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A LIFE-HISTORY APPROACH TO THE  
BIOLOGY OF OREOCHROMIS MOSSAMBICUS  
(PISCES : CICHLIDAE) IN THE EASTERN  
CAPE, SOUTH AFRICA.

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the Requirements for the Degree of  
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Frontispiece. The two largest Oreochromis mossambicus caught at Mill Farm Dam during sampling in 1987. The upper photograph is of a 2464 g male, 385 mm standard length, caught on 28th July. The lower photograph is of a 2332 g female, 385 mm SL, caught on the 31st August.

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Resume

The phenotypic plasticity of the cichlid Oreochromis mossambicus was examined in fresh and brackish water populations living in the eastern Cape near the southern extremity of the natural range. The primary goal of the study was to examine the wide variety of life-history styles which were expressed in relation to the varying environmental conditions.

Four natural populations were studied during 1986 and 1987, and some experimental work under artificial conditions was carried out at the Rhodes University fishfarm during 1988. This comparative approach gave insights into the complex interactions between biotic and abiotic factors which are exploited by this hardy species.

O. mossambicus displayed a wide variety of life-history tactics under harsh environmental conditions. The growth of juvenile fish was rapid and mortality of the young-of-the-year was high. Age at first onset of sexual maturity ranged from one to three years. Under harsh conditions growth rate was markedly reduced after maturity, which occurred during the second or third summer and growth disparity between the sexes was more pronounced. Longevity was found to vary from five to ten years for different populations. Under more favourable conditions (resembling the typical "floodplain" habitats of this species at lower latitudes) very rapid juvenile growth, and a high maximum mass of over 2300 g for both sexes was

achieved. Sexual maturity under these conditions could be delayed until the third or fourth summer of life.

O. mossambicus demonstrated an ability to withstand and even benefit from fluctuating water levels, and adjusted its life style according to the prevailing conditions: at times of high water level recruitment was low and sexual maturity delayed. During low water periods reproductive rates increased.

O. mossambicus showed a distinct preference for gentle gradients and well-vegetated habitats for feeding , nesting and refuge. During the study winter temperatures were near and at some times below the generally accepted lower limits for this species. This implies that these indigenous populations have a degree of cold tolerance. A further implication is that O. mossambicus has the ability to thrive under adverse conditions which may partially explain its wide and successful colonisation of water bodies far from its natural range, and its obvious fisheries potential.

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## Introduction

Fishes are the most plastic of vertebrates in terms of their ability to adopt different life-history options in response to the co-evolving environment. The cichlid fish Oreochromis mossambicus (Peters 1852) is known for its wide phenotypic plasticity and survives and even flourishes under very diverse environmental conditions (Fryer & Iles 1972, Bruton & Allanson 1974, Bruton & Boltt 1975, Bowen & Allanson 1982, Philippart & Ruwet 1982, Noakes & Balon 1984) (Table 1). The natural distribution range of this species extends from southern Kenya, southward along the east African coast, and inland, to its southernmost limit in the eastern Cape of South Africa (Philippart & Ruwet 1982). Jubb (1967) suggests that the most southerly natural population may be that of the lower reaches of the Bushman's River, to the east of Port Elizabeth. Towards the southern end of its natural range O. mossambicus is commonly found in the brackish and hypersaline lagoons and estuaries of the south-east flowing rivers. This species is also found in large estuarine systems such as Lake St. Lucia where the salinity varies widely (0 - 120 ‰) according to freshwater inflow (Whitfield & Blaber 1979). At higher latitudes, and with increasing altitude, populations of O. mossambicus tolerate extremes in environmental conditions.

This study investigates the biology and life history of four such populations living in diverse but typical habitats within the eastern Cape, and attempts to relate the distinct life-history characteristics displayed to the prevailing

Table 1. The physico-chemical tolerances of O. mossambicus

Temperature

minimum	11 <sup>o</sup> C	Allanson et al. 1961
maximum	38,2 <sup>o</sup> C	Allanson & Noble 1964
preferred	32,2 <sup>o</sup> C	Stauffer 1986

Salinity

reproduction capability	0 - 49 ‰	Popper & Lichatowich 1975
acclimation capability	0 - 120 ‰	Assem & Hanke 1979a, Potts et al. 1967, Wallace 1975
direct transfer	0 - 27 ‰	Assem & Hanke 1979b

Dissolved oxygen

short periods	> 0,1 ppm	Maruyama 1958
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<u>pH</u>	5 - 10	Swingle 1961
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<u>Un-ionised ammonia</u>	> 2,4 mg/l	Redner & Stickney 1979
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<u>Current speed</u>	< 370 m/hr	Whitfield & Blaber 1979
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environmental conditions.

The life cycle of O. mossambicus

Whilst there is an abundance of information on experimental work carried out on this species there have been few studies on the life cycles of natural populations. Bruton (1973), Bruton & Allanson (1974) and Bruton & Bolt (1975) provided the most detailed descriptions of the general biology of O. mossambicus, and Bowen (1978, 1979) the nutritional requirements. Aspects of the life cycle of introduced populations are described by Bowen (1984), Hodgkiss & Man (1977a & b, 1978), De Silva (1985a & b, 1986) and De Silva & Sirisena (1988). There are numerous other publications, summarised by Trewavas (1983), that describe particular aspects of the life cycle of this species.

O. mossambicus (Frontispiece) is one of the best known tilapia due to its widespread introductions around the world for fish culture. It is a member of the maternal mouthbrooding group of tilapiines placed in the genus Oreochromis to distinguish them from the paternal or bi-parental mouthbrooders (Sarotherodon) and the guarders (Tilapia). O. mossambicus was formerly known as as Chromis mossambicus, Tilapia natalensis, Tilapia mossambica, and Sarotherodon mossambicus (Trewavas 1983).

The life cycle can be summarised as follows. Male O. mossambicus excavate simple crater-shaped nests, often in arenas. At this time male fish adopt an almost black colouration with red edges

to the dorsal and caudal fins and white lower parts of the head, and become aggressively territorial. Female fish in breeding condition are attracted to the nests by the males' colour and sexual displays. Spawning takes place over the nest into which the eggs and sperm are deposited and then immediately picked up by the female and retained in the buccal cavity where actual fertilisation may take place. Mouthbrooding females often congregate in schools in well vegetated areas (Bruton & Boltt 1975). Hatching usually takes place after approximately three to five days (Vaas & Hofstede 1952, Lombard 1962) during which time the developing eggs are continuously "tumbled" within the buccal cavity. After 10 to 14 days the young are ejected from the mouth for short periods and may begin exogenous feeding. The female usually finally releases the young after 14 to 22 days (Bohrer 1953), and they then utilise the warm and shallow littoral or eulittoral for feeding (Bruton and Boltt 1975, Bowen & Allanson 1982). O. mossambicus may spawn several times during the warm season, or almost continuously at intervals of four to six weeks under tropical conditions (Crass 1964, Jubb 1967, Bruton & Allanson 1974). Juvenile growth under favourable conditions is rapid, and males usually grow faster than females. This species is an opportunistic feeder, but concentrates on benthic algae, especially diatoms, although adults will take insects, crustaceans and occasionally small fish. Age at first maturity is highly variable and may range between three months and three years of age. Longevity may be as little as three to four years for populations under unfavourable conditions, but

up to 12 years under benign conditions. The maximum mass recorded is from 2,83 kg (Jubb 1967) to 3,30 kg (Bruton et al 1982), although the more typical limit for most waters would be 1,0 to 1,5 kg, and in dwarf populations as little as 15 to 30 g (Hecht & Zway 1984).

#### The eastern Cape environment

The waters of the eastern Cape consist mainly of short rivers flowing southwards from the edges of the Table Mountain Sandstones of the Cape fold mountains, and the Witteberg Group hills around Grahamstown (King 1963). These rivers have erratic flow regimes, and may cease flowing for many months, remaining as "reservoir" rivers, consisting of large deep pools, separated by rocky sections (Heydorn & Grindley 1982). They usually yield soft, mineral deficient and unproductive waters. However, the high pH (mean 8,2) and alkalinity (mean 139 - 185 ppm Ca CO<sub>3</sub>) of the waters of the Kowie River system indicates a higher natural productivity than many of the acidic streams further west (Bok 1983). In places, larger rivers which have their upper catchments in the Karoo (ie the Gamtoos, Gouritz, Sundays, and Great Fish Rivers) break through the montaine range of the escarpment and reach the sea usually via long meandering estuaries. The waters of these rivers carry fine Karoo sediments from the Stormberg, Beaufort, Ecca and Dwyka Groups and are highly mineralised and turbid in comparison to the short coastal streams (Noble & Hemens 1978). The coast has been uplifted (Marker 1988), and

the lower estuarine reaches of most rivers and streams consist of incised meanders that may extend up to 21 km inland, as in the case of the Kowie River. At times of low river flow these estuarine sections are brackish or saline, but become freshwater after flooding. Pools adjacent to the estuaries may become hypersaline at times of low water interchange. As this area is the extremity of the natural range of O. mossambicus, this species often only survives in these estuarine sections due to its increased tolerance of low temperature in brackish water (Allanson et al. 1962). Penetration of the shallow fresh waters upstream is limited by low winter temperatures. However, the construction of numerous small reservoirs at low altitude has created thermal niches which can sustain tilapia populations, but which can also block migrations. In some cases the tilapia in these dams are indigenous to the catchment, and in other cases have been stocked from nearby rivers.

It is evident therefore that O. mossambicus is found in a wide variety of environments within the eastern Cape. Most of these habitats have a simple fish community usually consisting of only a few species, which may be either freshwater, estuarine or marine in origin. Not only are the O. mossambicus in these small water bodies subject to low temperatures, but also to non-cyclical regimes of fluctuating water level, quality and salinity.

The ability of O. mossambicus to grow to a large mass (2,43 kg) in small water bodies near the extremity of its range

prompted the initial interest and fieldwork on which this study was based (James & Bruton 1987, 1988, James 1989). Further investigation revealed that this species is common in the eastern Cape coastal area, but adopts a widely variable life style depending on environmental influences.

#### Phenotypic plasticity

Growth in fishes does not conform to the pattern usually found in many of the more familiar animals, in that fishes continue to grow throughout their lives. Fishes are also unusual in the degree of plasticity exhibited in their life-history styles. This plasticity is manifested in ways such as growth rates, age at first maturity, life span, reproductive investment per individual young, and fecundity. Of all the African cichlids, the tilapiines show the greatest plasticity, with little specialisation compared to the species flocks of haplochromine cichlids of the great lakes of tropical Africa.

Fryer & Iles (1972) described several examples of "dwarf" tilapia populations resulting from environmental factors: O. mortimeri which replaces O. mossambicus in the Middle Zambesi catchment does not breed in Lake Kariba until at least 30 cm standard length (SL). In the lower reaches of the Malolo River, near the lake, this species matures at 18 to 20 cm, and in the upper reaches at 9 cm SL. O. mossambicus kept in aquaria may breed at only 7 cm SL and a few months of age (Peters 1963), whilst wild populations may delay breeding until their second year (Bruton & Allanson 1974).

"Stunting" or "dwarfing" in a population does not necessarily imply that food is scarce or that growth is slow (Fryer & Iles 1972): tilapia raised under favourable pond conditions may achieve growth rates of 8 cm in two to three months from fertilisation, and 18 cm in one year. These same fish matured at only three months of age, which is far earlier than in natural conditions (one to two years), and yet grew at a very much faster rate. The O. mossambicus population of Lake Sibaya studied by Bruton & Bolt (1975) was found to be fast growing and in good condition only whilst in the juvenile phase. Adult fish matured early, especially females (after only one year), and were in poor condition and grew little after maturation. This was attributed to complex reasons of which the most important was the low food abundance in the preferred habitat (sloping sandy terraces at the deep end of the littoral zone).

Another feature of dwarfing in tilapia is the ability of tilapia to produce smaller but more numerous eggs under adverse conditions. Cridland (1961) pointed out that dwarf O. esculentus produced eggs only one third the weight of those from the wild population in Lake Victoria. Various studies on O. mossambicus give a range of egg sizes from 1,9 to 3,6 mm for the long diameter (Vaas & Hofstede 1952, Chako & Krishnamurti 1954, Peters 1963, Fishelson 1966, Aravindan & Padmanabhan 1972, Bruton 1979, Trewavas 1983). Fecundity is largely size dependent, but may vary from 80 eggs per single spawning of an 80 mm total length (TL) female (Vaas &

Hofstede 1952) to between 360 and 1775 eggs for females of 20 to 31,9 cm TL (De Silva & Chandrasoma 1980, quoted in Trewavas 1983). Spawning frequency may vary from one to two broods per season in the Zambesi River (Fryer & Iles 1972) to almost continuous spawning throughout the year in dwarf populations from hot springs (Hecht & Zway 1984). In equatorial waters spawning may occur during two seasons annually for some tilapia that depend on the rainy seasons (Fryer & Iles 1972), or during the warmest months only where seasonal temperature variations are marked, irrespective of rainfall or flooding (Bruton & Allanson 1974).

There is a paucity of information on the longevity of O. mossambicus. Hodgkiss & Man (1977) found that this species had a short life cycle in Plover Cove Reservoir (Hong Kong) with few fish over three years of age. Bruton (1979) found the maximum age in Lake Sibaya to be 7 to 8 years old, and Hecht (1980) reported 9 years as the maximum age in the Luphephe Dam in Venda. It has usually been accepted that fish in benign environments will live longer than those living under harsh conditions or near their natural range limits.

This study attempts to investigate the variable life-history styles exhibited by O. mossambicus in the eastern Cape, and to relate the phenotypic plasticity expressed in the different populations studied to the prevailing environmental conditions.

In Chapter 1 the sampling sites are described. The physico-

chemical conditions and specific sampling methods for each site are detailed individually. The chapter concludes with details of general methods used.

Chapter 2 describes the population demography and general biology of O. mossambicus. Catch per unit effort data and visual observations are used to provide insights into diel and annual migrations, habitat preferences and population structure.

Age and growth is described in Chapter 3. Different ageing techniques are examined, together with validation of analysis of scale and otolith check marks. The length:mass relationship and longevity of the four populations is discussed. The chapter concludes with a general discussion on the reasons underlying the variable growth rates that were recorded.

Chapter 4 compares the reproductive biology of the four populations, with special emphasis on Bradshaw's Mill Dam and Mill Farm Dam. Age and size at first maturity, fecundity, nest building and spawning season are examined. Reproduction under controlled conditions is compared to the results of field observations of spawning in natural populations.

The study concludes with a general discussion on the alternative life-history styles adopted by O. mossambicus in the eastern Cape, and examines the extent of its phenotypic plasticity under harsh and benign environmental conditions.

## SAMPLING SITES

O.mossambicus occurs naturally in many fresh, and in some brackish, waters in the Albany area to the south of Grahamstown. The sites chosen for regular sampling had to meet the following criteria:

(a) As far as possible water bodies were selected that contained indigenous populations (as opposed to those originating from the Amalinda Fish Hatchery at East London which was the main source

of translocated fish). Sites were identified where land ownership had remained unchanged for lengthy periods and no record of stocking was recalled by the landowners.

(b) Sites were selected for their topographical variety and variations in water chemistry and quality.

(c) Populations of O. mossambicus which were exploited by anglers were avoided, as an absence of angling pressure was considered essential for accurate demographic study.

(d) The water bodies had to be of sufficient size to withstand regular sampling. Thus short riverine stretches or pools supporting limited numbers of O.mossambicus were unsuitable.

(e) Sites with and without predatory fish populations were selected in order to examine the effect of predator/prey relationships.

The four water bodies selected (Fig. 1) may be described briefly as follows:

Rufanes Pool: a large eutrophic pool on a small seasonal

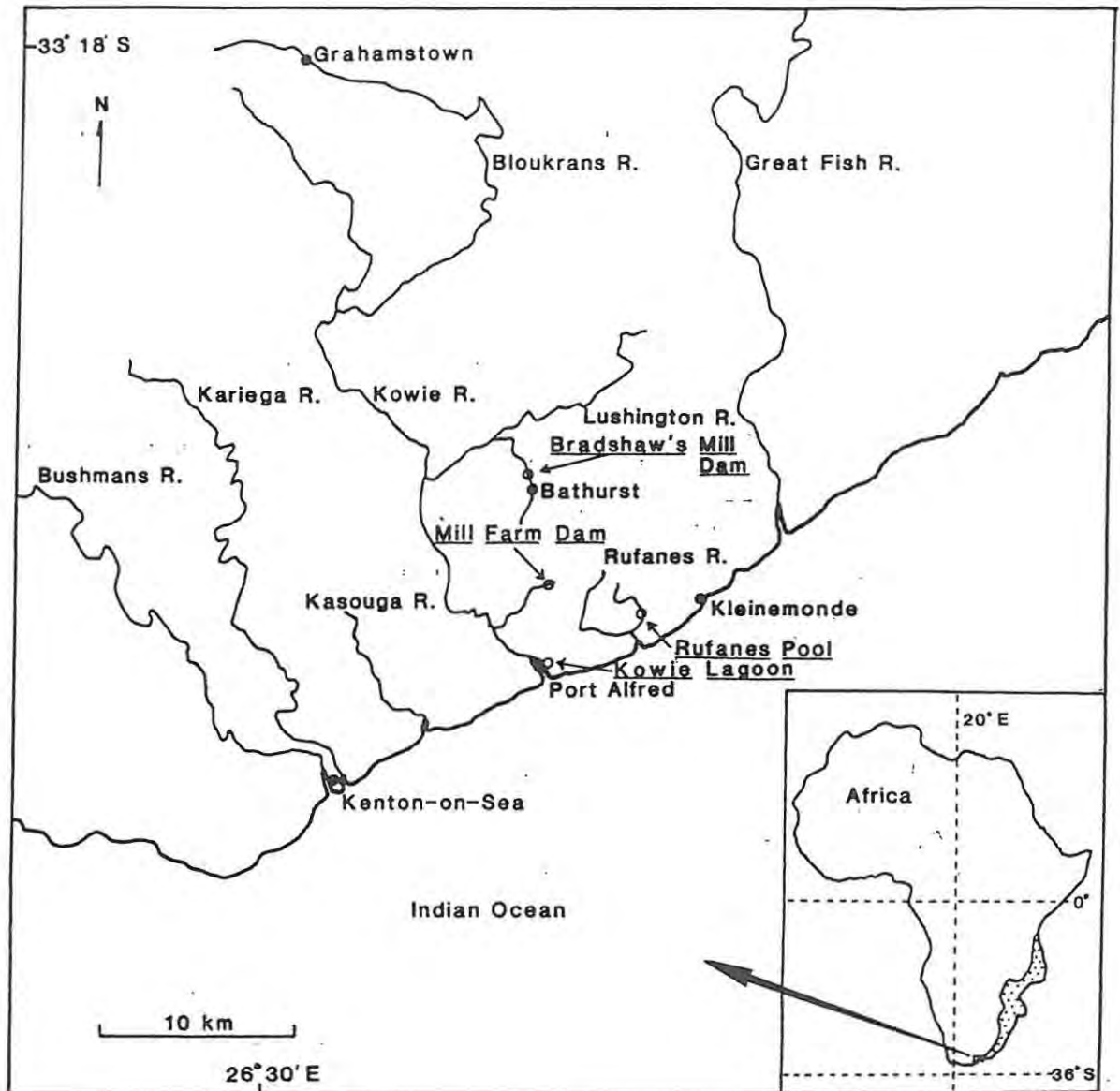


Fig. 1. Map of the eastern Cape showing the four study sites. The shaded area in the inset of Africa indicates the approximate natural range of *Oreochromis mossambicus* (after Philippart & Ruwet 1982).

stream.

Kowie Lagoon: a small estuarine salt marsh.

Bradshaw's Mill Dam: a clear water lake in a V-shaped valley.

Mill Farm Dam: a shallow gradient and nutrient-rich lake.

As external environmental factors play a major role in determining the life-history of the O. mossambicus populations, a comparison of these factors is important (Table 2).

In the next section the physico-chemical environment of each site is described. Whilst sampling techniques differed between sites, physico-chemical measurements were standardised using the instruments described in Table 3.

Table 3. The instruments used for recording the physico-chemical environment of the four sampling sites in the eastern Cape.

Dissolved oxygen	Simplair oxygen and temperature meter
pH	Kane and May meter
Transparency	Standard 20 cm Secchi disc
Salinity	Refracting salinometer
Temperature	Brannan minimum/maximum thermometers
Depth	Graduated line and plumb
Gradient	Zeiss dumpy level

Table 2. Environmental parameters for the four sampling sites.

	Kowie Lagoon	Rufanes Pool	Bradshaw's Mill Dam	Mill Farm Dam
Area (ha)	0.6	0.12	0.75	3 - 13
Max. depth (m)	1.0	2.0	3.6	4.6
Level fluctuation (m)	0.3	0.9	nil	3.0
Littoral gradient	1:30	1:4	1:2	1:25
Altitude (a.m.s.l.) (m)	0	40	165	90
Inflow	tidal	stream	stream	seepage
Emergent aquatic plants % area	15	10	30	0
Submerged rooted plants % area	70	0	10	60
Salinity (ppt.)	16-40	0-1	0	0
pH (range)	7.5-9.8	7.1-8.6	7.4-8.6	7.5-9.3
Min. temp (C at 1m)	9.5	11	10	11.5
Max. temp (C at 1m)	32	25	27	31
Secchi (range, cm)	100-100	13-100	30-315	70-190
Secchi disc mean	100	46,7	139.9	137.2
Sampling method				
adult fish:	Gill net	Seine net	Gill net	Gill net
juvenile fish:	Seine net	Seine net	Gill net	Electrofisher

## Bradshaws Mill Dam

### Site description

Bradshaws Mill Dam is a small artificial reservoir built in 1970 on the Bathurst Stream, a tributary of the Kowie River (Figs. 2,3 & 4). The dam wall lies astride a vee-shaped valley at the point where the Bathurst Stream begins to incise into the uplifted coastal plain. The Bathurst Stream is a perennial stream with a typical flow at this point of 0,5 - 3 litres per second. The stream has a degraded catchment and through much of its length above the dam flows through a semi-urban area, and is prone to floods carrying a high sediment load.

### Bathymetry

The reservoir is steep-sided (Table 2). The littoral gradient varies from 1:2 along the dam wall to 1:4 on the more gentle eastern bank. Much of the western side is a near vertical earthen cliff. The shape of the lake is forked, as a minor tributary enters from the eastern side. The maximum depth of the dam is 3,6 m, and the mean depth 2,5 m.

### Inflow/outflow

Water overflows from the lake via a 0,8 m high by 4 m wide brick spillway which forms the eastern end of the damwall. During the course of the study (December 1985 - December 1987) the reservoir was continually full, and overflow varied between a minimum of 0,25 litres/second and a maximum of



Fig. 2. Aerial view of Bradshaw's Mill Dam taken in April 1989. Note the extensive Typha capensis growth and the lack of open shoreline.



Fig. 3. A general view of Bradshaw's Mill Dam looking upstream.



Fig. 10. A general view of Rufanes Pool. The dam wall is on the left side of the photograph.

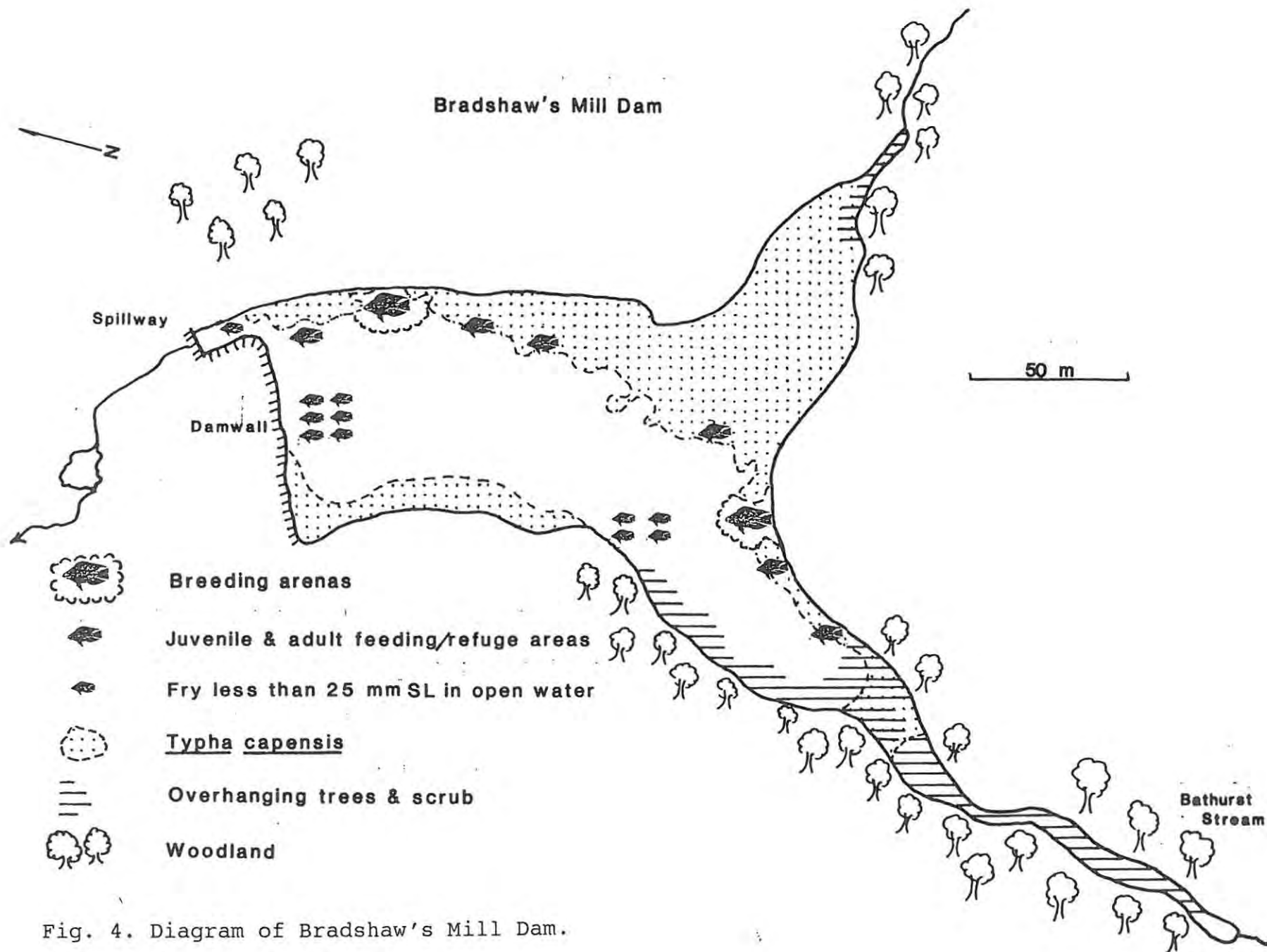


Fig. 4. Diagram of Bradshaw's Mill Dam.

