters, can be made.

MATERIALS AND METHODS

Age of mussels can be determined by length frequency studies, growth cessation lines, or by release recovery methods (Haskin, 1954; Negus, 1966). Length frequency methods could not be applied in this study as essentially this requires several years of study to obtain reliable results, and secondly, the continuous breeding of two of the species (C. mossambicensis and M. dubia) made year classes indistinguishable. Laurent (1971) made a similar observation on the gaper clam Tresus nuttalli in North America.

While all three species showed growth cessation lines, these were not easily interpretable in two species, (C. mossambicensis and M. dubia), possibly again related to

their lack of a clear spawning season, and it was decided not to rely on this method, although it was used as a check method for A. wahlbergi. This method has more validity in Northern climes, where clear - cut winter / spring marks facilitate its use (van der Schalie, 1963; Negus, 1966; Haynes and Hitz, 1971; Heard, 1965 & 1975; Wendell et al , 1976).

Growth and the subsequent establishment of age were determined by measuring and releasing mussels of varying sizes, periodically recovering these for measuring, and then returning them to the lake until they were measured again. Mussels to be released were placed within circular wire mesh cages planted on the lake floor.

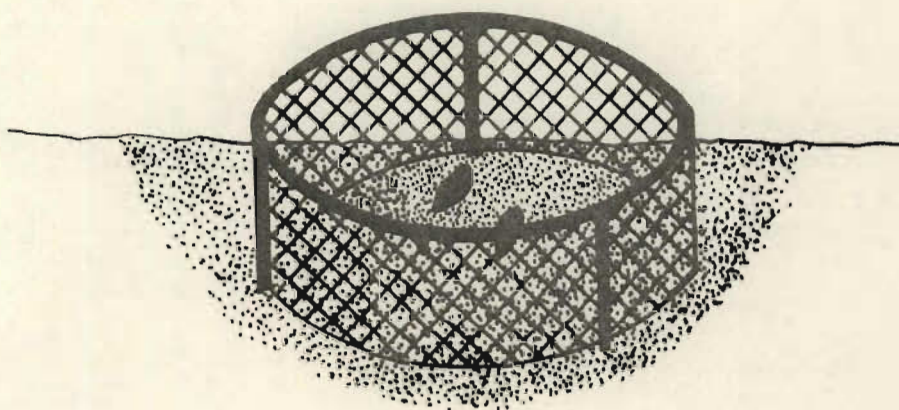


Figure 71 : Showing a wire mesh cage used for the release - recovery growth study

In the case of the smaller mussels, they were placed in removable containers which made their recovery much easier.

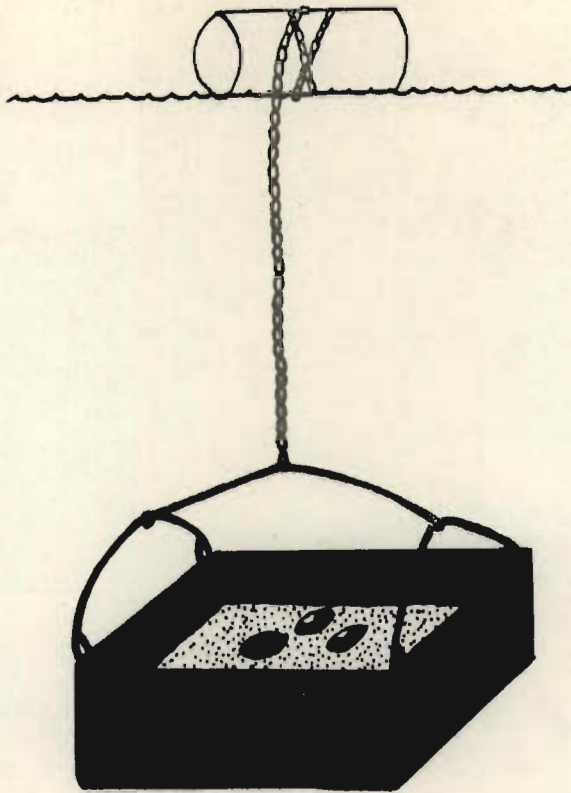


Figure 72 : Showing the mussel container used for smaller mussels in the release-recovery growth study

The smaller mussels were more liable to disappear due to predation and hence were measured at shorter intervals of time than the larger mussels. The interval between measurements varied because of other commitments, but was usually from one to three months. Several mussels did disappear after a few weeks or months, and were replaced, where possible, by mussels of similar length.

The growth data thus collected for each species were combined to form compound growth curves (Fig.74, Fig. 82 and Fig. 89), in which individual curves were connected one with another, and from which length at age t for the first few years was estimated. These estimates of length for age were then used to establish a von Bertalanffy growth equation :

$$l_t = l_{\infty} \left[1 - e^{-K(t - t_0)} \right]$$

where l_{∞} is the average maximum mussel length (the asymptote), K is the growth co-efficient, and t_0 the time when length would theoretically be zero. l_{∞} was determined approximately in a Walford plot, where length at age t is plotted against length at age $t + 1$ and a line fitted by eye to the plot to cut the 45° diagonal and establish l_{∞} by dropping a line to the x axis. The exact value of l_{∞} was then determined by plotting age t against $\log_e (l_{\infty} - l_t)$ - varying the value of l_{∞} until the straightest line through the plots was obtained. This was difficult to judge by eye, and a product moment correlation co-efficient calculation was used to determine the plot with the highest r value. Once this was established a linear regression equation, using the method of least squares, was calculated and a regression line fitted statistically. This then enabled t_0 in the von Bertalanffy equation to be calculated from the formula:

$$t_0 = \frac{\log_e l_{\infty} - y \text{ intercept}}{K}$$

where K is the slope of the line. Calculating the regression equation, where $y = a + bx$, is useful in that it enables an accurate estimate of K to be made, since this is b in the equation, while a is the y intercept. Normally estimates of these values are made by fitting a line by eye through the points.

Using the growth equation, a growth model was

then constructed and the data compared with the original growth data, derived from the growth curves. In two species, (C. mossambicensis and M. dubia) the calculated lengths at age t , t_1 , t_2 etc., were close enough to the estimated values to use the growth equation for construction of the age curves, and for subsequent production calculations. In A. wahlbergi the fit was only close from age 3 onwards, and a combination curve was drawn, employing estimated data for ages 1 and 2, and growth equation data from 3 onwards. The von Bertalanffy equation is more descriptive of the growth of older mussels (Crisp, 1971) and cannot always be expected to predict accurately the length of younger mussels at early ages.

Inspection of A. wahlbergi samples collected in the field had shown that many had very clear growth cessation marks, as illustrated below:

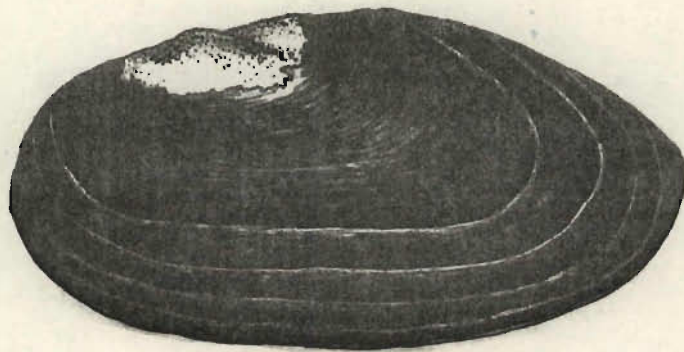


Figure 73 : Diagrammatic representation of an A. wahlbergi of 87 mm, showing five clear growth cessation marks, the first formed when the mussel was 56mm, and an estimated age of 1,8 years

These marks provided an opportunity to assess

age in a different way, and then compare the results with those obtained from the compound curve method described previously. If the results were comparable this would confirm that these growth cessation marks were in fact true annuli, and would endorse the validity of the von Bertalanffy age determination. The steps taken are outlined in point form:

- i.) 55 mussels out of several hundred examined were collected during 1976/1977 for measurements because of clear-cut growth cessation marks,
- ii.) the length of the mussel when the first, then successive marks, were formed was measured, using vernier calipers,
- iii.) age at these lengths was then determined from the growth curve. (e.g., Fig. 73 shows a mussel of 87 mm with a first clear mark formed when the mussel was 56 mm long, and, according to the growth curve, approximately 1,8 years old. Subsequent marks were thus assumed to have been formed when the mussel was 2,8 years old, 3,8 years old, etc.),
- iv.) length at estimated age was then plotted against estimated age and a mean length for each age could be determined; in order to allow for variation, and also for a margin of error, lengths encompassed by a small range of ages were summed to obtain an overall mean. Thus to determine length at 2 years, the lengths for mussels from 1,9 - 2,2 years

were used, giving a mean length of 59,2 mm (where N was 26, S.E. 0,70 and 95% confidence limits were 57,9 - 60,6 mm),

- v.) length/age results obtained this way were then checked against the earlier results obtained, as outlined previously.

A further check was made by deriving a von Bertalanffy equation from the results, constructing a growth model, and comparing the results with those obtained from a von Bertalanffy equation derived from the growth curve data.

A problem encountered in using compound growth curves to estimate age at length t was inability to find mussels of sufficiently small size in the field to follow growth from earliest sizes. Thus the smallest C. mossambicensis, A. wahlbergi and M. dubia used at the start of the release - recovery studies were 10 mm, 11 mm and 27,4 mm respectively. Several attempts were made to obtain post-parasitic juveniles by infecting fish and placing them in wire mesh enclosed containers in the lake, in the hope that mussels would drop off, or else caging fish in containers over substrates with several adult mussels, hoping the fish would become infected from the mussels. Half drums were used for these experiments. The containers were left for a few months in the lake and then removed and the substrate carefully washed through a series of graded sieves. However, no small mussels were ever discovered. Attempts were also made in the laboratory to obtain young mussels (described in PART TWO - REPRODUCTION). The only success was with M. dubia

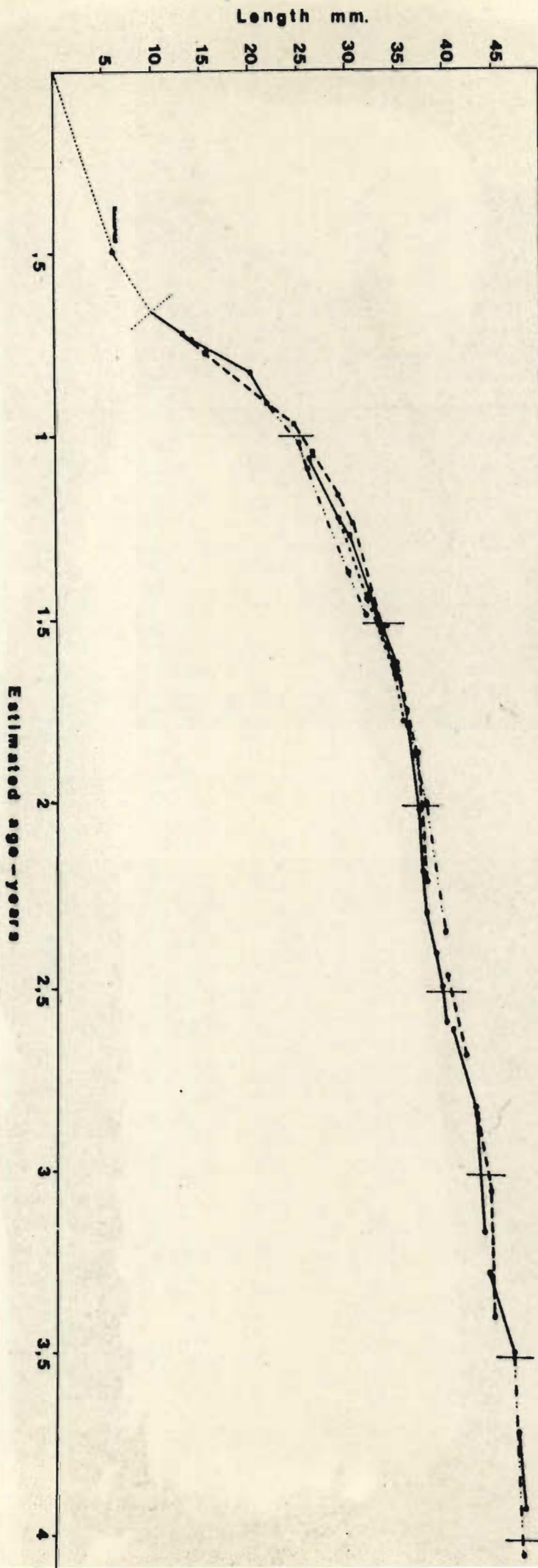
where two post-parasitic juveniles dropped off the cichlid, Pseudocrenilabrus philander. These were collected and placed in a wide-mouthed specimen jar with a thin film of substrate and lowered into the lake. Two months later the jar was examined but the mussels had disappeared. Lefevre and Curtis (1912) report similar difficulties in raising juvenile mussels, and failure to colonise a pond with infected fish, reporting that repeated attempts to raise post-glochidial stages for more than a few weeks met with no success. They attributed this to lack of suitable food. Harms (1907) managed to raise small Anodonta to six weeks, but these were destroyed by crustacea. As was pointed out in PART ONE, high mortality of post parasitic stages appears to be a common feature of freshwater bivalves, and the failure to obtain these stages artificially is not surprising if viewed against their virtual absence in the wild state in Lake Kariba. As a result, growth of the early stages had to be estimated from extrapolation and deduced from observations.

RESULTS

1. Caelatura mossambicensis

The steps taken for the derivation of the growth equation for this species are all presented here. The compound growth curve is seen in Fig. 74, where the growth pattern from 10 mm to beyond 45 mm is shown. Below 10 mm a hypothetical curve has been extrapolated to zero age, and the estimated time between zero age and age when 10 mm has been estimated as 8 months.

Figure 74: Compound growth curve comprised of individual growth curves of C. mossambicensis



This estimate is based on the estimated age of the small mussels found in the tree line of Sanyati East in October 1978, described in PART ONE. These mussels must have started colonizing this area only after silt deposition from the Sanyati River stopped, probably in March/April 1978, and they could not have been older than 6 mths - 7 mths. Their mode was 6 mm, and hence 6 mm in this graph has been assigned a theoretical age of 6 mths, and therefore 10 mm on the graph has an estimated age of 8 mths. On this basis, age 1 is determined as 24,9 mm, age 2 as 37,5 mm, age 3 as 43,8 mm and so on.

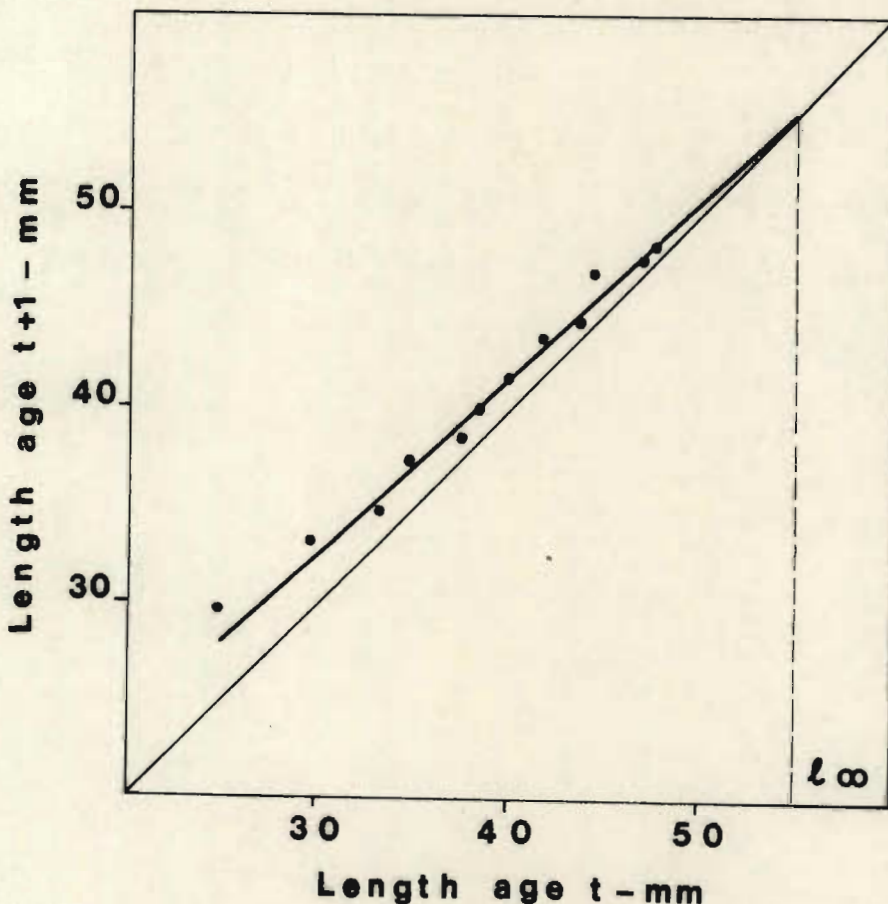


Figure 75: Walford graph for *C. mossambicensis*. Intercept of the two diagonal lines indicates l_{∞} = approximately 55mm (dotted perpendicular)

Using these data, length at age t was then plotted against length at age $t + 1$, in a Walford graph, and a line fitted by eye through the points to cut the 45° diagonal. (Fig. 75). The intercept of the two diagonal lines indicated that l_∞ was approximately 55 mm. This was checked against the length frequency field data of PART ONE (Fig. 21), which showed the average maximum length to be approximately 55 mm. Using lengths varying about 55 mm as trial values of l_∞ , values of $\log_e (l_\infty - l_t)$ were plotted against age and r values calculated for each set of figures to determine which set gave the highest r value. The highest r value (0,999541) was derived when a trial value of 54,2 was used (Fig. 76 B).

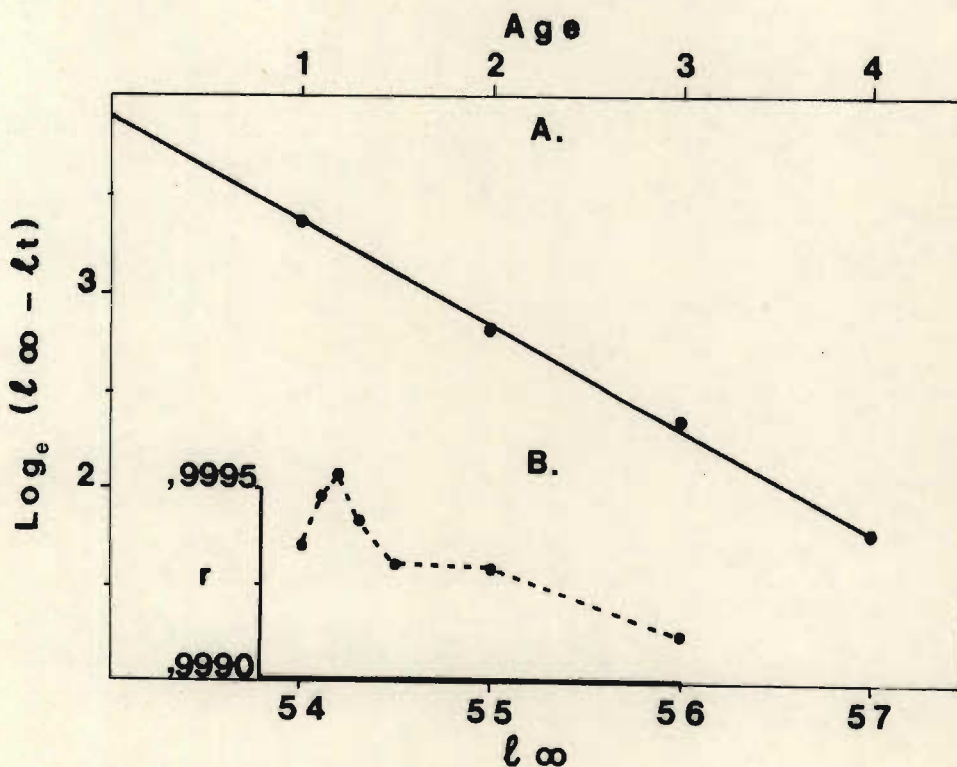


Figure 76 : Age plotted against $\log_e (l_\infty - l_t)$ where $l_\infty = 54,2$ mm (A), and r values for different estimates of l_∞ (B)

The values of age against $\log_e (l_{\infty} - l_t)$ were then plotted, where l_{∞} was 54,2 mm, and a line fitted statistically in order to obtain K and t_0 (Fig. 76,A), as described earlier.

The von Bertalanffy growth equation was then derived and had the following form:

$$l_t = 54,2 \left[1 - e^{-0,528 (t - 0,175)} \right]$$

Using the formula, lengths at given ages were calculated, and these compared with the original estimates of length at given ages, derived from the compound growth curve. These are shown in Table 17.

The model was considered to be a good fit as the largest deviation of calculated length from estimated length was 11,1%, with an overall mean of 4,8%, and the equation was thus used to calculate age curves for C. mossambicensis, plotting age against length, total mass, dry tissue mass, and energy content. (Fig. 77). Mass for given ages was derived from the regression equations already established for the relationship between length and mass, and energy content was calculated from dry mass, at 23,442 kJ g⁻¹ ash-free dry mass.

The construction of reliable growth curves allows the population to be positively age identified, thus allowing an assessment to be made of the general virility or maturity of the population, i.e. is it composed mainly of young, middle-aged or old individuals ?

Table 17: Compound curve estimates (A), and von Bertalanffy calculations (B) of length-age of C. mossambicensis

	A	B	
AGE	ESTIMATED LENGTH mm	CALCULATED LENGTH mm	% DEVIATION
1,0	24,9	22,3	10,4
1,5	33,3	29,6	11,1
2,0	37,5	35,4	5,6
2,5	40,0	39,7	0,8
3,0	43,8	43,0	1,8
3,5	47,0	45,7	2,8
4,0	48,3	47,6	1,4

Age distribution of the population of C. mossambicensis was determined from the sample population of mussels collected from the transect grid sampling in the Sanyati East cleared area, and is shown graphically in Fig. 79, where numbers, whole wet mass, and dry tissue mass are plotted against age. Annual incremental growth is shown in Fig. 78 a.

Average specific growth rates (g) for the various age groups (0 - 1, 1 - 2, etc.,) were calculated from the equation :

$$g = \frac{1}{t} \ln \frac{w_2}{w_1}$$

where w_1 and w_2 are the mean masses at the beginning of each time period, and t is the time period, i.e. 365 days.

These had a wide range, obviously with the lowest values in the oldest age groups, where growth had diminished considerably and it was necessary to plot the data (g against age groups) on a semi - log scale. (Fig. 78 b).

Calculation of average specific growth rate is necessary for the determination of production rates, and also provides a valuable comparative index of instantaneous growth rates for various age sections of the population. The much reduced growth rate of the older individuals, in comparison with the younger ones, is reflected in the graph.

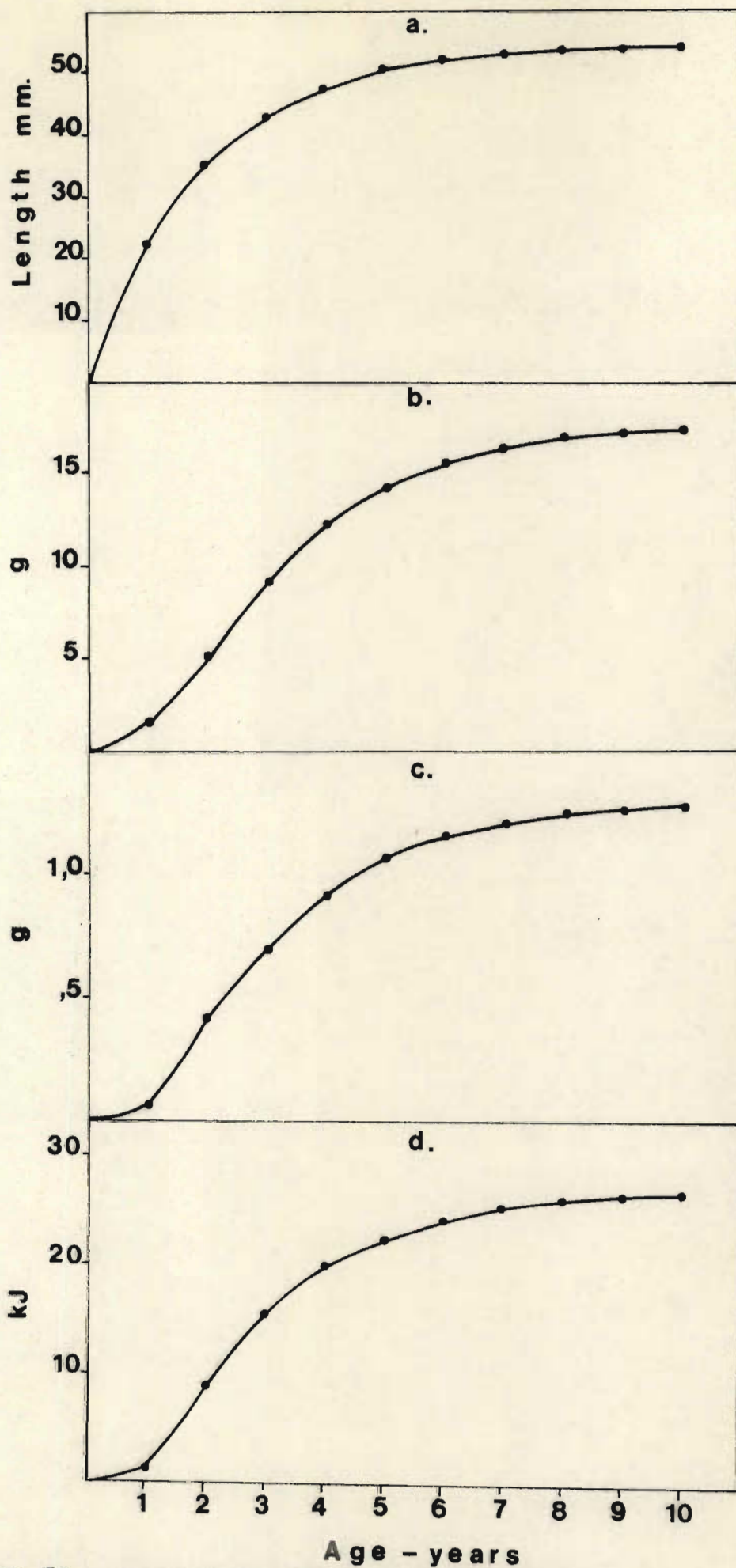


Figure 77: Age curves of *C. mossambicensis* in terms of length (a), total mass (b), dry mass (c) and energy content (d)

The plot of annual growth increments is shown in Fig. 78a. Growth is rapid in the first few years but then slows down noticeably. Fig. 78b shows average specific growth rates

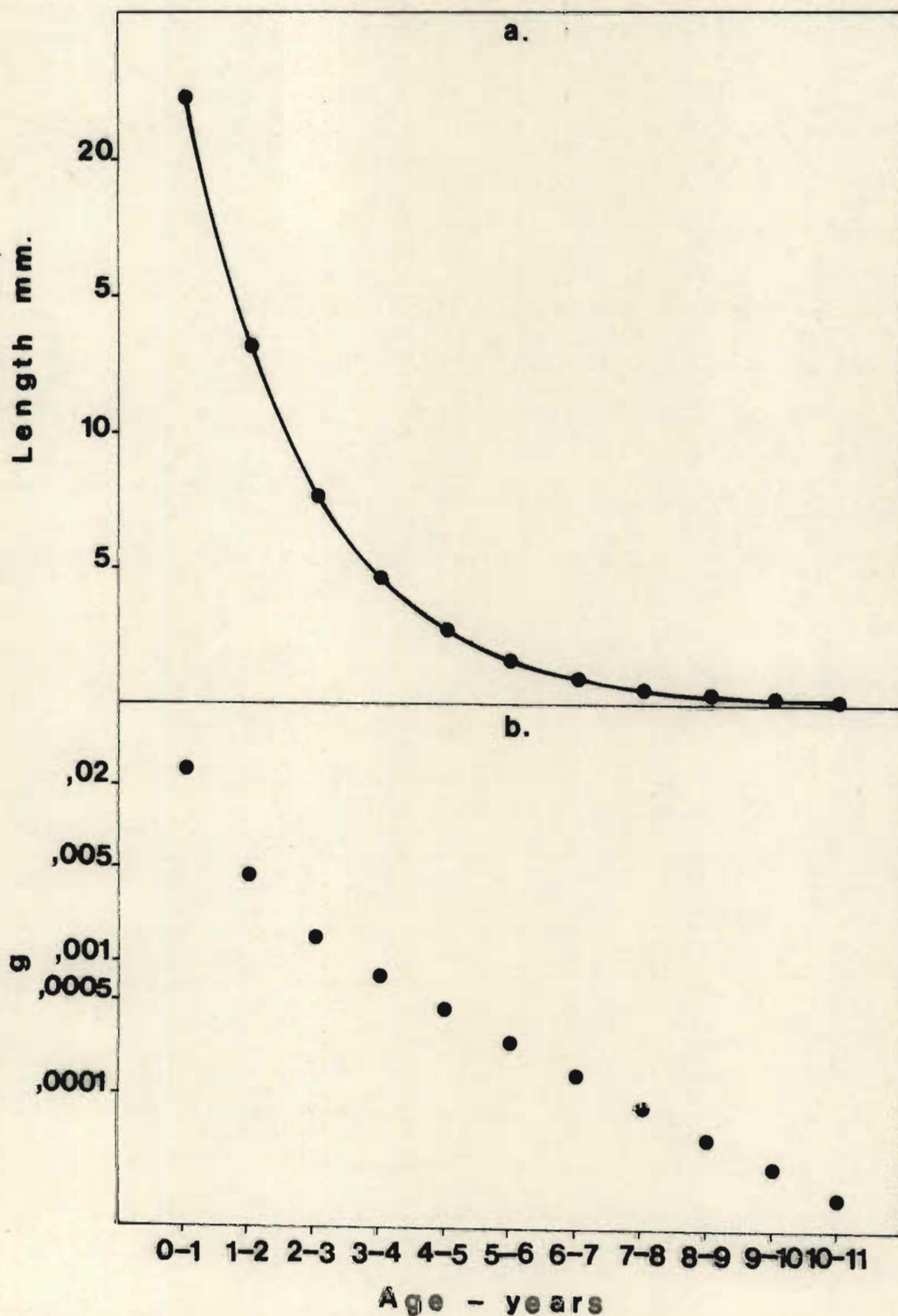


Figure 78: Annual growth increments (a) and average specific growth rates (b) for C. mossambicensis

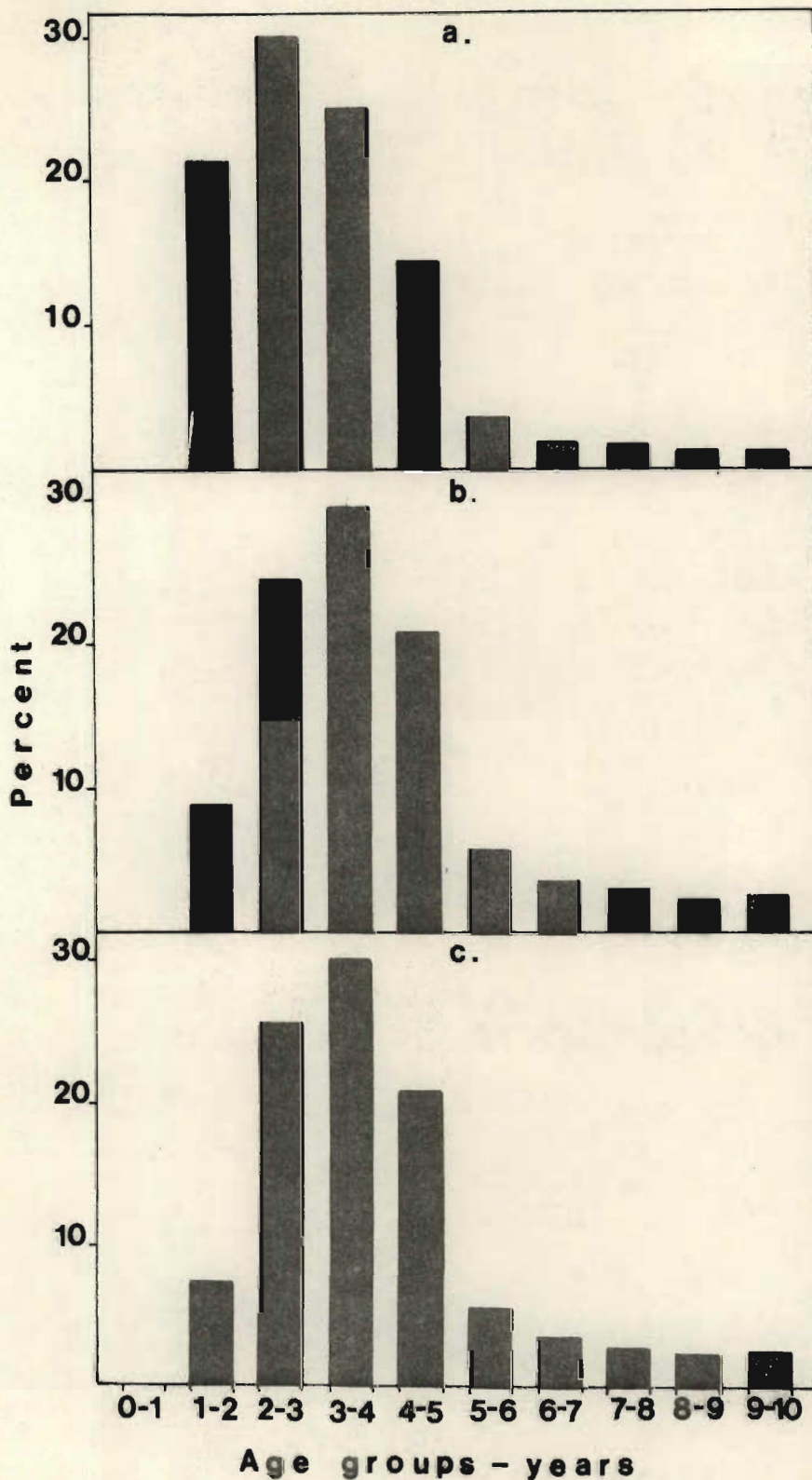


Figure 79: Age distribution of the sample population of *C. mossambicensis* from the Sanyati East cleared area - numbers (a), whole mass (b) and dry tissue mass (c)

The graphs clearly show the population is composed mainly of individuals from 1 - 5 years of age, with very few less than 1 year old. The same picture emerges for mass, where the main biomass is composed of individuals from 1 - 5 years old. The important contribution of the younger age groups to the population is shown clearly in Fig. 80 and 81, where accumulative numbers and biomass have been plotted against accumulative age groups (0 - 1, 0 - 2, 0 - 3, etc.).

These show that the 0 - 5 age group comprises 86% of the numbers and over 83% of the total biomass, with the remaining 14% and 17% respectively made up of mussels older than 5 years. The fairly small contribution to the overall biomass of mussels under two years is also evident.

The conclusions one can draw from a population age structure such as this are that

- i) the population is not overburdened with more older individuals than younger individuals, and is therefore not in a state of stagnation or decline,
- ii) the population is not comprised to a large extent of smaller individuals, and is therefore not in the process of development or expansion,
- iii) the gradual and regular decrease in numbers from younger to older members indicates that recruitment to the population is regular from one year to the next.

The overall impression is one of a young and vigorous population, in a stable state of existence.

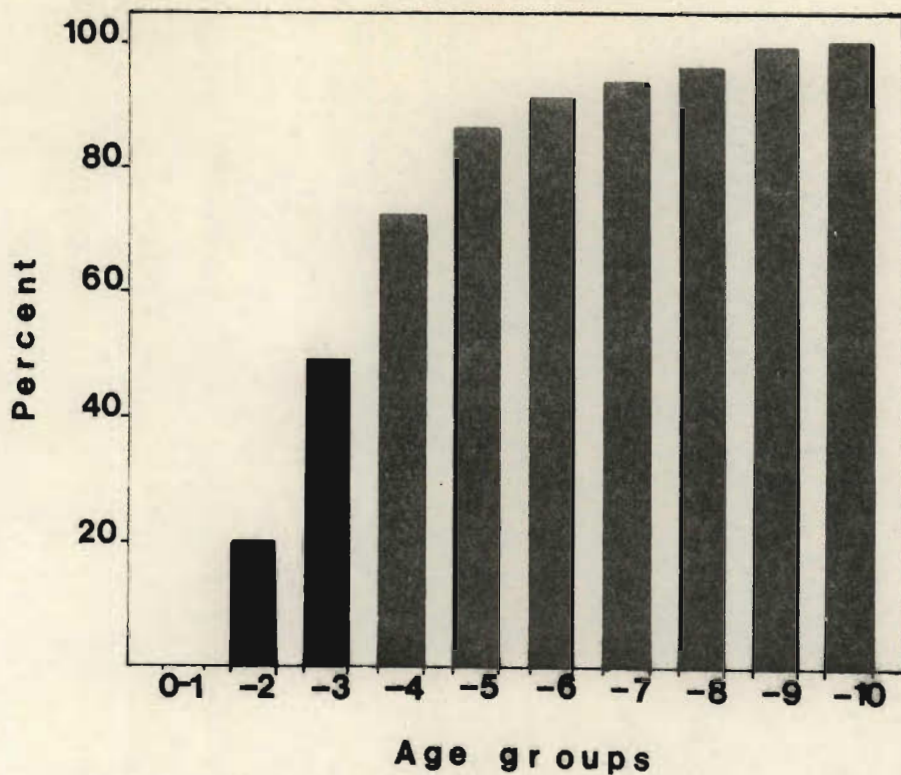


Figure 80: Accumulative numbers of the sample of *C. mossambicensis* from the Sanyati East cleared area

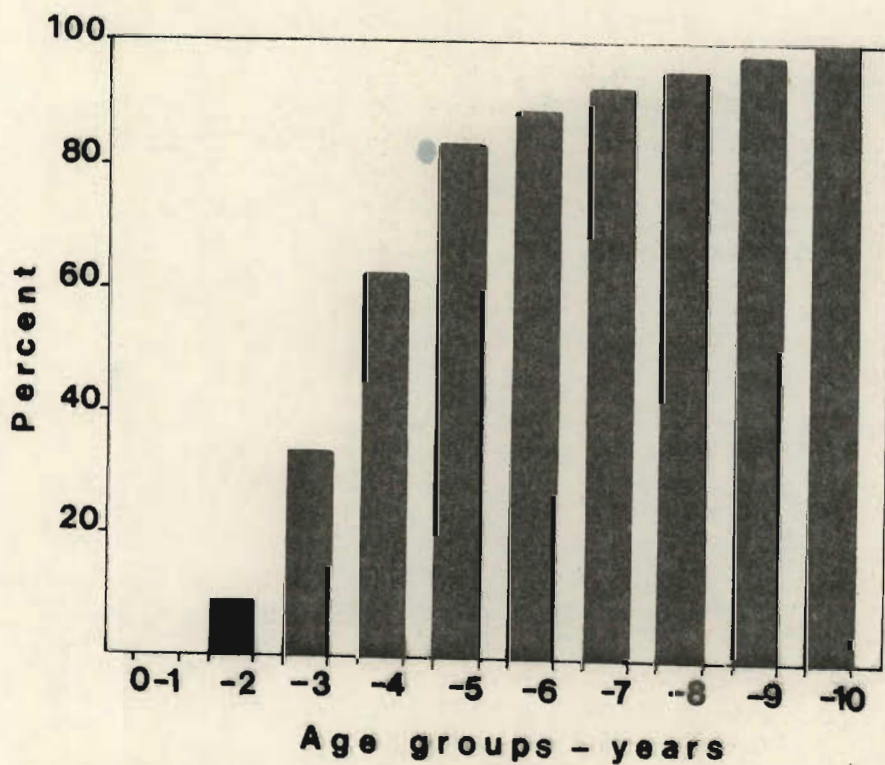
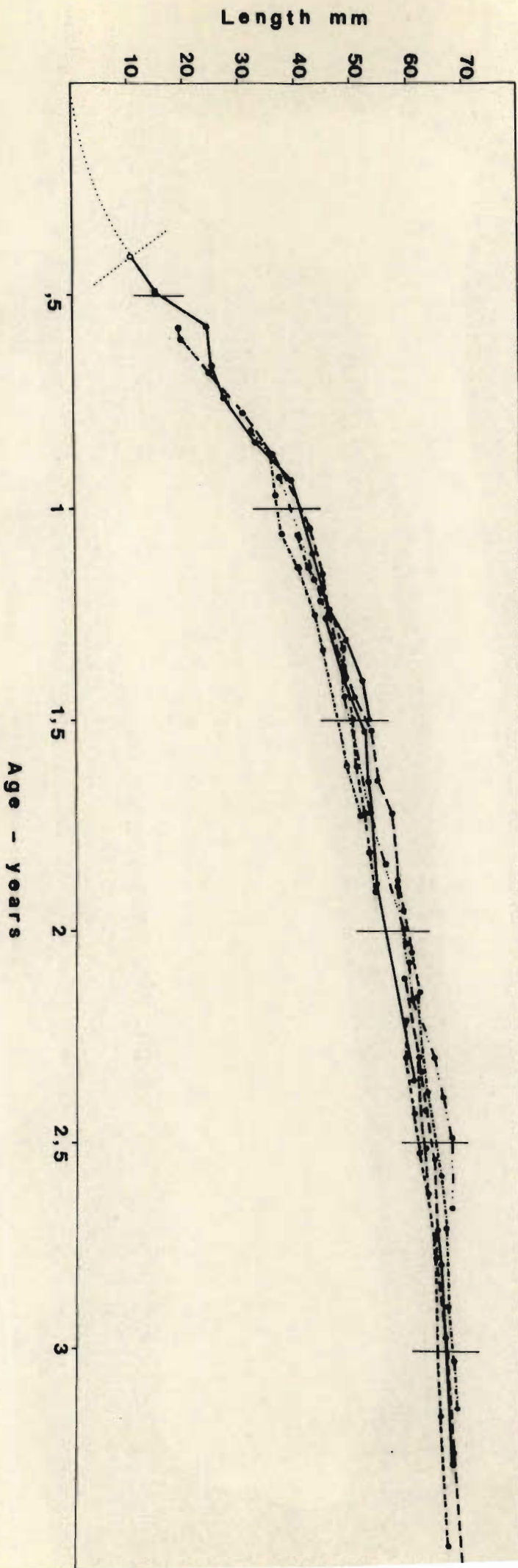


Figure 81: Accumulative biomass of the sample of *C. mossambicensis* from the Sanyati East cleared area

Figure 82: Compound growth curve comprised of individual curves of A. wahlbergi



2. Aspatharia wahlbergi

The compound growth curve from which estimates of length and age were derived is shown in Fig. 82 . Here again a theoretical curve was extrapolated from 11 mm to the point of origin of the axis, and 11 mm was assigned an estimated age of 4 months. This seemed a reasonable estimate, as the mussel of 11 mm trebled its length to 33,5 mm in 5 months, indicating very fast early growth.

Following the same procedure as was used for C. mossambicensis and described in detail earlier, a von Bertalanffy growth equation was derived from the age - length estimates from the curve, with the following formula:

$$lt = 94 \left[1 - e^{-0,410 (t - 0,313)} \right]$$

Using the formula, lengths at given ages were calculated and these compared with the original estimates of length at given ages, derived from the compound growth curve. These results were then compared with two other sets of results, length - age estimated from growth - cessation marks on shells, and von Bertalanffy calculations from these data, in which the growth equation had the form :

$$lt = 95 \left[1 - e^{-0,40 (t - 0,320)} \right]$$

These results are shown in Table 18.

Table 18: Compound curve estimates and calculations (A), estimates and calculations from growth cessation marks (B) and combined (C) for A. wahlbergi

	A			B			C
AGE	ESTIM.	CALC.	% DEV.	ESTIM.	CALC.	% DEV.	COMBINED
1,0	38,2	31,6	17,3	40,5	31,3	22,7	38,2
1,5	50,2	43,4	13,5				
2,0	57,8	52,6	9,0	59,2	52,3	11,7	55,2
2,5	64,0	60,1	6,1				
3,0	66,0	66,5	0,8	69,6	66,4	4,6	66,5
4,0	-	75,8		77,1	75,8	1,7	75,8
5,0	-	81,9		84,0	82,2	2,1	81,9
6,0	-	86,0		87,5	86,4	1,3	86,0
7,0	-	88,7		89,7	89,2	0,6	88,7
8,0	-	90,5		90,5	91,1	0,7	90,5
9,0	-	91,7		-	92,4		91,7

A significant feature of these results was the closeness of the two sets of calculated results despite having been derived from bases using different ageing techniques. Admittedly, the initial estimate of age for the first "annulus" was based on the compound curve, and thereafter estimates of age of subsequent "annuli" based on the initial age estimates of the first "annulus", but nevertheless the validity of the final equation still depended on whether or not the growth cessation marks were true annuli. The closeness of the two sets of results strongly suggests that the growth cessation marks are in fact true annuli*, and this being the case, justifies using these results as a check against estimates and calculations from the compound curve.

Calculated results agreed fairly closely with estimates from age 3 on, but gave lower length values for ages 1 and 2 than estimated ages, as indicated by the percentage deviations. Since the study of annuli on the sample of 55 mussels had shown that the smallest length when the first annulus was formed was 39 mm, it was decided that the calculated values of 31,6 mm and 31,2 mm for age 1 were too low. Hence calculated lengths for age 2 (52,6 mm and 52,3 mm) were probably also too low.

* These annuli are probably laid down during the first half of summer (September to December), when food reserves and nutrient levels are low, as shown by Cochrane (1978). A comparison of growth rates of several A. wahlbergi ranging in size from 55 mm - 74 mm, for three periods: April to September, September to February, and February to September, gave mean growth rates of 0,44 mm day⁻¹, 0,24 mm day⁻¹ and 0,503 mm day⁻¹. Clearly the middle period, which incorporates this unproductive period had the slowest growth rates and in fact two of the mussels stopped growing altogether during this period.

As a result, estimated lengths from curve data at ages 1 and 2 were combined with calculated lengths (from curve data), from age 2 onwards, shown in Column C of Table 18, where 55,2 mm is the mean of 57,8 mm and 52,6 mm. These length - age data were then used to construct growth curves for length, mass and energy content, shown in Fig. 83 and Fig. 84.

The length-age curve shows a similar form to that for C. mossambicensis, with rapid growth in the first few years and much slower growth of later years. The length - mass curves have a normal sigmoid slope, showing that mass increase is greatest in the middle years, and least in early and later years. Rather similar shaped curves were obtained by Negus (1966) on the Thames River Unio spp. and Anodonta. Anodonta anatina, which attains a similar size to A. wahlbergi, reached a length of approximately 34 mm in heated effluent water by the first winter in this river, and approximately 49 mm by the second winter. Growth increments for the first three years of life were 34 mm, 15 mm and 10 mm, rather similar to the 38 mm, 17 mm and 11 mm of A. wahlbergi. Pennak (1953) says that freshwater mussels usually grow to a length of 30 mm - 80 mm in two growing seasons, which is in agreement with these results. It is interesting to note that despite the differences in the climatic environment of these two species, (Anodonta and Aspatharia), both have restricted growing seasons. A. anatina stops growing in winter, while A. wahlbergi slows growth or stops growing during early summer. Thus a favourable climatic regime is not necessarily a guarantee of year round growth.

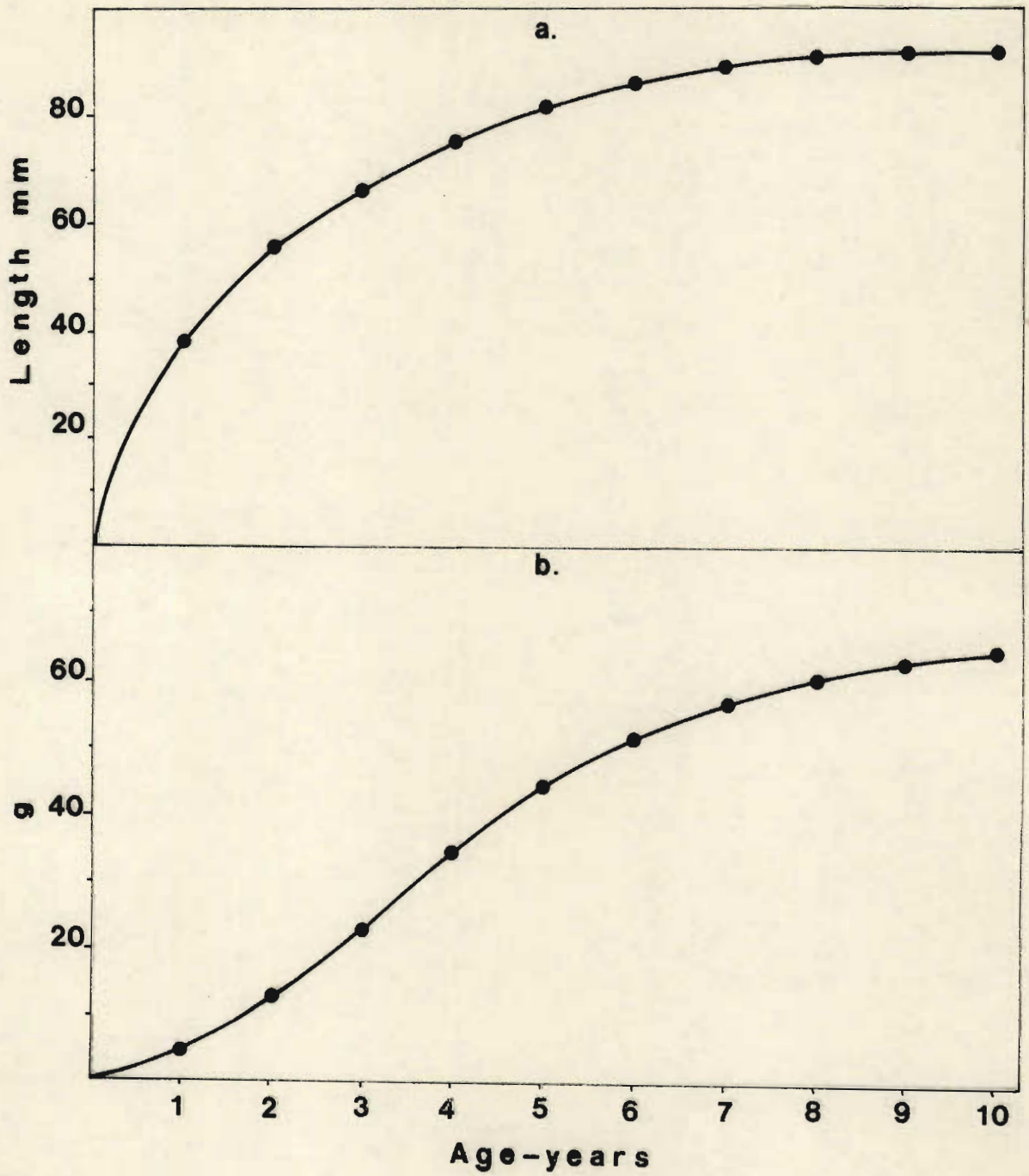


Figure 83: Length - age curve (a), and total mass - age curve (b), for A. wahlbergi

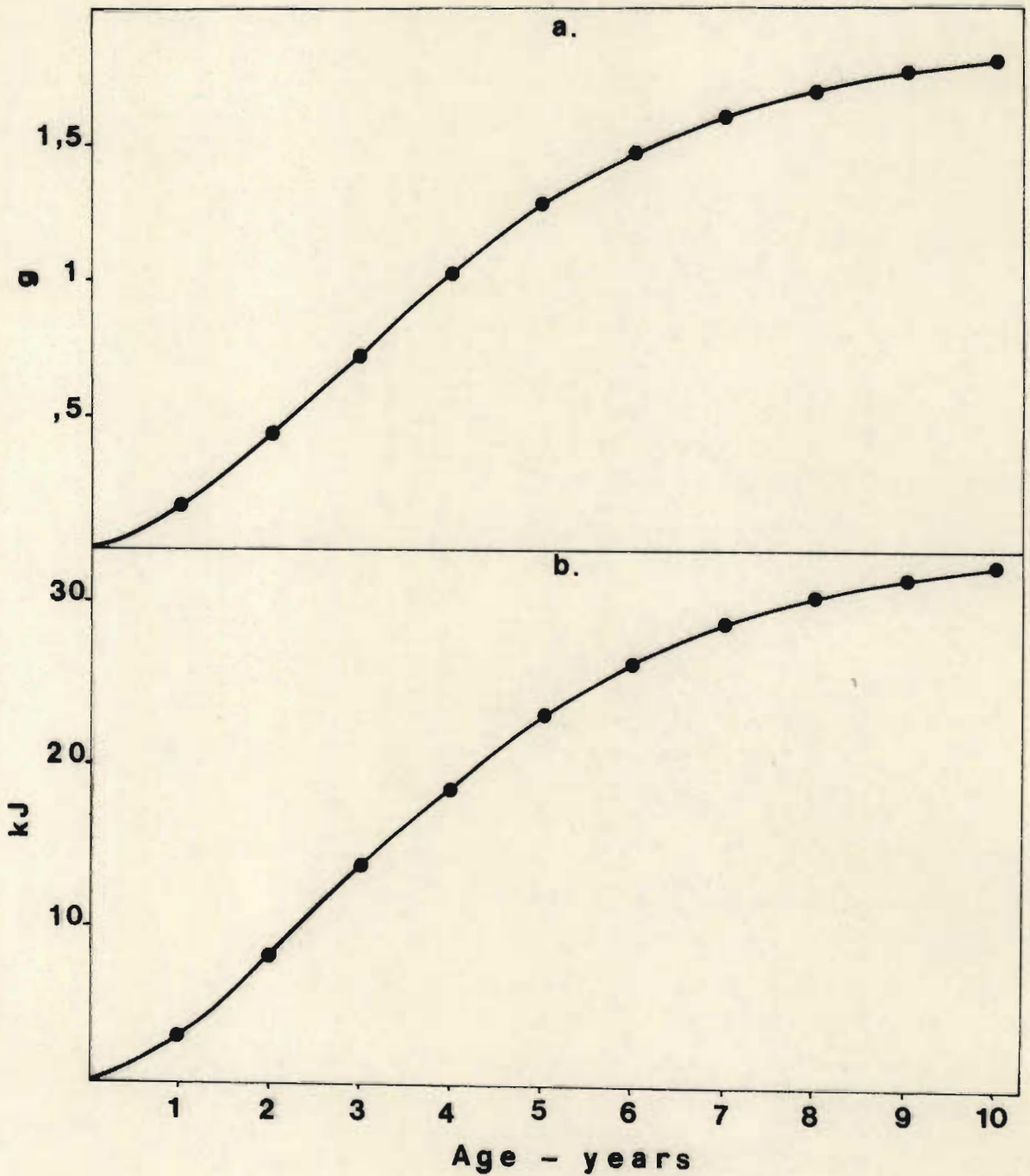


Figure 84: Dry - mass age curve (a), and energy content-age curve (b) for A.wahlbergi

The annual growth increments and average specific growth rates are shown in Fig. 85.