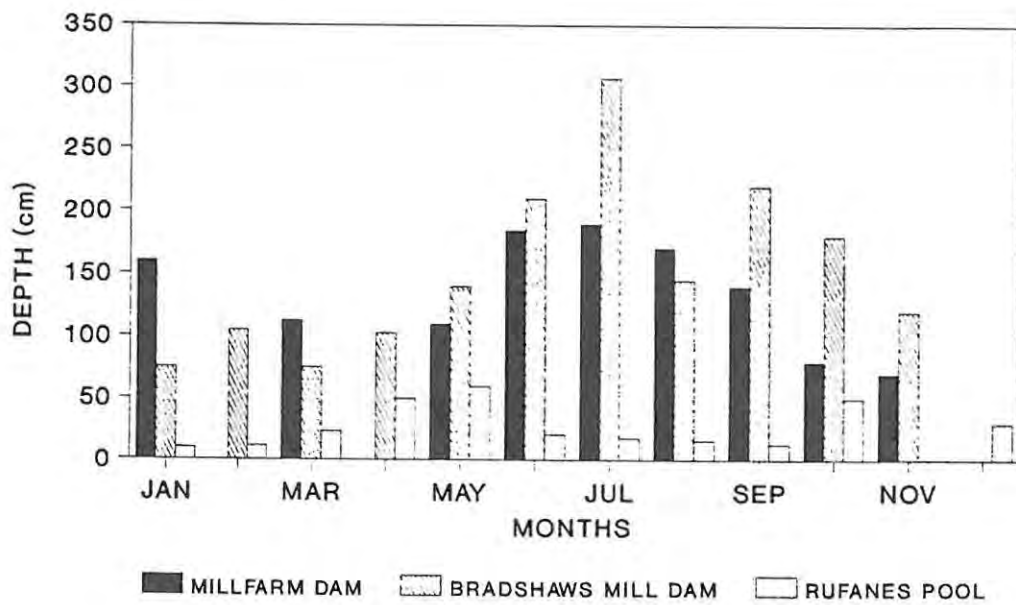


Fig. 5. Monthly water transparency recordings (Secchi disc) from three of the four sampling sites. The fourth site, Kowie Lagoon, remained clear to its maximum depth of one metre throughout the year.

several hundred litres/second for short periods after heavy rainfall. After periods of heavy precipitation the inflow became turbid, but due to the small area of the catchment, strong stream flow was short-lived and the lake soon cleared as the inflow was reduced. Table 4 details the fluctuations in transparency recorded during the sampling period. Comparisons with other sites are shown in Fig. 5.

Table 4. Transparency at Bradshaw's Mill Dam during 1986/87 (- indicates no record available)

Month	Transparency cm.	
	1986	1987
January	-	75
February	30	105
March	115	75
April	76	103
May	210	140
June	-	210
July	315	307
August	102	145
September	110	220
October	165	180
November	45	120
December	90	-

The trend towards greater clarity during winter when phytoplankton growth is reduced was interrupted by occasional increased turbidity due to flooding. Transparency in this water body was the highest recorded in any of the sites monitored and could be an indicator of low primary productivity. This is discussed in a later section.

## Temperature

Due to the steep underwater profile of the lake basin, its constant depth and sheltered aspect, a degree of thermal stratification was expected. To attempt to record this, minimum/maximum thermometers were placed at 30 cm, 100 cm and 360 cm (the maximum depth) and monthly recordings were taken (Table 5).

Table 5. Minimum monthly water temperatures at Bradshaw's Mill Dam in degrees Celsius (- indicates no record available)

Depth	30 cm	100 cm	360 cm
January 1986	19,5	21	-
February	22	-	-
March	21	-	-
April	18,5	17,5	-
May	15	14	-
June	-	-	-
July	10,5	10	11
August	12	11	11,5
September	14	12,5	13
October	14,5	13,5	14
November	15,5	15	15
December	18	16,5	16
January 1987	21,5	21	17,5
February	21,5	21	19,5
March	21,5	20,5	20,5
April	18,5	17	17
May	16	14,5	15
June	11	10	11
July	12	11	11
August	13	11,5	11,5
September	15	13	14
October	18	15	16
November	19	18	18

The lowest temperatures were recorded during June and July each year when minimum temperatures between 10 and 12 °C were experienced at all depths.

Flora: aquatic and terrestrial.

The steep shore of the lake is vegetated with short pasture grasses and Acacia thorn scrub of similar species composition to that found on most of the eastern Cape coastal plain, and described as Savanna verging on Valley Bushveld by Lubke & van Wijk (1988). The south-western (upstream) part of the dam is overhung in places with thickets and small trees. Numerous terrestrial birds were observed nesting in these trees (predominantly weavers), but waterfowl were rare, although the Cape cormorant Phalacrocorax capensis visited the lake occasionally.

Approximately 30% of the lake surface area is dominated by a vigorous growth of the Cape bullrush, Typha capensis, which has colonised all the substrata less than 2 m deep, with the exception of the dam wall, a section of bank of only 5 to 7 m length on the eastern shore, and in the vicinity of the spillway. Where Typha has not colonised the substrate Potamogeton pectinatus forms a dense growth during the warmer months, at depths up to 2,5 m, but largely dies off during winter. The growth of Typha is so dense that the bay formed by the eastern tributary is completely choked and sediment deposition is taking place amongst the stems, rapidly reducing the depth and area of the bay. Typha seems to prefer water of 20 cm depth or more, and a narrow band of open water separates the reed bank from the littoral. This has an effect on the

diurnal thermal regime of the water, as illustrated in Table 14.

Due to the dense vegetative growth surrounding the lake, the substratum consists of black anoxic mud, overlain with a layer of coarse, decaying Typha stems of variable thickness. Finer detritus on the substrate is found in the vicinity of Potamogeton pectinatus.

#### Fish species

Two fish species were recorded from the impoundment:

Oreochromis mossambicus (Peters 1852), the Mocambique tilapia.

Micropterus dolomieu (Lacepede 1802), the smallmouth bass.

O. mossambicus may be indigenous to this locality and occurs in permanent pools both above the dam and below. This species has colonised the newly built (1988) Bathurst Stream Dam (Sarel Hayward Dam) a few kilometres downstream at the confluence with the estuarine section of the Kowie River.

M. dolomieu was probably stocked after 1970, but has not sustained a viable population. Only three large adults were caught (mass: 1260 g, 990 g and 660 g.) during the first three months of netting, and despite use of various catch techniques no further bass were caught or observed. It is likely that the specimens caught were relics of the original stocking, as the rocky substrate habitat preferred by this species (P H Skelton, J L B Smith Institute of Ichthyology, pers. comm.)

is not found in this dam. Reproduction does not appear to have taken place, and due to the low number caught their presence is not considered to be significant in terms of biological impact.

No small Barbus species were present which is surprising as both B. pallidus and B. anoplus are present in the catchment (Skelton, pers. comm.). The spotted bass M. punctulatus, which has recently been reported from the ebb and flow of the Kowie River, downstream of the dam (A Bok, Cape Department of Nature and Environmental Conservation, pers. comm.), was also absent. Largemouth bass M. salmoides are also found in the catchment (Bok 1983) but not in the dam.

#### Other aquatic macrofauna

Large freshwater crabs, Potamonautes perlatus, with carapace lengths up to 12 cm were abundant and often found entangled in gill nets where they scavenged enmeshed fish. Water leguaans, Varanus niloticus, were present, as evidenced by their occasional entanglement in gill nets.

#### Specific sampling techniques and methods

An initial survey was undertaken during November 1985 to establish the presence of Oreochromis mossambicus, and thereafter monthly sampling commenced in January 1986, for two years. Catch techniques were limited to a standard fleet of gill nets (100 m long by 2,5 m deep comprising 10 m panels of the following stretched mesh sizes (mm): 15, 25, 40, 50, 80,

100, 125, 150, 180 and 200) set adjacent to the reed bank along the eastern shore. During the first two months, day-set nets recorded high catches, possibly due to the low transparency. Net catches decreased inversely with water clarity, and gill nets were set overnight after the August sample to compare night and day catches. Thereafter nets were left overnight as standard practice from September onwards.

Various other catching techniques were attempted: baited traps, consisting of a triangular net-covered frame with invaginated wire entrance cone, were found to be ineffective. Small juveniles were occasionally caught by electrofishing but this could only be practised in the few shallow areas. Rod and line fishing proved to be very variable: at times numerous sub-adult (SL 80-150 mm) O. mossambicus were caught, but more usually this method proved ineffective.

Seine netting was effective in two ways:

(a) Short distance pulls with a 7 m x 1 m x 15 mm stretched mesh net, covering 3 to 5 m of the substrate opposite the grassy bank on the eastern shore.

(b) The net placed amongst the stems of Typha such that the base lay on the substrate, and the upper part near the surface forming a cross-section similar to the letter "C", in water 30 to 50 cm deep. The net was left for 15 minutes and then lifted rapidly at each end by two assistants, trapping fish in the "U" section. At times when catches were low, juvenile fish were actively chased into the net-trap before lifting. This method proved to be either highly effective, or caught

virtually no fish at all, with little variation between the two extremes. As "chasing" of the fish into nets is a qualitative and non-standardised exercise, catches could not be used for quantitative comparisons.

Due to the small area of this lake, the extended period of sampling (two years), and the effectiveness of night-set gill nets, it is possible that the number of adult fish removed (117 x > 100 g mass, 159 x 11 to 99 g) could have had a significant effect on the demography of the population, which is likely to number hundreds of adults rather than thousands (Table 13). For this reason sampling was limited, and curtailed as soon as possible. Repetitive samples large enough for statistical analysis of population estimates were therefore not available.

## Kowie Lagoon

### Site description

The upper east bank lagoon on the Kowie River estuary (Fig. 6 & 7) is one of several salt-marsh lagoons situated adjacent to the main channel approximately 0,5 km north of the river mouth. The lagoon is not a natural feature of the estuary, as the river channel was canalised in 1838 (Heydorn & Grindley 1982), and the main outlet to the sea which was previously on the east bank was re-routed to the west bank. The lagoon is probably the remains of the original sand flats that existed between the original river mouth to the east and the channeled mouth to the west. Despite its historical disturbance, the lagoon is typical of many similar salt-marshes that occur naturally along this and other nearby river estuaries.

During the sampling period (December 1985 to December 1987) the lagoon was connected to a similar lagoon (the lower east bank lagoon) through a culvert under the main East London road. These two lagoons were originally one and were separated by construction of the road and bridge in 1970. Both lagoons are separated from the river channel by a "berm" or dyke, and tidal effects are largely dampened. In 1988 the lower east bank lagoon was drained and dredged to form a small boat harbour, and the dyke was breached that connected it to the estuary, making it tidal. The upper east bank lagoon dried up completely. All aquatic macrophytes and invertebrates suffered desiccation and the fish population was removed. This lagoon



Fig. 6. A general view of the Kowie Lagoon.

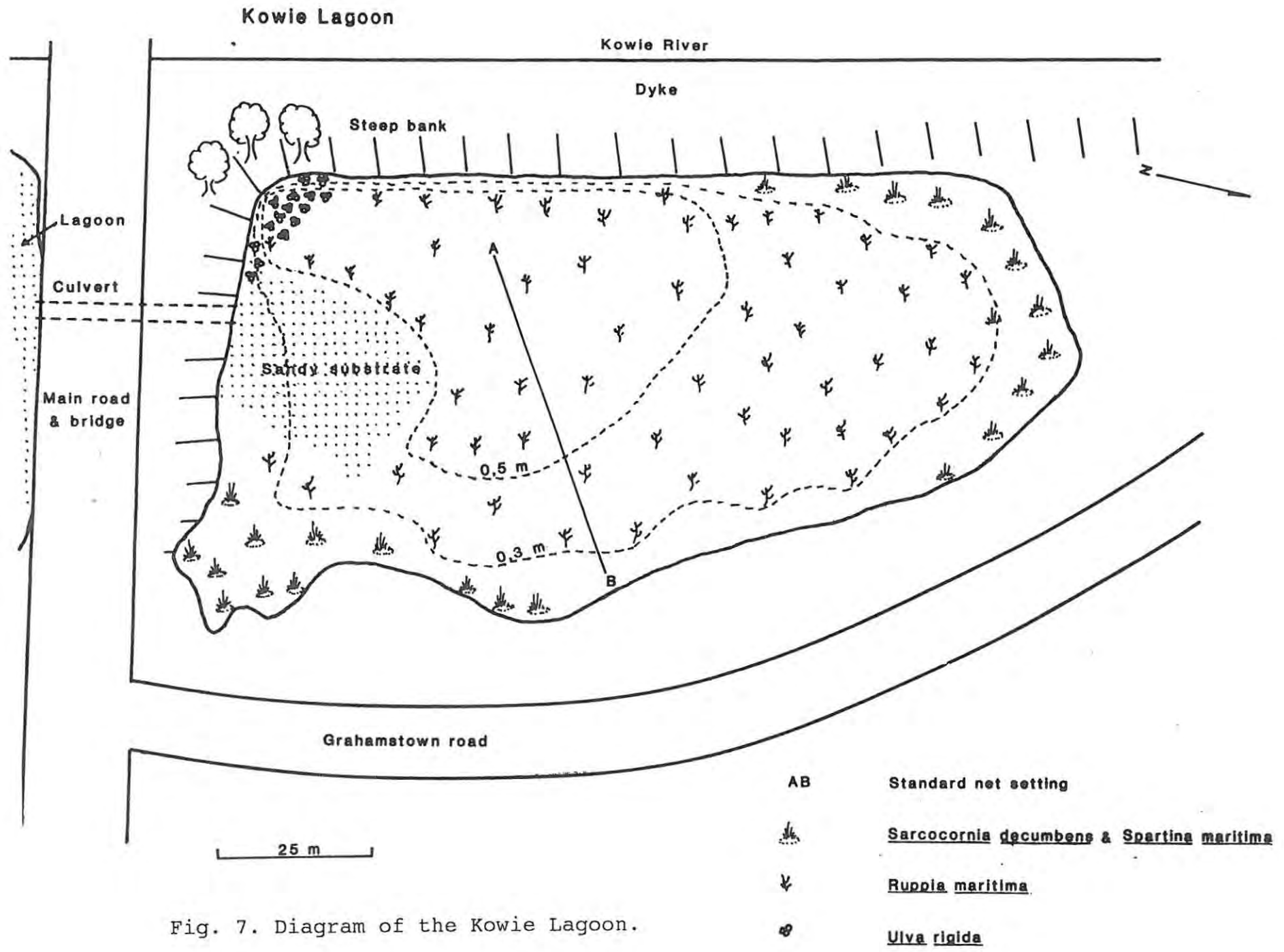


Fig. 7. Diagram of the Kowie Lagoon.

has since refilled, and through the culvert connection and breached dyke, is now tidal and accessible to estuarine and marine animals. In the following site description the lagoon will be described as it was during the sampling period.

Flora: aquatic and terrestrial

On the north-east side the lagoon bank had been landscaped and grassed. The south and west banks are steep dykes separating the lagoon from the river and road, and support grass and small shrubs. There is little overhanging cover with the exception of the southern corner which has a small thicket of thorn scrub.

Within the lagoon the macrophyte Ruppia maritima covers 70% of the substratum, and due to the shallow nature of the water (<1 m) extends to the surface and is exposed at low water level.

Table 6. Common aquatic macrophytes in the Kowie Lagoon (adapted from Heineken 1985).

<u>Sarcocornia decumbens</u>	Shallow fringes of the lagoon
<u>Spartina maritima</u>	Shallow fringes of the lagoon
<u>Ruppia maritima</u>	Covering much of the substrate
<u>Grateloupia</u> spp.	Attached to <u>R. maritima</u>
<u>Ulva rigida</u>	Free floating

The only area not vegetated is a shallow sandbank in the proximity of the culvert. The reason for the absence of macrophytes in this area may be due to currents, rapidly varying salinity, or lack of nutrients. The total absence of macrophytes in the lower lagoon, from which some water originates, may also be due to it being sandy and more

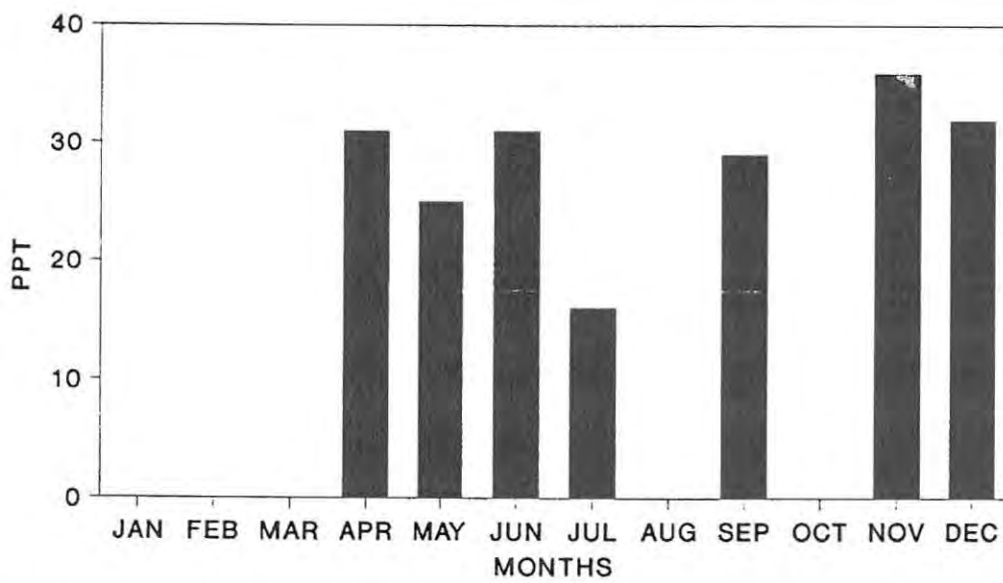


Fig. 8. The monthly salinity recorded in the Kowie Lagoon during 1986. Note that records were not available every month.

affected by tidal exchange than the inflow of water from urban runoff as is the case with the upper lagoon.

#### Inflow/outflow.

As the lagoon is isolated from the tidal estuary it appears to receive its water from seepage through the dyke and through the culvert connecting it to the lower east bank lagoon. Heineken (1985) conducted a 36-hour survey of tidal fluctuation using a tide gauge, and recorded no diurnal tidal movement. He also carried out a 7-14 day observation, and this revealed a 15-25 cm change in water level which coincided with spring and neap tides. During the course of this study fluctuations of up to 30 cm were recorded. After rain there was some inflow from stormwater drains and urban runoff at the north-eastern corner which may account for some degree of eutrophication.

#### Bathymetry

The average depth varied between 30 and 50 cm with a maximum of 1 m. The water surface area is approximately 6000 m<sup>2</sup>. At low water level (maximum depth 70 cm), the total area is reduced by approximately 30 %. The substratum consists of black organic mud, except for the sandbank in the vicinity of the culvert. Microscopic examination reveals that this consists of decaying plant material, with a high concentration of diatoms and dinoflagellates.

## Salinity

Salinity ranged between 16 and 40 ‰ (Fig. 8), and depended on inflow from either rainfall or water from the lower lagoon (Table 7). Salinity levels were highest when the lagoon level was low and evaporation high.

Table 7. Salinity fluctuations at the Kowie lagoon during 1986 (- indicates no record available)

Month	Salinity ‰	Comments
April	31	Level recently risen
May	-	
June	25	Recent rain, muddy around edges
July	31	Level high, connected to lower lagoon
August	16	Heavy rain, water flowing through culvert
September	-	
October	29	Water level dropped 20 cm
November	36	Water level low
December	32	Low water, spring tides
January	40	Water recently risen. Weather hot and windy. <u>O. mossambicus</u> suffering eye disease.

## Temperature and aspect

This was the most typically estuarine site examined in which O. mossambicus was indigenous. The coastal location and open aspect of the lagoon had the following important influences on the thermal regime of the water:

(a) Windy days were more common than inland.

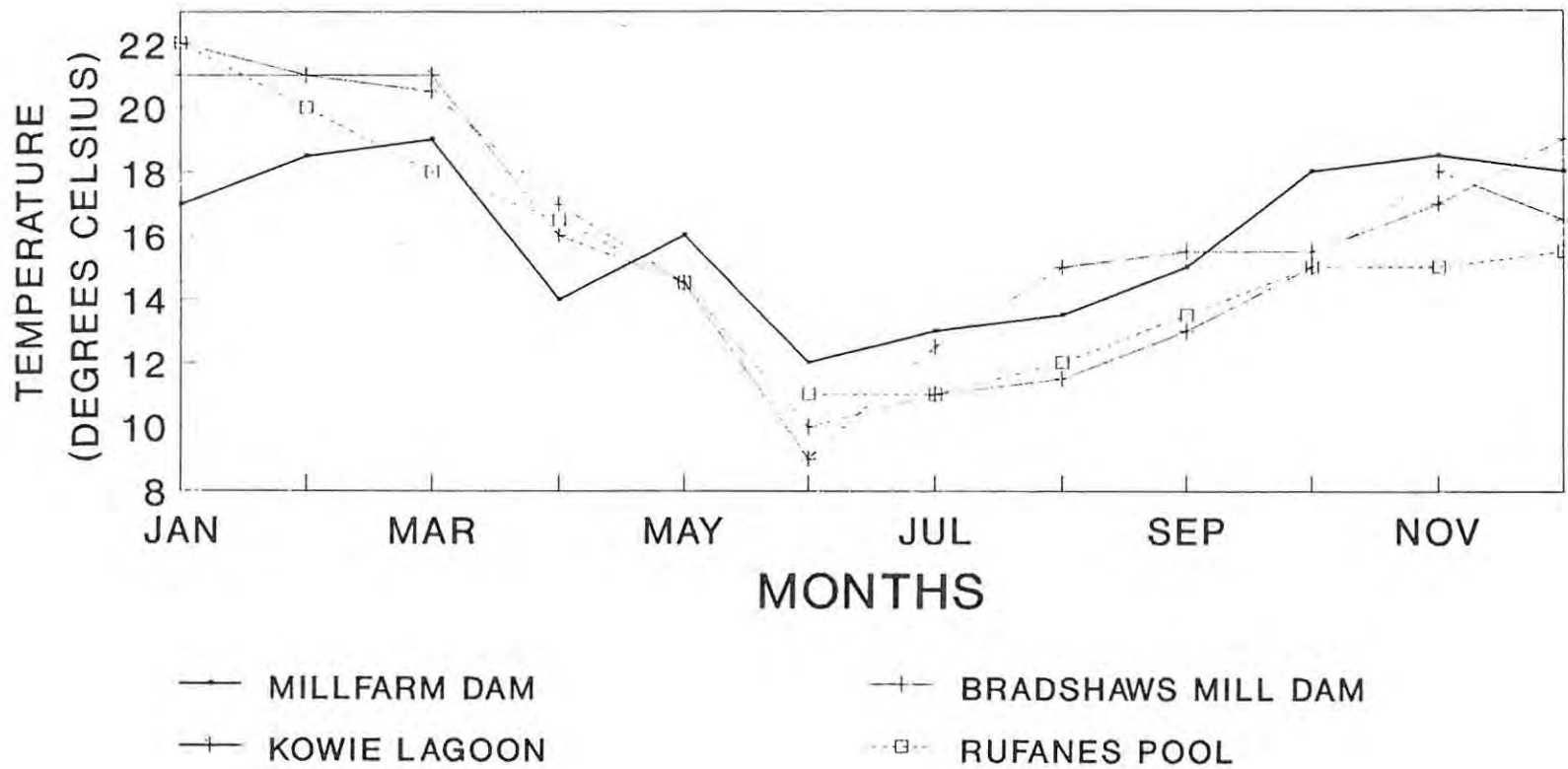


Fig. 9. The monthly minimum water temperatures recorded at 30 cm depth at the four sampling sites in the eastern Cape.

(b) The shallow depth, high transparency and small volume allowed rapid temperature fluctuations and wider extremes than in the main river estuary.

(c) The proximity to the sea moderated air temperature extremes compared to inland sites.

(d) Thermal stratification was absent due to wind mixing, except in the shallows (<20 cm) where surface warming on calm sunny days elevated shallow water temperature above that of the deeper water.