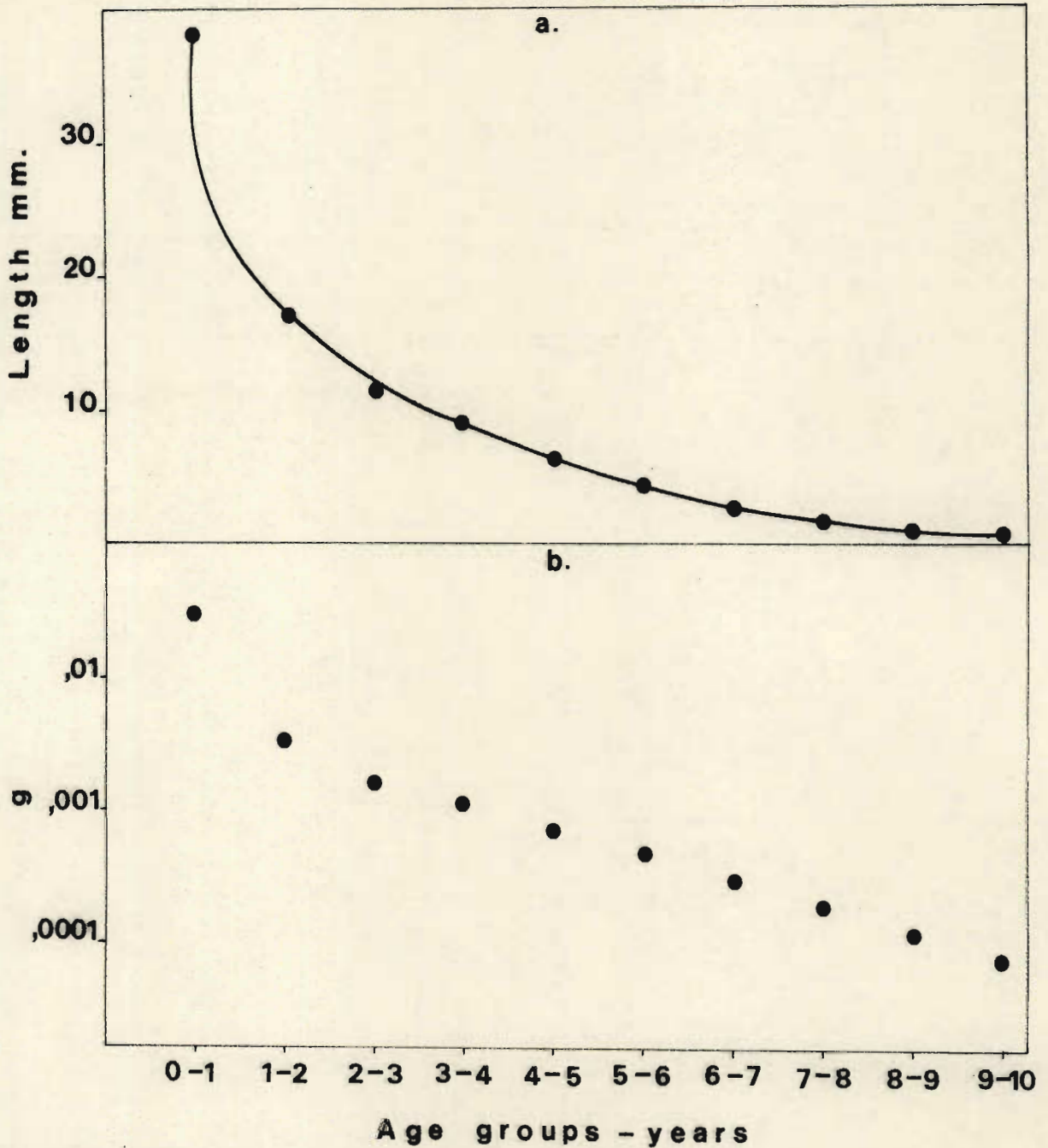


Figure 85: Annual growth increments (a), and average specific growth rates (b) for A. wahlbergi

The pattern here is similar to that of C. mossambicensis and other animals whose growth pattern tends toward asymptotic growth. A semi logarithmic axis

was used to present age - average specific growth rates because of the very large differences in values between the youngest and the oldest age groups.

The distribution of the population in terms of numbers and mass in the Sanyati East cleared area determined from the transect data is shown in Fig. 86.

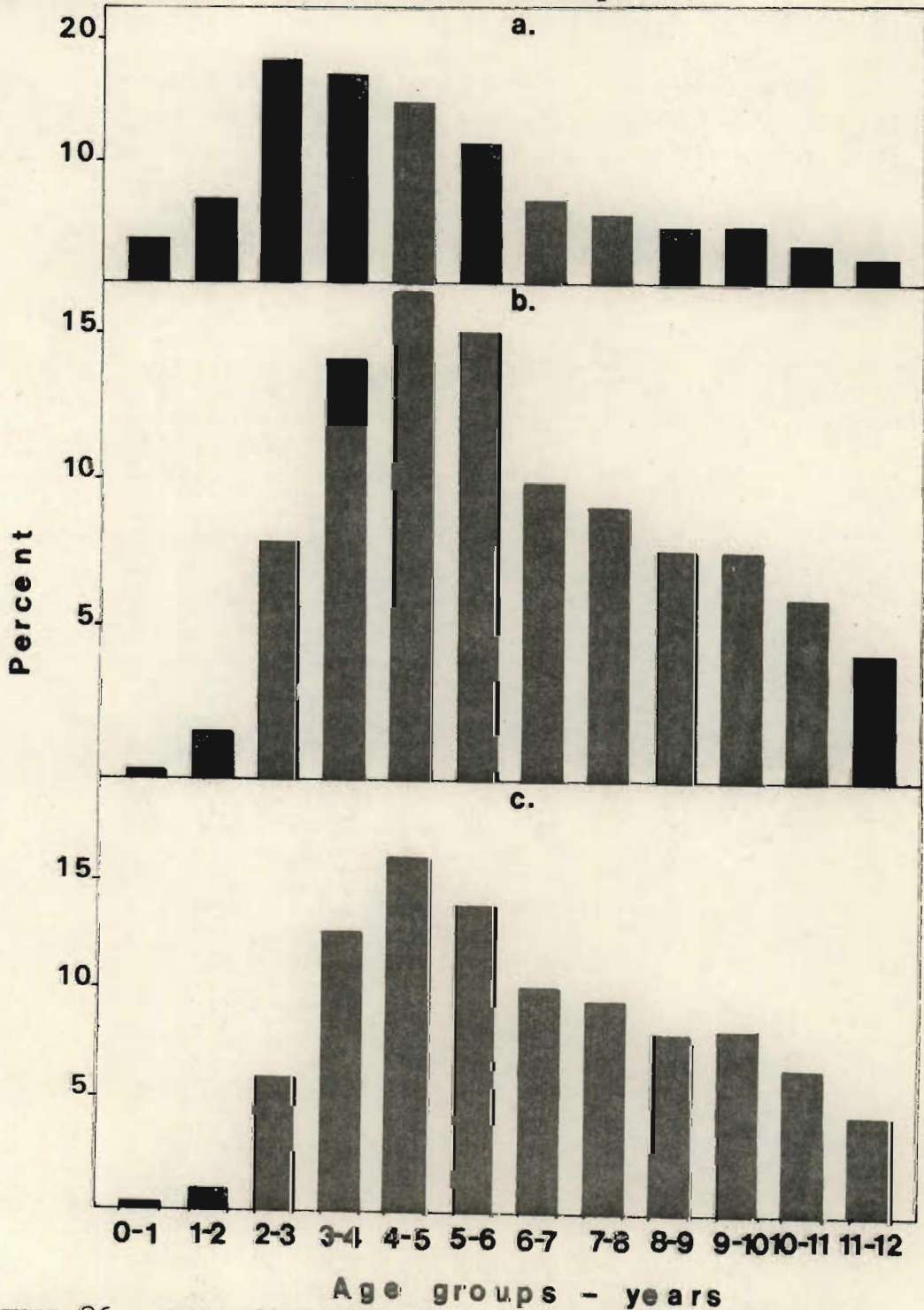


Figure 86: Age distribution of the sample population of *A. wahlbergi* from the Sanyati East c/a numbers(a) whole mass(b) dry tissue mass(c)

Accumulative percentages for numbers and biomass are shown in Fig.87 and Fig. 88.

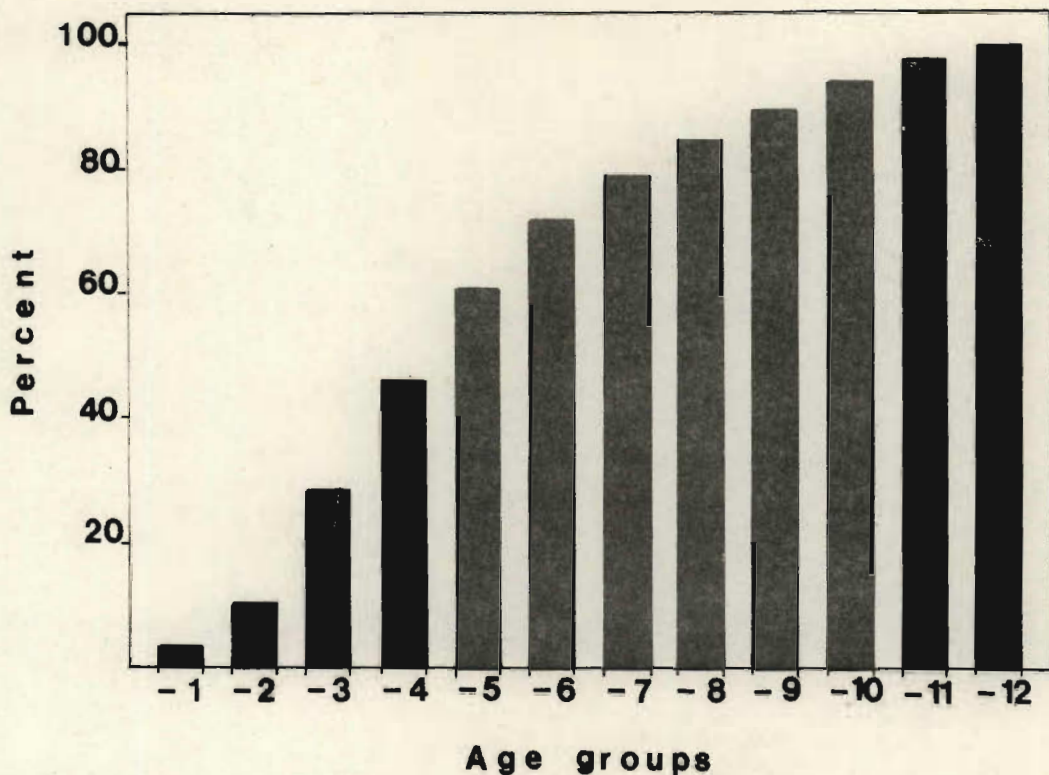


Figure 87: Accumulative numbers of the sample of A. wahlbergi from Sanyati East c/a

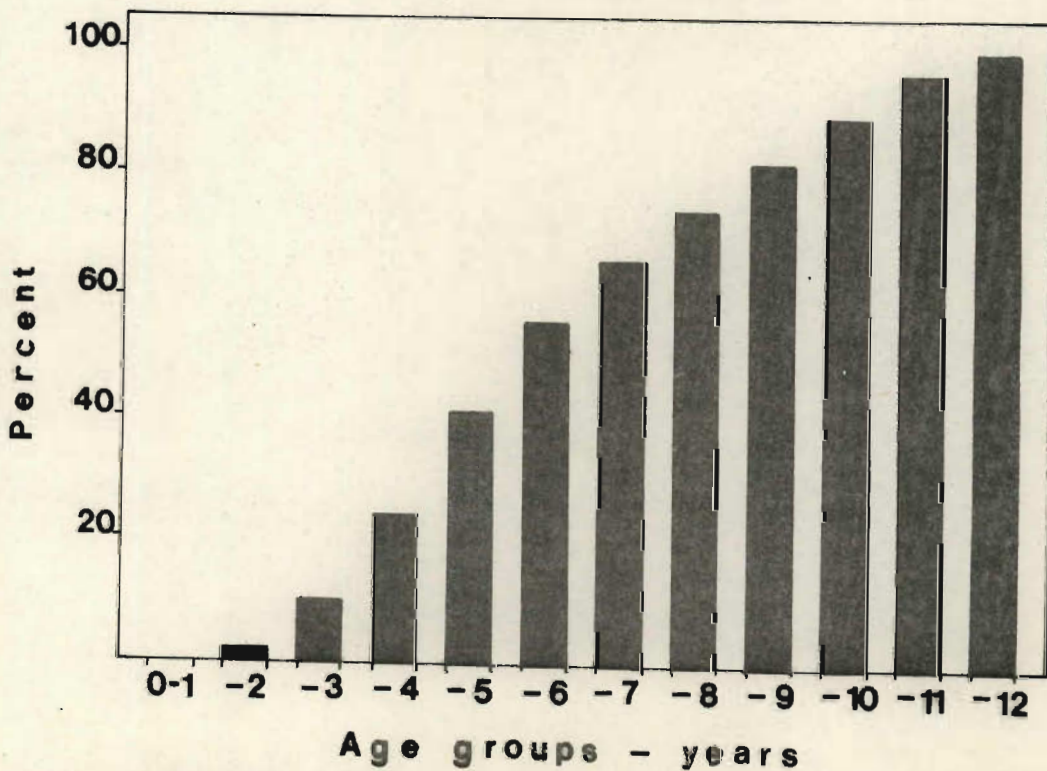


Figure 88: Accumulative biomass of the sample of A. wahlbergi from Sanyati East c/a

Unlike the C. mossambicensis population where there is a sharp rise in accumulative percentage up to age 5, the increase shown is very much more gradual, and the 0 - 5 year age group accounts for only 60% of the population by number and slightly over 40% by mass, compared with respective values of 86% and 83% for C. mossambicensis.

The greater contribution to the total standing crop by older mussels is also indicated by the mean length of 78,4 mm of mussels collected in the Sanyati East cleared area. (Fig. 24 c, - PART ONE), which is in the 4 - 5 year age group. The comparative mean length for C. mossambicensis of 41,7 mm has an age of approximately 3 years.

Despite the impression given by length frequency histograms that the A. wahlbergi population has an imbalanced preponderance of older mussels, the age frequency distributions show that this is not the case. Over 70% of the population is comprised of mussels under 6 years, or nearly 80% under 7 years. This factor, plus the regular nature of the decline in numbers with increasing age suggests regular recruitment to the stock, and a stable, but long - lived population. This latter aspect, of long life, is responsible for the important biomass contribution to the standing crop by the older individuals, while the stable nature of the population will account for the lack of juveniles found.

3. Mutela dubia

The same procedure as used for C. mossambicensis and A. wahlbergi to determine growth equations was followed for M. dubia. The compound growth curve using release - recovery data is shown in Fig. 89. Here again, because of lack of growth data on the post-parasitic stage, a theoretical growth curve was extrapolated to the origin of the x axis, relying on the actual growth curves as a guide.

Early growth of this thin-shelled and elongate species appeared very much faster than the other two species, indicated by the doubling in size of a mussel of 27,4 mm - 53,9 mm in only 8 months, or shown by the increase from 27,4 mm to 37,0 mm in 71 days. Lefevre and Curtis (1912) and Harms (1907) have shown on the species they studied that once the young mussel drops off growth is immediate, and since juvenile M. dubia drop off at a length of approximately 1,5 mm growth must be fairly rapid from this point onwards. (See p. 342*).

Using the estimated length - age data derived from the curve, a von Bertalanffy growth model was constructed with the following growth equation:

$$l_t = 94 \left[1 - e^{-0,49 (t - 0,637)} \right]$$

Length at age was calculated from this to provide the model, and estimated ages were then compared with it. These are shown in Table 19.

Figure 89: Compound growth curve comprised of individual growth curves of M. dubia

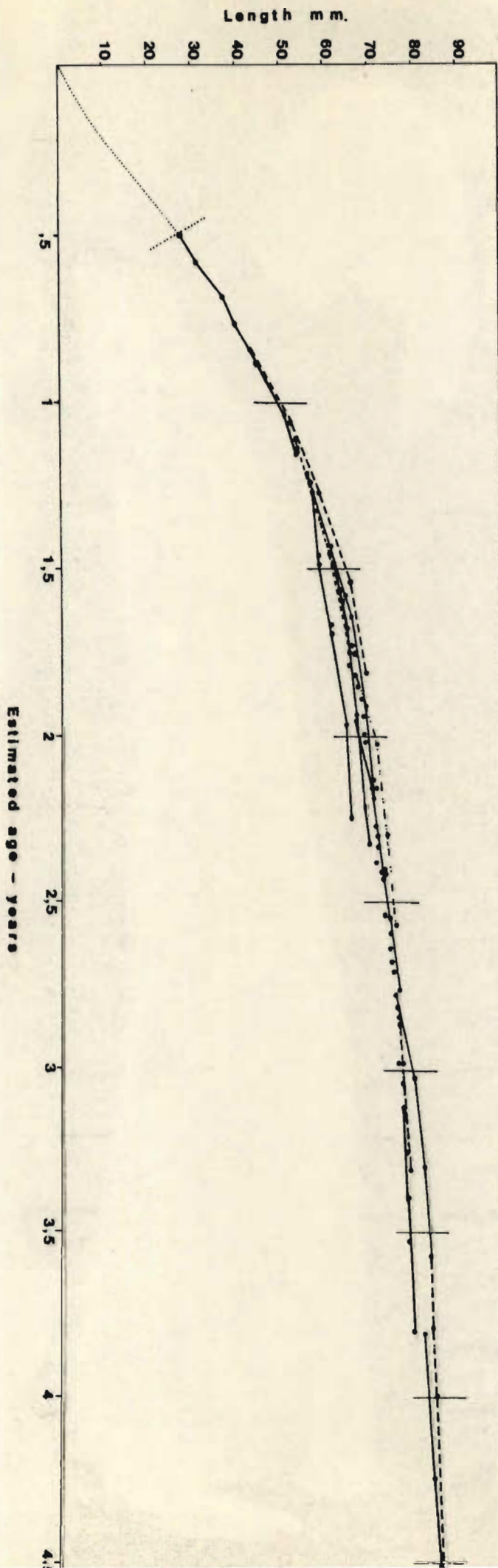


Table 19: Compound curve estimates (A) and von Bertalanffy calculations (B) of length-age of M. dubia

	A	B	
AGE	ESTIMATED LENGTH mm	CALCULATED LENGTH mm	% DEVIATION
1,0	49,5	53,4	7,9
1,5	62,0	61,1	1,5
2,0	69,0	68,1	1,3
2,5	74,0	73,8	0,3
3,0	78,0	78,2	0,3
3,5	81,5	81,7	0,2
4,0	84,0	84,3	0,3
4,5	86,0	86,4	0,5
5,0	-	88,1	
6,0	-	90,3	
7,0	-	91,8	
8,0	-	92,6	
9,0	-	93,1	
10,0	-	93,5	

The model proved to be a good fit and was used in its entirety to draw the length - age, mass - age and energy content-age curves, shown in Fig.90 and Fig.91.

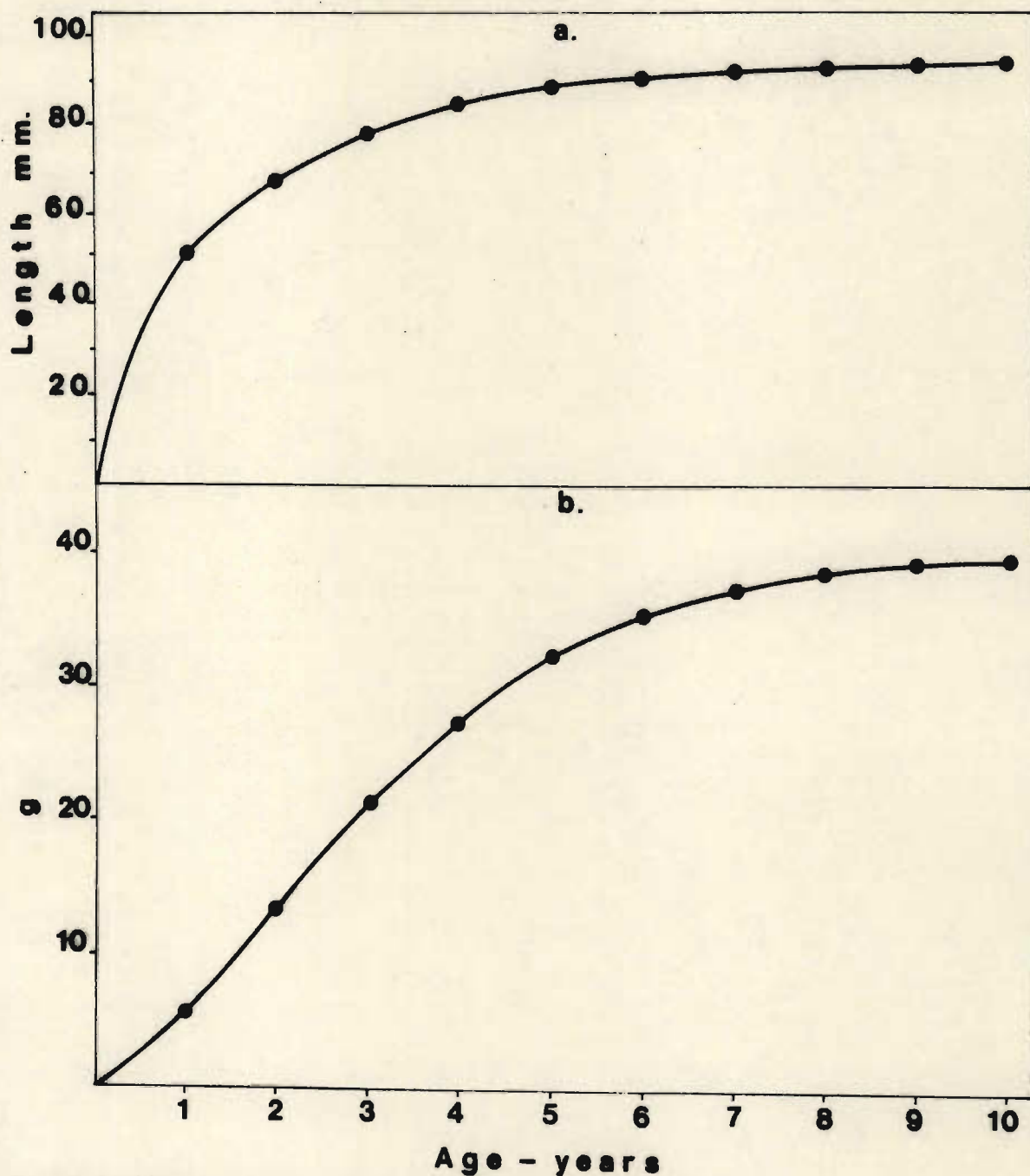


Figure 90: Length - age curve (a), and total mass - age curve (b) for M. dubia

The pattern of growth is similar to that of the other two species, with rapid growth in the early years compared with much slower growth later on. A plot of 49 mm

for the first year may have proved more suitable and given the curve a less steep increase from zero age, but the remaining estimated data, if plotted, would follow an almost identical pattern to the calculated plots.

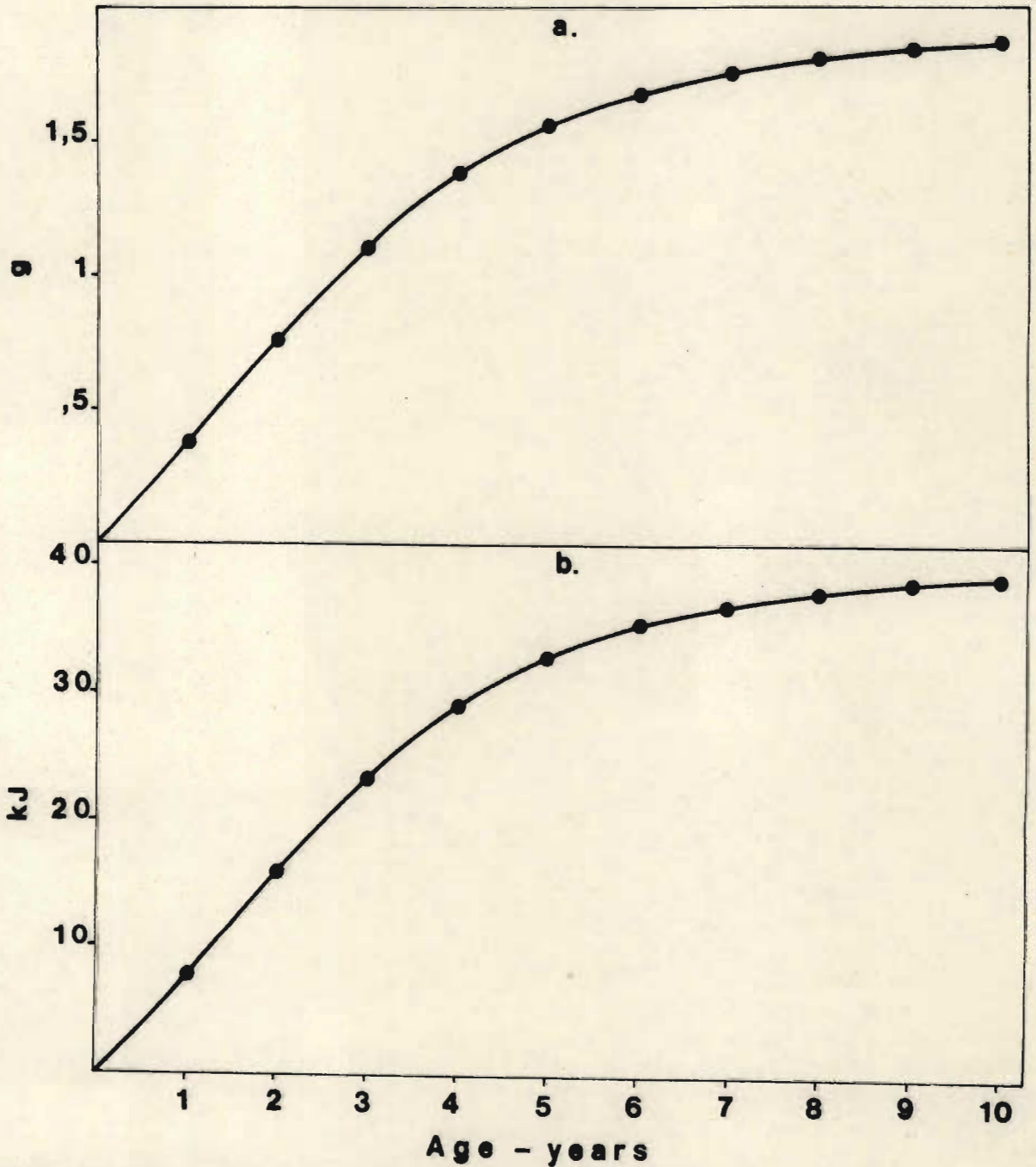


Figure 91: Dry mass - age curve (a) and energy content - age curve (b) for M. dubia

The mass - age curves show a sigmoid form, not quite as pronounced as that of A. wahlbergi, where the younger

specimens are lighter relative to the older ones than in M. dubia. Growth in the first two years falls within Pennak's range of 30 mm - 80 mm in two growing seasons.