Despite the moderating influence of the sea, the widest temperature extremes of the four sampling sites were recorded at Kowie Lagoon, when measured at 1 m depth. The highest temperature recorded at 1 m depth was 32° C, which was recorded for two consecutive months (January, February 1986). This was 7° C warmer than at (the sheltered) Rufanes Pool and Bradshaws Mill Dam, and 1° C warmer than at (the exposed) Mill Farm Dam, where wind mixing also influenced the temperature of the surface water.

The lowest minimum monthly temperatures were recorded at this site, i.e. 9° C in June 1986 (Fig. 9). This can again be attributed to aspect, as this cold snap was caused by a cold weather frontal system with accompanying high winds, causing a rapid fall in surface temperature. Other water bodies deeper than the shallow Kowie Lagoon were less affected by this short-lived cooling. Apart from this brief period of very low temperatures the minimum temperatures at Kowie Lagoon were

usually equal to, or 1 degree higher than, those at the other sites.

#### Fish species

During this study the following species were encountered:

Oreochromis mossambicus (Peters 1852), Mocambique tilapia  
Gilchristella aestuaria (Gilchrist 1914), estuarine roundherring

Liza richardsonii (Smith 1846), southern mullet.

#### Specific sampling methods and observations

The Kowie Lagoon was the second smallest sampling site selected for this study, and the sample size had to be adjusted accordingly. If seine netting for adult fish had been possible, a catch-and-release method would have provided an adequate sample size. Thick plant growth prevented the use of this method except along short (2 to 5 m) transects for juveniles. Gill netting was the only effective sampling technique, as the salinity precluded use of the electric fishing gear.

The standard fleet of gill nets was set monthly in the same location, diagonally across the lagoon with an east to west orientation. Due to the shallow nature of the water and its clarity, adult O. mossambicus were easily alerted to the presence of people and remained sedentary during sampling,

which made passive fishing gear ineffective. It was found that a catch could usually be made by driving the fish into the net by wading through the shallows, and this was adopted as standard practice. As with other sites, an initial survey was undertaken during December 1985, and standardised sampling commenced in January 1986, and then continued monthly for 13 months.

## Rufanes Pool

### Site description

The Rufanes River is a typical eastern Cape seasonal stream, which has its source 6 km north of the coast (Fig. 1). The stream flows strongly only at times of heavy rain, but has perennial pools along its lower reaches. The estuary is usually lagoonal except after flooding, when it opens to the sea.

The Rufanes River catchment is characterised by dense coastal thicket vegetation in its upper reaches and dune thicket (Lubke 1988) along the short estuarine section. Geologically, the catchment falls within the belt of coastal limestone, and reflects typical geomorphological features of an uplifted coastline (Marker 1988) such as inland plains and deeply incised estuarine meanders.

Rufanes River Pool is a semi-natural pool on a tributary of the Rufanes River, approximately 1 km north-east of the estuary, and a few hundred metres north of the Port Alfred/East London national road (Figs. 10 & 11). The stream at this location is at a transition stage from the shallow gradient coastal plain to the steeply graded incised meanders leading to the estuary. The pool is at an altitude of 36 m a.m.s.l.

About 50 years ago an earthen wall was constructed by the local farmer to deepen an existing pool on the stream for

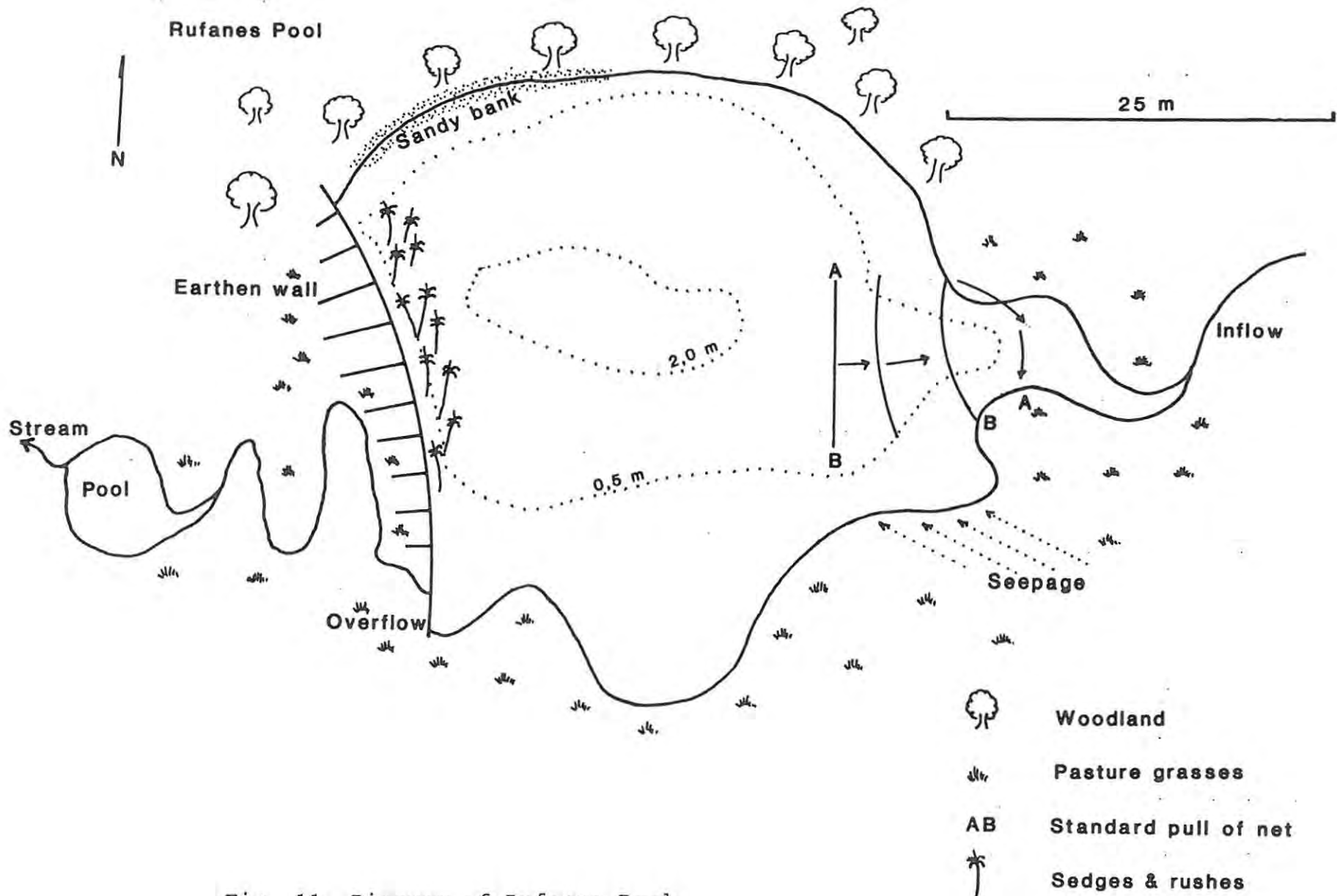


Fig. 11. Diagram of Rufanes Pool.

stock watering. The wall is 2 m high and 25 m long, and forms a pool of 1200 m<sup>2</sup>.

#### Inflow/outflow

The pool receives water from the periodic flow of the Rufanes River tributary, and perennial seepage from the south-east bank. The importance of seepage should not be underestimated as with no measurable inflow at times the pool was found to be overflowing at an estimated rate of 1 litre/sec. On the upstream and downstream reaches are similar smaller pools, which were never seen to dry up, and which provided refuges for small populations of O. mossambicus when surface flow ceased. Stream inflow to Rufanes Pool was highly variable: after heavy rain a maximum measured flow of 0.018 cumecs was recorded, and after several months of drought this flow ceased altogether. The spring on the south-east bank varied from 2 l/sec surface flow to immeasurable seepage. At no time was inflowing water carrying a high sediment load, even at peak flood. In the pool itself a high organic load was sustained by daily livestock defecation whilst drinking, and fluctuations in water level that inundated marginal areas and incorporated organic material into the water body. At all times the pool had a brown-coloured appearance due partially to organic matter in suspension and partially to stirring up the benthos by livestock. During the study period precipitation was very erratic and the maximum pool depth varied between 210 cm (overflow) and 120 cm.

## Aquatic macrofauna

Two fish species are found in Rufanes Pool:

Barbus pallidus Smith, 1841, goldie barb

Oreochromis mossambicus Peters, 1852, Mocambique tilapia.

B.pallidus is a small cyprinid minnow that is found in clear streams of the Cape, and is almost certainly indigenous to Rufanes Pool.

Macroflora: aquatic and terrestrial

The pool is surrounded by Eastern Cape thorn thicket, comprising the following dominant species: Acacia karroo, Chrysanthemoides monilifera, Rhus crenata, Maytenus procumbens and Passerina rigida, which are typical of this area (Lubke & van Wijk 1988). Planted pasture grasses (kikuyu) cover the southern bank and the wall. The northern bank is wooded, with little undergrowth, and forms a steep sandy bank at the edge of the pool (Fig. 10).

Within the pool aquatic macrophytes are restricted by the low light penetration of the turbid waters, and limited to small clumps of sedges (Scirpus nodosus and Mariscus congestus). Potamogeton pectinatus, which is usually abundant in most freshwaters in the area, is absent.

Table 8. The growth of tagged and recaptured *O. mossambicus* from Rufanes Pool.

Tag number	Date	Mass at capture (g)	Days at liberty	Mass change (g)
R04391	21/2/86	650		
	21/3/86	648	28	-2
	5/6/86	644	75	-4
R04390	21/2/86	950		
	5/6/86	902	103	-48
	9/7/86	881	33	-21
	4/9/86	914	54	+33
R04389	21/2/86	850		
	5/6/86	795	103	-55
	9/7/86	826	33	+31
R04388	21/2/86	901		
	21/3/86	866	28	-35
	5/6/86	832	75	-34
	9/7/86	859	33	+27
	9/8/86	858	31	-1
Y01794	21/2/86	749		
	5/6/86	758	103	+9
	9/7/86	752	33	-6
	9/8/86	768	31	+16
R04375	21/2/86	29		
	5/6/86	28	103	-1

## Specific sampling methods and observations

Due to the small size of the pool and ease of sampling, standardised catches were possible. A standard monthly 10 m drag of a 15 mm stretched mesh seine net, 15 m long by 1 m deep, followed by two random drags, effectively sampled the fish population on a comparative basis. After counting and sorting for size, most fish were returned to the water, after removing a sub-sample. Due to the small size of the population, gill nets, the use of the ichthyocide rotenone and other sampling methods lethal to fish were avoided for conservation reasons. Several adult and sub-adult fishes were tagged with spaghetti-type FD 69 Floy tags and released. Later recaptures were re-measured and released again (Table 8). Electrofishing was attempted but found to be ineffective due to the high turbidity which obscured the stunned fish.

## Temperature

Careful attention was paid to the recording of water temperature, especially minimum temperature. Thermometers were hung from poles pushed into the substratum such that the bulb of the instrument was at the selected depths of 30 cm from the surface, at 1 m, and at the pool bottom, (a depth of about 2 m). During the latter part of the study, in early 1987 when the water level dropped markedly, the instrument near the surface had to be moved frequently to deeper water to prevent exposure to the atmosphere, or extremely shallow water temperatures. At various times of the year vertical

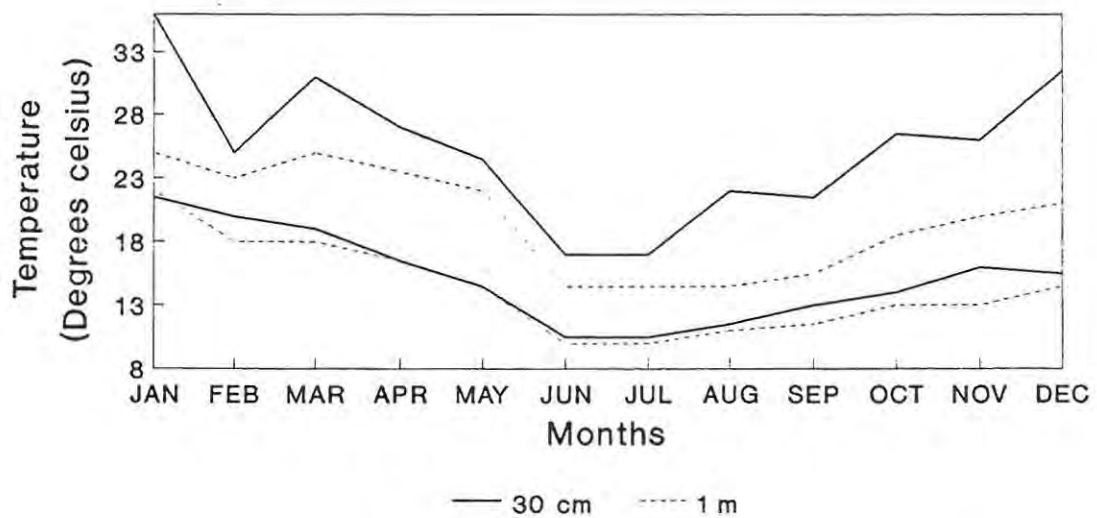


Fig. 12. Temperature stratification as a result of high turbidity at Rufanes Pool. The solid lines represent minimum and maximum temperatures recorded at 30 cm depth, and the broken lines at 1 m depth.

temperature profiles were recorded to ascertain thermal stratification.

Rufanes Pool has a sheltered aspect which offers a degree of protection from the strong coastal winds that affected two of the other sites (Kowie Lagoon and Mill Farm Dam). Wave action did not occur. Thermal stratification was more pronounced at this site than at any other, despite its shallow maximum depth of 2 m (Fig. 12).

Monthly maximum and minimum temperatures did not reach the extremes recorded at the more exposed sites. The warmest months were December to March, and the coolest June and July, as recorded at 1 m. Due to lack of wave action there was little vertical mixing of the water column, and the extreme shallows at times became several degrees warmer than that recorded at 30 cm depth.

Due to the thermophilic nature of O.mossambicus juveniles (Allanson & Noble 1964), and both the extreme warming of the eulittoral water and the protection from predation offered by high turbidity, the shallows were fully utilised by the fish. Warming of surface waters, coupled with a steep thermal gradient encouraged adult O.mossambicus to construct nests and breed in much shallower water (30 to 50 cm) than in clear lakes such as Sibaya (Bruton & Boltt 1975) and Kariba (Donnelly 1969), where depths of up to 5 m are the preferred habitat of breeding adults. The highest temperature recorded

at 30 cm depth was 36° C which is just within the upper lethal limit for O.mossambicus and considerably above the preferred temperature for juveniles (27 - 33,5° C) as measured in a thermal gradient tank (Badenhuizen 1967).

The lowest temperatures (Fig. 9) were recorded during the month of June 1986. Without the measurement of daily min/max temperatures it is unclear for how long the temperature remained at near-lethal levels. During the first 10 days of June air temperatures were consistently below 15°C and water temperatures during this period must have been at or near the minimum recorded. Surface and bottom temperatures as low as 10°C, and 11 °C at 1m were measured. On 4th July, after slightly warmer weather, and under sunny conditions at an air temperature of 18 °C, the water temperature at 30 cm depth was 13°C at 1600 hrs. The maximum recorded during the previous 30 days at 1m depth was 14,5 °C.

#### Temperature stratification

The effects of turbidity and depth on temperature stratification were examined over a 12-month period (Fig. 12). At no time was water in the pool homothermal, although the occasional inflow of surface runoff after rain partially disrupted the thermal gradient in the pool. This water body is too small and shallow to experience thermoclines and turnovers as found with some large dams and lakes in southern Africa (Walmsley and Butty 1980), and vertical thermal gradients are

a result of daily temperature variations, and turbidity.

### Transparency

Average transparency was low (Fig. 5). Frequent stirring up of the substratum by livestock, and rapid fluctuations in water depth appear to be responsible for a mean Secchi disc reading of 0,47 m (n = 12, SD = 0,32). This is atypically low for pools or dams on streams in this catchment (Table 9).

Table 9. Typical water transparency in pools and dams on the Rufanes River.

Site	Disturbed by livestock use	Secchi (cm)
Rufanes Pool	yes	47
Rufanes Farm Dam 1	no	120
Rufanes Farm Dam 2	no	97
Pool upstream of study site	no	76
Pool downstream of study site	yes	27

Suspended matter was examined microscopically and found to consist of benthic detritus, silt particles and a high concentration of diatoms and dinoflagellates. Much of the organic input was observed to result directly from decomposing cattle manure, causing the waters of the pool to remain constantly eutrophic. Low transparency plays a direct role in the thermal regime of the pool and also explains the absence of submerged macrophytes. Low transparency may also indirectly affect the feeding behaviour of the fish due to distinct thermal stratification, as described by Caulton (1977) for Tilapia rendalli in tropical waters.

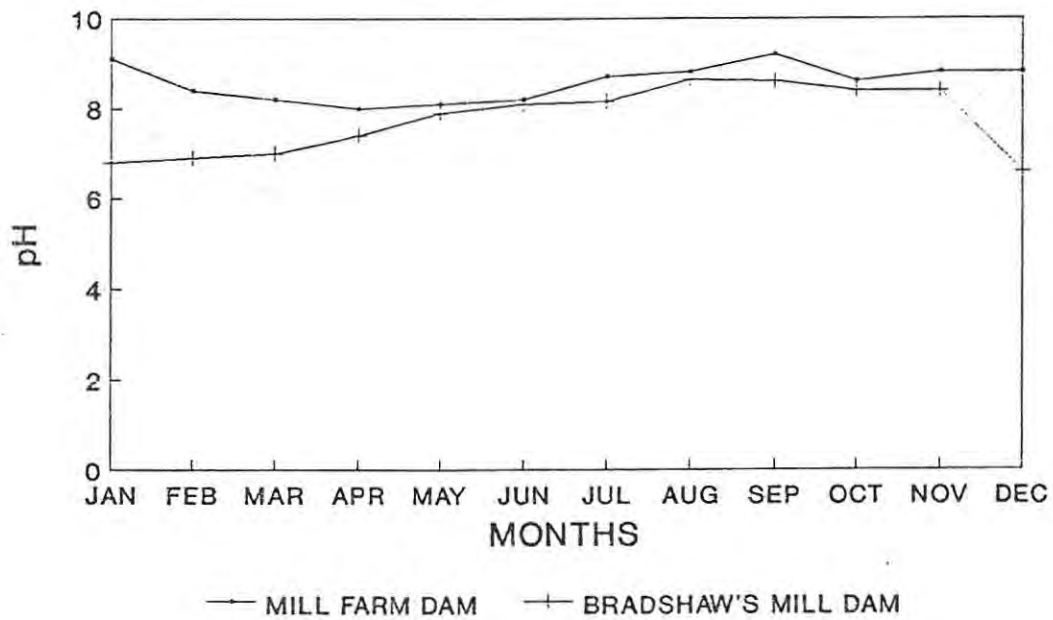
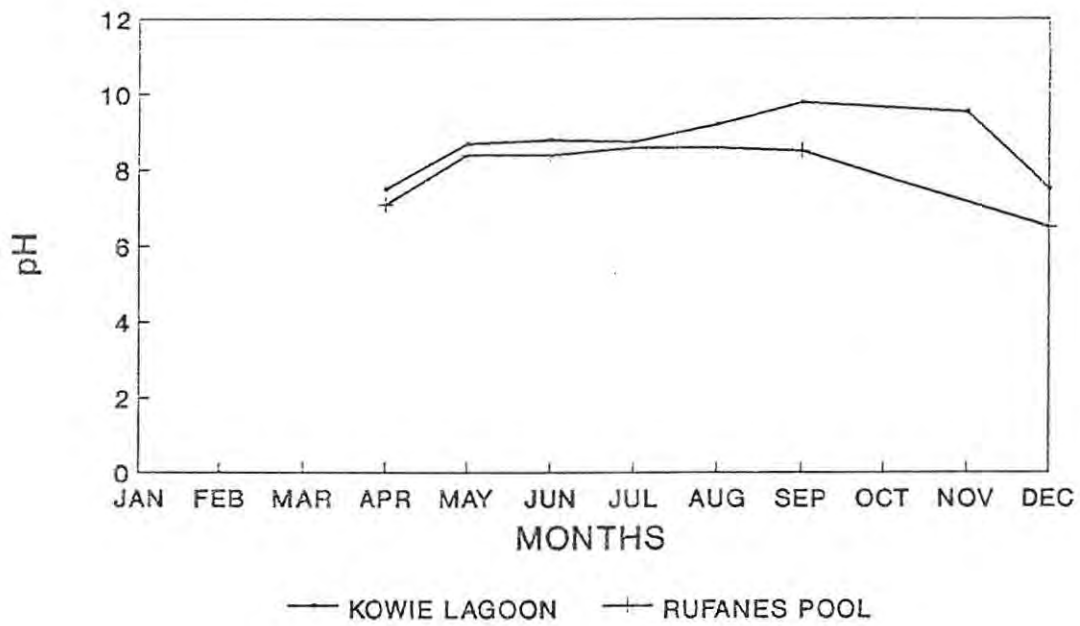


Fig. 13. The monthly pH recorded at each of the sampling sites during 1986 for Rufanes Pool and Kowie Lagoon, and during 1987 for Mill Farm Dam and Bradshaw's Mill Dam.

Seasonal variations in transparency were correlated with rainfall and inflow. Periods of clear inflow to the pool were followed by an increase in transparency (April/May and October 1986). Dilution of particulate matter in suspension by overflow of the pool increased transparency, and reduction of inflow was directly proportional to reduction of transparency, after a time lag of several weeks.

#### pH

Throughout the sampling period pH varied between neutral and alkaline (Fig. 13). Values between 7 and 8,6 were recorded, with the higher values recorded during the winter months. The pH of Rufanes Pool, as with all the sites studied, is within the acceptable limits of O.mossambicus (Chervinski 1982).

#### Zooplankton

Water samples were collected on an occasional basis and microscopically examined for presence of zooplankton. At no time was zooplankton a major source of food for O.mossambicus, although Daphnia sp. was the most common recognisable constituent of the diet of Barbus pallidus, the only other fish species present.

#### Sampling period and frequency

An initial survey was conducted during November 1985 to establish the presence of O. mossambicus, and any other fish

species. From January 1986, for a period of 13 months, fish were sampled monthly using the techniques described previously. Occasional visits were carried out at other times for specific objectives, such as cold water temperature monitoring, capture of live specimens for experimental work, and behavioral and breeding observations.

In analysing the data for this site the effects of habitat size had to be taken into account. By any standard this is a small natural population of O. mossambicus, and one may expect a degree of inbreeding and behavioural interaction not encountered in other larger natural populations (e.g. those studied by Bruton & Boltt 1975, Hodgkiss & Man 1977a & b, Cochrane 1985, De Silva 1985a & b).

## Mill Farm Dam

### Site description

Mill Farm Dam is a semi-natural impoundment which was constructed during the 1940's on an unnamed tributary of the Kowie River (Fig. 1). The lake (Figs. 14, 15, 16, 17, & 18), which is dammed by an earthen wall, floods four previously existing shallow "vleis" or swamps with an east/west orientation. At full storage the lake covers an area of 13 ha, and is wide and shallow. The lake is situated 300 m to the east of the Bathurst - Port Alfred main road, approximately four kilometres from the coast, at an altitude of 90 m a.m.s.l.

### Inflow/outflow

No distinct stream fills the lake, and water enters mainly in the form of surface runoff from surrounding farmland, and from groundwater and runoff within the lake basin; groundwater is probably the largest contributor. Only after heavy rainfall does a minor stream enter from the eastern end. As inflow is so largely dependent on the water table, lake level is variable, and maximum storage capacity and spilling is only rarely attained (Figs. 19 & 20). Minor fluctuations in level (20 to 30 cm) cause large changes in lake area due to the shallow cross sectional profile of the lake (Fig. 20).

During the drought of 1985 the level of Mill Farm Dam fell to an estimated maximum depth of 1,5 m and area of 2 ha. Good



Fig. 14. Aerial view of Mill Farm Dam taken in April 1989 when at a low level. In January 1986 and October 1989 the lake was full, and the track skirting the edge of the lake basin was submerged.

53



Fig. 15. The western basin of Mill Farm Dam during April 1987 when approximately 1 m down from maximum capacity. Note the wave action disturbing the substrate along the shoreline.



Fig. 16. The upper basin of Mill Farm Dam during April 1987. The upper basin is becoming separated from the central basin. Note the very gentle littoral gradient.

54

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Fig. 17. The middle basin of Mill Farm Dam during July 1988 when approximately 1,5 m down from maximum capacity.