Annual growth increments and calculated values of specific growth rate are shown in Fig. 92.

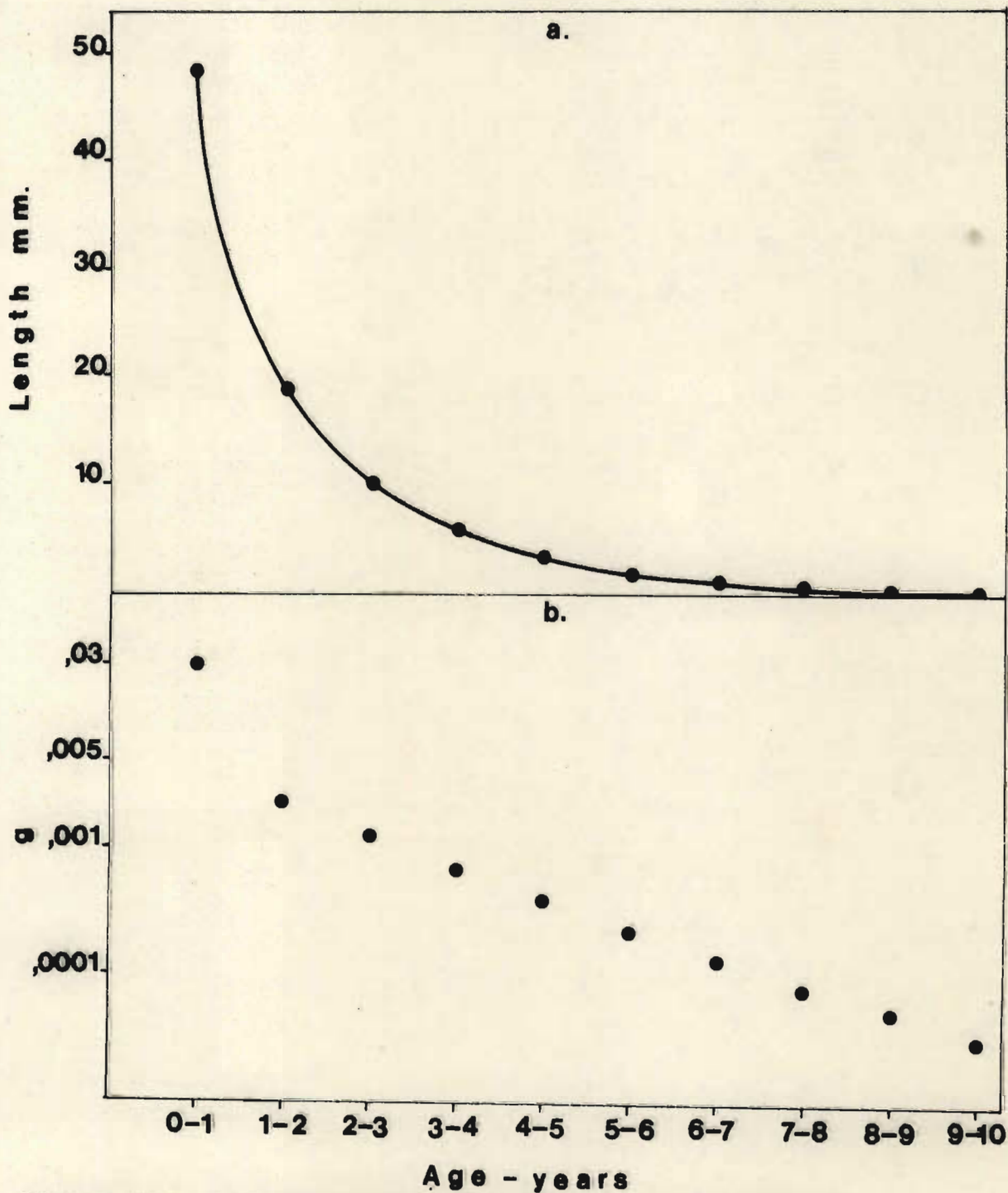


Figure 92: Annual growth increments (a) and average specific growth rates (b) for M. dubia

The curves here are similar in pattern to those of the other species, with rapidly decreasing increments and average specific growth rates in the older individuals.

The length - age and mass - age distributions of the sample collected using all methods of sampling in the Sanyati East cleared area in 1976 and 1977 are shown in Fig. 93 .

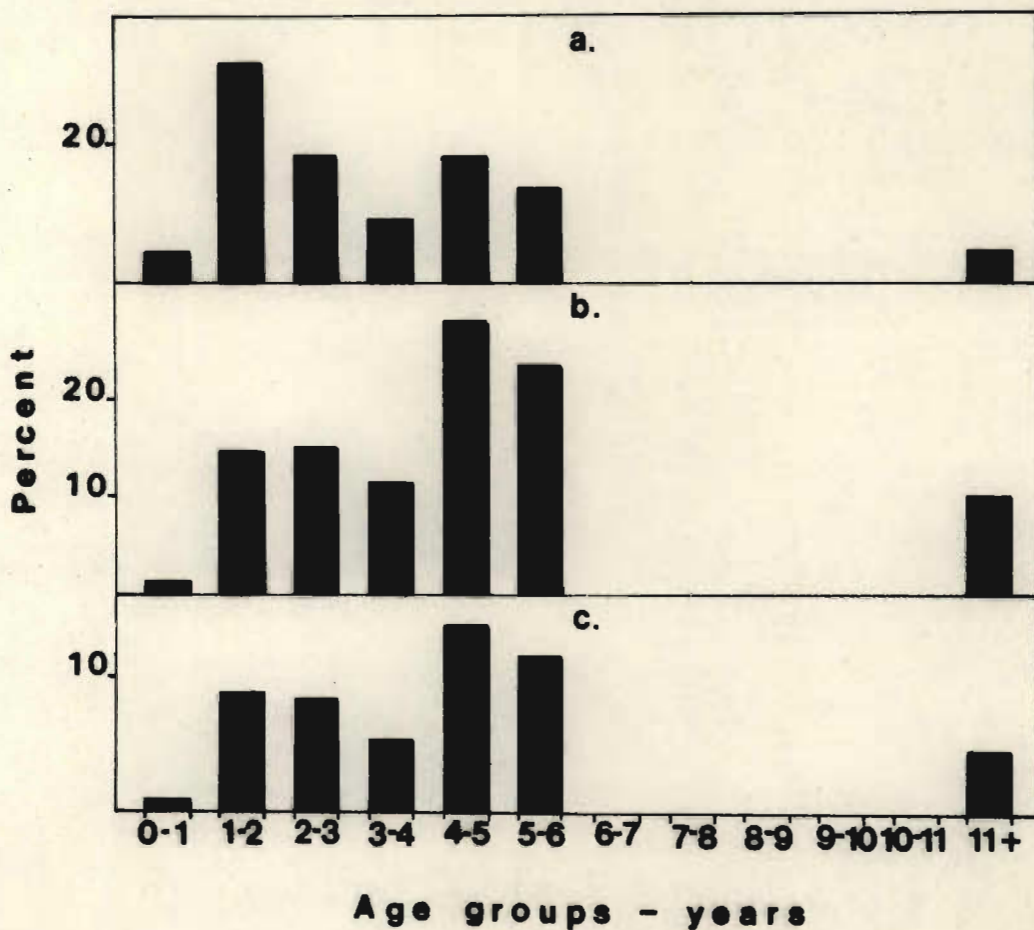


Figure 93: Age distribution of the sample population of *M. dubia* from the Sanyati East c/a : numbers (a), whole mass (b), and dry tissue mass (c)

Since the total number collected was only 22, these graphs are unlikely to represent the true age distribution of the

entire population in the Sanyati East cleared area.

The irregular nature of these distributions is evident, and perhaps the only conclusion is that the population is composed of younger rather than older individuals.

Accumulative numbers and biomass are shown in Fig. 94.

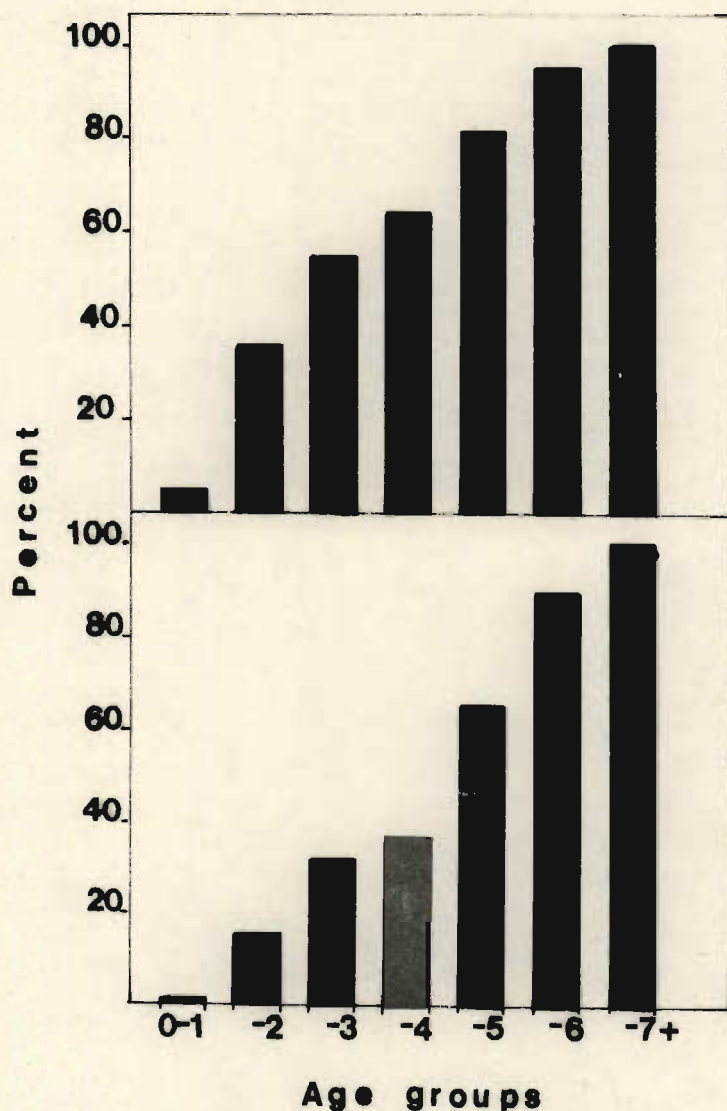


Figure 94: Accumulative numbers (a) and biomass (b) of the sample of M. dubia from the Sanyati East cleared area

The bulk of the sample population is comprised of individuals less than 6 years old, with a fairly even distribution between 2 and 6 years old. Consequently, the main biomass is comprised of the older individuals, with the 0 - 4 year olds comprising less than 40% of the total biomass. It is not possible to say for certain whether this population is in a stable state or not; the lack of juveniles indicates it is not increasing in size, but on the other hand it is composed essentially of young to middle age members, with few older ones, and appears not to be stagnating. Possibly, therefore, it is in a fairly stable but virile state.

D. STANDING CROP

In PART ONE, the stock of a typical cleared area (the Sanyati East cleared area) was described in terms of mean densities per species, and the individual species have now been described in terms of gross body composition (i.e. shell, viscera and water composition, wet and dry tissue mass, and mean energy content). Utilizing these statistics it is now possible to estimate the standing crops in this cleared area, and to calculate in broad terms the standing crops over a wider area of the lake.

METHODS

Surface areas at a lake level of 488 m.a.m.s.l. (the 1 600 ft contour - full supply level) were calculated for all designated cleared and uncleared fishing areas from

the Sanyati to the Sengwa Basin by Minshull, using contoured maps and an accurate planimeter (pers. comm.). Since he calculated areas according to various depth contours, and since the mussel crop extends to a depth of approximately 12 m, the areas covering a water depth from 4,6 m - 15,2 m (15 ft - 50 ft) at 488 m.a.m.s.l. were considered to approximate to the mussel grounds, as this is equivalent to 0,6 m - 11,2 m depth at 484 m.a.m.s.l. (normal operating level). To allow for the fact that mussels were not generally recorded from 0,6 m to approximately 2,5 m depth, which in terms of surface area will constitute some 17% of the total surface area, (assuming equal bottom gradient from 0,6 m - 11,2 m), but also allowing that mussels undoubtedly extend to at least 12 m depth (an extra 7% on the surface area, assuming equal bottom gradient), the actual surface areas given have been corrected to a more representative figure for the mussel grounds by subtracting 10% (17% - 7%) from the figures given by Minshull.

Using these surface area figures the standing crops of the fishing areas, which are also the main mussel grounds, were calculated in terms of numbers, total mass, wet viscera mass, dry viscera mass, and shell mass. For the Sanyati East cleared area, the density figures given in Table 2 of PART ONE were used to estimate standing crops for each species, while the overall mean values of all species combined were used to calculate approximately the additional standing crops available in the uncleared areas of Sanyati East. For the determination of standing crops in other areas arbitrary figures of 20 mussels m^{-2} and 250 g m^{-2} were chosen

as the basis for the calculation. Table 3 of PART ONE shows densities in various fishing areas ranged from 31 - 52 mussels m^{-2} and from 261 - 1 175 m^{-2} , and it was felt the arbitrary densities chosen would not result in either gross over- or gross under-estimation of the true standing crop. These densities are somewhat lower than the mean densities for Sanyati East cleared area. (29 mussels m^{-2} and 378 g m^{-2}), but this area is served by the Sanyati, second largest inflowing river, and is considered by Begg (1970) to be slightly more productive as a result.

RESULTS

The surface area of the Sanyati East cleared area with a depth of 2,5 m - 12 m at 484 m.a.m.s.l. is estimated as 30,5 km^2 , and that of the uncleared areas as 13,4 km^2 . Standing crops for the cleared area have been estimated for each species, and to this has been added an overall standing crop for all three species for the uncleared area, utilizing the mean density figures of the cleared area.

Table 20 shows that the Sanyati East cleared area supports a standing crop of over 11 000 tonnes of mussels (total mass) and if the contribution of the uncleared area is considered this rises to over 16 000 tonnes. The numbers of mussels present in both areas is estimated as being over one thousand million. It should be remembered that these figures do not take into account the contribution of Corbicula africana.

Table 20: Estimated standing crops of the Sanyati East cleared and uncleared areas. Biomass is given in tonnes, energy content in $\text{kJ} \times 10^6$. Figures in parenthesis express biomass as kg ha^{-1}

CLEARED AREA (30,5 km ²)						
SPECIES	TOTAL NUMBER (MILLIONS)	TOTAL BIOMASS	VISCERA BIOMASS	SHELL BIOMASS	DRY TISSUE BIOMASS	ENERGY CONTENT
C.m.	757	7 198 (2 360)	2 382 (781)	2 800 (918)	477 (156)	29 800
A.w.	110	4 506 (1 330)	1 416 (464)	1 639 (537)	283 (93)	14 588
M.d.	15	275 (90)	94 (31)	86 (28)	19 (6)	1 168
TOTAL	881	11 529	3 892	4 525	779	45 556
UNCLEARED AREA (13,4 km ²)						
ALL 3 SPECIES	268	5 065	1 710	1 988	342	20 013
GRAND TOTAL	1 149	16 594 (3 780)	5 602 (1 276)	6 513 (1 483)	1 121 (255)	65 151

The most vital figures, from a commercial production point of view, are those of viscera and shell mass - 5 600 tonnes and 6 500 tonnes respectively - a total of over 12 000 tonnes including both areas.

The significance of these figures can perhaps best be appreciated by comparing them with standing crop figures obtained by other workers for benthic invertebrates and fish. Mitchell (1976) sampled the fish fauna of marginal habitats of Lake Kariba in the Sanyati and Bumi Basins (Basin Five and Basin Four) and obtained a range for standing crop (all species) of 46 - 1 400 kg ha⁻¹ with a mean of 470 kg ha⁻¹. This is considerably lower than the overall mean obtained for the Sanyati East cleared area of 3 780 kg ha⁻¹ of mussels and some five times lower than the mean of 2 360 kg ha⁻¹ for one species alone, C. mossambicensis.

These differences are emphasized if one considers that Mitchell's findings applied to relatively small areas of the shoreline with higher than normal densities, and his figures are not applicable to the vast areas of shallow open water, where standing crops will be considerably less. Balon (1973), also sampling marginally but to deeper depth than Mitchell, obtained a range of 276 - 1 225 kg ha⁻¹ for Lake Kariba, with the highest mean for a single species, (Sarotherodon mortimeri) being 97 kg ha⁻¹. Thus it can be seen that standing crops of mussels outweigh quite considerably those of even the most common fish species, or even all species considered together in the most favourable habitats.

Extrapolation of these figures to the lake as a whole further emphasize the importance of the mussel crop. Balon (1973) estimated that the area of the lake inhabited by fish amounted to 25% of the area covering a depth of 0 m - 20 m (i.e. 33 422 ha) and on this basis he calculated the total standing crop of fish in the whole of Lake Kariba as 17 814 tonnes. If one considers that the mussels probably occupy some 50% of the depth area of 0 m - 20 m (i.e. 66 844 ha) and if for the whole lake one assumes a very conservative mussel density of 50 g m^{-2} (500 kg ha^{-1}), the total standing crop is 33 422 tonnes, almost twice that of fish. Using 250 g m^{-2} as a mean density, a quite realistic figure on the basis of present findings, the standing crop is 167 110 tonnes for the whole lake. This assessment is comparable with that derived from considering fishing areas on the South shore individually, summing the separate standing crops, and extrapolating the total (Table 21).

The total standing crop (whole mass) for these areas including the already calculated data for Sanyati East, amounts to 75 669 tonnes. The surface area, $280,2 \text{ km}^2$, is equal to 42% of the $668,4 \text{ km}^2$ (66,844 ha) estimated as occupied by mussels and hence an extrapolation of the standing crop of the 42% gives a figure of 180 164 tonnes whole mass for $668,4 \text{ km}^2$. Clearly this exceeds quite considerably the estimated biomass of fish in the lake. The total tonnage of mussels in the lake, including river estuaries, islands, etc., might well reach 200 000 tonnes.

Table 21 : Standing crops (tonnes) of individual fishing areas (cleared and uncleared) on the South shore of Lake Kariba. (Estimated using mean 20 mussels m⁻² and 250 g m⁻²)

AREA	km ²	NUMBER (MILLIONS)	TOTAL BIOMASS	VISCERA BIOMASS	SHELL BIOMASS	DRY TISSUE BIOMASS
Charara	21,2	424	5 300	1 789	2 080	358
Naodza	12,7	254	3 175	1 072	1 246	214
Gache Gache	30,0	600	7 500	2 532	2 943	506
Sanyati West	61,7	1 234	15 425	5 207	6 054	1 041
Sengwa West	71,3	1 426	17 825	6 018	6 996	1 203
Sengwa East	39,4	788	9 850	3 325	3 866	665
TOTAL	236,3	4 726	59 075	19 944	23 185	3 989
Including Sanyati East	43,9	1 367	16 594	5 603	6 513	1 120
GRAND TOTAL	280,2	6 093	75 669	25 547	29 698	5 109

A further indication of the size of the mussel standing crop is provided by the estimate of French (1980) of one and a quarter billion mussels stranded on approximately 250 km^{-2} of shoreline in January and February of 1980, when lake level dropped to 484,5 m.a.m.s.l. If a mean mass of 10 g per mussel is assumed the biomass estimate of these stranded mussels will be 12 500 tonnes over the whole lake. Since the area exposed represents only a fraction of the total area colonised by mussels a figure of 180 000 tonnes is easily visualized.

Considered numerically the mussels far outnumber fish densities, as estimated by Balon (1973). The standing crop of the Sanyati East cleared area amounted to a mean density of 28,9 mussels m^{-2} , or 289 000 ha^{-1} . The highest figure attained by Balon in his poisoning of bays was 63 900 ha^{-1} , and his average for all species was 36 633 ha^{-1} (excluding the abundant pelagic shoaling species, Limnothrissa miodon). Mitchell's largest mean standing crop for a single species was 3 707 ha^{-1} for Alestes lateralis, and 16 424 ha^{-1} for all species. Unfortunately it is not possible to compare the Lake Kariba standing crops of mussels with those of fish in Lake McIlwaine, i.e. a more productive lake than Lake Kariba, as no standing crop figures are available, although Marshall (1978 a) mentions that standing crops of juvenile fish in shallows can be as high as 250 kg ha^{-1} . Various standing crops for fish given by Balon (1973) for rivers and dams of Europe and North America range from 15 - 605 kg ha^{-1} - all below the standing crop of mussels in the Sanyati East cleared area.

Negus (1966) obtained comparable figures for mussels in a short stretch of the Thames. Her overall density for four species was 22 mussels m^{-2} (c.f. 29 mussels m^{-2} in the Sanyati East cleared area) and 2 922 kg ha^{-1} whole mass (c.f. 3 780 kg ha^{-1} in the Sanyati East cleared area). She estimated that the standing crop of mussels, excluding shells represented more than 90% of the biomass of the bottom fauna, and was twice that of the fish population. This latter aspect is in agreement with these findings, where the standing crop of shell free biomass in the Sanyati East cleared area (1 276 kg ha^{-1}) is approximately twice that of Balon's mean standing crop of 588 kg ha^{-1} for fish (and two and a half times that of Mitchell's mean of 470 kg ha^{-1}).

Negus's observation that mussels formed over 90% of the bottom fauna biomass appears to be applicable to Lake Kariba as well. In the Sengwa cleared area, at 2 m - 12 m McLachlan (1967) obtained benthic fauna densities of 105, 229 and 343 mg m^{-2} (shell and cuticle free dry mass) in 1963, 1964 and 1965 respectively. Compare these values with 25,5 g m^{-2} for mussels (dry tissue mass) in the Sanyati East. (His largest value was only 1,3% of this.) Despite the development of a varied population of snails since McLachlan's work was done (1963/1964) the bivalve population still dominates the benthic fauna as shown by Mitchell and Gahamadze (1976) in the Lakeside cleared area of the Sanyati Basin, where, from 3 m - 6 m, snails numbered 37 m^{-2} and heavier bivalves, (mostly C. africana), 44,1 m^{-2} (no mass figures are given). This sampling was done with a van Veen grab and it

is unlikely the mussel population was adequately sampled, as only one mussel species, A. wahlbergi, was recorded here, whereas three species occur. There is no doubt of the great importance of the bivalve crop in the benthic faunal community of Lake Kariba. This is consistent, as, unlike Lake McIlwaine, the crop is not subject to periodic drastic reductions caused by falling lake levels, and remains from year to year as the major benthic component at the depths it occupies.

E. PRODUCTION

Production represents a way of describing the dynamism of the population, and essentially indicates its vitality. It is variously described, and when applied to consumers is termed secondary production, which means the net production of consumer organisms, above respiration and excretion, in a community (Edmondson and Winberg, 1971). In more specific terms net production is the sum of the growth increments of all species of the population over a given period of time (Winberg et al, 1971)

Two types of approach to the study are possible. The first is a descriptive field study, such as this, where various parameters of the population, such as age and growth, structure, densities etc., are described through extensive field work and then utilized to determine net production of the particular population under study. This approach is an extremely valuable one, in that it allows the attainment of two objectives:-

- i.) the description of the population in various terms, which constitutes a considerable source of biological and management knowledge, and
- ii.) the calculations of production which stem from this fund of knowledge.

The second approach is a laboratory one, involved with rates of feeding, respiration, excretion etc., and in most cases the results are meaningless unless they can be related to field population characteristics of the animal or animals under study.

In this study, the primary aim of calculating production was to identify the most productive components of the population to enable best harvesting size to be determined, in order to exploit maximum production. A second objective was to determine the daily or annual turnover rate of material, since in a stable population production is balanced by mortality and production rate indicates the quantity of nutrients being recycled in the form of dead mussels. Such information would help assess their role in the nitrogen and possibly other cycles, and be of relevance in understanding their role in the ecosystem as a whole.

METHODS

In a population which reproduces continuously, the age groups or cohorts are indistinguishable, and it is impossible to follow their change in abundance with time.

To assess production of such a population it is necessary to use methods not requiring the recognition and following of a cohort. Most of the methods of estimating production of populations with continuous reproduction are based on the finite rate of growth of individuals, requiring the knowledge of the weight increment of the individual during its life span from hatching to death.

The generalised formula for production in a unit of time takes the form:

$$P = \frac{N_1 w_1}{T_1} + \frac{N_2 w_2}{T_2} + \frac{N_3 w_3}{T_3} \text{ etc.,}$$

where w means the weight increment of an individual, the numerals indicate different stages, and T is the time of duration of that stage. Most of the methods can be reduced to this generalized formula, but the method selected will depend on the nature of the organism and the material available (Winberg et al, 1971). Obviously the more complete the data the more precise the estimate. Alternatively, where gaps exist, the final estimates are approximate values and this should be indicated by the author.

The method selected for calculation of production was that provided by the formula:

$$P = ngw$$

(from Winberg et al, 1971), where n is the density of the

size or age group under consideration, g is the average specific growth rate of the group, and w is the mean mass of the group. Obviously this formula depends on a knowledge of growth. Production of the population per unit of time is then the sum of production of the single size or age groups. In this case age groups were selected rather than size groups as growth had been calculated on a yearly basis, making 365 days an obvious time interval for the calculations. The method is a basic one which can be applied to populations in which reproduction is continuous, and in which growth rate of size - age groups is known. Average specific growth rates were calculated using the formula :

$$g = \frac{1}{t} \ln \frac{w_2}{w_1}$$

which has been described earlier.

In addition to production rates, figures for the ratio of daily production to biomass (P/B co-efficients) are given , for comparison with useful data provided by Zaika (1973). Krebs (1972) considers that this ratio is a measure of maturity of an ecosystem, and therefore it also might be applicable to single populations. The higher the value, the greater the turnover rate in the population, which in itself could be a measure of instability. One would expect a developing population to have a high P/B co-efficient, and a more stable population to have a relatively lower value.

The range of P/B co-efficients quoted by Zaika, expressed as average diurnal values, is from 0,0003 - 0,03 ,

with highest values attained by short - lived species with high turnover rates.

RESULTS

The three species are dealt with separately first, and then production rates of all three are summed later to provide an overall figure for the Sanyati East cleared area.

1. Caelatura mossambicensis

Calculated production rates for various age groups are shown in Table 22. Energy content has been calculated from dry tissue mass minus ash mass.

The total production for all age groups was determined as $0,2454 \text{ g m}^{-2} \text{ day}^{-1}$ (whole mass), or $2,454 \text{ kg ha}^{-1} \text{ day}^{-1}$. This equates to a daily production rate of $7\frac{1}{2}$ tonnes (whole mass) per day over the whole Sanyati East cleared area (approximately 0,5 tonnes dry mass, and 2,5 tonnes viscera mass). Negus (1966) obtained a production figure of $0,056 \text{ g m}^{-2}$ for body weight (approximately $0,168 \text{ g m}^{-2}$ total mass, assuming body mass is equal to a third of total mass), for three species in the Thames.

Relative rates of production for each age group are shown graphically in Fig. 95 and Fig. 96.

Table 22: Calculated production rates of C. mossambicensis in the Sanyati East cleared area

AGE GROUP	SIZE mm	WHOLE MASS kg ha ⁻¹ day ⁻¹	ACCUMULATIVE WHOLE MASS	DRY TISSUE kg ha ⁻¹ day ⁻¹	ACCUMULATIVE DRY TISSUE	ENERGY CONTENT kJ ha ⁻¹ day ⁻¹
0 - 1	-22,3	,0064	,0064	,0003	,0003	7,405
1 - 2	-35,4	,8527	,8591	,0633	,0636	1 335,752
2 - 3	-43,0	,8259	1,6850	,0599	,1235	1 263,335
3 - 4	-47,6	,5220	2,2070	,0369	,1604	777,759
4 - 5	-50,3	,1993	2,4063	,0139	,1743	292,601
5 - 6	-51,9	,0306	2,4369	,0021	,1764	44,581
6 - 7	-52,9	,0097	2,4466	,0007	,1771	14,107
7 - 8	-53,4	,0058	2,4524	,0004	,1775	8,288
8 - 11+		,0020	2,4544	,0001	,1776	2,930
TOTAL DAY ⁻¹		2,4544		,1776		3 746,763
TOTAL ANNUM ⁻¹		895,8560		64,8240		1,368 x 10 ⁶
kg 30,5km ⁻² day ⁻¹		7 485,9200		541,6800		11,302 x 10 ⁶

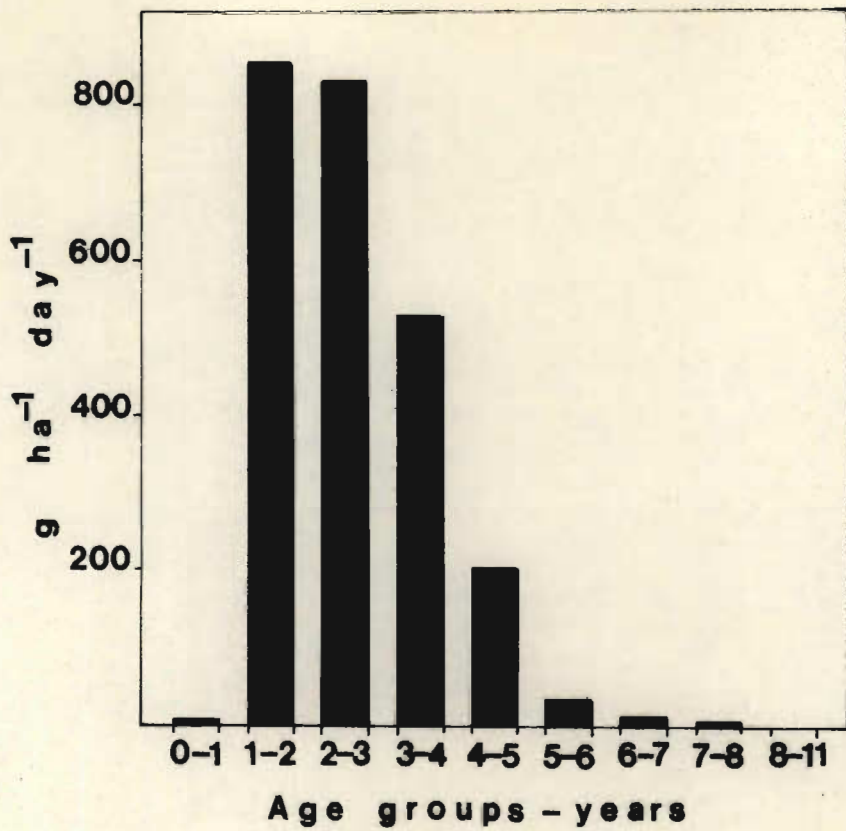


Figure 95: Relative production rates (whole mass) for different age groups of C. mossambicensis

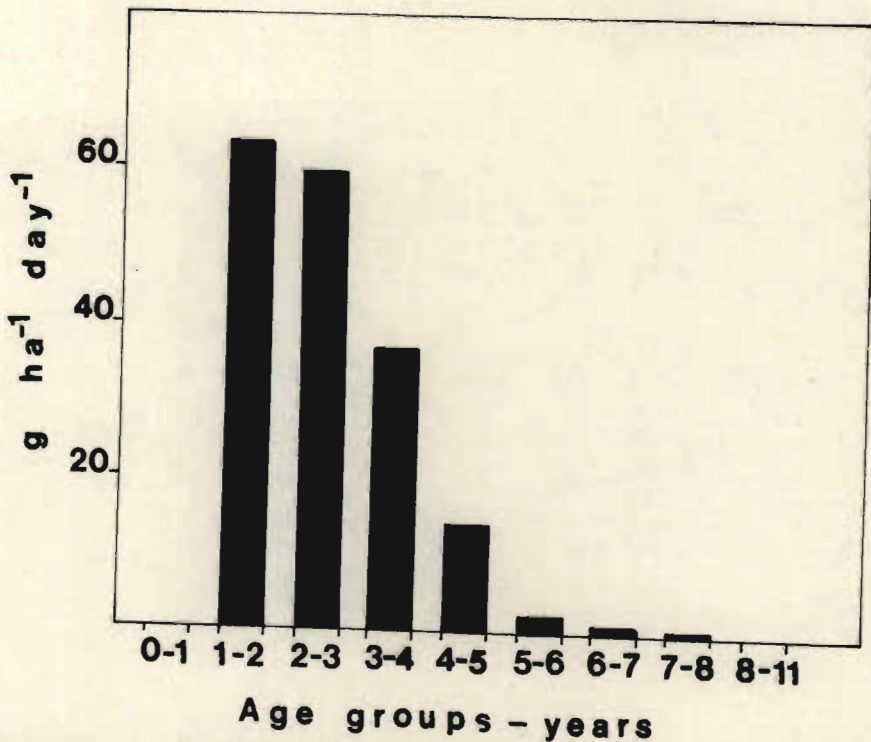


Figure 96: Relative production rates (dry tissue mass) for different age groups of C. mossambicensis

Quite clearly the most productive years of the population are from one to four years (22 mm - 48 mm), after which production rates fall off rapidly. Greatest production rates are attained by ages one to three. Production rate in the first year group is very low because of the low densities of this age group. The important contribution of the early age groups to total production is also seen when accumulative production is plotted (Fig. 97).

The proportional contribution to total production, represented by the shaded area, is negligible from age 5 onwards. Approximately 90% of the total production is contributed by the 0 - 4 age group, and the remaining 10% by mussels older than 4.

The production to biomass ratio (P/B co-efficient) for this age group (0 - 4) calculated by dividing their total daily production ($0,2207 \text{ g m}^{-2} \text{ day}^{-1}$) by the mean density of this age group ($140,4 \text{ g m}^{-2}$), was 0,0016, while that of the 0 - 5 age group was 0,0013, and for the 0 - 7 age group it was 0,0012. These values are of interest in that they approximate to the values provided by Zaika (1973) of specific production (C, equivalent to P/B) as a function of a life span of 6 - 7 years old. Zaika calculated the C value of the two species, Acmaea testudinalis, (Barents Sea), and Dreissena polymorpha, (Kuibyshev reservoir) as 0,0011 - 0,0013 and 0,0014 respectively. If one considers that over 90% of the biomass of C. mossambicensis is composed of individuals up to 7 years old. (Fig. 80) perhaps the similarity in values is not surprising.

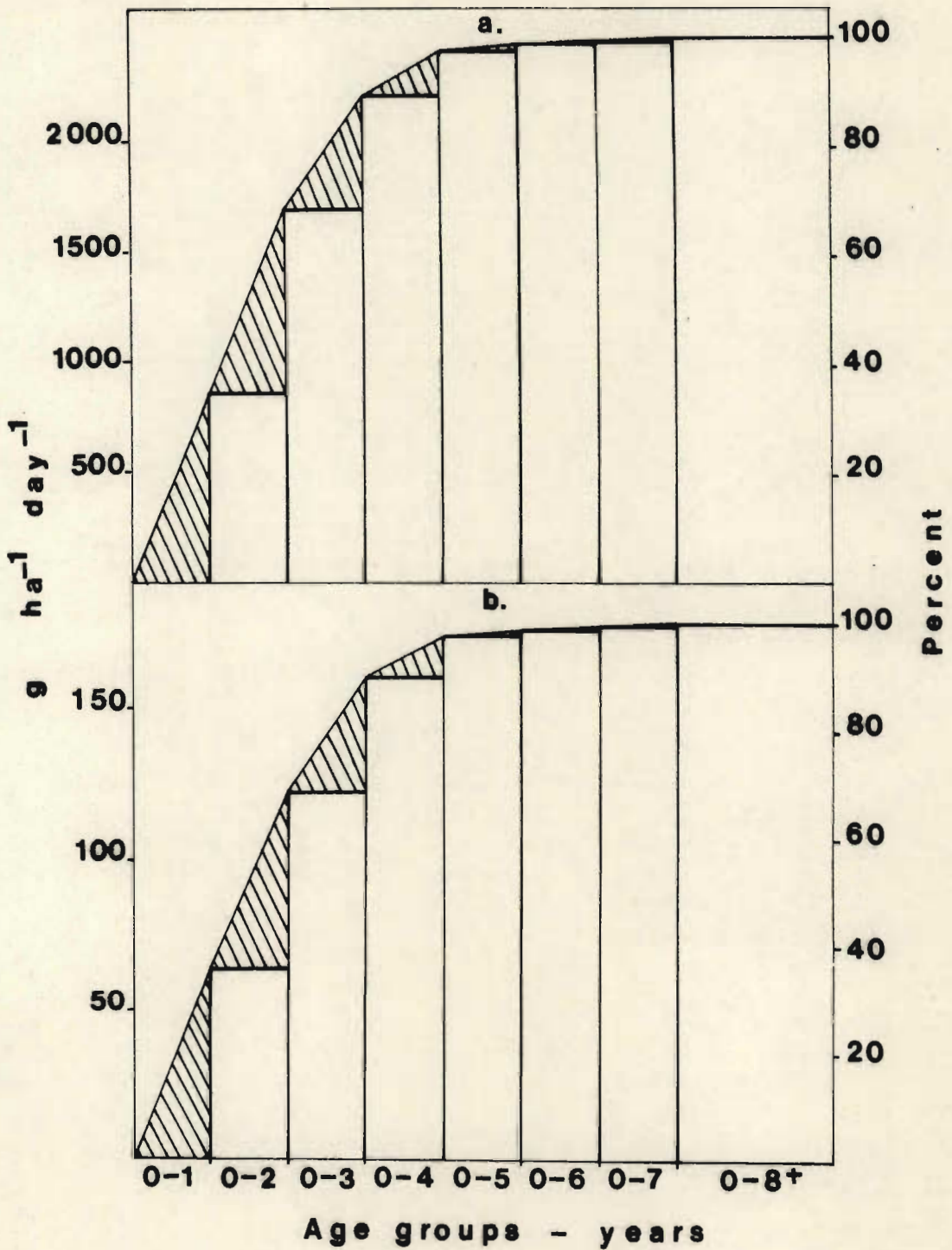


Figure 97: Accumulative production for different age groups of *C. mossambicensis* : whole mass (a), and dry tissue mass(b)

The P/B ratio for all age sectors of C. mossambicensis was calculated as 0,0011. This value falls within the range of 0,0035 - 0,00035 given by Zaika for molluscs with life spans from 6 - 13 years. The highest P/B co-efficient was 0,027 in age group 0 - 1. The values given by Zaika apply to temperate zone marine and freshwater species, but in view of the fact that Lake Kariba mussels experience a slow growing or nil growth season comparable to a similar season in Northern climes (winter) there is some justification in comparing them with values presented here. In general there is an inverse relationship between specific production and individual life span (Zaika, 1973) and since the bulk of the C. mossambicensis population only reaches 7 years the more correct co-efficient for comparative purposes with other species is probably 0,0012.

2. Aspatharia wahlbergi

The calculated production rates for various age groups are shown in Table 23.

Total production for all age groups was assessed as 0,0768 g m⁻² day⁻¹ (whole mass), or 0,7676 kg ha⁻¹ day⁻¹. Total production over the whole of the Sanyati East cleared area therefore amounts to some 2,3 tonnes whole mass per day. This is approximately 71% of the production rate obtained by Negus (1966) for A. anatina in the Thames (0,108 g m⁻² day⁻¹). However , whole mass standing crop of A. anatina was some 32% higher than that of A. wahlbergi, which probably accounts for the difference in rates between these two species.

Table 23: Calculated production rates of A. wahlbergi in the Sanyati East cleared area

AGE GROUP	SIZE mm	WHOLE MASS kg ha ⁻¹ day ⁻¹	ACCUMULATIVE WHOLE MASS	DRY TISSUE kg ha ⁻¹ day ⁻¹	ACCUMULATIVE DRY TISSUE	ENERGY CONTENT kJ ha ⁻¹ day ⁻¹
0 - 1	-38,2	,0994	,0994	,0038	,0038	68,399
1 - 2	-55,2	,0591	,1585	,0029	,0067	52,702
2 - 3	-66,5	,1500	,3085	,0086	,0153	154,882
3 - 4	-75,7	,1840	,4925	,0191	,0344	344,759
4 - 5	-82,0	,1330	,6255	,0097	,0441	175,393
5 - 6	-86,0	,0722	,6977	,0055	,0496	99,208
6 - 7	-88,7	,0307	,7284	,0024	,0520	42,948
7 - 8	-90,5	,0186	,7470	,0015	,0535	26,874
8 - 9	-91,7	,0101	,7571	,0008	,0543	14,693
9 - 10	-92,4	,0059	,7630	,0005	,0548	8,623
10 - 12	-93,3	,0030	,7660	,0002	,0550	4,479
12 +		,0016	,7676	,0001	,0551	2,344
TOTAL DAY ⁻¹		,7676		,0551		995,305
TOTAL ANNUM ⁻¹		280,1740		20,1115		363 286
kg 30,5 km ⁻² day ⁻¹		2 341,1800		168,0550		3,036 x 10 ⁶

This suggests that if biomass densities were equal very similar production rates would have been attained.

The relative rates of production for each of the age groups are shown graphically in Fig. 98.

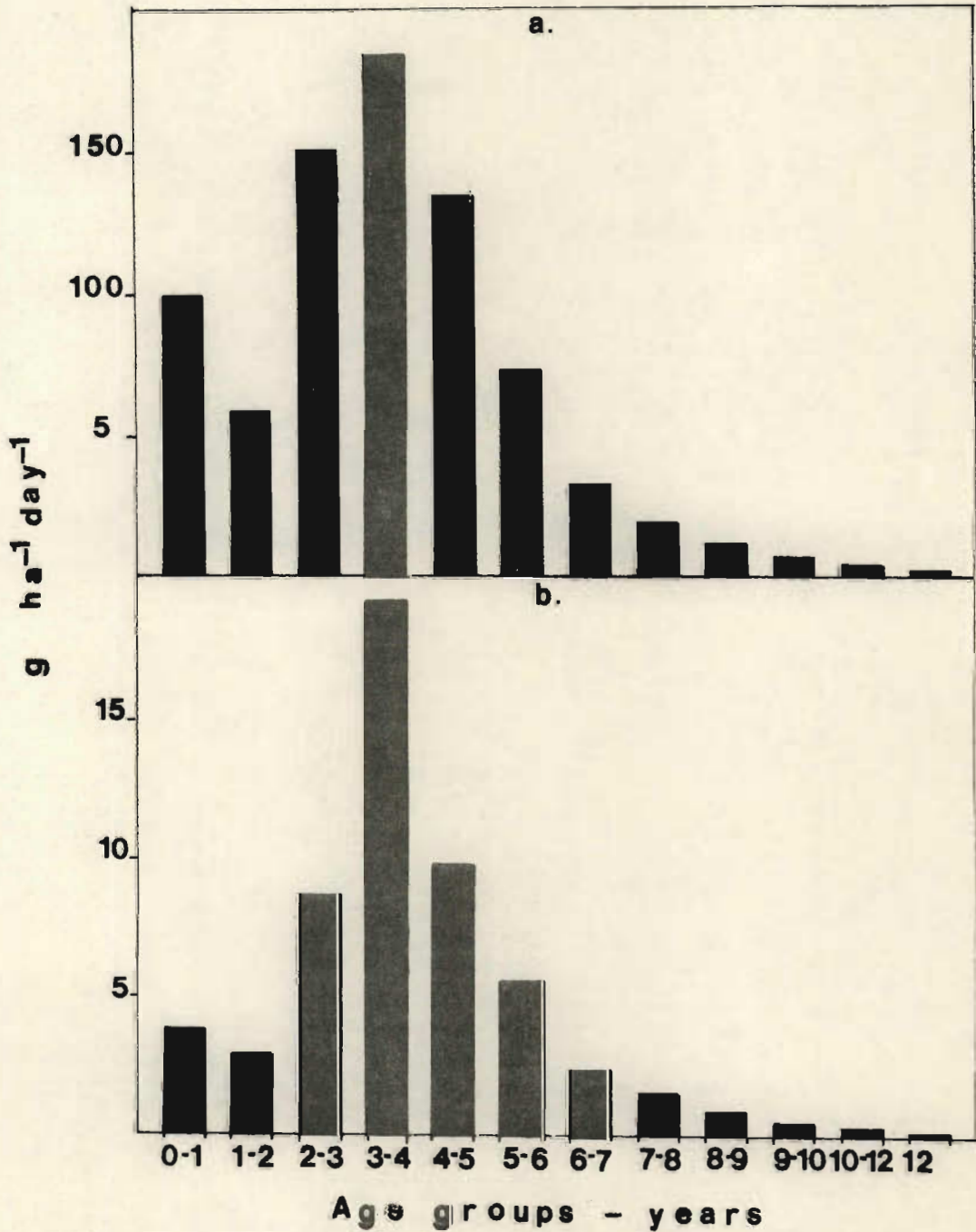


Figure 98: Relative production rates for different age groups of *A. wahlbergi* : whole mass (a), and dry tissue mass (b)

The most productive one year age groups were those from 2 - 6 years old, or from 55 mm - 86 mm . Beyond this age production rates dropped rapidly, as shown in the graphs of accumulative production (Fig. 99.)

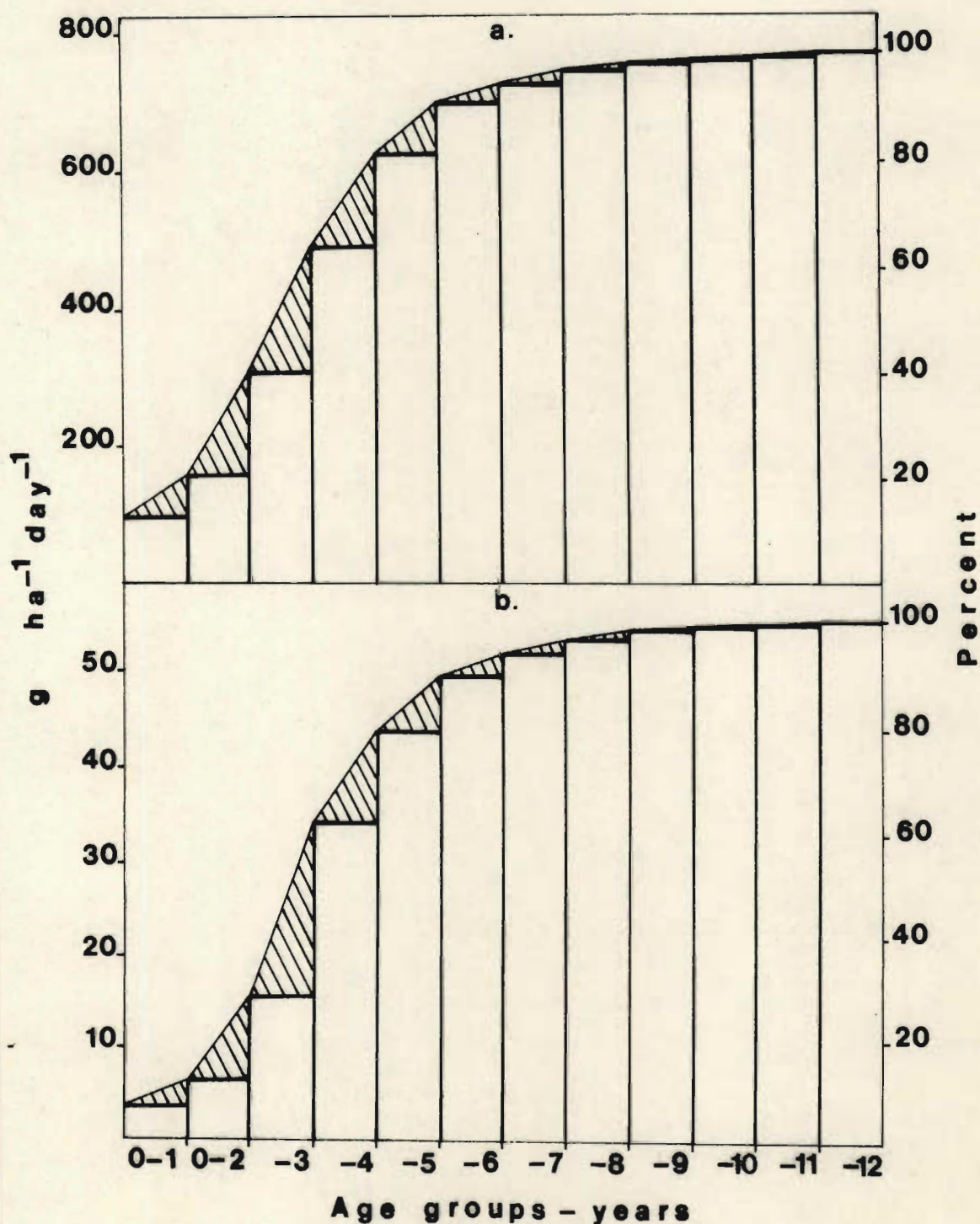


Figure 99: Accumulative production for different age groups of *A. wahlbergi* : whole mass (a), and dry tissue mass (b)

The graph shows the negligible proportion contributed by age groups over 6, and the major portion (90%) contributed by the 0 - 6 year age group. Reference to Fig. 86, 87 and Fig. 88 , showing age distribution of the population, and accumulative age distribution respectively, shows that mussels over 6 years old contribute substantially to the population, forming 28% of the population numerically, and 45% by mass, and yet they account for only 10% of the production. The overall daily production rate ($0,0768 \text{ g m}^{-2}$) is more than three times lower than that of C. mossambicensis even though density (g m^{-2}) is only half (32,8% as opposed to 65,0% - Table 2 , PART ONE). Obviously the lower production rate is not entirely due to a lower density, but is partly attributable to the age distribution of the population, with a large portion of the biomass comprised of relatively unproductive individuals.

The high productivity of the younger age groups is indicated by the P/B co-efficient ($0,0013$) for the 0 - 6 year old age group ($\frac{0,0636}{47,6147}$) which compares favourably with the values of $0,0016$ and $0,0013$ for the most productive age groups of C. mossambicensis, i.e. the 0 - 4 year, and 0 - 5 year age groups. The mean P/B co-efficient for all age groups was calculated as $0,0008$, much lower than that of C. mossambicensis ($0,0011$) which also suggests that the unproductive group over 6 years tends to lower the overall production rate quite considerably. However, A. wahlbergi is a longer lived species than C. mossambicensis , and , in accordance with Zaika's observation that specific production is inversely related to longevity, can be expected to have

a lower P/B co-efficient. The value of 0,0008 is similar to that of 0,0005 for A. anatina (Negus, 1966) which reaches 11 years, and falls well within the range of 0,0003 to 0,03 recorded by various workers on various species. As with C. mossambicensis, the highest P/B co-efficient recorded was in age group 0 - 1, with a value of 0,030.

3. Mutela dubia

Although the standing crop of this species in the Sanyati East cleared area was calculated as approximately 275 tonnes, the actual density was extremely low ($0,5 \text{ m}^{-2}$) and less than 20 mussels were recorded in the grid transect samples. Thus the production calculations are based on a very low representative sample and probably represent only a rough estimate of the actual production rates.

The daily production rate was calculated as $0,0119 \text{ g m}^{-2} \text{ day}^{-1}$, which equates to 363 kg day^{-1} (whole mass) over the whole of the Sanyati East cleared area. This rate is much lower than that of C. mossambicensis and A. wahlbergi (0,2454 and 0,0768, respectively), and represents only 3,6% of the total daily production. Negus (1966) obtained a similar production rate for Unio tumidus (approximately 0,014 for whole mass) and a slightly higher production rate for Unio pictorum. No relative or accumulative production graphs were drawn for M. dubia because of the scant data. In view of the fact that of the few mussels recorded the majority were less than 5 years old, a fairly high overall P/B co-efficient was expected.