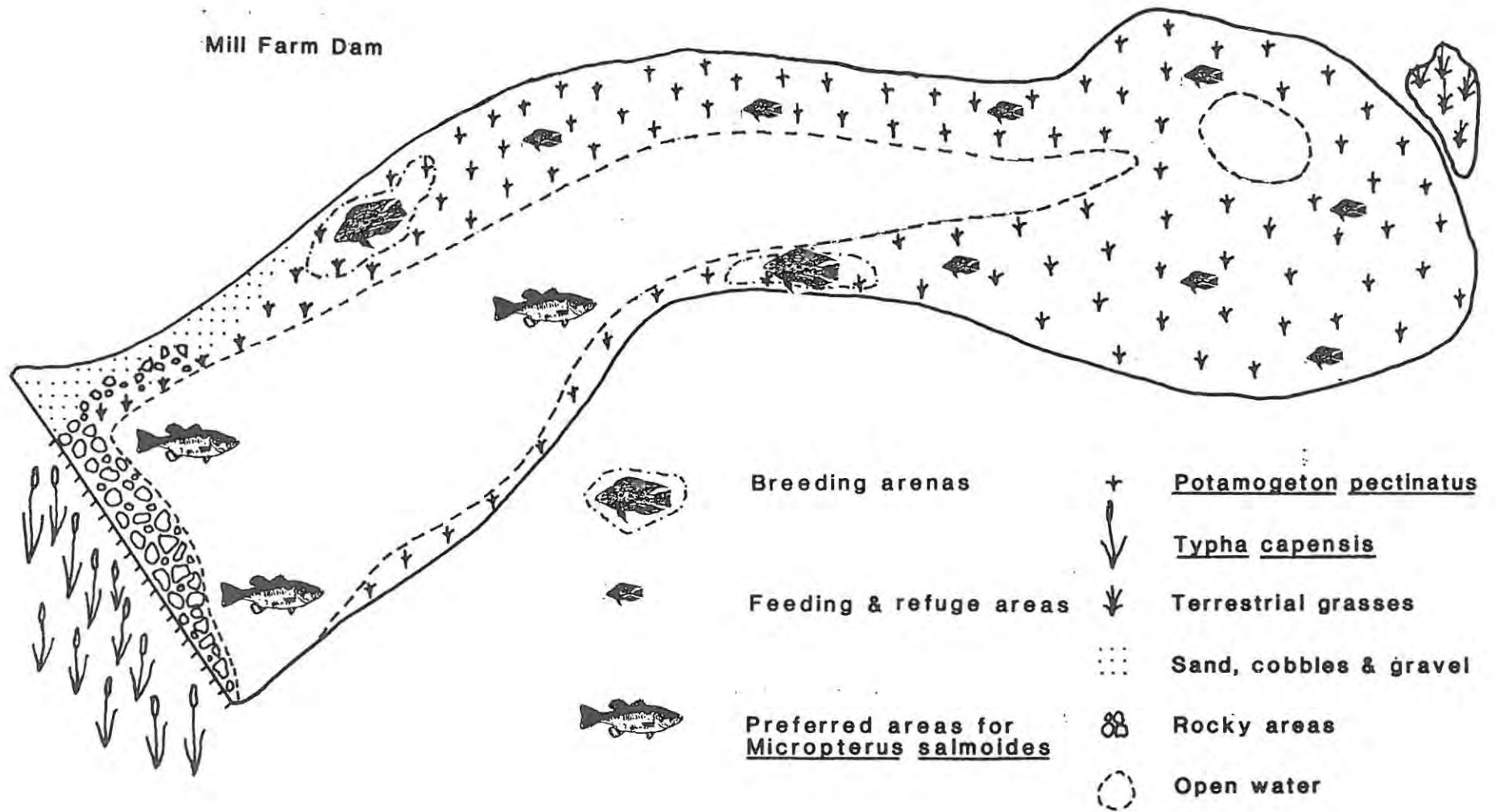


Fig. 18. Diagram of Mill Farm Dam showing the underwater habitat.

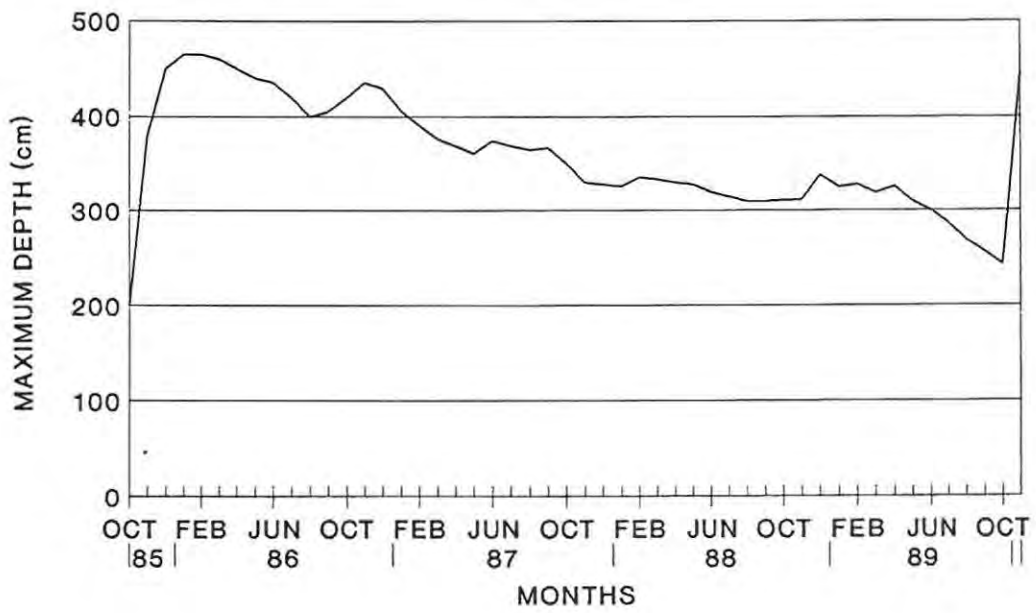


Fig. 19. The water level fluctuations of Mill Farm Dam from October 1985 to October 1989.

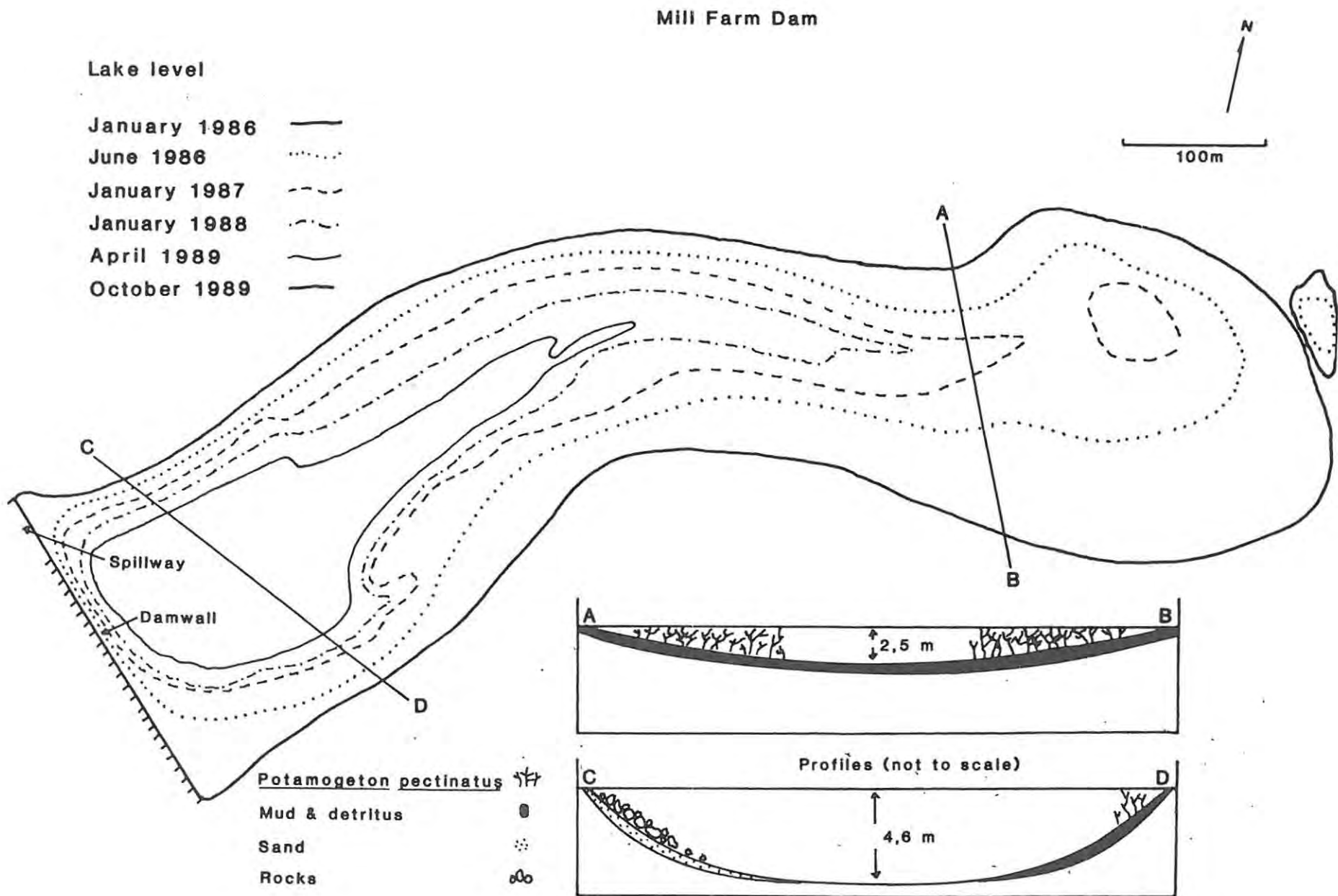


Fig. 20. The fluctuations in water level of Mill Farm Dam from 1986 to 1989.

rains during November/December 1985 filled the lake to its maximum depth of 5 m and area of 13 ha. The lake overflowed strongly for two months and then decreased to an estimated capacity of 70 % and depth of 4 m, and remained at this level for most of 1986. Poor rains during 1987/88/89 resulted in a gradual decrease in level and desiccation of much of the lake bed, until April 1989 when the maximum depth was 2,1 m and the area approximately 2,5 ha, at which stage the aerial photograph (Fig. 14) was taken.

Sampling started in August 1986 to establish the species composition of the lake, and regular sampling with the standard gill nets was carried out from November 1986 until December 1987. The lake was again briefly sampled during April/May 1989 to observe the effects of the drought on the fish population.

#### Aquatic macrofauna

Two fish species have been recorded from the lake:

O. mossambicus (Peters 1852), Mocambique tilapia

Micropterus salmoides (Lacepede 1802), largemouth bass.

No small species were recorded in catches despite the abundance of Barbus pallidus in nearby streams. The freshwater terrapin, Pelomedusa subrufa, and the crab, Potamonautes perlatus, are both common.

## Waterfowl

One of the characteristics of this lake is the large resident and migratory population of waterfowl and terrestrial birds (Table. 10). At times flocks of birds consisted of many hundreds of individuals, for example on 13 August 1986, 117 ducks of various species, and on 4 December 1986 270 Egyptian geese were recorded. As the lake level declined the numbers of waterfowl decreased, and seasonal variations which could be attributed to migration were noted.

Table 10. Waterfowl and terrestrial birds commonly encountered at Mill Farm Dam during 1987.

Common name	Scientific name
Egyptian goose	<u>Alopochen aegyptiacus</u>
White backed duck	<u>Thalassornis leuconotus</u>
South African shelduck	<u>Todorna cana</u>
Blacksmith plover	<u>Vanellus armatus</u>
Blackwinged stilt	<u>Himantopus himantopus</u>
Spoonbill	<u>Platalea alba</u>
Spurwinged goose	<u>Plectropterus gambensis</u>
Coot	<u>Fulica</u> spp.
Dabchick	<u>Tachybaptus ruficollis</u>
Heron	<u>Ardea</u> spp.
Cattle egret	<u>Bubulcus ibis</u>
Cormorant	<u>Phalacrocorax</u> spp.
Pied kingfisher	<u>Ceryle rudis</u>
Giant kingfisher	<u>C. maxima</u>
Moorhen	<u>Gallinula chloropus</u>

An attempt was made to quantify the mass of bird droppings in the littoral, as this was obviously an important source of nutrients to the lake. Between high water mark and the existing water level the exposed littoral area was divided into three zones comprising heavy, medium and slight

defecation levels by waterfowl. Criteria for the divisions included the distance from the water and the slope of the shore: most bird droppings were concentrated within 10 m of the water's edge on gentle slopes (1:30) and became sparse on steeper slopes (1:10) and towards the high water mark. Dam level at the time of sampling was down 1,2 m from the maximum. Three randomly selected sample squares each 1 m square were selected in each zone and pegged with a marker. All avian faeces were collected from these squares and weighed to the nearest gram. An estimation of total mass of faeces lying on the surface was then made by extrapolating to the total exposed littoral area in each division. One month later the bird droppings were again collected from the sample points and re-weighed to estimate the rate at which renewal took place (Table 11).

Table 11. Estimation of avian defecation in the exposed littoral zone at Mill Farm Dam (April 1987).

Total exposed littoral area			41 000 m <sup>2</sup>
(a) Area of high defecation			6 000 m <sup>2</sup>
(b) Area of medium defecation			11 000 m <sup>2</sup>
(c) Area of low defecation			24 000 m <sup>2</sup>
Mean mass over 1 m <sup>2</sup> sample from (a)			74 g
Mean mass over 1 m <sup>2</sup> sample from (b)			17 g
Mean mass over 1 m <sup>2</sup> sample from (c)			8 g
Mean mass after 1 month from (a)			24 g
Mean mass after 1 month from (b)			7 g
Mean mass after 1 month from (c)			2 g
(a) Total mass	444 kg	Monthly addition	144 kg
(b) Total mass	187 kg	Monthly addition	77 kg
(c) Total mass	192 kg	Monthly addition	48 kg
Total mass	823 kg	Monthly addition	309 kg.

Fertilisation of ponds is known to stimulate indirectly the growth of O. mossambicus. Due to its habit of consuming plant and algal detritus (Trewavas 1983), this species benefits from the increased biomass of macroflora and the microfauna associated with its decomposition. The input of phosphates in the form of bird faeces to the water column brought about by water level increases (Fig. 19) means that during and after water level rises the lake becomes eutrophic. The lasting effect of enrichment with natural manures has been determined by numerous aquaculture trials worldwide (Hickling 1950, Huet 1968, 1972, Rabanal 1968, Swingle 1968).

#### Temperature

Mill Farm Dam, at high or near high water level (November 1985 - January 1987) was the largest water body studied. Despite the large area, the depth at the time of this study (2,1 to 4 m) was similar to Bradshaws Mill Dam (3,6 m), although the mean depth was significantly less: 1,5 m. vs. 2,5 m. Aspect was important as windy days were common, with strong winds prevailing along the long axis of the lake. Figure 15 illustrates the wave action and water mixing that was commonly experienced.

Minimum/maximum recording thermometers were placed at 30 cm, 100 cm and on the substrate at the deepest point to establish whether thermal stratification existed (Table 12).

Minimum temperatures did not reach the low level attained in the other sites, probably due to the larger volume of the lake and intermixing with warm surface water. The winter temperatures, though cool for O. mossambicus, were more stable and less extreme than at other smaller sites.

Table 12. Minimum water temperatures recorded during 1986/87 at Mill Farm Dam (- indicates no record available).

Depth	30 cm	100 cm	400 cm
November 1986	15	16	-
December	20	18	-
January 1987	17	17	-
February	-	18,5	-
March	-	19	-
April	-	14	-
May	15,5	16	15
June	11,5	12	11,5
July	12	13	13
August	12,5	13,5	13
September	15	15	15
October	19	18	18
November	18	18,5	18

#### Aquatic macrophytes

The lake supports a dense growth of Potamogeton pectinatus at times covering 60 % of the lake surface, mostly at depths of less than 2 m (Fig. 18). During periods of stable or rising water level a narrow band of clear water remains uncolonised by P. pectinatus around the periphery of the lake (from the littoral edge to approximately 20 cm depth). This area is utilised by juvenile O. mossambicus. Water temperatures in this zone are elevated on hot days to 30 to 33 C. At times of decreasing water levels this zone is choked with stranded and

rotting Potamogeton and juvenile O. mossambicus are restricted to deeper water.

Below the dam wall the Cape bullrush, Typha capensis, is abundant but has not succeeded in colonising the lake basin, probably due to periods of desiccation of the littoral. When the lake level is relatively constant for several months as in 1986, the miniature water lily, Limnosella capensis, establishes itself in the upper basin in shallow water (<50 cm deep). The tubers must be able to survive desiccation as this part of the lake basin is only flooded occasionally (for 8 months during 1985/86), and after desiccation is colonised by terrestrial grasses and grazed by livestock. At high lake level the flat leaves of Limnosella were noted to offer shelter to juvenile Micropterus salmoides which were preying on odonatid larvae.

#### Specific sampling techniques

Gill netting with the standard fleet of nets was the most effective catch technique. Nets were set (at first during the day, later overnight) with the smaller meshes set perpendicular to the shore amongst Potamogeton, and the larger meshes parallel to the Potamogeton bank on its deep water side. Thus the nets covered a range of depths from 30 cm for the smallest mesh, to 2 m for the larger mesh sizes. Nets were also bottom-set occasionally, using weights and anchors, in deep water, and along the rocky dam wall. As the water level

declined and the upper two basins became isolated from the main body of the lake, these were intensively netted to establish if fish were stranded. These isolated basins produced very low fish yields, and it appears that fish retreat to the main basin before the interconnection becomes too shallow.

The dense growth of Potamogeton made seine netting impractical, and juvenile O. mossambicus were usually caught by electrofishing. M. salmoides was occasionally caught in gill nets, but was more readily taken on rod and line using either artificial flies or lures. Rod and line fishing for O. mossambicus proved to be an unreliable catching technique and was abandoned.

#### Sample size

It was only possible to do one year of sampling at this site, therefore the sample size is small and data sets are not conducive to elaborate statistical analysis. Phenotypic variations between this population of O. mossambicus and others studied locally were so distinct that these methods were considered to be unnecessary as the observed data showed clear trends when plotted graphically.

The lake was again sampled during April/May 1989, during a low water phase, in order to establish how drought and deteriorating environmental conditions were affecting the fish population.

## Discussion

### Water depth

During the survey period (Nov 1985 to Dec 1987) the rainfall in the Albany district was typically erratic (Stone 1988) and stream flow and runoff into dams varied accordingly. Water bodies such as Mill Farm Dam and Rufanes Pool experienced wide fluctuations in both area and depth, whereas other dams such as Bradshaws Mill Dam, that are on perennial streams, remained at a constant depth but with varying inflow/outflow (Table 2). The Kowie Lagoon was influenced by spring tides seeping through the dyke separating the lagoon from the river, and periodic fluctuations of up to 0.3 m were recorded.

Prior to the abundant rains during November/December 1985 Mill Farm Dam covered an area of about 2 ha, with a maximum water depth of 2 m. By late December that year, the lake had filled to maximum capacity, covering 13 ha and reaching a maximum depth of 4,6 m. With minor fluctuations, lake level declined gradually thereafter, until September 1989 when the water level equalled the low 1985 level (Fig. 19 & 20). Heavy rain in October 1989 refilled the lake.

The initial increase in the nutrient status which has been recorded by many workers after the flooding of virgin land may sustain improved growth rates (and juvenile survival) for up to three years (Fryer & Iles 1972). The growth of O.mossambicus in Mill Farm Dam, subsequent to filling in late 1985 was near optimum for this species, although juvenile

survival was still subject to winter cold (see below). Other habitats nearby which underwent no or minor level fluctuations during the same period due to sustained inflow, retained cyclical fluctuations in population number according to the season only (Bradshaw's Mill Dam and Kowie Lagoon), and considerably lower growth rates. These populations did not benefit from inundation of nutrients.

#### Transparency and turbidity

Water clarity was highest at all sites during mid-winter and declined thereafter until February. Phytoplankton blooms during the warmer months reduced light penetration except in the brackish Kowie Lagoon where transparency remained constant at 1 m (the maximum depth of the lagoon). Transparency was low at Rufanes Pool throughout the year due to high nutrient enrichment and regular disturbance by stock which made this the most turbid of the habitats investigated. The most extreme fluctuations in turbidity occurred at Bradshaw's Mill Dam, due to flooding of the Bathurst stream. Whilst turbidity has been reported to have a negative effect on fish production for such species as Oncorhynchus mykiss (Alabaster & Lloyd 1982), this study suggests that increased turbidity as a result of stock disturbance and enrichment of water can enhance growth rates of O. mossambicus despite limited water area or depth.

#### Temperature

The lowest water temperatures were recorded during June/July each year. Thereafter temperatures rose above the level

generally considered to be the lethal minimum for O. mossambicus (Trewavas 1983).

Due to the small size and shallow depth of the habitats studied, fluctuations in temperature were rapid. Vertical thermal stratification was absent in the shallow open lakes such as Mill Farm Dam and the Kowie lagoon, but marked in small, turbid habitats like Rufanes Pool due to inhibition of infra-red penetration. Where emergent and submergent macrophytes were abundant, horizontal thermal stratification occurred, and this had important behavioural implications on the fish.

The maximum temperature recorded at 1 m depth was 32° C at Kowie Lagoon, compared to 25° C at Rufanes Pool. This illustrates the variation resulting from environmental differences in depth and water transparency. The importance of aspect and surface area in temperature stratification can be illustrated by noting that the surface and bottom temperature at Mill Farm Dam differed by usually not more than 2° C over a depth of 3 to 4 m, whereas at a sheltered locality of similar depth (Bradshaw's Mill Dam) variation was 5° C or greater. Frequent strong winds resulted in an almost total intermixing of epilimnion and hypolimnion at Mill Farm Dam, where windy days were recorded as follows: calm 44%, strong breeze 20%, strong wind 36%.

## pH

The waters of the coastal region of the Eastern Cape are slightly alkaline (Fig. 13), in comparison to the highly acidic streams which flow from the Cape fold mountain system further west (Bok 1983). The pH showed little variation between localities, although the Kowie Lagoon was consistently the most alkaline.

## Methods

### Population structure

Gill nets and seine nets were used to obtain regular samples either on a monthly or bi-monthly basis. Cochrane (1986) used gill nets for mortality assessment in Hartbeespoort Dam (Transvaal), but in this study gill nets were found to be unsatisfactory as a universal catching technique. Due to the behaviour of juvenile fish during winter, and the obstruction of nets by emergent and submergent macrophytes in some habitats, gill nets did not provide representative samples of the fish present. Only seine netted samples were used for mortality estimates. This obviated the necessity for omitting low catches from gill nets or other sampling methods due to behavioral reasons as reported by Cochrane (1986), as the catching technique was considered to be effective for all length frequencies in the small habitat selected (Rufanes Pool).

Depending on temperature O. mossambicus in the eastern Cape usually spawns from December to March, although distinct populations such as in Mill Farm Dam had a shorter breeding season (see section on reproduction). During this period individual females could have spawned three or four times, although these were poorly reflected by length frequencies in catches of juveniles from December to July. The mortality of 0+ year class was determined by fitting catch curves to length frequencies obtained from samples taken during 1986 and 1987

from January until July each year. Hodgkiss & Man (1977b), Bruton & Taylor (1979) and Cochrane (1986) made substantial collections of dead O. mossambicus found floating in the water during winter, and used these to substantiate winter mortality. Very few such fish were located during this study, and this method was therefore not used.

For the purposes of this study it was felt that the extrapolation of inshore catch data to the entire surface area of impoundments to calculate standing stock and mortality, did not take into account important behavioral aspects affecting habitat preferences, as noted by Bowen (1984) in Lake Valencia, Venezuela (Hodgkiss & Man 1977b working on the 1200 ha Plover Cove Reservoir; Cochrane 1986 working on the 2000 ha Hartbeespoort Dam). These aspects were outlined by Bruton and Boltt (1975) for another large lake, Sibaya (6 500 ha). In this lake it is suggested that a depth limitation of 10 m for O. mossambicus would limit habitation of the lake to 45 % of its area. They also report that the maximum compensation depths for adults were higher in summer than in winter. The choice of Rufanes Pool for assessment of winter mortality is therefore acceptable as it has a limited area and shallow depth, rendering it an homogenous and accessible environment for O. mossambicus. Regular sampling over a designated area could therefore be representative of the population as a whole. The assumption that standing stock and mortality as measured in Rufanes Pool can be extrapolated to the other three habitats studied is questionable.

Rufanes Pool was seine netted repeatedly on three visits during 1987 (January, June, and September) until no further catches were made. All fish caught were placed live in drums of pool water according to length group, and the sex of adults was noted. To check the efficacy of this method of stock assessment, one further pull of the net was made after sorting all the fish caught. This was usually about 30 minutes after completion of the previous catch, after which time it was assumed that the remaining fish would have recovered from the initial disturbance, and be equally easily caught, having re-distributed randomly in the pool. Any further fish caught were counted and their number taken as a percentage of the number already caught. This percentage represented the "uncatchable" proportion of the population remaining in the pool due to the avoidance of the net, and was added to the total caught. After counting, most fish were returned to the water. To increase the accuracy of estimation of the total catch on the last occasion (September), the pool was seined with gill nets of variable mesh after all "catchable" fish had been removed from the pool. No further fish were caught despite repeated pulls of the net, confirming that the methods used were efficient, and that the catches made were representative of the population as a whole as suggested by Ricker (1975).

Using the fish caught during the regular monthly sampling, the populations from each sampling site were divided into three

arbitrary groups which could be loosely termed: juveniles, subadults and adults. These groups were based on the size range up to which 50 % of the population at that size showed signs of sexual differentiation of the gonads (ie GMI = 1), and then up to the size at which 50 % of the population had attained sexual maturity. The third group consisted of fully mature fish. In assessing the female:male ratio, the two latter groups were used, ie subadults and adults.