Table 24: Calculated production rates of M. dubia in the Sanyati East cleared area

AGE GROUP	SIZE mm	WHOLE MASS kg ha ⁻¹ day ⁻¹	ACCUMULATIVE WHOLE MASS	DRY TISSUE kg ha ⁻¹ day ⁻¹	ACCUMULATIVE DRY TISSUE	ENERGY CONTENT kJ ha ⁻¹ day ⁻¹
0 - 1	-53,4	,0546	,0546	,00376	,00376	79,325
1 - 2	-68,1	,0230	,0776	,00141	,00517	29,762
2 - 3	-78,2	,0157	,0933	,00086	,00603	18,125
3 - 4	-84,3	,0071	,1004	,00035	,00638	7,451
4 - 5	-88,1	,0094	,1098	,00046	,00684	9,670
5 - 6	-90,3	,0061	,1159	,00029	,00713	6,195
6 +		,0030	,1189	,00014	,00727	2,930
TOTAL DAY ⁻¹		,1189		,00727		153,459
TOTAL ANNUM ⁻¹		43,3985		2,6536		56 013
kg 30,5 km ⁻² day ⁻¹		362,6450		22,1736		468 049

This was calculated as 0,0012 , which agrees with the figures obtained for the other two species for their young to middle-age groups. The youngest age group had a co-efficient of 0,31 which is in agreement with results for C. mossambicensis and A. wahlbergi.

4. Total production rates

Total production rates for the Sanyati East cleared area, and the relative contributions of each species in relation to their total biomass are presented in Table 25.

The total daily production (whole mass) for the Sanyati East cleared area is calculated as over 10 tonnes per day , or approximately 3,4 tonnes of wet body mass (viscera). These are obviously approximate estimates, as most production calculations have embodied in them the sampling and experimental errors of the various steps taken along the way. While a daily production rate of 10 tonnes of material resulting from growth alone might seem an extravagant figure, this reduces to a less spectacular figure of 0,334 g m⁻² day⁻¹. The P/B co-efficient calculated from the overall production rates and the overall calculated standing crop is calculated as 0,0009 , which agrees with similar values calculated by Zaika (1973) for various mollusc species, including bivalves. Unfortunately the only really comparative work is that of Negus (1966) and until such time as more studies appear on this aspect of freshwater bivalves the nature of the production reported here in relation to other populations will remain unknown.

Table 25: Total production in the Sanyati East cleared area, and percentage proportions of production in relation to percentage proportions of biomass

	WHOLE MASS		DRY TISSUE		ENERGY CONTENT	
	PRODUCTION %	BIOMASS %	PRODUCTION %	BIOMASS %	PRODUCTION %	BIOMASS %
<u>C. mossambicensis</u>	73,4	65,0	74,0	61,2	76,3	61,2
<u>A. wahlbergi</u>	23,0	32,8	23,0	36,5	20,3	36,5
<u>M. dubia</u>	3,6	2,2	3,0	2,4	3,1	2,4
TOTAL						
kg ha ⁻¹ day ⁻¹	3,34		0,240		(kJ) 4 897,62	
kg ha ⁻¹ annum ⁻¹	1 219,00		87,6		(kJ) 1,787 x 10 ⁶	
kg 30,5 km ⁻² day ⁻¹	10 187,00		732,0		(kJ) 14,9377 x 10 ⁶	
P/B co-efficient	0,0009		0,0009			

Negus obtained a production rate of $0,14 \text{ g m}^{-2} \text{ day}^{-1}$ (whole mass) which represents 41% of the value presented here. However her standing crop was only 77% that of Lake Kariba's, (kg ha^{-1} whole mass), which suggests that at a similar density of mussels her production rate would have been $0,18 \text{ g m}^{-2} \text{ day}^{-1}$, or slightly more than half (53%) that of the rate reported here. In relation to the Thames, therefore, Kariba has a much higher rate of production. Zaika (1973) quotes figures of $4,2 \text{ g m}^{-2} \text{ day}^{-1}$, $5,46 \text{ g m}^{-2} \text{ day}^{-1}$, and $1,79 \text{ g m}^{-2} \text{ day}^{-1}$ for three species from the Sea of Azov, in Russia. (Mytilaster lineatus - life span 3 years, Cardium edule - life span 5 years, and Abra (Syndesmia) ovata - life span 4 years.) Other figures given are $2,52 \text{ g m}^{-2} \text{ day}^{-1}$ (Dreissena polymorpha - Kuibyshev reservoir - life span 6 years) and $0,79 \text{ g m}^{-2} \text{ day}^{-1}$ (Lacuna pallidula, Barents Sea). These simply provide data on the degree of production that is attainable, and obviously cannot be compared with the Lake Kariba figures.

The relationship of the percentage proportions of production and biomass are interesting (Table 25) and appear to exemplify the general rule that specific production is related to the age distribution of the population (Zaika, 1973). For example, A. wahlbergi formed 36,5% of the biomass (dry tissue) but only 23% of the production (a ratio of 1,6 : 1). Conversely, C. mossambicensis formed 61% of the biomass but contributed a greater proportion to production (74%) than its contribution to the biomass (a ratio of 0,8 : 1). The larger number of older age groups in the A. wahlbergi population is probably the reason for the lower contribution

to production in relation to biomass, while the converse situation applies to the C. mossambicensis population. Individual growth rates, maximal life span and age composition operate together to determine the value of specific production and the indications are that the annual average diurnal specific production (C) decreases the longer the population lives. Postulating this, Zaika (1973) constructed a model to test the theory and derived one which accurately described actual data, and explained the behaviour of C as a function of T (age in years). The P/B co-efficients, or C, for the three species discussed here is accurately described by this model in terms of their ages, and the overall age distribution of the populations. This can be shown by considering the overall P/B co-efficients of Kariba mussels and the general average life span of the mussel community. If one considers the overall P/B co-efficients of Kariba mussels and the general average life span of a population to be the age encompassing approximately 95% of the population, then general life spans of 10 years for A. wahlbergi and 7 years for C. mossambicensis are obtained (Fig.87 and Fig. 81). A less reliable figure of 7 years is proposed for M. dubia, on the basis of the small sample (Fig. 94). This gives an overall mean general life span of almost 8 years for the three species. According to Zaika's model, and taking into account the shape of the age distribution curves of the three species, a specific production of between 0,0009 and 0,001 is predicted by his model. This is in agreement with the figure of 0,0009 actually obtained for the overall specific production rate of the Sanyati East populations.

DISCUSSION

Zaika (1973) writes: "The data obtained from natural mollusc populations indicate that the very youngest groups usually do not predominate. Most age distribution curves are bell-shaped with the bell situated in the left part of the curve. Clearly such populations are in a transitional, rather than stationary stage." Obviously the pattern of age distribution as reported here for C. mossambicensis and A. wahlbergi is not unique, and has also been recorded for a wide variety of species. Both A. wahlbergi and C. mossambicensis age distributions are bell-shaped, (see Fig. 79 and Fig. 86), with the bell skewed to the left part of the curve. Both species are characterised by a lack of the youngest age groups, and the "bell" is composed of young to middle-age groups. Zaika also notes: "To some extent the observed condition can also be attributed to a poor catch of small specimens". To a certain extent this is probably true, but there can be little doubt that the Sanyati East cleared area has a very small population of juveniles in relation to adults. Several methods of sampling consistently yielded large samples of juvenile to adult Corbicula africana which attain an average size of approximately 20 mm, but no comparable sizes of the three mussel species studied were collected. This situation contrasted with that on Lake McIlwaine, where juveniles were frequently recorded on the unstable drawdown zone, as the lake level dropped.

Presumably, by "transitional", Zaika does not

mean unstable, or developing or evolving, but virile or vigorous. A developing population should be characterised by a large population of recruits as found on many Lake McIlwaine beaches. The age structure of the Kariba population can be characterised as young and vigorous. This is shown by the fact that the age - production curves are virtually identical to the age - frequency curves, as are the accumulative frequency and production curves. Clearly the bulk of production is contributed by the younger (not youngest) sector.

While this is true of both main species, the A. wahlbergi population has a greater proportion of older members relative to younger members, than C. mossambicensis. This has the effect of lowering the overall production rate of the population, indicated by the lower specific production or P/B ratio. Harvesting would have the effect of removing these older less productive individuals and would probably improve the overall production rate, since they would probably be replaced by younger individuals. If harvesting is to be governed by consideration, amongst other things, for production rates, then clearly the accumulative production curves will indicate at what size or age the mussels start becoming unproductive. They become dispensible at this age since they are no longer contributing usefully to the population in terms of production, relative to time. Their intake of food is utilized mostly for processes other than growth and their competition for food resources and living space becomes a handicap to growing individuals.

Reference to the graphs for C. mossambicensis suggests that this situation occurs at an age of 5 years, or a size of 50 mm. Beyond this size production is negligible, and little would be gained in yield in relation to time beyond this age. The 0 - 5 years age group contributes 98% of the total production and constitutes 84% of total biomass. In considering harvesting size a second factor to consider is age at maturity. C. mossambicensis starts breeding at \pm 23 mm, or an age of 1 year. By the end of their first year of breeding life, by which time they will probably have produced several broods, they have reached a size of approximately 36 mm. The 0 - 2 year age group constitutes less than 10% of the biomass, and contributes approximately 35% of the production. Obviously, from a cropping point of view, it would be wise not to crop before the mussels have had an opportunity to breed, and this suggests that \pm 36 mm should be the size at which cropping commences. Some production would be sacrificed in the interests of maintaining a breeding population. Thus a harvesting age of 2 - 5 years suggests itself, as this allows for a period of breeding and takes advantage of maximum production. The age group 2 - 4 provides 55% of production, 2 - 5 provides 63%, 2 - 6 provides 64,3% and 2 - 7 provides 64,7%. Clearly beyond 5 years little gain is made, and the law of diminishing returns comes into effect. C. mossambicensis is the most important species in all potential fishing areas, and harvesting practice will essentially be guided by how best this species can be exploited.

With regard to A. wahlbergi, the point at which

the mussels are no longer relatively productive is less clear-cut than C. mossambicensis because of the greater number of older age groups. However, since one is looking for the greatest production in the shortest space of time, the 0 - 4 age group (up to 76 mm) offers approximately 60% of production and the 0 - 5 age group (up to 82 mm) offers approximately 80%. The species appears to start breeding at 64 mm, or an age of 2 - 3. Allowing it one season of breeding (since it is a seasonal breeder) minimum harvesting size would be approximately 73 mm, or almost 4 years. This age group contributes only 24% of the biomass but over 60% of the production. Clearly harvesting conditions are not as favourable for this species as they are for C. mossambicensis, if allowance is to be made for breeding. Only 17% of the total production (whole mass) will be utilized if a best harvesting size is fixed as 73 mm - 82 mm. (4 - 5 years old). Fixed at 4 - 6, it is 27%, from 4 - 7 it is 31%, 4 - 8 it is 33% and so on, the returns diminishing rapidly. It is debatable whether there is much point in placing restrictions on the cropping of this species, since the return over a long period will be small. For example, a five year period will allow a return of only 17% of the total production for this period. Doubtless this production rate will improve as a probable result of increased growth rate and densities if the older, less productive section is removed, but the increase, at a guess, is not likely to be more than 15% or 20%. Placing size restrictions on one species that differ from the size restrictions on a smaller and more common species being fished concurrently would be virtually impossible to enforce. A practical proposition, if some form of protection for this

species was desired, would be protected areas in the middle of, or adjacent to, the fishing grounds, or to implement a closed season from December to March, during their breeding season.

M. dubia formed a minor segment of standing crops in nearly all areas sampled, and here again it is debatable whether any sort of restrictions should be imposed on its cropping. The species starts breeding from 1 - 2 years of age at a length of \pm 52 mm. Allowing it a year of breeding would take it to a length of approximately 70 mm.

Obviously any remarks made concerning the population are made on the assumption that the populations are in a stable state, and the remarks will be equally valid in the future. Krebs (1972) has pointed out that populations are very rarely in a state of immobility, but are almost constantly changing. In most cases increasing populations typically have a predominance of the younger age groups, while stable or declining populations tend to have fewer young organisms. As already discussed, the Sanyati East populations appear to be stable, indicated by a lack of young and old, and a general preponderance of middle-age mussels. The length - frequency structure of the C. mossambicensis sample population collected in October 1978 has been compared with that of February/March, 1977 (Fig. 21 , PART ONE), and was found to be similar , with comparable mean lengths of 41,6 mm and 40,9 mm, not differing significantly at the 95% level. When described in terms of age this sample had a structure very similar to the age

structure found in February/March 1977, some 20 months earlier. (Fig. 100).

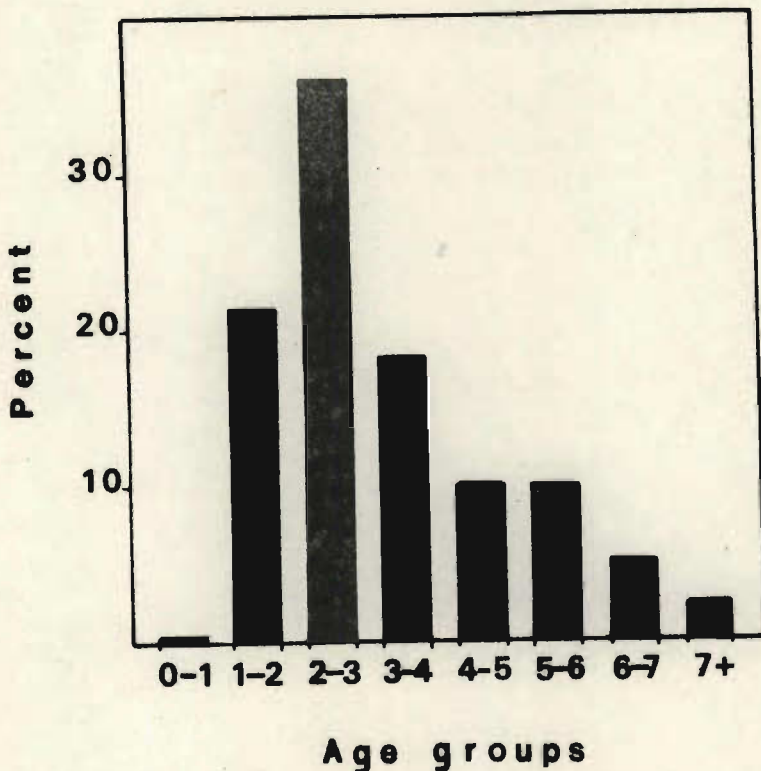


Figure 100: The age structure of the sample population of C. mossambicensis from the Sanyati East cleared area, October 1978

The graph shows that there is a similar lack of young, the three dominant age groups are from 1 - 4 with 2 - 3 outstanding as in the 1977 sample, and there is a similar, although not identical lack of older mussels. The structure retains its bell shape. There has been some shifting of age groups, but the basic structure is similar, and exemplifies the essential stability of the population over a period of time. Only 18 A. wahlbergi were collected in October 1978, and the sample is too small to make a worthwhile comparison. However, the two dominant age groups in

this sample were the 2 - 3 and 3 - 4 year age groups, similar to the 1977 sample. The environment of the mussels in the lake - where annual temperature ranges are not great, exposure does not affect the bulk of the population, food reserves are presumably very similar from year to year, and mortality from predation is virtually nil - is one where a general state of equilibrium probably exists from year to year, with probably only minor changes in population structure occurring. Greater changes might occur in river estuaries where substrate conditions are less stable.

In view of the obvious importance of mussels as benthic animals a few suggestions for further research are put forward here. Work in these fields would contribute materially to our knowledge on African freshwater mussels.

On the morphological side , a field of interest is the relation of external dimensions to sex and habitat. Several authors have commented on the apparent relationship of shape to habitat. (eg. Wilbur and Yonge, 1964) and on the possibility of sexual differences in shape. (Heard, 1975). An evaluation of the evolution of characters to meet the demands of the physical environment would contribute appreciably to a better understanding of the process of natural selection. Mussels could provide an accessible and transportable subject to test hypotheses in this field.

Another field which could prove productive is the seasonal analysis of biochemical composition of mussel tissue, as this probably relates strongly to the physical

and chemical composition of the environment. Mussels are detritivores on the lowest step of the second trophic level, and as such could prove useful indicators to the status of nutrient supplies and food reserves. The usefulness of this approach in identifying unproductive periods has already been shown by Cochrane (1978) in seasonal biochemical analysis of the Lake Kariba freshwater sardines.

A third field which needs elucidating is the growth rate of mussels once they have left the host.* A greater degree of accuracy in production calculations would then be achieved.

Some recent papers published (e.g. Marshall, 1975; Jubb, 1976; Appleton, 1979) indicate an increasing interest in Southern African bivalves. Doubtless the stimulus needed to create an even greater awareness of this group would be provided if they became a commercial and economic resource in the same way the mussels of the Mississippi Valley were a valuable resource in the early part of this century. Quite clearly a group of animals whose standing crop might be anything from two to three times that of the marginal fish fauna is an element which cannot be ignored in future biological deliberations.

* Forty M. dubia collected on the draw-down zone at Pelican Point in July 1980 represented new elements colonizing a littoral zone decimated by draw - down the previous year. Rising lake level had re-submerged the exposed beach from 8th - 14th December 1979, and hence the oldest mussels could not be older than 7 months. (December 1979 - July 1980). They measured 10 mm - 29,8 mm in length (mean - 19,5 mm).

SUMMARY

1. Wet viscera mass comprises 33% - 34% of total mass, while shell mass comprises 39% - 40% in C. mossambicensis and A. wahlbergi, and 31% in M. dubia. The remaining mass is comprised of loose water.
2. Linear relationships were observed for the function of length against height and width, and height against width. A single possible exception to linearity was the length - height relationship of M. dubia.
3. Single regressions adequately described the relationship of length - mass for A. wahlbergi and M. dubia, but not for C. mossambicensis.
4. The gross biochemical composition of a sample of the three species was water 80%; fat 1,14% - 1,4%; ash 1,8% - 4,6%; protein 8,8% - 9,8%. Seasonal variation in biochemical values is likely, and these are not mean values.
5. Proteins of the mussels contained 18 of the 24 known naturally occurring amino acids. Nine of the 10 known essential amino acids were present.
6. Calorific values of ash-free dry mass for the three species ranged from 20,93 - 24,70 kJ g⁻¹.
7. The C. mossambicensis population is composed mainly of mussels under 5 years old (87%). The major portion is composed of individuals 2 - 5 years old, giving the population a bell-shape, characteristic of mollusc populations. Mussels 0 - 1 years were extremely scarce.
8. Growth in C. mossambicensis is rapid for the first few years but slows down after age 4.
9. The A. wahlbergi population has a bell-shaped age

- distribution, with the "bell" to the left of the curve. There are relatively more older age groups than in the C. mossambicensis population, with mussels over 5 years old forming nearly 40% of the population by number, and nearly 60% by mass. Mussels 0 - 2 years old were scarce.
10. The growth cessation marks on the shells of A. wahlbergi were shown to be annual marks (annuli). A season of slower or nil growth occurs in summer.
 11. The small sample of M. dubia obtained indicated that the population is composed predominantly of individuals under 6 years old. Mussels 0 - 1 years old were very scarce.
 12. Total standing crop of the Sanyati East cleared area (30,5 km²) was calculated as 11 529 tonnes whole mass (62% C. mossambicensis; 35% A. wahlbergi; 2% M. dubia). This was equivalent to 3 780 kg ha⁻¹.
 13. The Sanyati East uncleared area standing crop was estimated approximately as 5 065 tonnes, giving the whole of Sanyati East an estimated standing crop of 16 594 tonnes whole mass. This was equivalent to 5 602 tonnes viscera, and 6 513 tonnes of shell mass.
 14. The standing crop of the designated fishing areas from the Sanyati Basin to Sengwa West was estimated at approximately 75 669 tonnes (whole mass). Standing crop for the lake as a whole in the areas likely to be occupied by mussel beds was estimated as 167 000 - 180 000 tonnes (whole mass).
 15. Standing crop of mussels was estimated as being at least two or three times more than that of the marginal fish fauna.

16. Net secondary production in the Sanyati East cleared area was calculated as 10,19 tonnes day⁻¹ whole mass (3,34 kg ha⁻¹ day⁻¹), contributed by C. mossambicensis (73,5%), A. wahlbergi (23%) and M. dubia (3,6%).
17. The gross energy content production rate was estimated as 4 897,62 kJ ha⁻¹ day⁻¹.
18. The P/B co-efficient for the mussels in the Sanyati East cleared area was calculated as 0,0009.

GENERAL DISCUSSION

Appleton (1979) states : "Virtually nothing is known of the ecology of the freshwater bivalves of South-Central Africa, nor, indeed, of Africa generally. This is despite the fact that although poor in numbers of species, the Unionacea of the river systems under discussion are amongst the largest members of the benthos. Indeed, they may attain high population densities and may therefore constitute an important proportion of the benthic biomass" This is an apt assessment of the current state of knowledge of the mussel fauna of this continent, and reference to the importance of mussels in the benthic fauna is certainly true in the case of Lake Kariba and Lake McIlwaine. With due regard to this paucity of information I would like to take the opportunity in this section of discussing the mussel fauna of Lake Kariba and Lake McIlwaine in broad ecological terms, and to relate this to, or compare it with, situations elsewhere. Some of the ideas put forward are tentative, often based on slender evidence, and as such are open to contradiction or affirmation as more information on mussels accumulates. Tenuous ideas can stimulate interest, discussion or controversy, however, and it is hoped that some of the suggestions put forward will not be wanting in this respect

While it is clear from the resume of van der Lingen (1973) that many biotic and abiotic aspects of Lake Kariba have been investigated over the years, little consideration, if any, has been accorded the bivalve component of the benthic fauna in Lake Kariba, and, until this study,

its magnitude and importance were unknown. Since the standing crop of mussels in the lake is obviously a large one it is probable that mussels will feature more prominently in future scientific deliberations. Their importance in the benthos could well extend beyond these borders. What, for example, is the position in the other great man-made lakes in Africa, - Volta, Kainji, Aswan, Cabora Bassa? Or the natural Lake Victoria? Or the smaller but highly productive Lake George? If these lakes do support similar crops these would represent a massive but unexploited food resource, not to mention the biological implications. Scientific investigation is warranted, since many of the larger man-made lakes have been in existence long enough now to develop mussel resources.

Leading on from this the question that might be asked is how long does it take mussel stocks to develop in a new lake? The situation in Lake Kariba (and observations made on Lake McIlwaine) suggests this is not a long process. The work of McLachlan (1967) in the Sinamwenda area of the lake showed that the first bivalves appeared in the substrate of the Sengwa cleared area in mid 1964, some 5½ years after the dam started filling in December 1958. The lake only reached full capacity in September 1963, but then was allowed to drop nearly 7 m through into 1964, when the lake began its existence as a stable water body subject to minor annual lake level fluctuations. Thus 1964 might be considered as the first year in which bivalves had an opportunity to establish. By 1975, eleven years later, the mussel beds were well established, and may already have been in existence

for a few years at an asymptotic level of abundance. Isom (1969) mentions that only nine years after the Wheeler Reservoir on the Tennessee River was built (1936) large beds of mussels were found, resulting in an increase in the mussel harvest for the button industry. On Lake McIlwaine a lake level drop of two metres in the latter half of 1979 eradicated the mussel fauna on the draw-down zone. The following year, in July, exposure of the shoreline resulted in the stranding of numbers of juvenile M. dubia, showing that re-population of a denuded area can be fairly rapid provided a source of adults is available to provide recruits. Of interest in this case was that whereas in 1979 C. mossambicensis dominated numerically in the shallows, M. dubia formed 97% of the juveniles collected on the draw-down zone in 1980. This reversal in dominance resulted from the 1979 draw-down of two metres eradicating most of the C. mossambicensis population whereas the bulk of the M. dubia population, occupying deeper water, was unaffected, and provided the source for re-population of the shallows at high water level in 1980.

Source of the colonization of Lake Kariba's shallow marginal areas was probably tributary rivers, rather than the drowned Zambezi, where oxygen depletion in deeper water as the lake filled must have killed the populations. The nature of the colonization is not known, but it probably followed the normal sigmoid pattern of development and indications are that the asymptotic level has been reached and the lake is carrying the maximum standing crop for conditions obtaining at this time. There was probably a species succession, or change in species composition as the

community developed. Begg (1971), for example, recorded only A. wahlbergi in Peterson grab samples taken in 1968 (disregarding C. africana which he also recorded), which suggests this species was the dominant element at that time. In 1973/1974 only A. wahlbergi were noted on the exposed shoreline in the Lakeside area, whereas in 1980 all three species were recorded at higher altitudes on the draw-down zone. Thus A. wahlbergi may have been an early successful species with the other two increasing in more recent years. A possible reason for this is suggested later.

A point of interest is that the population was developing at the same time as the population of Kariba weed, Salvinia molesta, was showing a steady annual decline (L.K.F.R.I. records). This emphasizes the dynamism shown by a new lake, with the assemblage of organisms in a continual state of change over many years. There may have been an inverse relationship between the development of the mussel beds and the decline of Kariba weed, due to the influence of the bivalve stock on available nutrients (Marshall, pers. comm.).

This raises the question of what role this enormous pool of animal life is playing in the inorganic cycles of the lake. Animals tend to modify the environment in which they live (Russell-Hunter, 1970) and a standing crop of mussels which probably exceeds 100 000 tonnes must have modified and caused ramifications which as yet can only be guessed at. Because mussels are long lived animals the turnover rate of material is relatively slow (in comparison,

say, with chironomids) and a considerable amount of nitrogen must be locked up in the standing crop, and made available to the ecosystem only through mortality. For a biomass of 160 000 tonnes (whole wet mass) an estimated 850 tonnes of N (kjeldahl) is locked up (assuming 50% protein in dry flesh mass). If mortality equals production the actual amount of N released by mortality must be very small (equivalent to about $0,018 \text{ kg ha}^{-1} \text{ day}^{-1}$). In view of this it seems likely that the importance of mussels lies more in the contribution of their excretory products, particularly if they utilize food resources that are not utilized to any extent by other animals (detritus, for example). Freshwater mussels can filter water at a rate of 1 - 3 litres per hour. In an area like the Sanyati East cleared area, 884 million litres of water could theoretically be filtered in a single hour (at a density of 29 mussels m^{-2} and a filtration rate of 1 l hour^{-1}). A considerable amount of suspended matter must be filtered out of the water every day, resulting in a steady supply of easily recycled excreta. Junor (pers. comm.) has suggested this supply could be utilized rapidly by phytoplankton, to the benefit of zooplankton, and thus freshwater sardines, at present the basis of a thriving fishing industry. If this reasoning is correct there might even be a relationship between the recent increase of the phytoplankton feeding cichlid, Sarotherodon macrochir, and the mussels. Whatever the case there are good grounds for examining more explicitly the relationship between mussels and nutrients, particularly if large scale cropping of the stock for commercial purposes is envisaged. Results of such a study could show whether mussels are beneficial or detrimental to a system. If the

former is shown to be the case then the introduction of mussels to dams might represent a useful way of increasing the productivity of a water body. Apart from their possible effect on nutrient cycling their burrowing activities might assist oxidation processes, with the consequent release of nutrients, as chironomids are suspected of doing (McLachlan, 1967).