#### Marked fish

In two habitats (Rufanes Pool and Kowie Lagoon) a number of adult and sub adult fish were caught by seine nets, and tagged with Floy FD 69 "spaghetti" tags in the dorsal musculature. After weighing (g) and measuring (mm SL) they were then released for estimation of standing stock and growth rates (Ricker 1975). Field experience indicated that this could only be done where fish could be caught with seine nets without damage, as it became clear that survival after catching with gill nets was low due to fungal infections of wounds inflicted by the net, and stress whilst struggling after capture. At Kowie Lagoon, 36 fish were gill netted, tagged and released in April 1986. Over a period of nine monthly samplings thereafter, none were recaptured, although one was observed on one occasion. At Rufanes Pool, adults and juveniles over 90 mm SL were tagged and released after having been caught in seine nets. Adults were caught and recaptured several times (Table 8) but smaller fish appeared to succumb to the wound of the tag and recaptures were low. Population

size was estimated by calculating the proportion of tagged to untagged fish in each standardised catch and extrapolating the results to the area of the pool.

Hodgkiss and Man (1977a), using opercular tags, reported a tag-life of only two to three months, and a total tag loss after four months. Floy "spaghetti" type tags inserted through the dorsal musculature were found to last well if inserted sufficiently deep in the musculature, but were eventually lost from all fish after 12 to 15 months. Wound infection was still apparent in some cases six months after tagging, and most fish showed little positive, and occasionally negative growth, after tagging. The tag legend tubes rapidly became obscured with algae which delayed reading whilst cleaning. Bruton (1973) reported that spaghetti tags were still legible up to 570 days in the wild, and that tag retention was good in the wild, but poor under artificial conditions due to repeated sampling. Larger fishes (> 300g) appear to accept tags more readily than small ones.

## RESULTS

### Population demography and general biology

#### Introduction

The population demography and biology of wild populations of O.mossambicus has been described by several workers (Bruton & Allanson 1974, Bruton & Boltt 1975, Bruton 1979, 1980, Bowen & Allanson 1982, Whitfield & Blaber 1979, Bowen 1984, Cochrane 1985, Hecht & Zway 1984, Hodgkiss and Mann 1977 a & b, 1978, De Silva 1985).

Populations of O.mossambicus in the small water bodies of the eastern Cape, South Africa, tend to be limited to isolated stretches of rivers at low altitude, and to dams and brackish water estuaries. There is a possibility of natural inter-catchment transfer between populations at times of high flood when this euryhaline species may migrate from estuary to estuary along the coast (Jubb 1967).

It is well known that O.mossambicus has been widely translocated within the eastern Cape (Bruton & Merron 1985, De Moor & Bruton 1988) especially since the construction of farm dams, which have created thermal refuges where winter survival is enhanced. Many of the introduced fish originated from the Amalinda Hatchery at East London (Bok, pers. comm.) although numerous intra-catchment transfers have probably been carried out by private individuals. Most of the south-flowing rivers within the study area have indigenous populations living in their lower reaches, some of which have since become

established in nearby dams. It is these populations that were of most interest in this study.

#### Lateral and vertical distribution

Catch-per-unit-effort (CPUE) records were utilised to ascertain the following:

(a) Horizontal and vertical distribution of the fish, at various times of year.

(b) Reasons for their presence, or absence, from various locations.

Monthly overall catch per unit effort showed the expected trend of high adult catches during the early months of summer (August/September) with few juveniles, followed by increasingly larger juvenile cohorts during mid and late summer (Figs. 21, 22 & 23). Similar trends were reported by Cochrane (1986) and Bruton & Boltt (1975). The numbers of juvenile fish netted declined sharply from April to June, after which very few fish smaller than 100 mm SL were caught.

Gear selectivity was probably responsible for some of this trend, but Figure 21 which shows the CPUE at Rufanes Pool, gives a strong indication of the changes in population structure throughout one annual cycle. This habitat was the only one where effective seine netting could be carried out, and, due to its small size, monthly catches are probably representative of the existing population structure. The mortality of juvenile fish was high for length cohorts up to

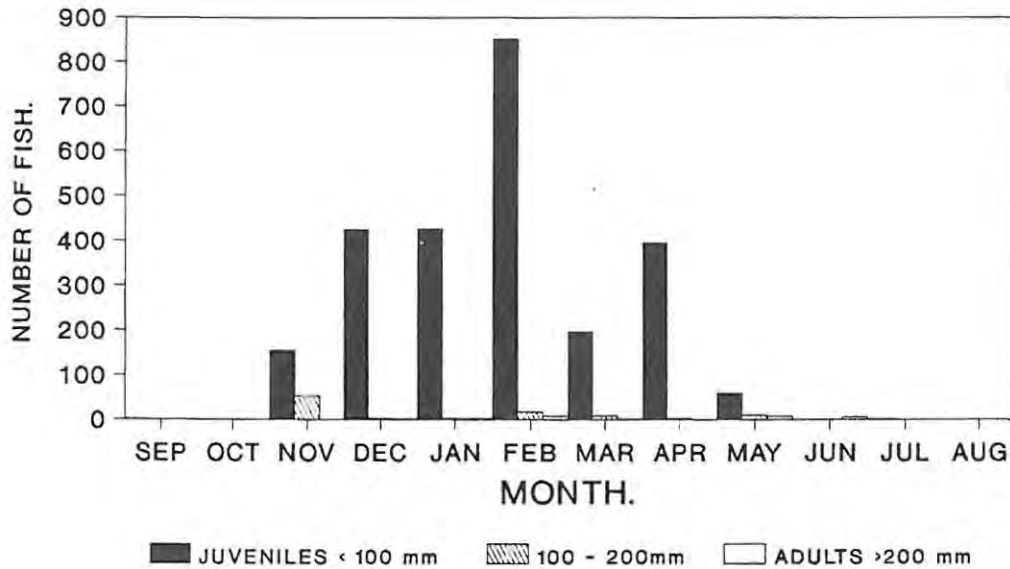


Fig. 21. The monthly catch per unit effort using the standard seine net of juvenile, sub-adult and adult *O. mossambicus* from Rufanes Pool.

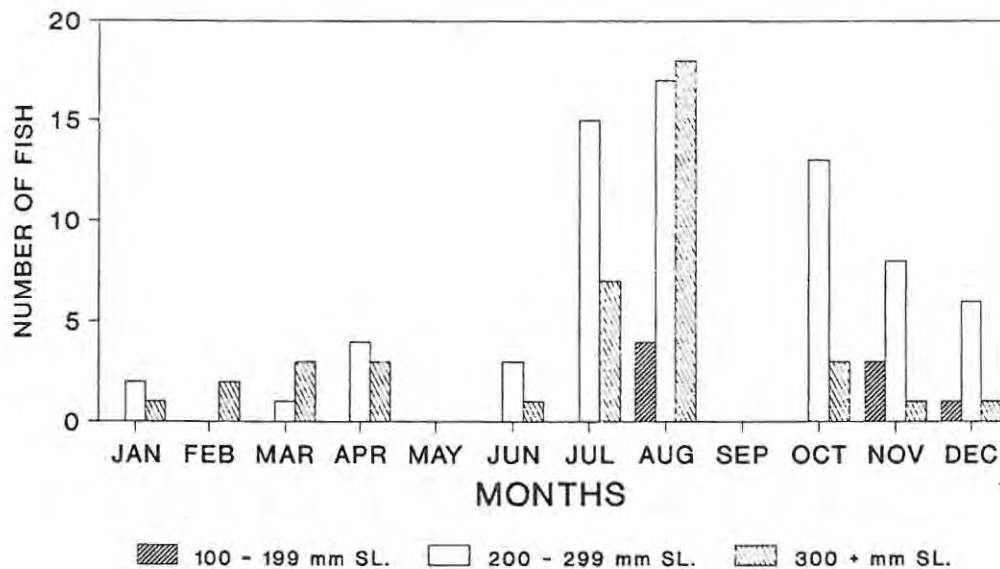
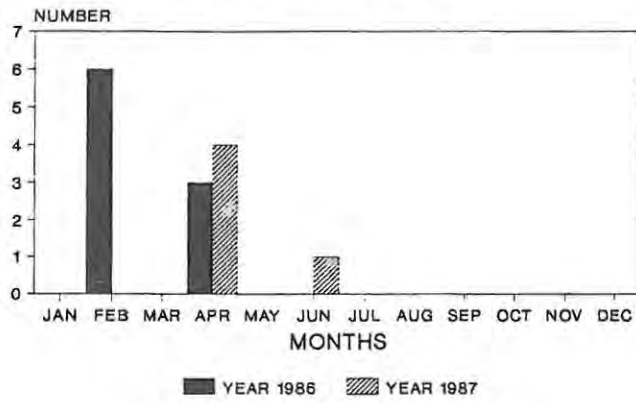
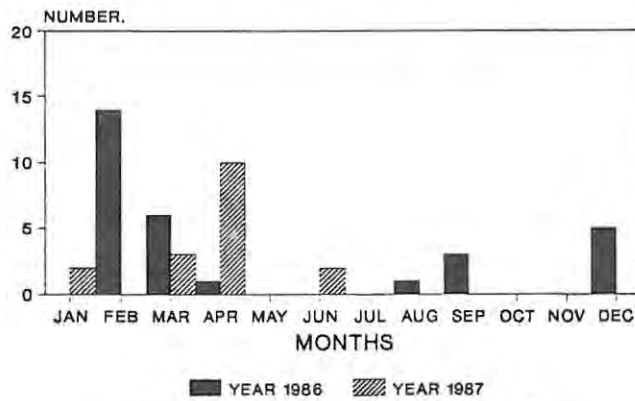


Fig. 22. The monthly catch per unit effort using the standard fleet of gill nets of three length groups of *O. mossambicus* in Mill Farm Dam.

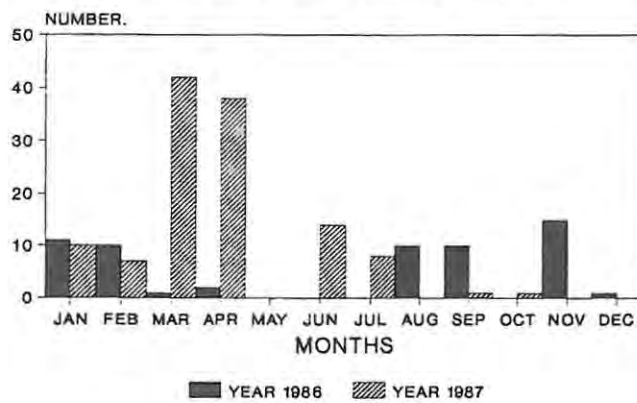
JUVENILES <50 mm SL.



JUVENILES 50 - 99 mm SL.



SUB-ADULTS 100 -199 mm SL.



ADULTS 200 + mm SL.

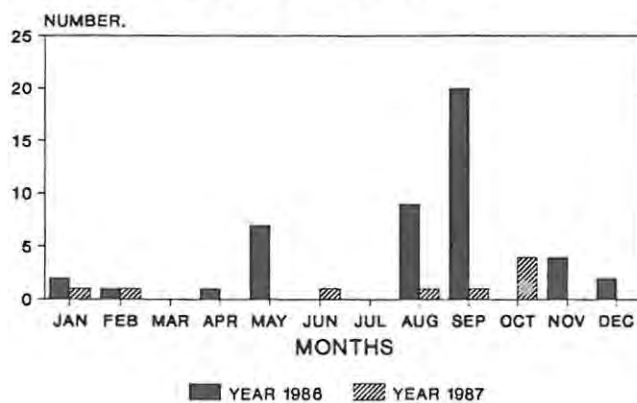


Fig. 23. The monthly catch per unit effort using the standard fleet of gill nets of *O. mossambicus* at Bradshaw's Mill Dam during 1986 and 1987.

Table 13. Standing stock of O. mossambicus at Rufanes Pool. Estimated stock is based on catch per unit effort data, and actual standing stock is based on repetitive seine netting over the total pool area.

		Juveniles 20-49 mm	Sub adults 50-149 mm	Adults >150 mm
<u>Rufanes Pool</u>				
January:	estimated stock	4 888	112	32
	actual stock	10 480	38	11
June:	estimated stock	0	472	56
	actual stock	44	59	7
September:	estimated stock	0	0	0
	actual stock	1	11	7

100 mm SL in all the habitats examined. It is assumed that this may be attributable to lethal low water temperatures during winter, which seems likely in view of experimental work reported on later in this study, which suggests that juvenile O.mossambicus are more susceptible to cold than adults. This theory conflicts with the findings of some earlier workers (Bruton & Boltt 1975, Bruton & Taylor 1979) who suggested that adult tilapia have narrower temperature tolerances than juveniles.

In some habitats certain year classes (e.g. the 1+ cohort at Kowie Lagoon) were poorly represented in the catches. It is possible that this could be due to almost total mortality of the young of the year during severe winters, or as a consequence of unsuccessful reproduction. This was especially marked in the smaller habitats such as Rufanes Pool, and shallow lagoons such as Kowie Lagoon where temperature fluctuations are more rapid (Heineken 1985).

None of the habitats examined in this study were prohibitively deep for either adult or juvenile O. mossambicus. Despite this, a marked preference for certain depths was recorded. The general trend was for a movement into deeper water during cooler months and a return to the shallows in the warm season. This trend was at times superceded by a temporary migration either into or away from the shallows, depending on wind, wave action and surface water temperature. Wave action increased turbidity in the shallows and intermixed the warm surface waters with cooler deeper water (Fig. 15). This

temporarily interrupted the diel migration to shallow water during the heat of the day.

Lateral migration of both adults and juveniles varied between habitats. During the period November to April many adult male fish were observed guarding nests in shallow water (50-75 cm depth) in association with the macrophyte Potamogeton pectinatus which is common in most habitats. At this time adult females were only seen in nests in the shallows whilst actually spawning, after which they returned to the deeper water at the edge of macrophyte beds.

After release of the young, female fish were frequently netted in deeper water (2-3 m) at the base of the P. pectinatus or T. capensis growth at its deepest extension. The stomach contents of these fish indicated that feeding had taken place, and they had possibly retreated to deeper water to digest the food, as suggested by Caulton (1973).

In localities where predator pressure was high due to piscivorous fish and birds (Mill Farm Dam), newly released fry, and juveniles less than 120 mm SL, rarely ventured out of the cover of P. pectinatus, and were most common during daylight in the vegetation-free zone in the extreme shallows (0-15 cm depth) (Figs. 26 & 28.) In those habitats from which piscivorous fish were absent (Bradshaws Mill Dam), newly released fry frequented open water at the surface, and moved freely between open water and the extreme shallows (Figs. 27 & 28). Larger individuals (SL 25-80 mm) were the targets of

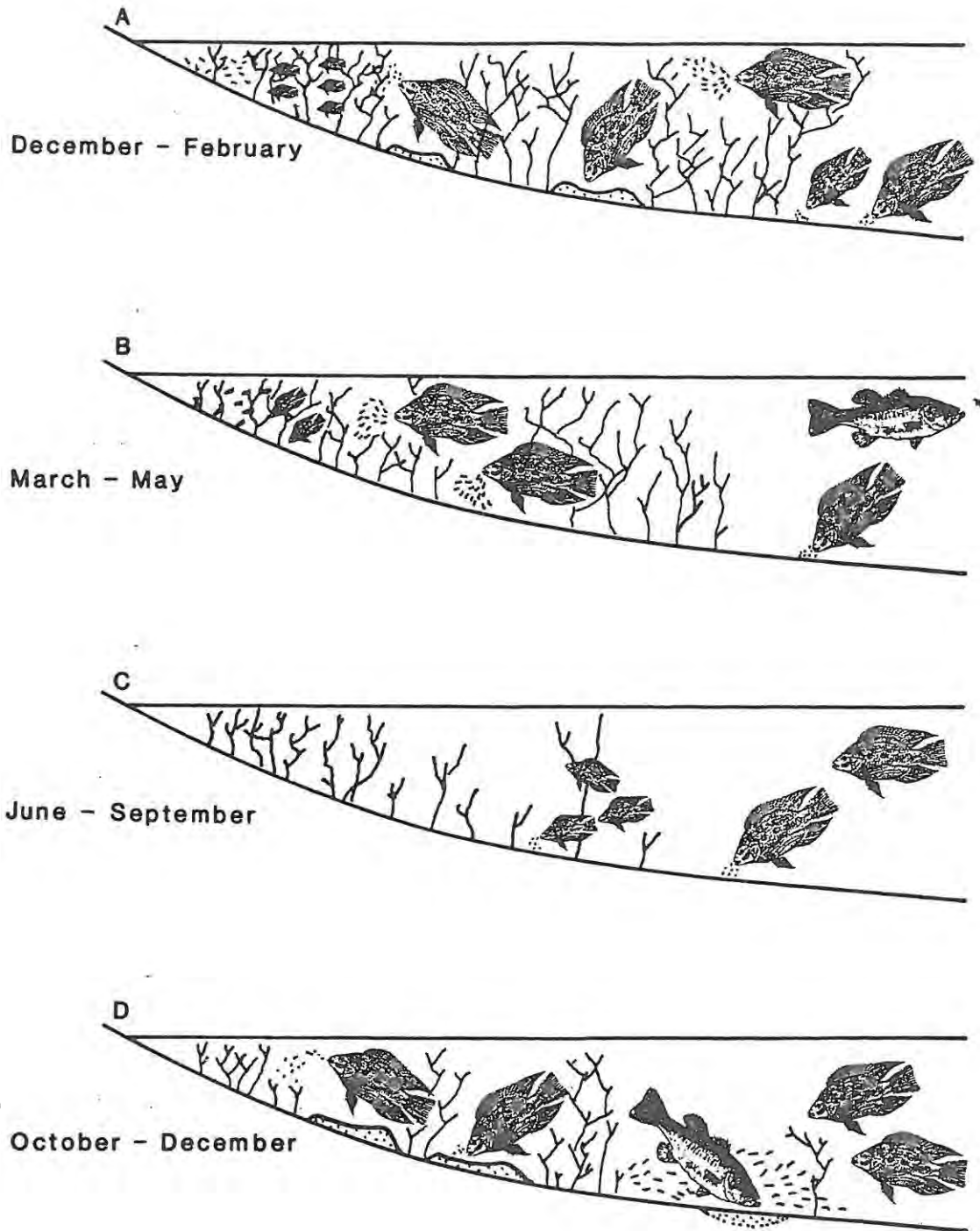


Fig. 26. The life cycle of *O. mossambicus* in Mill Farm Dam. (A) During mid-summer large males and females spawn amongst *Potamogeton pectinatus*. Newly released fry congregate in the warm littoral areas, and larger juveniles in adjacent vegetation. (B) After the spawning season fry and larger juveniles remain amongst vegetation safe from *Micropterus salmoides* which patrols more open waters. (C) During winter juveniles and sub-adults retreat to deeper water but remain amongst the reduced *P. pectinatus* growth. (D) At the time of rising water temperatures adult males begin nest-construction in shallow water. *M. salmoides* nestguards and defends its young in deeper waters, and young adults feed at the edge of *P. pectinatus* growth.

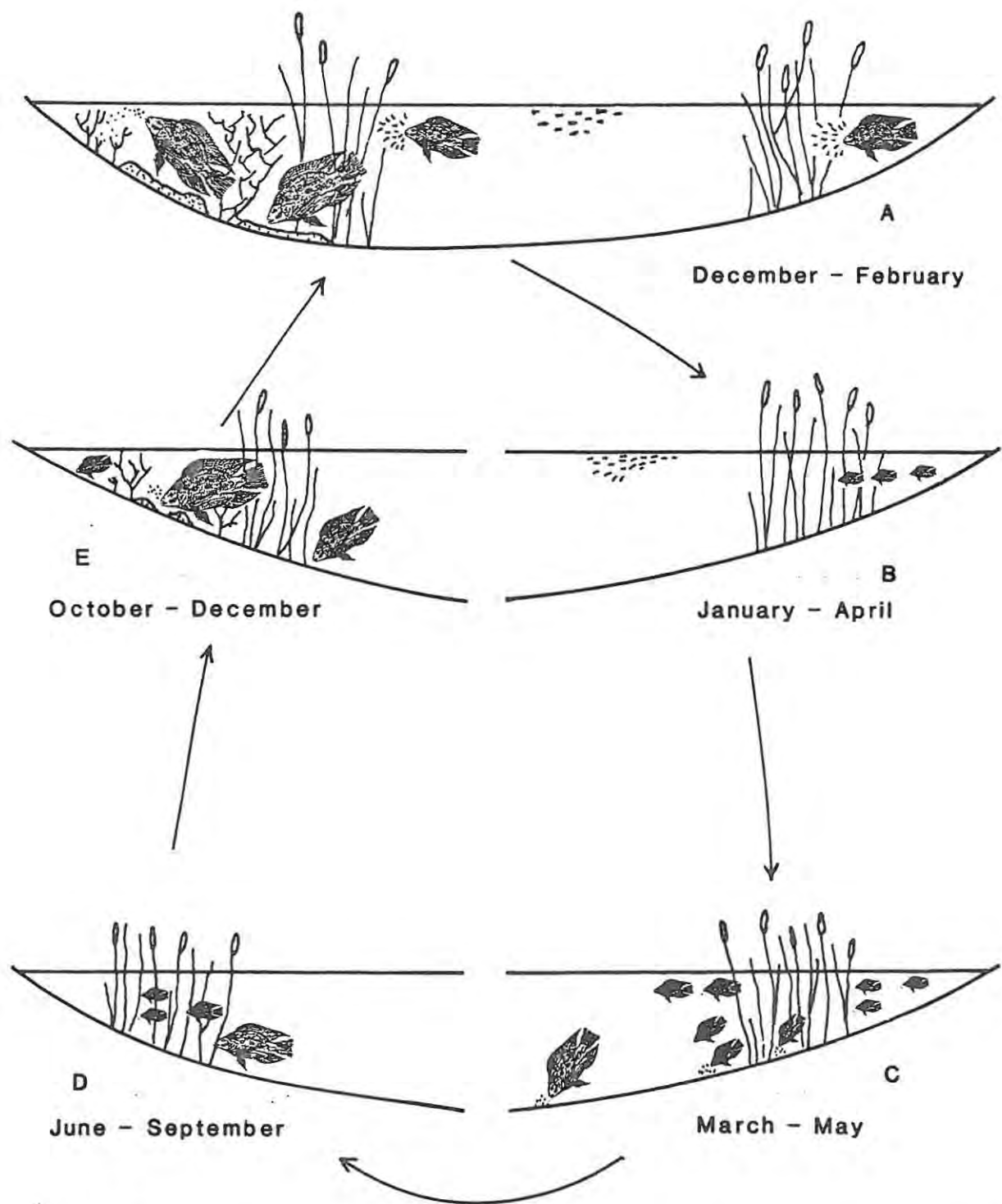


Fig. 27. The life cycle of *O. mossambicus* in Bradshaw's Mill Dam. (A) During the hottest months males construct nest colonies amongst vegetation, mouthbrooding females release their young near *Typha capensis* and the fry shoal in the warm open surface waters. (B) Larger juveniles seek refuge from avian predators amongst *T. capensis*, and utilise the warm littoral areas. (C) Progressively larger juveniles are found in deeper waters. (D) During the coldest months all fish seek deeper water amongst or at the edge of vegetation. (E) As temperatures increase males begin nestbuilding and sub-adults return to the littoral areas.

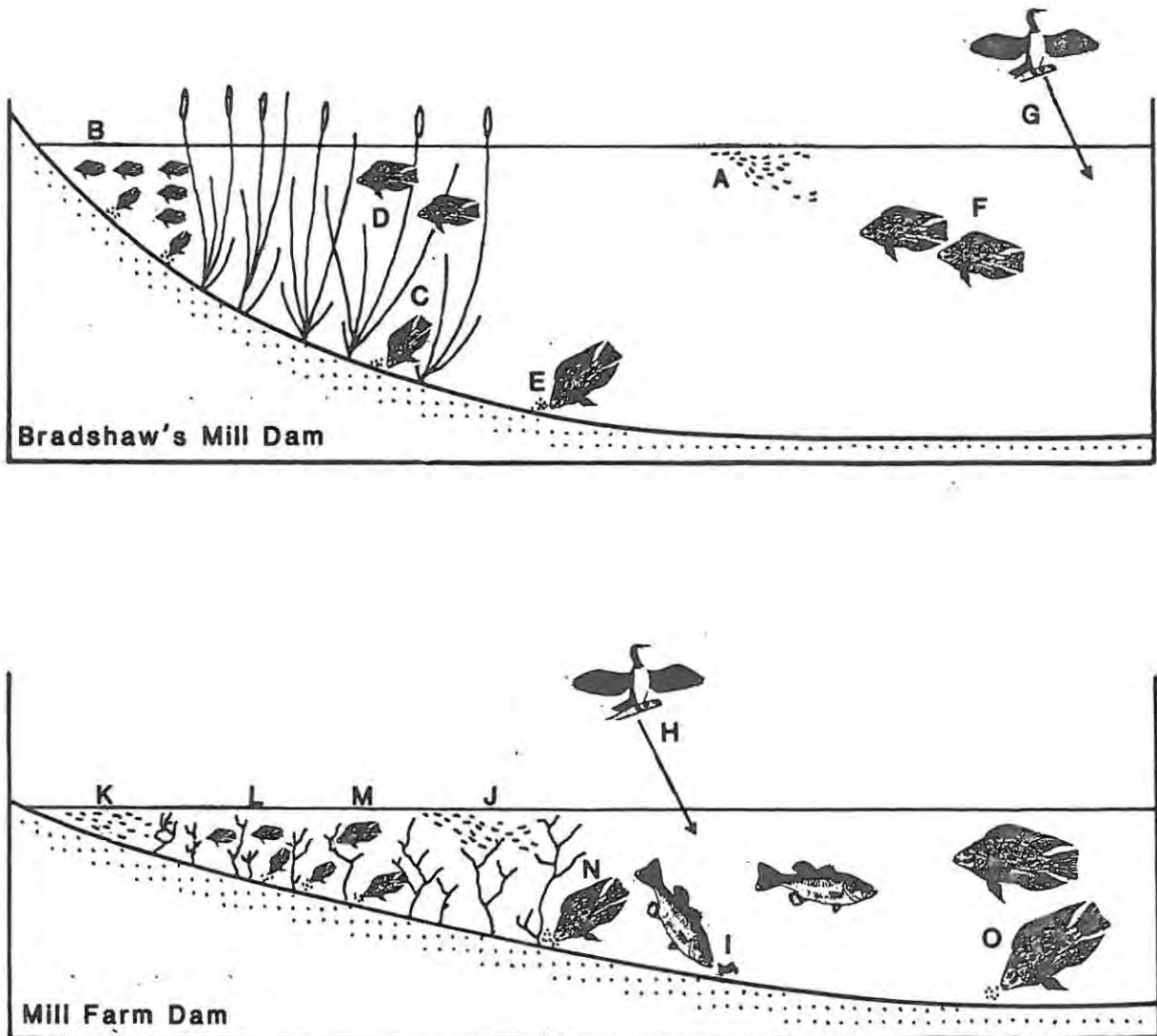


Fig. 28. The effect of predation on O. mossambicus in two eastern Cape lakes.