Certainly, Kariba has shown that where environmental conditions are suitable a very large standing crop of mussels can develop. At this stage one might ask what factor or factors have contributed to the success of their development. The size of the crop can probably be attributed to nature acting in accordance with the ecological principle that animals occupying the lowest levels in food chains tend to dominate numerically and in most cases by mass (the Eltonian pyramid). The apparent superiority of the mussel standing crop over the fish standing crop probably reflects their lower position in the trophic organization, since they represent a primary consumer level, whereas the majority of fish species in Lake Kariba are secondary or even tertiary consumers (Kenmuir, 1977). This does not, of course, undermine the importance of the fish community, where turn-over of material and productivity are undoubtedly much greater. However, it is interesting to note that in Lake McIlwaine where three of the four dominant larger species are primary consumers (S. macrochir, Tilapia rendalli, and Labeo altivelis) the mussel crop is proportionally much smaller than in Lake Kariba. Possibly a greater degree of competition exists here between fish and mussels for food

resources. Other factors contributing to the success of mussels in Lake Kariba are probably the quality of the water (clean, oxygenated and silt free), the mussels high reproductive potential in the warm water temperatures (year-round breeding, repetitive spawning etc.), the negligible degree of predation on the stocks, and suitability of the substrates (soft, penetrative). Undoubtedly water quality is one of the most important factors. Isom, (1969) has pointed out that siltation of dams on the Tennessee River has a detrimental effect on mussels, and many areas are uninhabited because of this.

The nature or make-up of the mussel crops warrants some consideration. A feature of the populations of both Lake Kariba and Lake McIlwaine is the existent low diversity of species. In Lake McIlwaine four large mussel species were recorded in the upper estuarine reaches (A. wahlbergi, M. dubia, C. mossambicensis and U. caffer) whereas in the rest of the lake only two species represented the population (M. dubia and C. mossambicensis) In Lake Kariba certain areas are dominated almost entirely by only one species, in some areas two species occur, and only in or in proximity to the river estuaries does a greater diversity occur. A similar situation has been recorded in many smaller dams in Zimbabwe (Marshall, pers. comm.) e.g. Gwonorah Dam (one species), Sebakwe Dam (Two species) Mandara Dam (one species), Mwenje Dam (one species), Inkomo Dam (two species) and in Karoi, Mazoe and Savory Dams, one species (pers. obs.) These results may not be conclusive as they are based on shell collections on shorelines made at low water level, but they

do suggest a pattern of low species diversity in dams. Results from elsewhere suggest a similar situation. Bates (1962) describes a situation in the Tennessee River where 14 bivalve species were recorded prior to impoundment, and only eight after impoundment, six being newcomers to the fauna. Cvancara et al (1976) report 12 mussel species from the Sheyenne River, but only four species from Lake Ashtabula on this river. Three large mussel species are recorded from the Pongolo River floodplain (Appleton 1977). However, Pretorius et al (1975) recorded only one species per pan in six out of 18 pans examined for molluscs. Again a low diversity pattern is evident

The situation observed in dams might be a manifestation of a principle of Thienemann (1954, quoted in Hynes 1970) which states the more the conditions in a locality deviate from normal, and hence from the normal optima of most species, the smaller is the number of species which occur there and the greater the number of individuals of each of the species which do occur there. Here again, if the intrusion of an artificial dam into a natural river system constitutes a condition largely deviating from normal, then the situation recorded in Lake Kariba and Lake McIlwaine would appear to hold true to this principle. In both lakes the bulk of the population comprises only one species, and in Lake Kariba, in particular, this species occurs in very large numbers.

The situation in rivers differs. At two localities on the Hunyani River, above Lake McIlwaine

and below Lake Robertson, three and four species were recorded in June 1980, these being M. dubia, A. wahlbergi, C. mossambicensis, and U. caffer. At Mana Pools, on the Zambezi river below Lake Kariba, all three of the Kariba species have been recorded (Marshall pers. comm.)

Appleton's collation of all records for South Central Africa (1979) also suggests a greater diversity of species in rivers. This difference between riverine and lacustrine faunas can possibly be explained in terms of another of Thienemann's principles which states the greater the diversity of the conditions in a locality the larger is the number of species which makes up the biotic community. The situation of greater species diversity in rivers appears to accord with this principle. A river presumably offers a greater variety of habitats than a dam or lake, where homogeneity tends to prevail, particularly in the smaller waterbodies, and is also more likely to offer a greater variety of fish hosts for the parasitic larvae than a dam, where invariably fewer species dominate rather than a variety. A short stretch of river might meet the environmental requirements for all life cycle stages of several mussel species, whereas a large stretch of dam might meet the environmental requirements of only one mussel species. The smaller rivers might deviate from the situation of greater species diversity. For example, only one species was recorded from the Gwebi, a tributary of the Hunyani. Sampling was not exhaustive, however, and this result is not conclusive.

Another ecological principle with which the mussel distribution accords is that of greater species diversity

occurring where two different habitats meet, or overlap. In Lake McIlwaine, as mentioned, greater species diversity occurs where the riverine and lacustrine habitats merge. In Lake Kariba greater diversity generally occurred in the river estuaries or in close proximity to the river estuaries. This principle also applied in certain areas of the lake proper. In the Sanyati East cleared area two species dominated (C. mossambicensis and A. wahlbergi), whereas in the uncleared areas adjacent to them, where dead trees represented a new element in the otherwise similar habitat, a third species (M. dubia) increased in numbers. It might be a general rule in dams that the larger the dam the more diverse the mussel fauna, due to an increase in habitats, or elements within the overall habitat providing microhabitats. The small Pongolo pans appear to have only one large species present per pan, many smaller dams in Zimbabwe seem to have only one, Lake McIlwaine has two dominating, and Lake Kariba (in the Eastern basins) has three overall, although one or two dominating in most localities.

An interesting observation on the mussel distribution in Zimbabwe, albeit based on as yet fairly scant data, is that up to the present time, with two exceptions, no two Unionid species have been recorded in the same dam (Marshall, pers. comm; pers. obs.). Even in a situation such as Lake McIlwaine where it is known that two species of Unionids occur in the inflowing river, only one dominates the lake, and only one specimen of the other species (U. caffer) has ever been recorded in the lake proper, despite intensive sampling in 1973 (Marshall, 1975) and again in 1979. The other

exception is the new Lake Robertson (built in 1976) below Lake McIlwaine, where both C. mossambicensis and U. caffer were recorded on the drawdown zone in 1979. (pers. obs.) It is probable, however, that as the lake matures one species will disappear. Marshall (pers. comm.) has suggested that some type of exclusion principle might be involved. There may be something to this, as Appleton (1979) has shown distinct regional differences in the Unionid fauna existing in the different river systems of South-Central Africa. C. mossambicensis is categorized as essentially an eastern species, C. kunenensis as essentially a western species, and C. framesi as a southern species, with no overlap of ranges recorded as yet. If mutual exclusion exists on a geographical basis it could possibly also exist on a more local basis, as for example between C. mossambicensis and U. caffer in Zimbabwe.

What factor or factors influence the nature of the mussel fauna which does develop in a lake environment? This is a difficult question, since any one of a number of factors might tip the scales in favour of one species over another. An advantage gained might be related to breeding requirements, predation or lack of it, food and feeding requirements, siltation or lack of it, etc.. These are specific aspects, and precise answers for each situation could only be forthcoming if the complete biology and ecology of all the species were known (as well as the exact nature of the environment.) Since this is not possible at present, the best approach is to deal with the question in more general terms, basing premises on observations arising from

this study and those of other workers. The most logical approach is to start at the beginning, i.e. to consider first the faunal complement in the more natural riverine environments from which lacustrine fauna originates, and to proceed from there. A starting point is to say that a dam can be considered to approximate to one particular biotope or habitat type in a river, and therefore the species occupying this particular habitat are the species most likely to successfully colonize a dam. The most likely analogy is that of a dam approximating to a deep calm-water pool, or backwater, on a river. Vancara et al (1976), for example, noted that the most successful species in Lake Ashtabula (Anodonta grandis) was generally found in greatest numbers in stagnant or slow-moving parts of the river. What species are likely to inhabit deep pools or backwater in rivers? Here again, only extensive river sampling could answer this question satisfactorily, and since this has not yet been done suggestions are based on various observations, rather than established facts. Depending on the locality, the rivers in Zimbabwe seasonally either dry up completely, or are reduced to a series of disconnected pools, or to a series of pools connected by minimal water flow. An observation arising from this study was that only one of the three species under study (A. wahlbergi) was capable of resisting desiccation. The other two (C. mossambicensis and M. dubia) died within a few days of being exposed to the atmosphere. It follows that the species most subject to mortality from exposure are the species most likely to be found in the deeper pools or channels of rivers, where this danger is minimised. This may or may not be a valid conclusion, but

the fact that in Lake Kariba C. mossambicensis is the dominant species, and in Lake McIlwaine M. dubia, suggests this line of reasoning may be correct. Obviously the fish species occurring in deeper quieter habitats in rivers, or in backwaters, are also the species most likely to successfully colonize a new dam, and are likely to be the main hosts for the larvae of the mussels occurring in their habitat. The observation that C. mossambicensis and M. dubia breed throughout the year suggests running water is not a strict requirement for successful breeding and neither species would be at a disadvantage in a dam. The thinner, lighter shells of these two species, relative to that of A. wahlbergi suggests they are to be found in localities in rivers not subject to the bruising or abrasive effects of strong currents and hard or coarse substrates. A. wahlbergi, by virtue of its hard shell and resistance to desiccation might normally occupy habitats not usually occupied by the former two species, e.g. shallow water sandbanks or bars, river channels, and flood plains subject to seasonal flooding followed by drying out. A further pointer to a deep water pond type habitat for C. mossambicensis is its ability to withstand extremely low oxygen concentrations of a magnitude that could be expected in the depths of a deep pool in the late dry season. This might also apply to M. dubia. An examination of the respective tolerances to low oxygen tensions of the various species could be rewarding.

There are some observations which tend to support these suggestions. P.A. Reavell, quoted in Appleton (1979)

commenting on mussels in the Okavango, wrote :

"Caelatura kunenensis (typical form) prefers soft clay bottoms of streams in seasonally inundated areas. Very common along Thamalakane River where in the dry season water may become stagnant with very low dissolved oxygen content. Mutela dubia usually together with C. kunenensis but more sporadic in distribution and of lower population density. Aspatharia pfeifferiana found only on clean, sandy bottoms where water was always flowing and dissolved oxygen content always high." Appleton notes that in specimens of large C. kunenensis and M. dubia from the Thamalakane River, erosion of the prismatic layer around the umbone and dorsal areas was unusually severe, a condition he suggested could be attributed to the action of aggressive carbon dioxide in stagnant conditions. Kensley, quoted in Appleton (1979), noted that in a small muddy pool below the Ruacana Falls on the Kunene River, C. kunenensis was the most abundant species in the ooze substrate (6 - 10 m⁻²). M. dubia and two species of Aspatharia were present but much less common (seldom more than one per square metre). There was no water movement through this particular pool. In June 1980 C. mossambicensis and M. dubia were recorded from the muddy bank of a long pool above a weir on the Hunyani River, above Lake McIlwaine (pers. obs.). In October 1979 the dominant species recorded on a sandy river bank in less than one metre depth in the extreme upper reaches of Lake McIlwaine was A. wahlbergi. A few M. dubia were present. Heeg (pers. comm.) recalls seeing large mussels which he presumes were Aspatharia on the banks of the Zambesi (between high and low river levels) above the Victoria Falls. River flow was fairly strong at

this locality.

These observations tend to reinforce the view-point that the species most likely to be found in the "pool" type habitat of rivers are C. mossambicensis and M. dubia .

The argument that C. mossambicensis and M. dubia are "dam" types, appears to be to some extent contradicted by the fact that many small dams in Zimbabwe are occupied by A. wahlbergi (Marshall, pers. comm; pers. obs.), and the fact that this species is also quite widespread in the Sanyati Basin of Lake Kariba. The occurrence of this species in many smaller dams can probably be related, in part, to their resistance to desiccation. Many smaller dams in Zimbabwe tend to either dry up completely, or suffer drastic water loss and lowering of water level during the dry season, particularly in drought years. Most of these dams are used for irrigation and/or drinking purposes water, which further aggravates the situation. Dams falling into this category, particularly abundant in the drier Western half of the country are liable to be colonized or dominated by A. wahlbergi rather than less resistant species. Selection here is by exclusion of species not adapted to such conditions. This can be seen on a small scale in the crocodile ponds of the Lake Kariba Crocodile Farm, some of which are colonized by A. wahlbergi. These ponds are periodically drained. Pretorius et al (1975) recorded an aestivating specimen of A. petersi in the completely dry Mfongosi pan on the Pongolo River flood plain. Of significance is that this was the only mollusc species recorded from this pan. In July / August

1980 Savory Dam, outside Salisbury, was emptying revealing the presence of aestivating A. wahlbergi in hard sand and stone substrates in the upper sections of the draw-down zone. Out of a total of 27 collected from a 5 x 5 m⁻² quadrat in a more populated area nine (33%) were alive. These had been exposed for several months. No other mussel species were recorded. Heeg (1977) has suggested that pulmonates living in ephemeral habitats will experience selection for a high proportion of successful aestivators whereas lake populations never subjected to drying will include a lower proportion of individuals able to survive out of water. It would be of some interest to know if the same considerations apply to A. wahlbergi populations living in such habitats.

The distribution of A. wahlbergi in Lake Kariba tends to support the suggestion that this species is essentially fluviatile, or orientated towards flowing, rather than stagnant water, since its distribution pattern appears to be closely associated with the inflowing rivers and river estuaries. Begg (1971) similarly noted that this species occurred in "riverine localities". This association could be related to their breeding habits and requirements. A first indication of this is the breeding season, which coincides with the rainy season and river flow and, coincidentally, with the breeding season of some of the potamodromous fish species in Lake Kariba. Heeg (pers.comm.) has suggested that a second indication that the breeding of this species is adapted to fluvial conditions is the nature and behaviour of the larvae. These are highly infective,

lethal to heavily infected fish and very small in size. These characteristics could be adaptations to flowing water, since if successful infection of fish hosts is to take place in floodwaters a species would require large numbers of infective larvae, and secondly the smaller and more resistant these are the greater their chance of being carried safely in the current into contact with fish. Obviously in flowing water the larvae would be distributed and dispersed sufficiently to render them non-lethal to fish hosts. It is interesting to note that the bivalve fauna of the rivers of the Kruger National Park is dominated by two Aspatharia species (Oberholzer and van Eeden, 1967).

A. wahlbergi and A. petersi were recorded at 19 and 21 localities respectively, whereas the two Unionids, U. caffer and U. framesi were recorded at 5 and 3 localities respectively. This tends to support the view that A. wahlbergi is a river orientated species.

If this argument is valid, it suggests that the main host species for the larvae will be potamodromous fish species, which in Lake Kariba tend to be confined to localities in the proximity of the main inflowing rivers. This in turn could explain the association of A. wahlbergi with areas in the proximity of inflowing rivers in Lake Kariba, or within their influence. It could also explain the suspected status of this species as one of the early colonizers of the lake, since early successful fish species in Lake Kariba were potamodromous species (Donnelly, 1970; Kenmuir, 1977). Small dams will obviously fall under river influence during the rains and in any case many of them

support populations of riverine type fish, such as Labeo and Barbus species (Donnelly, pers. comm.)

If, among other aspects (e.g. shell characteristics, reaction to low oxygen concentrations, reaction to atmospheric exposure, etc.), the nature of the larvae can indicate the preferred or likely habitat of the adult, then the larvae of C. mossambicensis and M. dubia should also provide some clues to their origin and distribution. The larvae of C. mossambicensis are large relative to those of A. wahlbergi, somewhat spherical in shape and of a rather fragile nature, each possessing a long sticky thread which combines with others to gel the larval brood together. In still water this brood sinks to the bottom, or adheres to whatever it comes into contact with. There are apparently no attachment hooks, and attachment would seem initially to be made by adherence of the sticky threads, and then by chance snapping of the bivalved larvae on to some part of the fish's anatomy (usually fins or gills). Attachments to fins are frequently of a tenuous nature, and encystment in the hosts tissues takes up to three hours. The entire process seems to suggest calm or fairly calm water as the best medium for successful infections to take place. It seems unlikely that such larvae would survive the bruising likely to be sustained in strong currents, and attachment to fish could be difficult under such conditions. If, as seems likely this species is adapted to calmer conditions, the presence of aquatic plants, sticks or other litter in the habitat could facilitate successful infections by providing places of attachment for the sticky larval mass,

with which fish might make contact. The size of the larvae suggests that a period of waiting for a suitable host is catered for by adequate reserves.

Concerning M. dubia, the fact that the larvae successfully infected fish in aquaria at Lake McIlwaine after being sucked up from the lake and circulated through pipes and a reservoir suggests the larvae are hardy and not adversely affected by currents. While they are expelled in a conglutinous mass, resulting from the inter-twining of individual threads, this retaining material appears to disintegrate after a while, leaving the larvae in an apparently dispersed form. At this stage some form of current might be necessary to circulate them for successful attachment to the fins and scales of fish. It is tentatively suggested that the higher numbers of this species in the river estuaries of Lake Kariba and the wave disturbed littoral zones of some of the islands (e.g. Redcliffe Island) as well as their presence on Lake McIlwaine's wave disturbed littoral zones, might support this possibility. Fryer (1961) noted that the specimens of M. bourquignati he examined were living up to eight feet deep, perhaps more, where river flow was moderately rapid. The elongate, rather streamlined nature of the adults shell, plus the animal's habit of lying diagonally to the substrate (in alignment with the current ?), might be adaptations to life in deeper water subject to milder and less abrasive currents. This factor might separate this species from C. mossambicensis. Of the three live specimens collected from the Hunyani River near Sinoia in June 1980, one was from a rocky sub-

strate in water adjacent to the steady, but not strong, current of the main stream, and the other two were collected downstream of this in an expanded and calmer section, on sandy, plant-free substratum near the river bank, and subject to a very slight current.

Further research elsewhere in South, and Central Africa, will undoubtedly shed more light on the behaviour, distribution, habitat preferences and general requirements of local mussel species, and elucidate further the environmental factors which influence and govern these aspects of their ecology. It is hoped that this discussion will have helped in pinpointing some of the areas or fields of freshwater mussel ecology which require further attention.

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REFERENCES

- ANCEY, C.F. (1906) Reflexions sur la fauna malacologique du Lac Tanganika et catalogue des mollusques de ce lac. Bull. Scient. Fr. Belg. (5) 9.
- ANSELL, A.D. (1974) Seasonal changes in biochemical composition of the bivalve Lima hians from the Clyde Sea area. Marine Biology 27 : 115 - 122.
- APPLETON, C.C. (1977) The fresh-water Mollusca of Tongaland, with a note on molluscan distribution in Lake Sibaya. Ann. Natal Mus. 23 : 129 - 144.
- APPLETON, C.C. (1979) The Unionacea (Mollusca, Lamelli-branchiata) of South - Central Africa. Ann. S. Afr. Mus. 77 : 151 - 174.
- AREY, L.B. (1932) A microscopical study of glochidial immunity. J. Morph. 53 : 367 - 379.
- AZEVEDO, J.F., DE MEDEIROS, L., & FARO, M (1957) Os moluscos de agua doce do Ultramar Portugues. 2. Moluscos do Sul do Save (Mozambique). Estudos Ensaios Docum. Jta. Invest. Ultramar. 31 : 1 - 116.
- AZEVEDO, J.F., et al (1961) Os moluscos de agua do Ultramar Portugues. 2. Moluscos de Mozambique, ibid : 88 : 1 - 394.
- BAER, J.G. (1952) Ecology of animal parasites. University Illinois Press, Illinois.
- BALINSKY, B.I. & JAMES, G.V. (1960) Explosive reproduction of organisms in the Kariba Lake. S. Afr. J. Sci. 56 : 101 - 104.
- BALON, E.K. (1973) Results of fish population size assessments in Lake Kariba coves (Zambia), a decade after their creation. In : Man - made lakes : Their problems and environmental effects. (ed.) Ackermann, W.C., White, G.F., and Worthington, E.B. Geophys. Monogr. Ser. 17 : 149 - 158, Washington D.C.
- BALON, E.K. (1974) Fishes of Lake Kariba, Africa. T.F.H. Publications, Neptune City, New Jersey.
- BATES, J.M. (1962) The impact of impoundment on the mussel fauna of Kentucky Reservoir, Tennessee River. Am. Midl. Nat. 68 : 232 - 236.
- BEADLE, L.C. (1974) The inland waters of tropical Africa. Longman, London.

- BEGG, G.W. (1970) Limnological observations on Lake Kariba during 1967, with emphasis on some special features. *Limnol. Oceanogr.* 15 (5) : 776 - 788
- BEGG, G.W. (1971) Notes on the molluscan constituents of the benthos of Lake Kariba. L.K.F.R.I. Proj. Rept. 3 : 1 - 20 (cyclostyled) *
- BELL-CROSS, G. (1972) The fish fauna of the Zambezi River System. *Arnoldia, Rhod.* 5 (29) : 1 - 19
- BLOOMER, H.J. (1932) Notes on the anatomy of some African naiades. Part 1. *Proc. malac. Soc. Lond.* 20 : 166- 173
- BOETTGER, C.R. (1913) Zur Mollusken fauna des Kongogebiets. *Annls. Soc.r. zool. malacol. Belg* : 47
- BOND, G. (1965) Preliminary observations on the development of shoreline features on Lake Kariba . In : Lake Kariba Fisheries Research Institute Symposium Report, (cyclostyled)
- BOURGUIGNAT, J.R. (1890) Histoire malacologique du Lac Tanganika (Afrique Equatoriale) *Annls. Soc. nat. zool.*, 7 serie, 10.
- BORGSTROM, G. (1961) *Fish as Food*. Academic Press, New York and London.
- BOUGHEY, A.S. (1963) The explosive development of a floating weed vegetation on Lake Kariba. *Adansonia* 3 : 49 - 61
- BOWMAKER, A.P. (1973a) An hydrobiological study of the Mwenda river and its mouth, Lake Kariba. Ph.D. thesis, Witswatersrand University, South Africa.
- BOWMAKER, AP., (1973b) Hydrophyte dynamics in Mwenda Bay, Lake Kariba. *Kariba Studies* 3 : 42 - 59
- BOWMAKER, A.P. (1976) The physico-chemical limnology of the Mwenda River mouth, Lake Kariba. *Arch. Hydrobiol.* 77 (1) : 66 - 108
- BURNE, R.H. (1971) A comparative study of the diets of Labeo congoro, Labeo altivelis and Tilapia mossambica in the Sanyati Basin of Lake Kariba LKFRI Proj. Rept. 12 : 1 - 10 (cyclostyled)*
- BROWN, D.S. (1967) A review of the fresh-water Mollusca of Natal and their distribution. *Ann. Natal Mus.* 18 (3) : 477 - 494
- BROWN, M.E. (1957) *The physiology of fishes* 1. Academic Press Inc., New York

- CARTENI, A. & ALOJ, G. (1934) Composizione chimica di animali marini del golfo di Napoli : Nota 11. Selaci, Mollusci, Crostacei. Quad. Nutr. 1 : 219 - 235
- CASTAGNOLO, L. (1978) The reproductive cycle of Anodonta cygnea L and Unio elongatulus Pfeiff in the Po River, Tolle area. Riv. Idribid. 17 (1 - 2) : 3 - 14.
- CAULTON, M.S. (1970) A quantitative analysis of the mode of replacement of inorganic phosphates and nitrates in waters of Lake Kariba during the period December 1969 - January 1970. Limnol. Soc. S. Afr. Newslett. 15 : 52 - 57.
- CAULTON, M.S. (1975) The ability of the cichlid fishes Tilapia rendalli Boulenger, Tilapia sparmanii A. Smith and Hemihaplochromis (= Pseudocrenilabrus philander (M. Weber) to enter deep water. J. Fish. Biol. 7 : 513 - 517.
- CAULTON, M.S. (1976) The energetics of metabolism, feeding and growth of sub-adult Tilapia rendalli Boulenger. Ph. D. thesis, Univ. of Rhodesia.
- CLARK, P., NYBAKKEN, J., & LAURENT, L. (1975) Aspects of the life history of Tresus nuttallii in Elkhorn Slough. Calif. Fish Game 61 (4) : 215 - 227.
- COCHE, A.G. (1968) Description of physico-chemical aspects of Lake Kariba, an impoundment in Zambia-Rhodesia Fish. Res. Bull. Zambia 5 : 200 - 267.
- COCHE, A.G. (1974) Limnological study of a tropical reservoir. In : Lake Kariba : Man-made tropical ecosystem in Central Africa. (ed) Balon, E.K. and Coche, A.G. Junk, The Hague.
- COCHRANE, K. (1978) Seasonal fluctuations in the catches of Limnothrissa miodon (Boulenger) in Lake Kariba. M. Phil. thesis, Univ. of Rhodesia.
- COE, W.R. (1943) Sexual differentiation in Mollusks. 1. Pelecypods. Q. Rev. Biol. 18 (2) : 154 - 164
- CONNOLLY, M. (1912) A revised reference list of South African non-marine mollusca, with descriptions of new species in the South African Museum. Ann. S. Afr. Mus. 11 : 59 - 306
- CONNOLLY, M. (1925) The non-marine Mollusca of Portuguese East Africa. Trans. R. Soc. S.Afr. 12 : 105 - 220
- CONNOLLY, M. (1931) Contribution to a knowledge of the fauna of South West Africa. 9. The non-marine Mollusca of South West Africa. Ann. S. Afr. Mus. 29 : 277 - 336

- CONNOLLY, M. (1939) A monographic survey of South African non-marine Mollusca. Ann. S. Afr. Mus. 33 : 1 - 660
- CRISP, D.J. (1971) Energy flow measurements. In : Methods for the study of marine benthos. (ed.) Holme, N.A., and McIntyre, A.D., I.B.P. Handbook No. 16. Blackwell Scientific Publications. Oxford and Edinburgh.
- CROSSE, H. (1881) Faune malacologique du Lac Tanganika. J. Conch., Paris. 29.
- CUMMINS, K.W. and WUYCHECK, J.C. (1971) Calorific equivalents for investigations in ecological energetics. Mitt. int. Ver. Limnol. 18 : 1 - 158
- CVANCARA, A.M. (1963) Clines in three species of Lampsilis (Pelecypoda : Unionidae). Malacologia 1 : 215 - 225
- CVANCARA, A.M., NORBY, R.D. and VAN ALSTINE, J.B. (1976) Mollusks of the Sheyenne River, North Dakota, U.S.A. : Present and Past. Malacological Review 9 : 25 - 38
- DARTEVELLE, E. (1939) Quelques mollusques fluviatiles du Cunene. J. Conch. Paris 83 : 327 - 331
- DAVID, F.N. and MOORE, P.G. (1954) Notes on contagious distributions in plant populations. Ann. Bot. Lond. N.S. 18 : 47 - 53
- DEJOUX, C., LAUZANNE, L., AND LEVEQUE, C. (1969) Evolution qualitative et quantitative de la faune benthique dans la partie est du Lac Tchad. Cah. O.R.S.T.O.M., ser Hydrobiol. 3 (1) : 3 - 58
- DEJOUX, C., LAUZANNE, L., and LEVEQUE, C. (1971) Nature des fonds et repartition des organismes benthiques dans la region du Bol. (Archipel est du Lac Tchad). Cah. O.R.S.T.O.M., ser Hydrobiol. 5 : 213 - 223
- DONNELLY, B.G. (1970) The fish population changes in Lake Kariba between 1960 and 1968. L.K.F.R.I. Proj. Rept. 4 : 1 - 20 (cyclostyled)*
- DONNELLY, B.G. and GROBLER, J.H. (1976) Notes on food and anvil-using behaviour by the Cape clawless otter, Aonyx capensis, in the Rhodes Matopos National Park. Arnoldia, Rhod. 7 (37) : 1 - 7
- DUPONT, B. AND LEVEQUE, C. (1968) Biomasse en Mollusques et nature des fonds dans la zone est du Lac Tchad. Cah. O.R.S.T.O.M. ser Hydrobiol. 2 : 114 - 126
- ELLIOT, J.M. (1971) Some methods for the statistical analysis

of samples of benthic invertebrates. F.B.A.
Scientific Publication No. 25.