Bradshaw's Mill Dam : (A) Newly released fry are not threatened by avian predation unlike larger juveniles (B) which seek refuge in the warm littoral. Larger juveniles feed (C) and find refuge (D) amongst Typha capensis, whilst adult fish (E) feed in deep water or bask near the surface (F) being too large to be susceptible to avian predation (G).

Mill Farm Dam: Avian predation (H) and Micropterus salmoides (I) restrict fry to areas of dense vegetation (J) and the littoral (K). Juveniles feed (L) and take refuge (M) amongst Potamogeton pectinatus whilst young adults (N) can feed safely in deeper open water.

piscivorous birds such as cormorants Phalacrocorax sp. and these fish rarely ventured away from the protection of T. capensis or P. pectinatus.

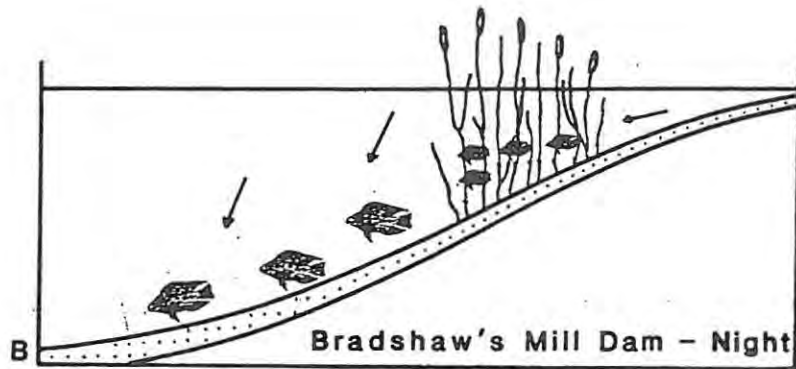
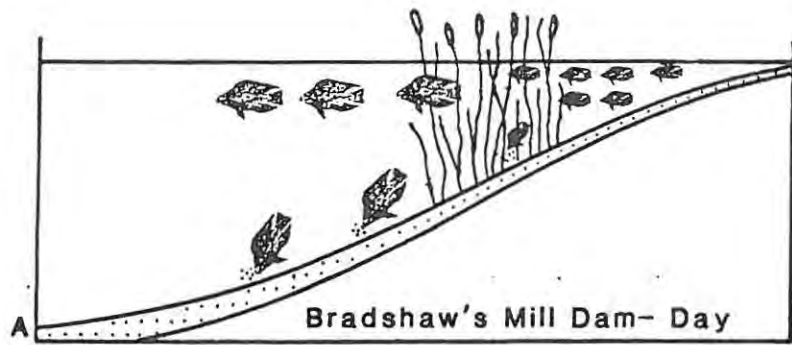
The vigorous growth of P. pectinatus in most habitats made standardised seine netting for juveniles impractical except at Rufanes Pool, and catches of juveniles using other methods were erratic and statistically incomparable. Electrofishing for tilapia was found to be less effective than for cyprinids and centrarchids, and poor catches were made using this method, although occasional juveniles were taken in shallow water at Mill Farm Dam. Particularly low catches were made during winter. At Mill Farm Dam electrofishing for juveniles in shallow water (10-50 cm depth) was only successful during the warmest months (January to March). When water temperatures fell below 20°C juveniles were no longer caught in the shallows and moved to deeper water amongst the P. pectinatus, despite the nearly homothermal nature of this lake. Whilst in this cover, no reliable catching technique could be used. Gill net catches of adults were confined to open water near the substrate during winter, whilst summer net catches were randomly spaced at all depths. Mouthbrooding females were common near the surface in deep water and nest-guarding males in shallower water during the peak spawning season. Difficulties in obtaining numerically adequate samples during colder months have also been reported by other workers (Cochrane 1985), and may reflect behavioral factors such as reduced mobility and feeding.

## Discussion

Experimental work by Caulton (1972) suggests that O. mossambicus can compensate for maximum water depth of 20 m (males) and 12,8 m (females), and individuals were found at this depth in Lake Sibaya by Bolt, Hill and Forbes (1969) and at 18 m by Bruton (1973). In Lake Valencia, Venezuela, Bowen (1984) reported that O. mossambicus was abundant only in the littoral zone, and is not found at depths greater than 5 m, or in open water away from the shore. As all the water bodies studied in the eastern Cape were less than 5 m deep, O. mossambicus was not excluded from any part of the habitat by depth limitations.

### Concentrations of fish due to breeding behaviour

Adult male fish constructed nests in colonies or arenas, similar to those reported from Lake Sibaya by Bruton & Bolt 1975, and the proximity of these nests (see section on reproduction) caused concentrations of fish during the breeding season in shallow water. At Mill Farm Dam, colonies of breeding or nest-building males included only large-sized individuals, and over an arena area of 50 m x 10 m could number as many as 20 large adults. Gill net catches indicated that adult females formed small shoals at the surface whilst mouthbrooding, but dispersed to deeper water after fry release (Figs. 26 & 27). Nets caught small groups comprising 2-3 females, within 1 - 2 m proximity, all either with fry in the



YK Potamogeton pectinatus

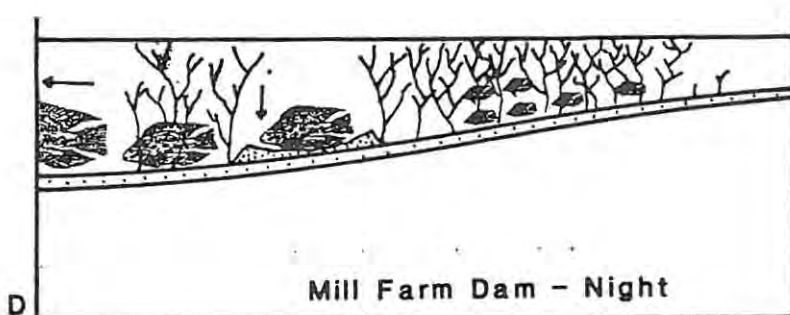
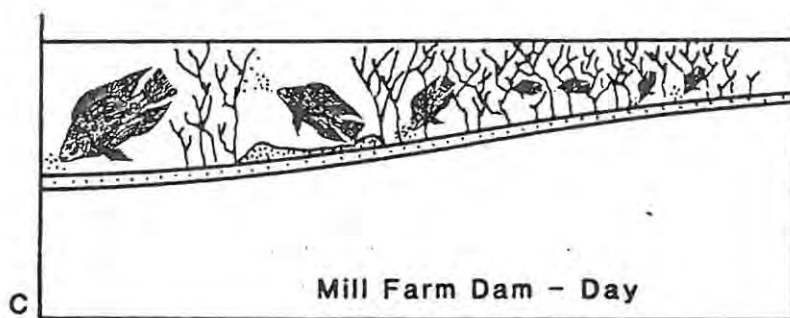
YK Typha capensis

..... Mud & detritus


•••• Sand


← Night time migration

Fig. 24. Diel migration at Bradshaw's Mill Dam. (A) During the day juvenile fish utilise the warm littoral areas for feeding and seek refuge in the adjacent emergent vegetation. Adults feed on the steeply sloping substrate in deeper water, and bask at the surface on the deep-water edge of T. capensis. (B) At night juvenile fish retreat into the vegetation and adult fish rest near the substrate in deep water.



 Potamogeton pectinatus

 Typha capensis

 Mud & detritus

 Sand


 Night time migration

Fig. 25. Diel migration at Mill Farm Dam. (C) During the day juvenile fish feed amongst P. pectinatus, adult males construct nests in dense vegetation, and females feed at the deep-water edge of P. pectinatus growth. (D) At night juveniles and adult male fish remain amongst vegetation in the shallows, and non-mouthbrooding females retreat to deeper water.

mouth or with the buccal cavity extended, presumably having ejected the young whilst struggling in the net.

#### Diel migrations

Similar patterns of winter behaviour were found at all sites with the exception of Bradshaw's Mill Dam where a diurnal migration of juveniles similar to that described by Bruton & Bolttt (1975) and Minshull (1978) was observed (Figs. 24 & 25). This was probably a reaction to the diel temperature zonation as the sheltered aspect and lack of intermixing by wave action in this habitat brought about a distinct thermal gradient perpendicular to the shore. Welcomme (1964) describes such shores as "gradient shores". The daily warming of shallows was utilised by juveniles, but these areas were unavailable to adults. Juveniles were observed pushing through thick growth of Typha from deep water, and congregating in water of 10 to 30 cm depth, between the reeds and shore where sunlight and protection from wind raised the water temperature substantially (Table 14).

Gill nets set overnight caught juveniles only along the immediate periphery of the reed banks, and neither in the extreme shallows nor in open water, indicating that the diurnal migration of juveniles did not extend into the deeper water occupied by adults. The diurnal migration of juvenile tilapia closely follows that described for tilapia species in Lake Victoria (Welcomme, 1964), Lake Kariba (Donnelly, 1969) and Lake Sibaya (Bruton & Bolttt 1975).

Table 14. Comparative winter water temperatures at the surface, in the shallows, and in open water at Bradshaws Mill Dam.

Depth (cm)	Aspect	Temperature (°C) at:		
		09h00	14h00	18h00
5	Sunny and open	13,5	18,5	16,5
10	" "	13,5	18	16
20	" "	14	17,5	16
30	Edge of reeds	14	16,5	15,5
35	Shadow of reeds	14	15	15
50	Within reeds	14,5	14,5	14,5
180	Open water	14	15	15,5

#### Habitat preferences

Habitat preferences were examined by repetitive gill netting over selected habitat types in two lakes: Bradshaws Mill Dam and Mill Farm Dam (Table 15).

Table 15. Habitat structure and utilisation by *O. mossambicus* in two eastern Cape reservoirs. The numbers represent the typical C.P.U.E. in each habitat type. M = male, F = females, Juv = juveniles.

Habitat (depth)	Mill Farm Dam (shallow slope)			Bradshaws Mill Dam (steep slope)		
	M	F	JUV	M	F	JUV
Mud (2-4m)	9	4	0	11	18	4
Gravel and cobble (0-3m)	0	2	0		N/A	
Boulders >10cm (0-3m)	0	1	0		N/A	
<u>Potamogeton</u> (0,5-3m)	30	2	18	46	34	87
Reeds (0,5-3m)		N/A		5	2	115
Mud/ <u>Potamogeton</u> edge (2-3m)	11	19	0	14	11	59
Reeds/mud edge (2-3m)		N/A		54	21	17
Open water surface (0-2m)	2	1	0	7	3	5
Eulittoral (0-0,3m)	0	0	12	0	3	108

## Discussion

There are interesting contrasts with Bowen's findings (Bowen 1984, Table 1.) in Lake Valencia, where females tended to prefer hard, sloping substrates and males gently sloping mud bottoms. In the eastern Cape, male fish were most common over shallow sloping substrates in association with Potamogeton pectinatus and on the edge of reed banks along steeply sloping littorals. Females were most numerous amongst the macrophytes or at the deep water limit of macrophyte growth. Steeply sloping habitats, with either stony or muddy substrates were the least preferred habitat. For comparison, habitat preferences during summer are described by Bruton (1975) for Lake Sibaya as follows: a catch per unit effort of 66,5 over terraces (0 to 2 m), 21,1 over barren slopes (2 to 7 m), 15.1 over sparsely vegetated slopes (2 to 7 m) and 4,1 over densely vegetated slopes (1 to 7 m).

The choice of habitat is correlated to the specific requirements of the males, females and juveniles for reproduction, feeding, mouthbrooding and defense against predation. Males selected protected areas with soft substrates where distinct territories could be established for nestbuilding and spawning. Females selected those areas where mouthbrooding could be safely completed and thereafter where feeding was optimal. Juvenile fish preferred warmer water and shelter against predation and predominated in shallow littoral areas.

Since each habitat type is utilised differentially by males, females and juveniles, an effort was made to assess the effect of the relative proportions of these in two of the sites. Habitats were divided into 10 major categories found in Bradshaws Mill and Mill Farm dams. These sites were selected due to their contrast. Based on these observations and catch data, the habitat utilisation patterns given in Table 16 were defined.

Based on these preferences the area for each habitat was calculated as a percentage of the whole. Each habitat was given an arbitrary score of 1 per function if utilised by juvenile or adult O. mossambicus and nil if not utilised (thus T. capensis habitats would score 1 for juveniles, whilst P. pectinatus growth habitats would score 2 for juveniles and 4 for adult fish). This score was then multiplied by the areal proportion to give an index of "preferability" or "utilisation" of the lake as a whole.

Table 16. Habitat utilisation by O. mossambicus in the E. Cape

Habitat type	Utilisation by fish	
	Juveniles	Adults
(a) Open shallows 0 - 50 cm	Feeding	-
(b) Open shallows 50 - 100 cm	-	Feeding Nesting
(c) <u>P. pectinatus</u> band	Feeding Refuge	Feeding Refuge Nesting Mouthbrooding
(d) <u>T. capensis</u> growth	Refuge	-
(e) Rocky substrate	-	-
(f) Deep-water edge of weed	-	Feeding
(g) Open water surface	-	-
(h) Open water depths	-	Refuge

From the results shown in Table 17, Mill Farm Dam was environmentally more favourable for O. mossambicus than Bradshaw's Mill Dam. Habitats preferred by adult fish were especially abundant at Mill Farm Dam. A "favourable" environment is taken here to be one that is similar to the stable natural environment that would cause the adoption of a precocial lifestyle in a natural water body (Noakes & Balon 1982); for example the rapid growth, late maturity, limited reproductive output coupled with a long lifespan that would be expected in a large nutrient-rich lake. A "harsh" environment would equate to conditions under which a natural population of O. mossambicus turn to early maturity and high reproductive output at the expense of somatic growth, as in for example a thermal or mineral spring.

Table 17. Habitat preferences of O. mossambicus in Bradshaw's Mill Dam (BM) and Mill Farm Dam (MF). Juv = juveniles, Ad = adults.

Habitat	% area		Preference			
	BM	MF	BM		MF	
			Juv.	Ad.	Juv.	Ad.
(a) Open shallows 0 - 50 cm	0	10			10	
(b) Open shallows 50 - 100 cm	5	10		10		20
(c) <u>Potamogeton</u> band	5	50	10	20	100	200
(d) <u>Typha</u> band	30	0	30			
(e) Rocky substrate	0	5				
(f) Deep side of <u>Potamogeton</u>	2	10		2		10
(g) Open water surface	30	10				
(h) Open water depths	28	5		28		5
	100%	100%	40	60	110	235

The above model is interesting if examined for favourability for growth, ie points scored for habitats utilised for feeding, as opposed to refuge, or reproductive behaviour.

If the model is re-arranged to emphasise favourability for growth, ie points are only scored where habitats which encourage feeding occur, the differences are more distinct (Table 18).

Table 18. The frequency occurrence of habitats used for feeding by O. mossambicus in the eastern Cape. (\* = preferred habitat).

	Area %		Feeding preference Juveniles/Adults	Score	
	BM	MF		BM	MF
(a) Open shallows 0-50cm	0	10	*	0	10
(b) Open shallows 50-100cm	5	10		0	10
(c) <u>P. pectinatus</u> growth	5	50	*	10	100
(f) Deep water edge of weed	2	10		2	10
				12	130

Mill Farm Dam has all four habitats favoured by both juvenile and adult fish for feeding, and these comprised 80 % of the area of the lake as opposed to 12 % for Bradshaws Mill Dam. The graded profile of the lake, the frequent level fluctuations, and the extensive submergent macrophytes strongly resemble the tilapia "nursery" areas of Lake Kariba described by Donnelly (1969).

## Population structure

### Sex ratio

In the smaller length classes females were generally more abundant than males, except at Bradshaw's Mill Dam. After sexual maturity all populations were predominantly male.

Table 19. The mean female-to-male ratio of O. mossambicus from four water bodies in the eastern Cape

Water body	Female to male Juveniles	Female to male Adults	Female to male Overall
Bradshaw's Mill Dam	1:1,32	1:1,38	1:1,35
Kowie Lagoon	1:0,82	1:1,50	1:1,10
Mill Farm Dam	1:0,96	1:1,94	1:1,35
Rufanes Pool	1:0,72	1:1,78	1:1,13
mean	1:0,96	1:1,65	1:1,23

### Fluctuation in population numbers

Population numbers fluctuated seasonally. Catch per unit effort reached a numerical peak during late summer (April/May) which coincides with the end of the spawning season, and a low during the coolest months (June - August). Where CPUE was based on gillnet sampling (Fig. 23), a bias may result due to selectivity; fish less than 6 cm were rarely caught by this method, and seine net catches indicated that the peak breeding season (January/February) was the period of maximum numerical population density (Table 13 & 20).

Table 20. The declining numbers of juvenile *O. mossambicus* as a reflection of catch-per-unit-effort in Rufanes Pool during the first five months of life.

Month	Standard length (mm)	Number caught	
		1986	1987
February	0 - 15	424	116
March	16 - 30	108	230
April	31 - 50	114	17
May	51 - 80	21	3
June	81 - 100	1	0

The greatest decrease in the number of juvenile fish caught per unit effort is during the months April and May. The minimum water temperature during this period was measured as 14,5<sup>o</sup> C which is within the natural tolerance of this species (Allanson et al 1962, Caulton 1978a, Bruton & Taylor 1979, Cochrane 1984, 1986), and would not be expected to result in mortalities. In November 1986, 52 juvenile fish aged 1+ years (standard lengths 100-130 mm) were caught after repeated pulls of the seine net. These fish were the young-of-the-year and were probably spawned during January-March that year. The very low catch (one fish) recorded in June 1986 indicates that the catching technique for small *O. mossambicus* was poor, and underestimated the number surviving in the pool during autumn.

### Discussion

The dominance by number of female fish in the juvenile length classes, and males in the adult component of the population is consistent with the findings of most other studies of this species (Bruton & Bolt 1975, Hodgkiss & Man 1978, De Silva

1986). De Silva (1986) recorded a higher proportion of females to males (1,0:0,88) in most man-made lakes in Sri Lanka, although the larger length groups were dominated by males (only 25 % female at lengths over 250 mm TL). However his overall numerical dominance of females:males of 1:0,88 contrasts with the figure of 1:1,23 for this study. The greater mortality of adult females in the eastern Cape compared to the reservoirs of Sri Lanka can be compared to similar results from Plover Cove Reservoir, Hong Kong (Hodgkiss & Man 1978) and Lake Moyua, Nicaragua (Riedel 1965). In the latter two studies, the proportional decline in adult female numbers is attributed to breeding activity and post-spawning mortality. Dominance of males in the larger size ranges is also due to the inherently faster growth of males and interference with growth by mouthbrooding in females (Fryer & Iles 1972). However, this is only significant if the respective ratios are calculated by length-groups, rather than by degree of sexual maturity as in this study.

The estimation of mortality in unexploited fish stocks (pristine resources) should present fewer problems than with populations subject to commercial or recreational fishing pressure. If a population is unexploited, the total mortality will equate with natural mortality. However natural mortality is expected to vary between age classes (Pauly 1980, Vetter 1988) and between differing populations of the same species. Where a species is an annual spawner, mortality can be assessed using length frequency occurrence in catch per unit

effort data. In the case of most tilapiines which are repeat spawners, cohort analysis becomes more difficult as spawning frequency increases. An individual fish may produce up to four or more broods, or breed continuously every six weeks in tropical areas (Siddiqui 1977, Bowen 1984).

Mortality during the early life phase is usually high, despite parental care, and can have a marked effect on subsequent year-class strength (Bagenal & Baum 1978). Backiel & LeCren (1978) suggest that density dependent mortality in the early life stages has a dominant influence on production. In temperate climatic waters it is suggested that a major cause of young-of-the-year mortality may be winter cold, and this can virtually eliminate entire year classes during severe years. Cochrane (1984) working in the highveld impoundment, Hartbeespoort Dam (near Pretoria), recorded similar year class mortalities of O. mossambicus during severe winters. In other water bodies, level fluctuations are held responsible for the failure of the fish to breed successfully, with the consequent virtual absence of entire year classes (Coche 1964, Donnelly 1969, De Silva 1985). The poor representation of the 1+ year age cohort in Mill Farm Dam (Fig. 22) could be explained by either exceptionally high winter mortality during the winter of 1986, or little breeding and therefore low recruitment to the population in the summer of 1985/86. As the lake level was high during late 1985 and early 1986, and the lake had recently filled (December 1985) after being at a very low level, recruitment during summer 1985/86 should have been more

successful than during the previous summer when the water level was decreasing. Rising water levels coinciding with breeding activity have been shown to enhance rather than reduce recruitment (De Silva 1985a, Fryer & Iles 1972, Lowe-McConnell 1982) but large numbers of young-of-the-year were not observed in the shallows during early 1986 in this study. The winter of 1986 was not unusually cold, by the standards typical of the region (Stone, 1988) and therefore the low numbers of 1+ year fish was probably a result of reduced reproduction rather than mortality due to low temperatures.

Hodgkiss & Man (1977b) suggested that the daily collection of dead fish during winter would provide a quantitative estimation of natural (chill-induced) mortality in the Plover Cove reservoir. Their results showed that mortality reached two peaks: a high mortality during winter (February peak) and a lower peak during late summer (August to October). During the course of this study, only three dead fish were found (two of which were suffering from an eye infection, and one which was injured), and difficulty was encountered in finding positive evidence of cold-induced mortality. Observations, in artificial pools subjected to low temperatures suggested that smaller fish succumb to cold at higher temperatures than large adults. These fish sank to the substratum, and due to their lower volume to mass ratio did not rise to the surface subsequent to death. Most water bodies in the Eastern Cape are populated by the freshwater crab, Potamonautes perlatus, and these were frequently noted to attack and consume fish caught

in gill nets, eating mainly the organs in the body cavity. Terrapins were also noted to do likewise. It seems likely that fish that become moribund due to cold are heavily preyed upon and few decay sufficiently intact to rise to the surface.

## Age and growth

### Scales and otoliths

Age composition, growth and body condition were examined on a comparative basis in the four populations of O. mossambicus. The most frequently used methods for determining age in fishes is the counting of growth zones, or rings, on bony parts during alternate periods of slow and fast growth. Both scales and sagittal otoliths were used in this study, and after a comparison of methods, scales were found to be a more practical means of rapidly determining the age (to acceptable limits) of large numbers of fish from habitats in this sub-temperate climatic area.

Several authors working on wild populations of O. mossambicus have experienced difficulties in the interpretation of the rings evident on most scales and otoliths. Hecht (1980) suggests that in the subtropical Luphephe-Nwanedzi impoundment in South Africa two rings are laid down annually on the otolith but only one on scales. Bruton & Allanson (1974), working on the Lake Sibaya population, reported that two rings were formed annually on scales, but did not compare this to otoliths, except to note that rings were also present on otoliths, and assumed that two were also formed annually. They also found that the preparation of otoliths for examination was tedious and time consuming for large numbers of fish.

Contrary to Hecht's (1980) findings that otoliths provide a better means for age determination in tropical climates, in

this study scales were found to have very clear rings in fish up to 5 years of age. After this age both scales and otoliths were lacking in clarity, and ring distinction became blurred. As the age of the fish in one of the populations studied did not exceed 5 years, this was not considered to be a problem, and the ease and rapidity of using scales became an advantage.

#### Laboratory methods

Fish were taken on the day of sampling and either processed immediately or frozen and processed later. Before freezing, fish were weighed in grammes to one decimal point and the standard length (SL) measured to the nearest millimeter, and a specimen number attached. The measurements were taken before freezing to avoid moisture loss, and possible tissue shrinkage. Formalin and alcohol were avoided due to chemical damage to scales and otoliths which may obscure ring identification (Ambrose 1983). Otoliths were removed and examined according to the methods described by Hecht (1980) and Japp (1986).

Scales were removed from the flank immediately behind the left pectoral fin. Scales in this area are generally uniform in size and symmetrical (Bruton & Allanson 1974, Bagenal & Tesch 1978). Initially up to five key scales were removed and used for ageing. On checking the accuracy of the readings it was found necessary on some fish to remove extra scales where the rings were indistinct, and the readings inconsistent when

checked. This method became standard practice during the second year of sampling, when up to ten scales were removed and the three with the most distinct rings were selected. Criteria for good scales, apart from clarity, were symmetry, the ring being visible from one lateral field to the other, uniform size, and no sign of either resorption or regeneration.