- EDMONDSON, W.T. & WINBERG, G.G. (1971) A manual on methods for an assessment of Secondary Productivity in Freshwaters. I.B.P. Handbook No. 17. Blackwell Scientific Publications. Oxford and Edinburgh.
- FALCONER, A.C. (1973) The phytoplankton ecology of Lake McIlwaine, Rhodesia. M. Phil. thesis. Univ. of London.
- FLANNAGAN, J.F. (1970) Efficiencies of various grabs and corers in sampling freshwater benthos. J. Fish. Res. Bd. Can. 27 : 1 691 - 1 700.
- FRANC, A. (1949) Unionidae d'Afrique occidentale française recueillis par Th. Monod. J. Conch. 89 : 157 - 187.
- FRENCH, R.A. (1980) An assessment of mussel mortality caused by a drop in the water level of Lake Kariba. L.K.F.R.I. Proj. Rept. 34 : 1 - 12 (cyclostyled)*
- FRETTER, V. & GRAHAM, A. (1964) Reproduction. In : Physiology of Mollusca. (ed.) Wilbur, K.M. and Yonge, C.M. Academic Press, New York.
- FRYER, G. (1959) Development in a mutelid lamellibranch. Nature, Lond. 183 : 1 342 - 1 343.
- FRYER, G. (1961) The developmental history of Mutela bourquignati (Ancey) Bourquignat (Mollusca : Bivalvia) Phil. Trans. R. Soc. B. 244 (711) : 259 - 298.
- FUZIWARA, T. (1978) On the ovulation of Corbicula leana Prime. Venus 37 (1) : 22 - 28.
- GAIR, E.H. (1959) The Karoo system and resources of the Gwembe District, North-west section. Zambia Geol. Surv. Dept. Bull. 1.
- GERMAIN, L. (1905) Liste des mollusques recueillis par M.E. Foa dans le Lac Tanganika et ses environs. Bull. Mus. Hist. nat. Paris.
- GIORGI, A.E. & DE MARTINI, J.D. (1977) A study of the reproductive biology of the red abalone, Haliotis refescens Swainson, near Mendocino, California. Calif. Fish. Game 63 (2) : 80 - 94.
- GIUSTI, F. (1973) The minute shell structure of the glochidium of some species of the genera Unio, Potomida and Anodonta. (Bivalvia : Unionacea). Malacologia 14 : 291 - 301.
- GIUSTI, F., CASTAGNOLO, L., FARINA, L.M., & RENZONI, A. (1975) The reproductive cycle and the glochidium of Anodonta cygnea L. from Lago Trasimeno Central Italy.

- Monitore zool. ital. (N.S.) 9 : 99 - 118.
- GREENWAY, J.P.C. (1969) Surveys of mussels (Mollusca : Lamellibranchia) in the Firth of Thames, 1961 - 67. N.Z. Jl. Mar. Freshwat. Res. 3 (2) : 304 - 317
- GRIFFITHS, A.B. (1905) On the composition of certain invertebrate pigments. Chem. News 91.
- HAAS, F. (1929) Die von der zweiten Deutschen Zentral - Afrika Expedition 1910 - 1911 mitgebrachten süßwassermuscheln. Senckenbergiana, 2.
- HAAS, F. (1941) Records of large freshwater mussels. Zool. Ser. Publs. Field Mus.nat. Hist. 24.
- HALVER, J.E. (1972) Fish Nutrition. Academic Press, New York and London.
- HARDING, D. (1961) Limnological trends in Lake Kariba. Nature, Lond. 191 : 119 - 121
- HARDING, D. (1962) Research on Kariba. In : Joint Fisheries Research Organization Ann. Rep. 10 : 32 - 40 Govt. Printer, Lusaka.
- HARDING, D. (1964) Hydrology and Fisheries in Lake Kariba. Verh. Internat. Verein. Limnol. 15 : 139 - 149
- HARDING, D. (1966) Lake Kariba : The hydrology and development of fisheries. In : Man-made Lakes. (ed.) Lowe-McConnel, R.H. Academic Press, London.
- HARMS, W. (1907) Ueber die postembryonale entwicklung von Anodonta piscinalis. Zool. Anz. bd., 31 : 801 - 814.
- HASKIN, H.H. (1954) Age determination in molluscs. Trans. N.Y. Acad. Sci. Ser. 2, 16 : 300 - 304.
- HATTINGH, E.R. (1961) Problem of Salvinia auriculata Aubl., and associated aquatic weeds on Kariba Lake. Weed Res. 1 : 303.
- HAYNES, E.B. (1966) Length - weight relation of the sea scallop Placopecten magellanicus (Gmelin). I.C.N.A.F. Res. Bull. 3.
- HAYNES, E.B., & HITZ, C.R. (1971) Age and growth of the giant Pacific sea scallop, Patinopecten caurinus, from the Strait of Georgia and outer Washington Coast. J.Fish. Res. Bd. Canada 28 : 1 335 - 1 341.
- HAYNES, E.B., & MCMULLEN, J.C. (1970) Relation between meat weight and shell height of the giant Pacific sea scallop, Patinopecten caurinus, from the Gulf of Alaska. Proc. Natl. Shellfish. Assoc. 60 : 50 - 53.

- HEARD, W.H. (1965) Comparative life histories of North American pill clams (*Sphaeriidae* : *Pisidium*) *Malacologia* 2 (3) : 381 - 411.
- HEARD, W.H. (1975) Sexuality and other aspects of reproduction in *Anodonta* (*Pelecypoda* : *Unionidae*) *Malacologia* 15 (1) : 81 - 103
- HEARD, W.H. and GUCKERT, R.H. (1970) A re-evaluation of the recent *Unionacea* (*Pelecypoda*) of North America. *Malacologia* 10 (2) : 333 - 355
- HEARD, W.H. and VAIL, V.A. (1976) The systematic position of *Unio caffer* (*Pelecypoda* : *Unionoida* : *Unionidae*). *Zoologica Africana* 11 : 45 - 58
- HEEG, J. (1977) Oxygen consumption and the use of metabolic reserves during starvation and aestivation in *Bulinus (Physopsis) africanus* (*Pulmonata* : *Planorbidae*) *Malacologia* 16 (2) : 549 - 560
- HOLLAND, D.A. and CHEW, K.K. (1974) Reproductive cycle of the Manilla clam (*Venerupis japonica*), from Hood Canal, Washington. *Proc. Natl. Shellfish Assoc.* 64 : 53 - 58
- HYNES, H.B.N. (1970) The ecology of running waters. Liverpool Univ. Press, Liverpool.
- IMLAY, M.J. (1971) Bioassay tests with naiads. Jorgensen and Sharp : 38 - 41
- ISOM, B.G. (1969) The mussel resource of the Tennessee River. *Malacologia* 7 (2 - 3) : 397 - 425.
- JACKSON, P.B.N. (1960) Ecological effects of flooding by the Kariba Dam upon middle Zambezi fishes. *Proc. 1st. Fed. Sci. Congr.* : 277 - 284.
- JOHNSON, M.J. (1941) Isolation and properties of a pure yeast polypeptidase. *J. biol. Chem.* 137 : 575 - 586.
- JOUBERT, C.S.W. (1975) A preliminary investigation into the biology and status of two Mormyrids *Mormyrops deliciosus* (Leach, 1818), and *Mormyrus longirostris* (Peters, 1852), (*Pisces* : *Mormyridae*) in Lake Kariba, Rhodesia. *L.K.F.R.I. Proj. Rept.* 22 : 1 - 121 (cycl)*
- JUBB, R.A. (1976) Freshwater mussels, *Unionidae*, what is their distribution in South African inland waters today? *Piscator* 97 : 73 - 75.
- JUNOR, F.J.R. (1964) Biological and legislative implications of river pollution in Rhodesia. *Dept. Nat. Parks and Wildlife Mngt. Rept.*
- JUNOR, F.J.R. (1969) *Tilapia melanopleura* Dum in artificial lakes in Rhodesia with special reference to its undesirable effects. *Rhod. J. Agric. Res.* 7 : 61 - 69.

- KUIPER, J.G.J. (1964) Contributions to the knowledge of the South African species of the genus Pisidium (Lamellibranchiata). Ann. S.Afr. Mus 48 (3) : 77 - 95
- KENMUIR, D.H.S. (1970) Results of an analysis of a few stomachs of five species of fish caught in gill and seine nets in Lake Kariba. L.K.F.R.I. Rept. (typed) *
- KENMUIR, D.H.S. (1975) Observations on the reaction of submerged hydrophytes to lake level rise, Lake Kariba. L.K.F.R.I. Proj. Rept. 24 : 1 - 25 (cyclostyled). *
- KENMUIR, D.H.S. (1977) Fish population changes in Lake Kariba Rhodesia L.K.F.R.I. Proj. Rept. 18 : 1 - 52 (cyclostyled)*
- KENMUIR, D.H.S. (1978) A wilderness called Kariba. Wilderness Publications, Salisbury.
- KREBS, C.J. (1972) Ecology. The experimental analysis of distribution and abundance. Harper and Row, New York.
- LAURENT, L.L. (1971) The spawning cycle and juvenile growth rate of the gaper clam Tresus nuttalli of Elkhorn Slough, California. Masters thesis. San Francisco State University.
- LEE, C.F. and PEPPER, L. (1956) Technological research with southern oysters. Southern Fisherman 10 :
- LEFEVRE, G. and CURTIS, W.C. (1912) Studies on the reproduction and artificial propagation of freshwater mussels. Document 756 from Bull. Bur. Fish., Wash. 30, 1910 : 105 - 201
- LELOUP, E. (1950) Lamellibranches : Exploration hydrobiologique du Lac Tanganika (1946 - 1947) 3 (1) : 1 - 153
- LEVEQUE, C. (1968) Mollusques aquatiques de la zone est du Lac Tchad. Bull. I.F.A.N., ser.A, 29 (4) : 1494 - 1533
- LEVEQUE, C. (1971) Equation de von Bertalanffy et croissance des mollusques benthiques du Lac Tchad. Cah. O.R.S.T.O.M., ser. Hydrobiol. 5 (3 - 4) : 263 - 284
- LEVEQUE, C. (1973) Dynamique des peuplements biologie, et estimation de la production des mollusques benthiques du Lac Tchad. Cah. O.R.S.T.O.M., ser. Hydrobiol. 7 (2) : 117 - 147
- LOOSANOFF, V.L. and DAVIS, H.C. (1963) Rearing of bivalve

molluscs. In : Advances in marine biology, 1.
(ed.) Russel, F.S. Academic Press, London and
New York.

- MACKIE, G.L., QADRI, S.U., and CLARKE, A.H. (1976a)
Reproductive habits of four populations of
Musculium securis (Bivalvia : Sphaeriidae) near
Ottawa, Canada. Nautilus 90 (2) : 76 - 86
- MACKIE, G.L., QADRI, S.U., and CLARKE, A.H. (1976b)
Intraspecific variations in growth, birth periods,
and longevity of Musculium securis (Bivalvia :
Sphaeriidae) near Ottawa, Canada. Malacologia
15 (2) : 433 - 446
- MCINTYRE, A.D. (1971) Efficiency of benthos sampling gear.
In : Methods for the study of marine benthos
(ed.) Holme, N.A. and McIntyre, A.D. I.B.P.
Handbook No. 16. Blackwell Scientific Publications,
Oxford and Edinburgh.
- MCLACHLAN, A.J. (1967) A study of the bottom fauna of Lake
Kariba (Rhodesia). Ph.D. thesis. Univ. of London.
- MCLACHLAN, A.J. (1969) The effect of aquatic macrophytes on
the variety and abundance of benthic fauna in
a newly-created lake in the tropics (Lake Kariba).
Arch. Hydrobiol. 66 : 212 - 231
- MCLACHLAN, A.J. (1970) Submerged trees as a substrate for
benthic fauna in the recently-created Lake Kariba
(Central Africa). J. appl. Ecol. 7 : 253 - 266
- MCLACHLAN, S.M. (1971) The rate of nutrient release from grass
and dung following immersion in lake water.
Hydrobiologia 37 : 521 - 530
- MANDAHL-BARTH, G. (1954) The freshwater molluscs of Uganda
and adjacent territories. Annls. Mus. r. Congo
belge. Ser. 8vo. Sci. Zool. 32 : 1 - 206
- MANDAHL-BARTH, G. (1972) The freshwater Mollusca of Lake
Malawi. Revue Zool. Bot. afr. 86 : 257 - 289
- MARSHALL, B.E. (1971) Ecology of the bottom fauna of Lake
McIlwaine, Rhodesia. M. Phil. thesis. Univ. of
London.
- MARSHALL, B.E. (1975) Observations on the freshwater mussels
(Lamellibranchia : Unionacea) of Lake McIlwaine,
Rhodesia. Arnoldia, Rhod. 7 (16) : 1 - 16
- MARSHALL, B.E. (1978a) An assessment of fish production in
an African man-made lake (Lake McIlwaine, Rhodesia)
Trans. Rhod. Sci. Ass. 59 (3) : 12 - 21
- MARSHALL B.E. (1978b) Lake McIlwaine after twenty five years.
Rhod. Sci. News. 12 (3) : 79 - 82

- MARSHALL, B.E. & FALCONER, A.C. (1973a) Physico-chemical aspects of Lake McIlwaine (Rhodesia), a eutrophic tropical impoundment. *Hydrobiologia* 42 : 45 - 62
- MARSHALL, B.E. and FALCONER, A.C. (1973b) Eutrophication of a tropical African impoundment (Lake McIlwaine, Rhodesia) *Hydrobiologia* 43 : 109 - 123
- MARSHALL, B.E. and LOCKETT, C.A. (1976) Juvenile fish populations in the marginal areas of Lake McIlwaine, Rhodesia. *J. Limnol. Soc. sthn. Afr.* 2 : 37 - 42
- MATTHES, H. (1968) The food and feeding habits of the tiger-fish *Hydrocynus vittatus* (Cast. 1861) in Lake Kariba. *Beaufortia* 15 (201) : 143 - 153
- MAUFFE, H.B. (1933) A preliminary report on the mineral springs of Southern Rhodesia. *Rhod. Geol. Surv. Bull.* 23.
- MELVILLE, J.C. and PONSONBY, J.H. (1898) Contribution towards a check list of the non-marine molluscan fauna of South Africa. *Proc. malac. Soc. Lond.* 3 : 166 - 184
- MERTZ, E.T. (1972) The protein and amino acid needs. In : *Fish Nutrition.* (ed.) Halver, J.E. Academic Press, New York and London.
- MINSHULL, J.L. (1978) Preliminary investigations of the ecology of juvenile *Sarotherodon macrochir* Boulenger. M.Sc. thesis, Univ. of Rhodesia.
- MITCHELL, S.A. (1976) The marginal fish fauna of Lake Kariba. *Kariba Studies* 8 : 109 - 162
- MITCHELL, S.A. and GAHAMADZE, C. (1976) *Haplochromis codringtoni* and bilharzia on Lake Kariba. *L.K.F.R.I. Proj. Rept.* 25 : 1 - 8 (cyclostyled)*
- MORTON, J.E. (1967) *Molluscs.* Hutchinson University Library, London.
- MUNRO, J.L. (1966) A limnological survey of Lake McIlwaine, Rhodesia. *Hydrobiologia* 28 : 281 - 308
- NEGUS, C.L. (1966) A quantitative study of growth and production of Unionid mussels in the River Thames at Reading. *J. Anim. Ecol.* 35 : 513 - 532.
- OBERHOLZER, G. & VAN EEDEN, J.A. (1967) The freshwater molluscs of the Kruger National Park. *Koedoe No.* 10 : 1 - 42.
- ORTMANN, A.E. (1909) The breeding season of Unionidae in Pennsylvania. *Nautilus* 22 :

- ORTMANN, A.E. (1910) The discharge of the glochidia in the Unionidae. *Nautilus* 24.
- ORTMANN, A.E. (1911) A monograph of the najades of Pennsylvania. Parts I and II. *Mem. Carnegie Mus.* 4 : 279 - 347.
- ORTMANN, A.E. (1918) The anatomy of two African naiades, *Unio caffer* and *Spatha wahlbergi*. *Nautilus* 31 : 75 - 78.
- ORTMANN, A.E. (1920) Correlation of shape and station in fresh water mussels (naiades). *Proc. Am. phil. Soc.* 59 : 268 - 312.
- PARODIZ, J.J. & BONETTO, A.A. (1963) Taxonomy and zoogeographic relationships of the South American naiades (Pelecypoda : Unionacea and Mutelacea) *Malacologia* 1 : 179 - 213.
- PEARSON, R.G., LITTERICK, M.R. & JONES, N.V. (1973) An airlift for quantitative sampling of the benthos. *Freshwat. Biol.* 3 : 309 - 315.
- PIELOU, E.C. (1969) An introduction to mathematical ecology. Wiley-Interscience, New York.
- PELSENEER, P. (1895) L'hermaphroditisme chez les Mollusques. *Arch. Biol.* 14 : 33 - 62.
- PENNAK, R.W. (1953) Freshwater invertebrates of the United States. The Ronald Press Co. New York.
- PILSBRY, H.A. & BEQUART, J. (1927) The aquatic Mollusks of the Belgian Congo, with a geographical and ecological account of Congo malacology. *Bull. Am. Mus. nat. Hist.* 53 : 69 - 602
- PRESTON, H.B. (1910) Further additions to the molluscan fauna of Central Africa. *Ann. Mag. nat. Hist.* 8.
- PRETORIUS, S.J., JENNINGS, A.C. COERTZE, D.J.R. & VAN EEDEN, J.A. (1975) Aspects of the freshwater Mollusca of the Pongola River floodplain pans. *S. Afr. J. Sci.* 71 : 208 - 212.
- PURCHON, R.D. (1951) Hermaphroditism. *Gazette King Edward VII Med. Soc., Univ. Malaya* 2.
- PURCHON, R.D. (1977) The biology of the Mollusca. Pergamon Press, Oxford.
- REEVE, W.H. (1963) The geology and mineral resources of Northern Rhodesia. *North. Rhod. Geol. Surv. Bull.* 3.

- RUSSELL-HUNTER, W.D. (1970) Aquatic productivity.
The MacMillan Company, London.
- SCHOUTEVDEN, H. (1935) Coquilles du Lac Tanganika. Bull.
Cerc. zool. Congol. 12.
- SCHWETZ, J. (1943) La faune malacologique du Lac Tanganika.
Bull. Cerc. zool. Congol. 18.
- SCHWETZ, J. (1949) Sur une nouvelle collection de mollusques
d'eau douce du Congo Belge et du Ruanda-Urundi.
Bull. Inst. R. Col. Belge, 20.
- SCHUTTE, C.H.J. & FRANK, G.H. (1964) Observations on the
distribution of freshwater Mollusca and chemistry
of the natural waters in the South-Eastern Trans-
vaal and adjacent Northern Swaziland. Bull. Wld.
Hlth. Org. 30 : 389 - 400.
- SEED, R. (1974) Reproduction in Mytilus (Mollusca; Bivalvia)
in European waters. Publ. Staz. zool. Napoli 39
Suppl. : 317 - 334.
- SESHAIYA, R.V. (1969) Some observations on the life histories
of South Indian freshwater mussels.
Malacologia 9 (1) : 286 - 287.
- SHANKS, W.E., GAMIMER, G.D., & HALVER, J.E. (1962)
Indispensable amino acids for rainbow trout.
Prog. Fish Cult. 24.
- SLOBODKIN, L.B. & RICHMAN, S. (1961) Calories / gm in species
of animals. Nature. Lond. 191.
- SMITH, E.A. (1880a) On the shells of Lake Tanganika and of
the neighbourhood of Ujiji. Proc. zool. Soc. Lond.
- Smith, E.A. (1880b) Diagnoses of new shells from Lake
Tanganika and East Africa. Ann. Mag. nat. Hist.
- SMITH, E.A. (1881a) On a collection of shells from Lakes
Tanganika and Nyasa, etc., Proc. zool. Soc. Lond.
- SMITH, E.A. (1881b) Description of two new species of shells
from Lake Tanganika. Proc. zool. Soc. Lond.
- SMITH, E.A. (1904) Some remarks on the Mollusca of Lake
Tanganika. Proc. malac. Soc. Lond. 6.
- SNEDECOR, G.W. (1956) Statistical methods. The Iowa State
University Press, Ames, Iowa.
- STANSBERRY, D. (1967) Growth and longevity of the naiades
from Fishery Bay in Lake Erie. Amer. Malac.
Union. Ann. Repts : 10 - 11 (abstract).
- STERKI, J. (1898) Some observations on the genital organs of
the Unionidae, with reference to classification.
Nautilus 12.

- STURANY, R. (1898) Catalog der....Sudafrikanischen land und süsswasser mollusken. S.A. Moll. Vienna.
- SUTCLIFFE, D.N. and DURRANT, P.M. (1977) Geometric mean shape of the shell in lacustrine and riverine limpets, Ancylus fluviatilis Muller. Freshwat. Biol. 7 : 479 - 485
- TEMPLETON, R.J. (1979) Some ecological and biological aspects of freshwater crabs, Potamonautes obesus obesus, in Lake McIlwaine, Rhodesia. Cert. in Field Ecology, thesis. Univ. of Rhod.
- THIENEMANN, A. (1954) Ein drittes biozonotisches grandprinzip. Arch. Hydrobiol. 49 : 421 - 422.
- TYNDALE-BISCOE, R. (1957) Explanation of the geological map of the country around Salisbury. S. Rhod. Geol. Surv. Short Rept. 36.
- *
VAN DER SCHALIE, H. (1966) Hermaphroditism among North American freshwater mussels. Malacologia 5 (1): 77 - 78
- VAN DER SCHALIE, H. (1969) Two unusual hermaphrodites. Science N.Y. 163 : 1333 - 1334
- VAN DER SCHALIE, H. and A. (1963) The distribution, ecology and life history of the mussel Actinonaias ellipsiformis (Conrad), in Michigan. Occ. Pap. Mus. Zool., Univ. Mich. No. 633 : 1 - 17
- VAN DEN BERGHE, L. (1936) Notes ecologiques sur quelques mollusques d'eau douce du Katanga (Congo Belge) Mem. Mus. Roy. Hist. Nat. Belge., 2 serie, 3.
- VAN DER LINGEN, M.I. (1973) Lake Kariba: early history and south shore. In : Man-made lakes : Their Problems and environmental effects. (ed.) Ackermann, W.C., White, G.F. and Worthington. E.B. Geophys. Monogr. Ser. 17 : 132 - 142
- VON MARTENS, E. (1883) Einige centralafrikanische conchylien. Sber.Ges. naturf. Freunde Berl.
- VON MEIER-BROOK, C. (1970) Investigations on the biology of some Pisidium species (Mollusca : Eulamelli-branchiata : Sphaeriidae). Arch. Hydrobiol/ suppl. 38. 1/2 : 73 - 150.
- VINOGRADOV, A.P. (1953) The elementary chemical composition of marine organisms. Mem. Sears. Fdn. mar. Res.2.
- WELCH, P.S. (1948) Limnology. McGraw-Hill, New York.
- WENDELL, F., DE MARTINI, J.D., DINNEL, P., AND SIECKE, J. (1976) The ecology of the gaper or horse clam, Tresus capax (Gould, 1850), (Bivalvia, Mactridae), in Humboldt Bay, California. Calif. Fish Game 62 (1) : 41 - 64

- WILBUR, K.M. and YONGE, C.M. (1964) Physiology of Mollusca.
Academic Press, New York and London.
- WILLIAMS, R.K. (1970) Practical methods to reduce the
intensity and occurrence of algal blooms at Lake
McIlwaine. Rhod. Sci. News. 4 : 54
- WINBERG, G.G. (1971) Methods for the examination of
production of aquatic animals. Academic Press,
London and New York.
- WINBERG, G.G., PATALAS, K., WRIGHT, J.C., HILLBRICHT - ILKOWSKA
A., COOPER, W.E., and MANN, K.H. (1971) Methods
for calculating productivity. In : Secondary
productivity in fresh waters. (ed.) Edmondson,
W.T., and Winberg, G.G., I.B.P. Handbook No.17
Blackwell Scientific Publications, Oxford and
Edinburgh.
- WOODWARD, F.R. (1974) A survey of the Mollusca of Lake Chad,
Central Africa. Appendix C. Notes on the
anatomy of Caelatura sp. from Lake Chad,
Northern Nigeria. Revue zool. afr. 88 : 346 - 351
- WOODWARD, S.P. (1859) On some new freshwater shells from
Central Africa. Proc. zool. Soc. Lond.
- YONGE, C.M. (1962) On Etheria elliptica Lam. and the course
of evolution, including assumption of
monomyarianism, in the family Etheriidae
(Bivalvia : Unionacea). Phil. Trans. R. Soc.
B. 244 : 423 - 458
- ZAIKA, V.E. (1973) Specific production of aquatic invertebrates.
John Wiley and Sons, New York and Toronto.
- * VANCARA et al (1976) Mollusks of the Sheyenne River,
North Dakota, U.S.A: Present and past.
Malacological Review, 1976, 9 : 25-38

* Lake Kariba Fisheries Research Institute Reports,
Lake Kariba Fisheries Research Institute,
P.O.Box 75, Kariba, Zimbabwe.