The scales were washed in tap water and, after drying, mounted between glass slides and viewed under a stereoscopic dissecting microscope. Determination of rings was aided by using both reflected and transmitted light, and varying the light intensity. The best clarity was found when using a low light intensity. Scale measurements were taken using an eyepiece graticule. Scale radii were measured in standard units (Japp 1986), and converted to millimeters when required by the following ratio:

Ratio of eyepiece to graticule = 0,69

Thus actual scale length (mm) = standard units x 0,69.

Measurements were taken from the scale focus towards the centre of the anterior edge. Measurements included the total scale radius, radius to the first ring, second ring and so on, as appropriate. Three scales were measured for each individual specimen, and the mean result was recorded. Where scale measurements differed by more than 10 % between the three selected scales, or the ring number was inconsistent, the scale specimen was discarded.

## Sample size

In conducting a statistical analysis of the age and growth of O. mossambicus, the importance of population and sample size had to be considered. All the habitats sampled were small, and the removal of large samples, as is done in assessing marine stocks, would have seriously affected the demography and growth rates of the uncaught population, which was numbered in hundreds rather than thousands. Sample size was of necessity therefore limited, and statistical analyses requiring large sample-sizes was not possible. Usable sample sizes were increased by back-calculating length-at-age. The small size of the populations of O. mossambicus in the eastern Cape is typical of many populations throughout its natural range due to the preference of this species for quiet backwaters, swamps, isolated pools and pans rather than large lakes and the open waters of major rivers. The study of these small populations is therefore of importance due to their frequent occurrence.

During 1986, fish collections were made at Rufanes Pool, the Kowie Lagoon and Bradshaw's Mill Dam by myself and D.W. Japp. A preliminary analysis of the age and growth of these three populations is described by Japp (1986). Further sampling was carried out at these three sites, and at Mill Farm Dam during 1987, and the data was pooled and re-analysed in this study.

## Determination of the time of scale ring formation

The accuracy of ageing techniques based on ring formation on bony parts of fishes depends on determining when these marks are formed, and whether this timing bears any correlation to climatic, seasonal or randomly unpredictable factors. Several of the studies which have examined wild populations of Oreochromis spp. differ in their suggestions for ring formation. This may be due to diverse environmental conditions affecting the formation of rings on hard bony parts. The studies detailed in Table 21 suggest either one or two rings formed on scales and otoliths annually.

Table 21. The number of rings or annuli formed on the scales or otoliths of different populations of O. mossambicus.

Population	Scales	Otoliths	Author
L. Sibaya	2	2	Bruton (1973)
Luphephe-Nwanedzi	1	2	Hecht (1980)
Transvaal Dams	1	-	Le Roux (1961)
Hong Kong Reservoir	1	-	Hodgkiss & Man (1977)
Hartbeespoort Dam	1-2	-	Cochrane (1985)
Kowie Lagoon	1	2	Japp (1986)

Due to the different results from various habitats shown in Table 21 it was considered essential to validate the ageing technique selected. The number of circuli in the marginal increment depends (a) on the time of sampling, and (b) the age of the fish. In young of the year, the number of circuli will increase from the focus to the margin until the first ring is formed. Thereafter, marginal increments (in number of

circuli) will increase until the second ring is formed (Bruton 1973). If a fish is caught shortly after ring formation the marginal increment will be either small or non-existent. Marginal increments will increase during successive months after this, until a rapid decrease in marginal width indicates that a new ring has recently formed. These monthly increments, measured in standard units, were plotted in length frequency histograms over two years, and a shift in the mode to the left indicated recent ring formation (Figs. 29 & 30). Where rings were crowded together in older fish (over 5 years age), the variations in marginal increment length became indistinct. Analysis was therefore limited to fish younger than 5 years.

Figures 29 and 30 indicate that only one ring was formed annually, during the part of the year shortly prior to recommencement of feeding when water temperature increased in October.

The method of measuring scale margin widths (for similar sized scales) as opposed to number of circuli as done by Bruton & Allanson (1974), and the clarity of scale rings in most cases made the assumption of one annual ring acceptable. There was no evidence of ring formation at any time of year except October/November. At this time of year the following events take place:

- (1) Surface waters warm up to temperatures at which active movement and feeding recommences (ie 16-20 C).

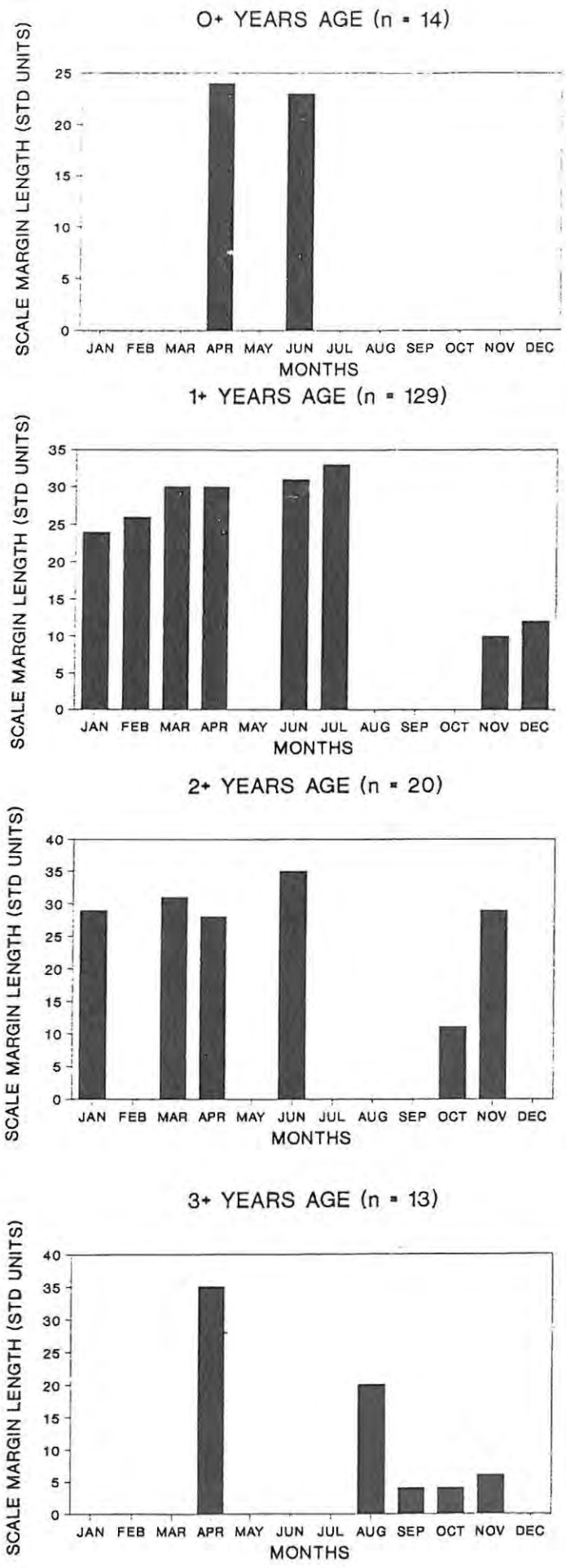


Fig. 29. Mean scale margin length for different age groups of *O. mossambicus* from Bradshaw's Mill Dam. Note the rapid decrease in length during October and November. Monthly data are not available for all age groups.

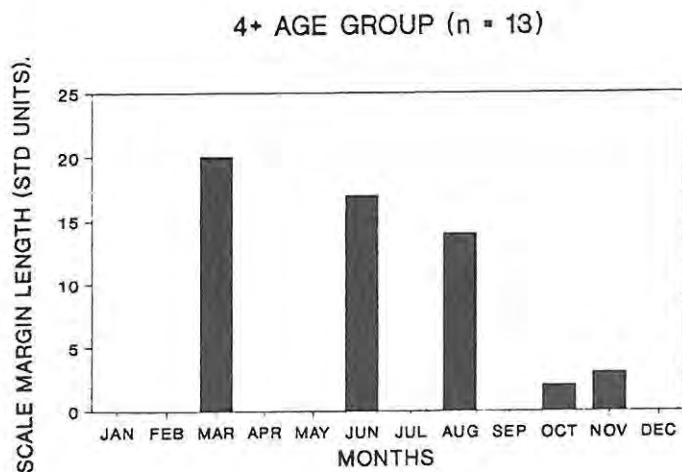
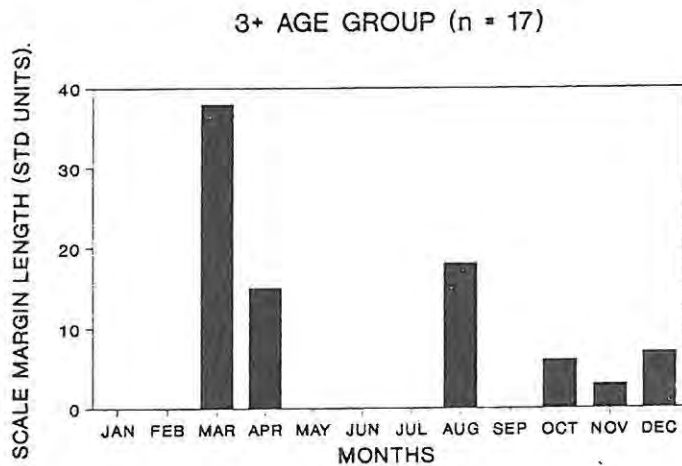
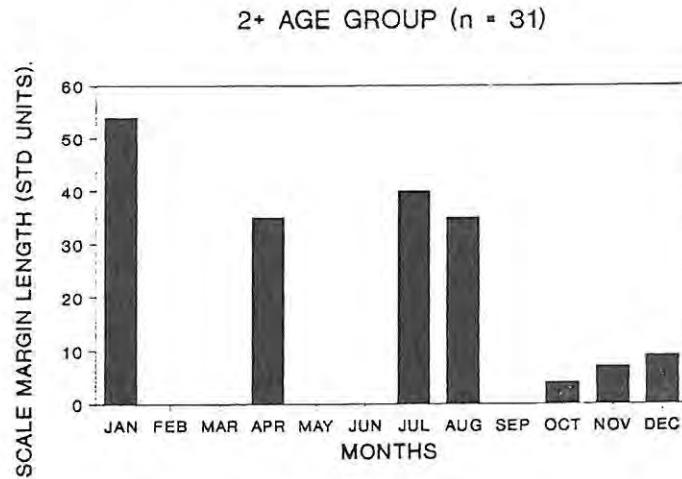
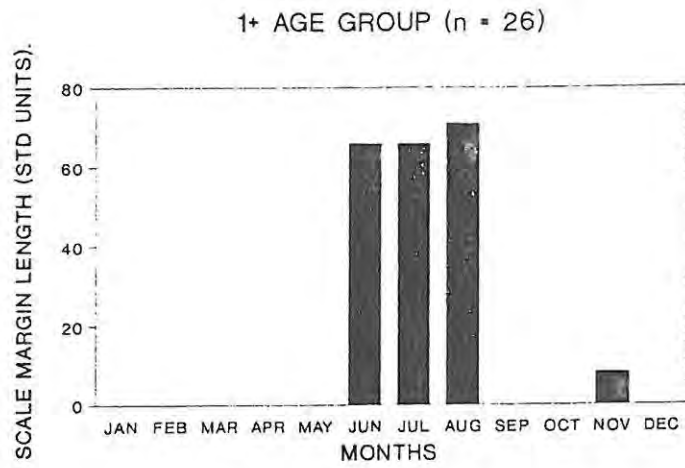


Fig. 30. Mean scale margin length for different age groups of *O. mossambicus* from Mill Farm Dam. Note the rapid decrease in length during October and November. Monthly data are not available for all age groups.

(2) Adult fish move into the shallows, and males begin nestbuilding.

(3) After the Spring rains, water levels have usually risen, flooding littoral areas, and stimulating food production.

Monthly examination of gonad condition indicates that gametes were already at stage IV - V at this time of year (ie near full development) having undergone gametogenesis during the cooler months, and so somatic growth is expected to increase without the expenditure of energy on gonad development for the period from October to first spawning in late December. Accelerated growth during this time would widen the gap between the circuli, forming a ring as described by Bruton & Allanson (1974) or Bruton (1979). Similar results have been reported by Gray & Setna (1931) (quoted in Bruton, 1973) who experimentally narrowed and widened the circuli spacing on the scales of rainbow trout by altering feed abundance.

It is important to note that rings only become distinct on the scale margin once the spacing of the circuli increases. The actual formation of the ring probably occurs during the coldest months (June - September) during which time the fish grows at a reduced rate, therefore closely bunching the circuli. Only after the growth rate accelerates in October/November is the ring detectible, after the circuli spacing increases.

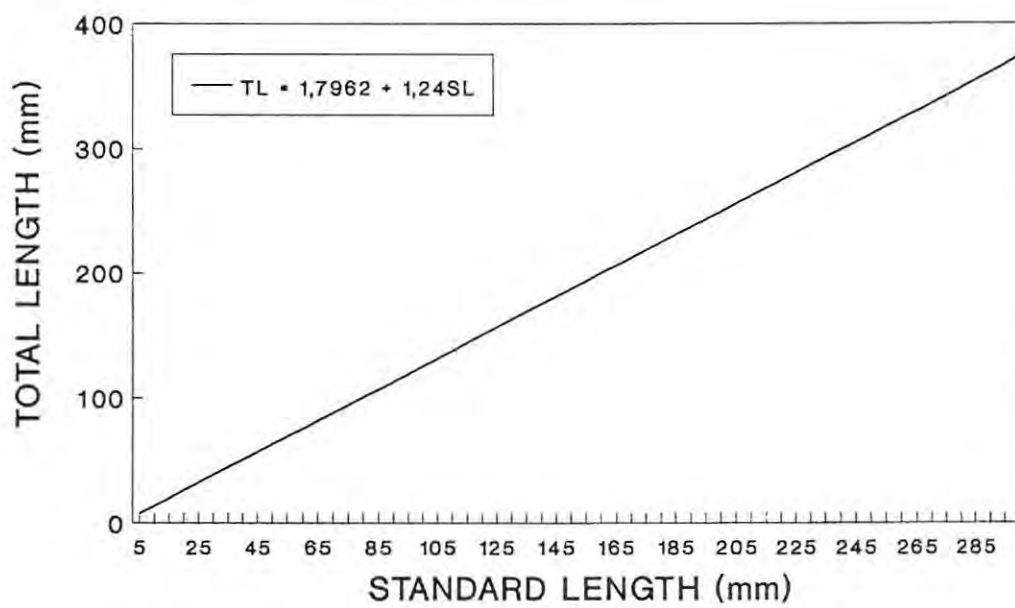


Fig. 31. The relationship between standard and total length of Q. mossambicus in the eastern Cape (n = 37, after Japp 1986).

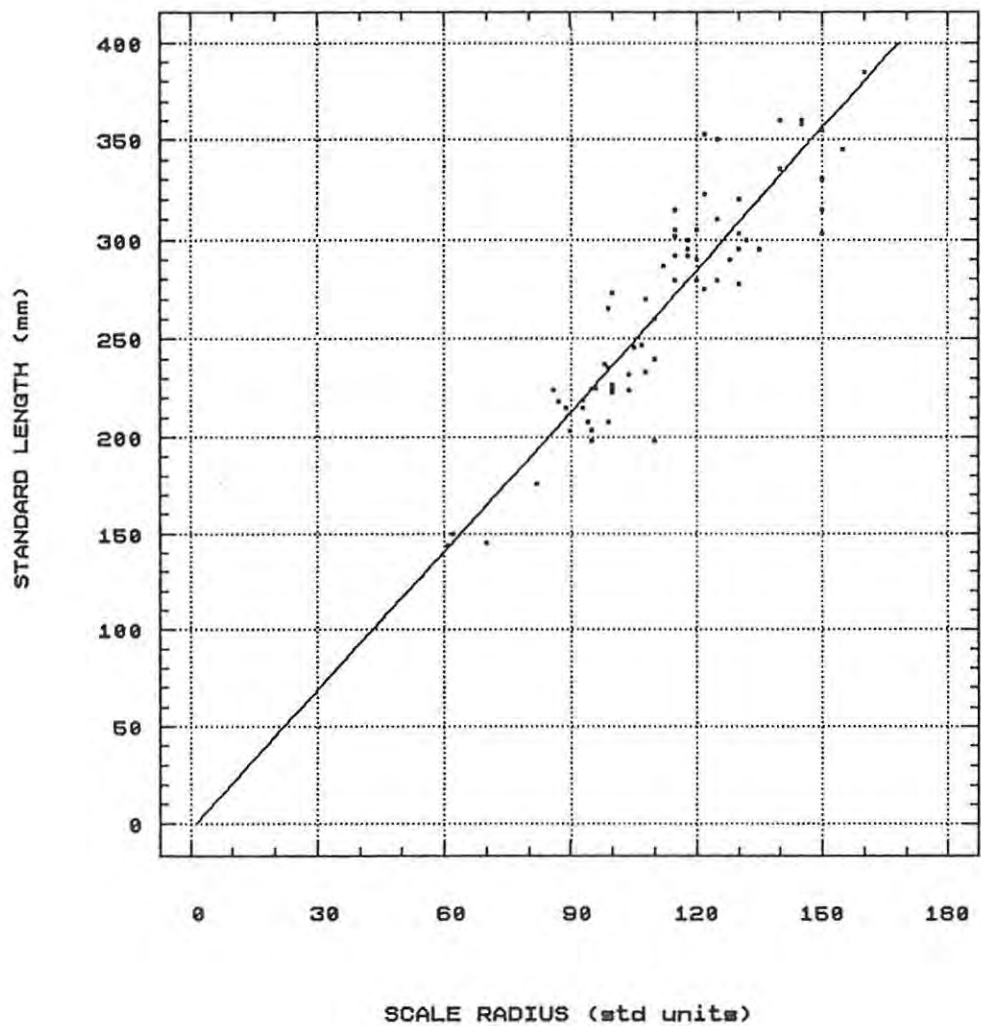


Fig. 32. The relationship of standard length to scale radius of the Mill Farm Dam (male) population of O. mossambicus.

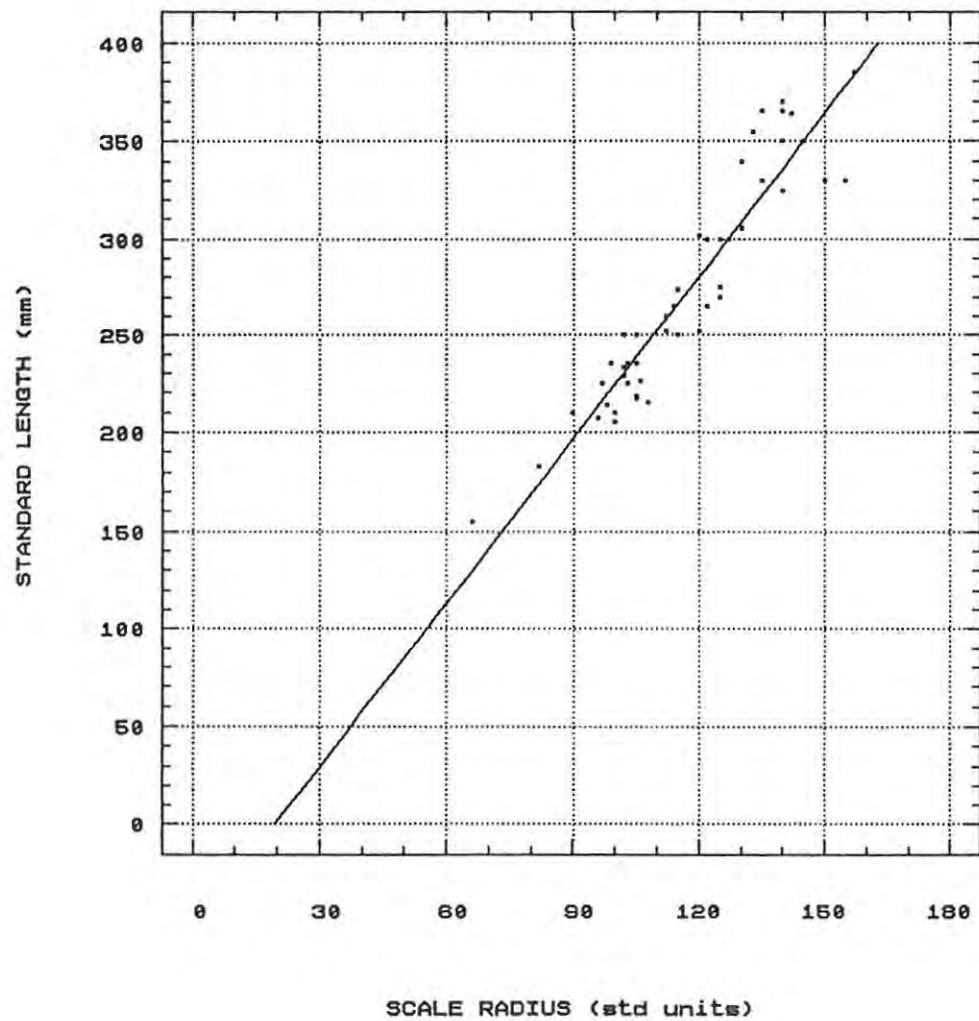


Fig. 33. The relationship of standard length to scale radius of the Mill Farm Dam (female) population of *O. mossambicus*.

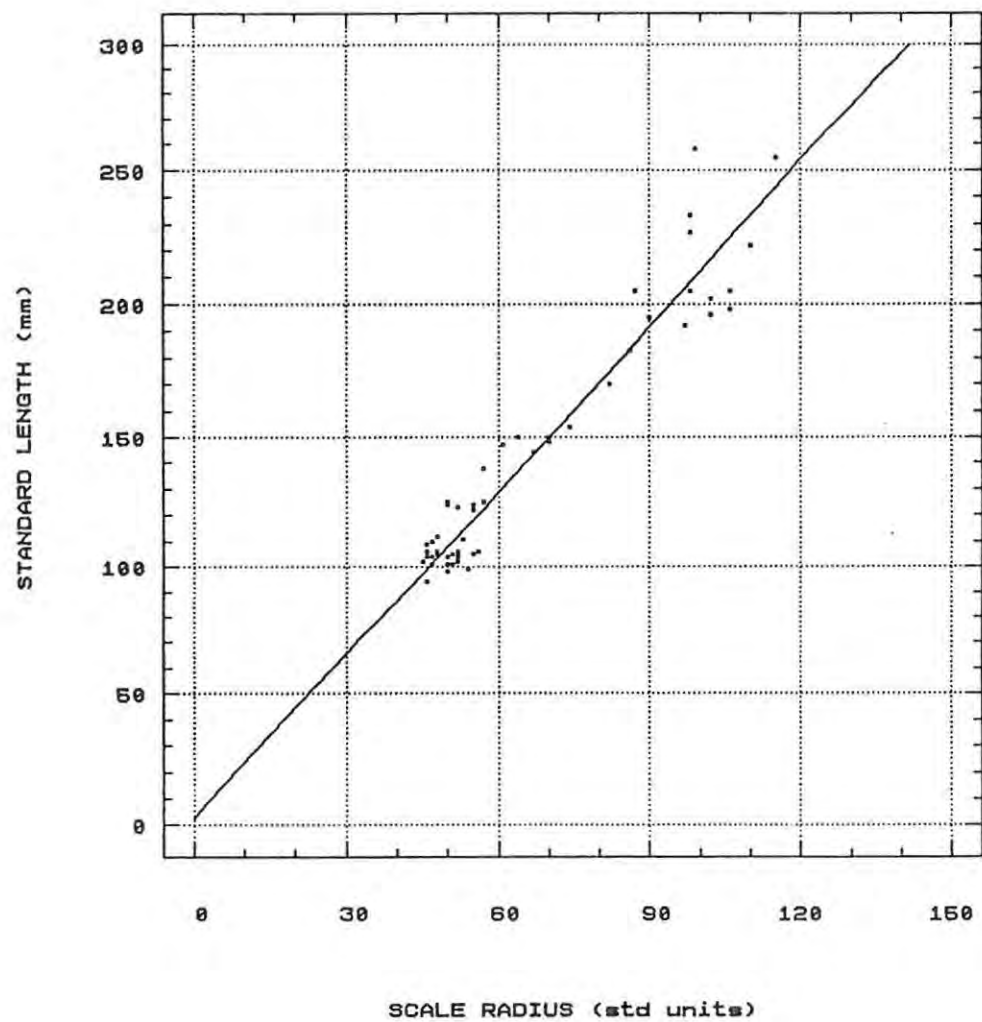


Fig. 34. The relationship of standard length to scale radius of the Bradshaw's Mill Dam (female) population of Q. mossambicus.

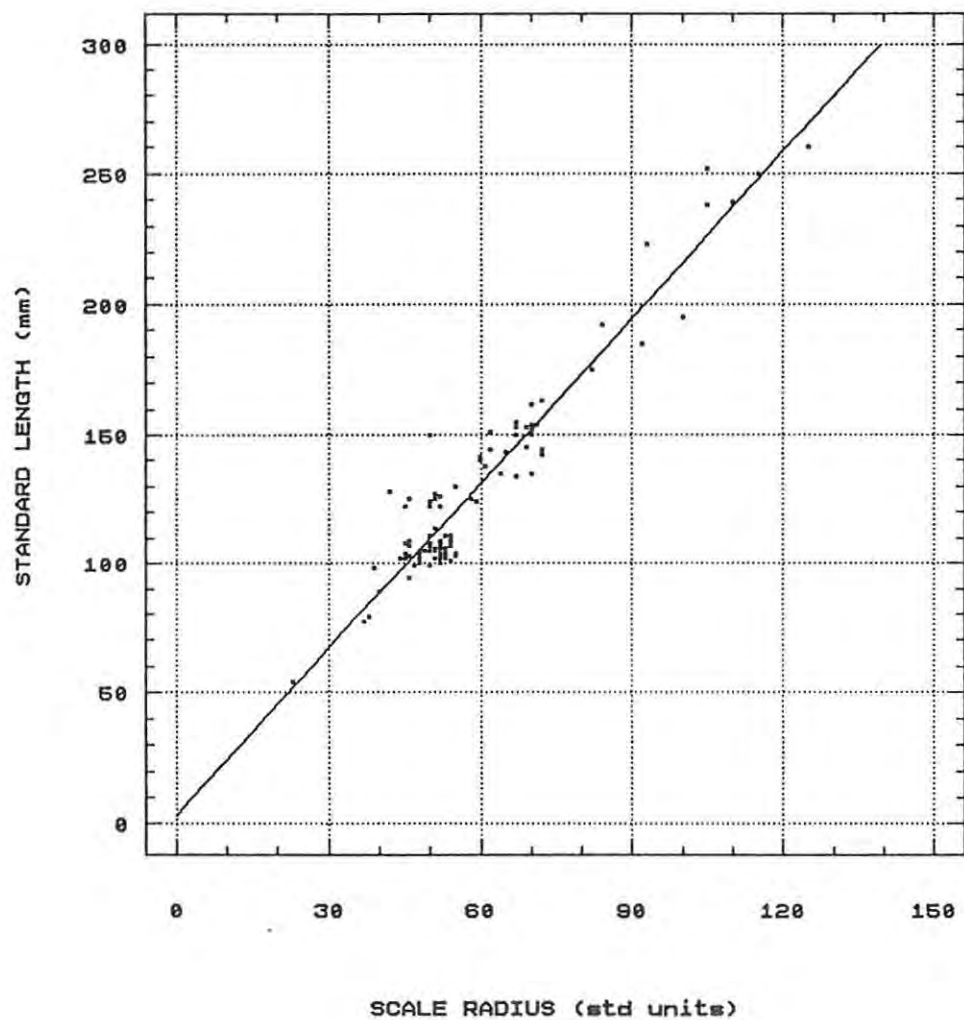


Fig. 35. The relationship of standard length to scale radius of the Bradshaw's Mill Dam (male) population of O. mossambicus.

## Results

### Relationship between standard length and total length

Japp (1986) calculated the relationship between standard and total length and found it to be linear and not significantly different for each of the three populations he studied. The linear relationship is expressed as:

$$\text{Total length} = 1,7962 + 1,24 \times \text{standard length (Fig. 31)}$$

The relationship was calculated so that growth rates recorded by this study could be compared with those from other populations where length had been measured as total length (TL).

### Relationship between standard length and scale radius

This ratio was calculated for the Bradshaw's Mill and Mill Farm Dam populations as well as for males and females separately. The linear relationship is shown in Figures 32, 33, 34 & 35 and the statistical data are presented in Table 22. In order that this relationship could be used to back-calculate standard length at age, it was necessary to establish the relationship between these two parameters. This was done for the Bradshaws Mill and Mill Farm Dam populations, and between males and females.

Table 22. Statistical data used in calculating the relationship between scale radius and standard length for O. mossambicus from various study sites in the eastern Cape.

	n	correllation coefficient	r <sup>2</sup>	p - value
<u>Bradshaw's Mill Dam</u>				
Both sexes	180	0,967036	0,94	0,001
Males	98	0,955204	0,91	0,001
Females	59	0,962271	0,93	0,001
<u>Mill Farm Dam</u>				
Both sexes	119	0,920492	0,85	0,001
Males	69	0,912115	0,83	0,001
Females	50	0,940735	0,89	0,001

The resulting equations describing the standard length:scale-radius relationship are:

Bradshaw's Mill Dam

Both sexes SL = 3,83946 + 2,10227 x SR

Males SL = 3,2358 + 2,12751 x SR

Females SL = 2,89129 + 2,0946 x SR

Mill Farm Dam

Both sexes SL = -20,6543 + 2,52953 x SR

Males SL = -3,13866 + 2,39619 x SR

Females SL = -54,2805 + 2,78948 x SR

## Growth rate

"The ability to increase in size by the replication of living material is one of the most fundamental characteristics of all living things, and because of this the study of growth phenomena in cichlid fishes is bound to throw light on almost every other aspect of their life history, ecology and evolution" (Fryer & Iles 1972).

Fryer & Iles (1972) described numerous examples of the plasticity in growth rate to be found in tilapiines, and compared this to the relative lack of plasticity in the haplochromines. There are several examples of studies on dwarfed or stunted natural populations of O. mossambicus that have been closely examined in the field (ie Bruton & Boltt 1973, Hecht & Zway 1984), but no detailed study of a population comprising fast-growing individuals which attain a large maximum size. During the course of this study widely variable growth rates were recorded in the four sampling sites. Although the Bradshaw's Mill Dam population could hardly be called "dwarfed", the limitations on mass and age of this population (600 to 700 g, 4 to 5 years old) serve as an interesting comparison to the Mill Farm Dam population (2100 to 2400 g, 8 to 10 years old). The growth rates of fish from this latter population are amongst the highest recorded for any natural population of this species.

Figure 36 shows the wide variations in growth rates between the populations of O. mossambicus. The most significant

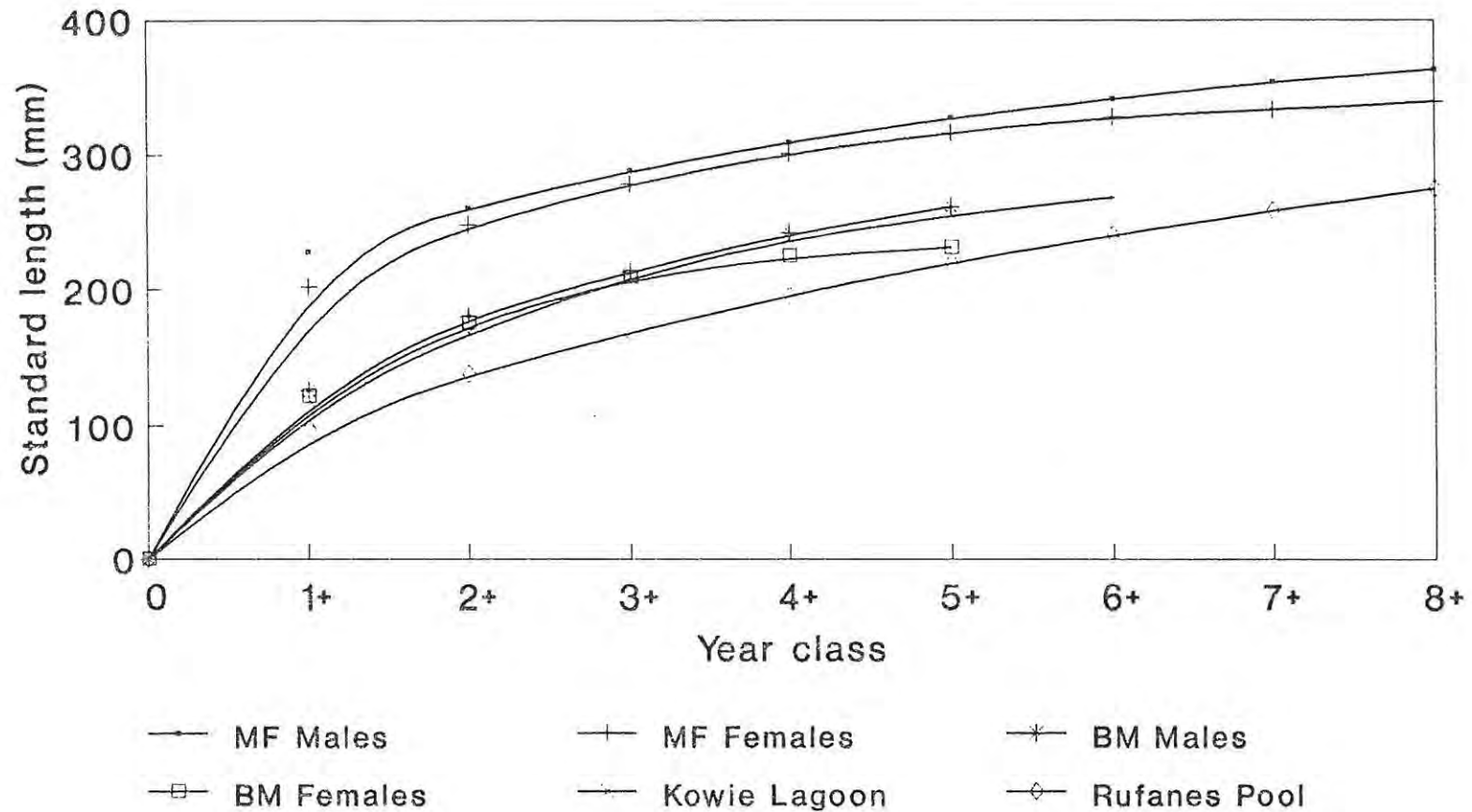


Fig. 36. Von Bertalanffy growth curves for different populations of *O. mossambicus* from the eastern Cape. MF = Mill Farm Dam, BM = Bradshaw's Mill Dam.

difference is the very rapid growth rate of young-of-the-year in the Mill Farm Dam population. Whilst juveniles of the 0+ age group (ie up to 10 months old) reach 98 to 115 mm SL by the time of first ring formation, similar aged fish from Mill Farm Dam average 215 mm SL. The difference is more extreme when the relationship between standard length and body weight is taken into account, due to the deeper body proportions of the Mill Farm Dam population.

In terms of rate of increase in length after year 1, the Bradshaws Mill and Kowie populations grow more rapidly than those from Mill Farm Dam (Fig. 37). This is misleading and illustrates the false impression that can be obtained from statistical analyses of biological phenomena: whilst both these populations are increasing in length at a rate greater than the Mill Farm population, the smaller length gains of the latter result in much greater mass increments due to the larger overall size of the fish. The slowest rate of growth was found in the Rufanes Pool population, in which growth was more linear. It is difficult to compare growth towards the theoretical maximum size as longevity varied between 4 and 10 years between populations.

#### Asymptotic length

The asymptotic length, or theoretical maximum length, was calculated as the parameter  $L_{\infty}$  in the von Bertalanffy growth equation, using the Walford plot:

$$l_{t+1} \text{ on } l_t$$

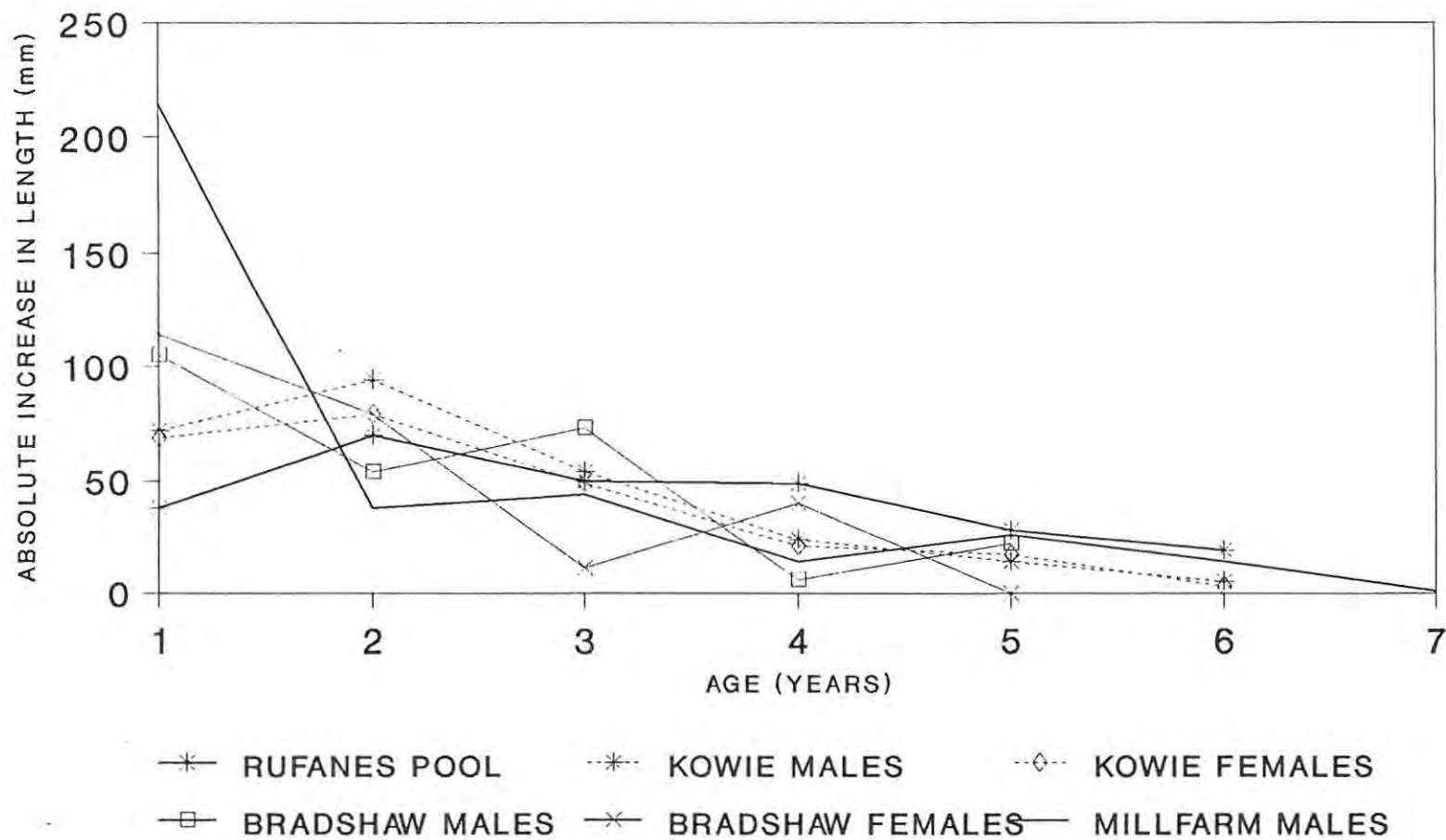


Fig. 37. The absolute rate of increase in standard length of O. mossambicus in the eastern Cape.

The Walford plot (Figs. 38, 39, 40 & 41) overestimates the asymptotic maximum length observed in Rufanes Pool, and underestimates that from the Kowie Lagoon (Table 23). Results for the other two sites are close to observed results. Despite this, the parameter  $L_{\infty}$  can still be used in the Von Bertalanffy equation to accurately describe growth rates.

Table 23. Asymptotic length and observed length of O. mossambicus from the study sites in the eastern Cape.

Site	$L_{\infty}$	Observed max SL
Rufanes Pool (males)	383,39 ( $r^2 = 0,89$ )	295
(females)		282
Kowie Lagoon (males)	267,52 ( $r^2 = 0,87$ )	300
(females)		275
Bradshaw's Mill Dam (males)	317,35 ( $r^2 = 0,93$ )	280
(females)		260
Mill Farm Dam (males)	406,25 ( $r^2 = 0,96$ )	385
(females)		385

One of the major drawbacks of the von Bertalanffy growth equation is the sole use of length to describe growth. Whilst this may be satisfactory within populations in which gross morphological proportions remain constant, it does not take into account variations in body shape between populations.

In order that body mass could be calculated from standard length, the relationship between these parameters was calculated for each population. The statistical data

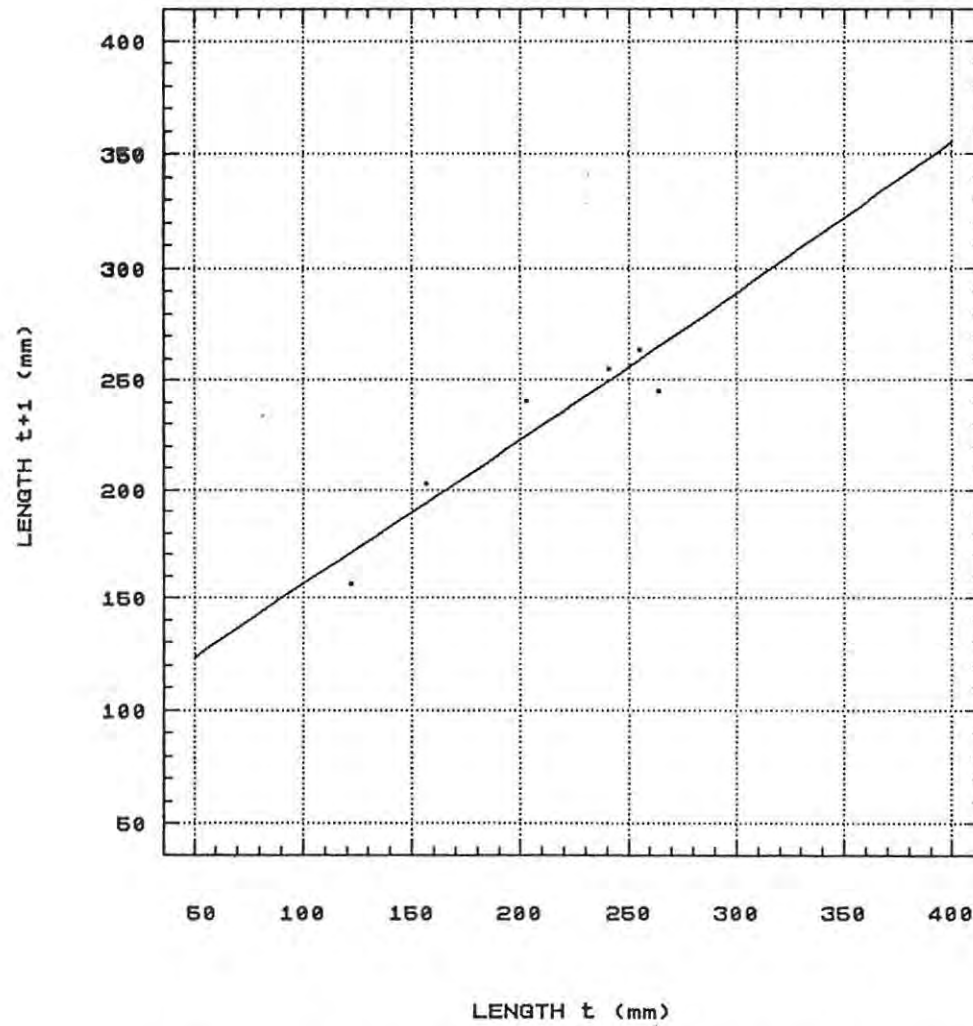


Fig. 38. The Walford plot used to estimate the parameters "K" and Loo in the Von Bertalanffy growth model for the Kowie Lagoon population.

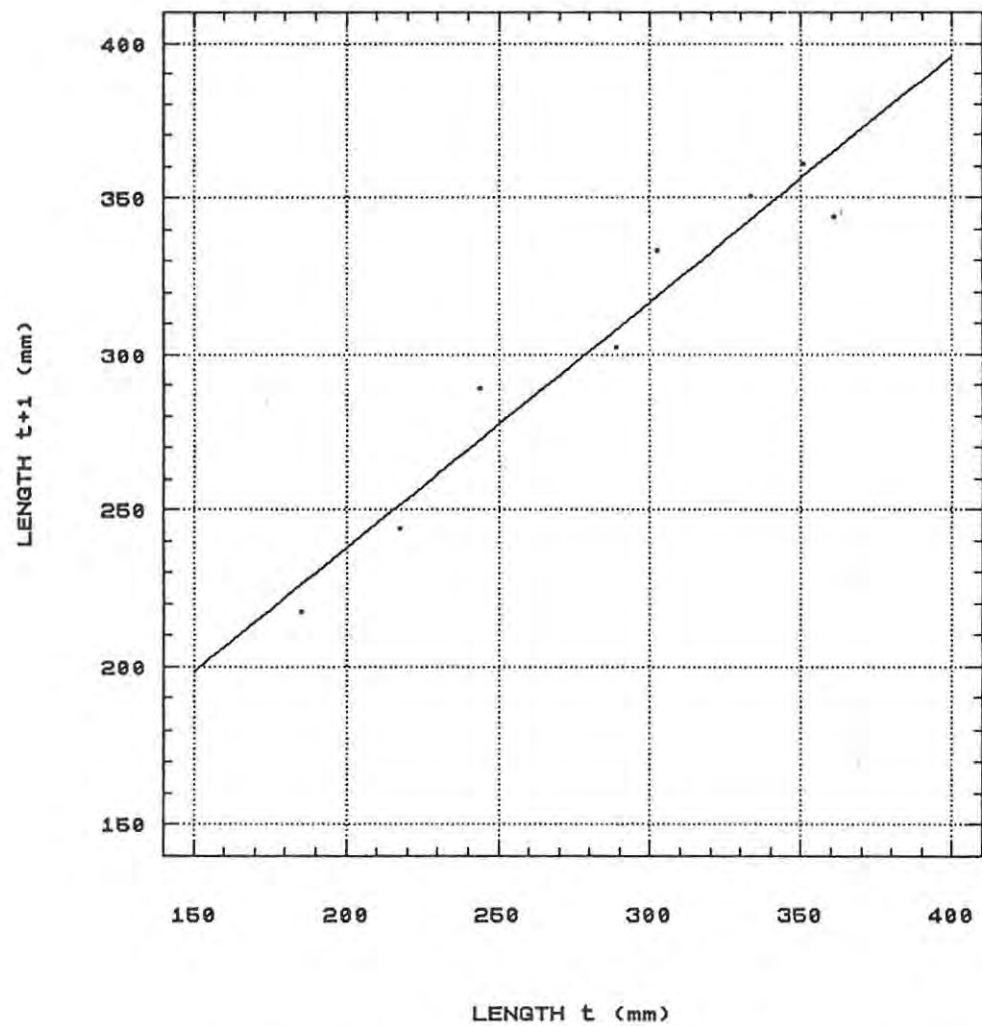


Fig. 39. The Walford plot used to estimate the parameters "K" and  $L_{\infty}$  in the Von Bertalanffy growth model for the Mill Farm Dam population.

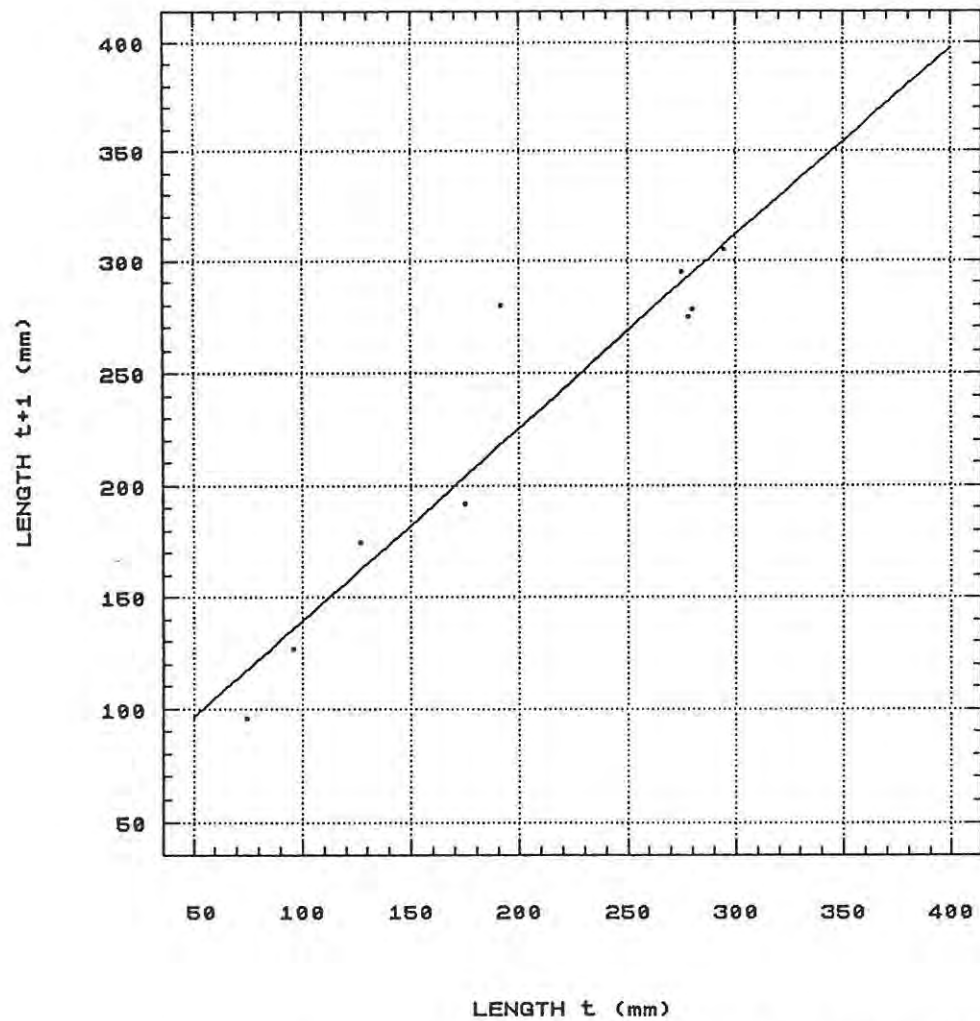


Fig. 40. The Walford plot used to estimate the parameters "k" and Loo in the Von Bertalanffy growth model for the Rufanes Pool population.

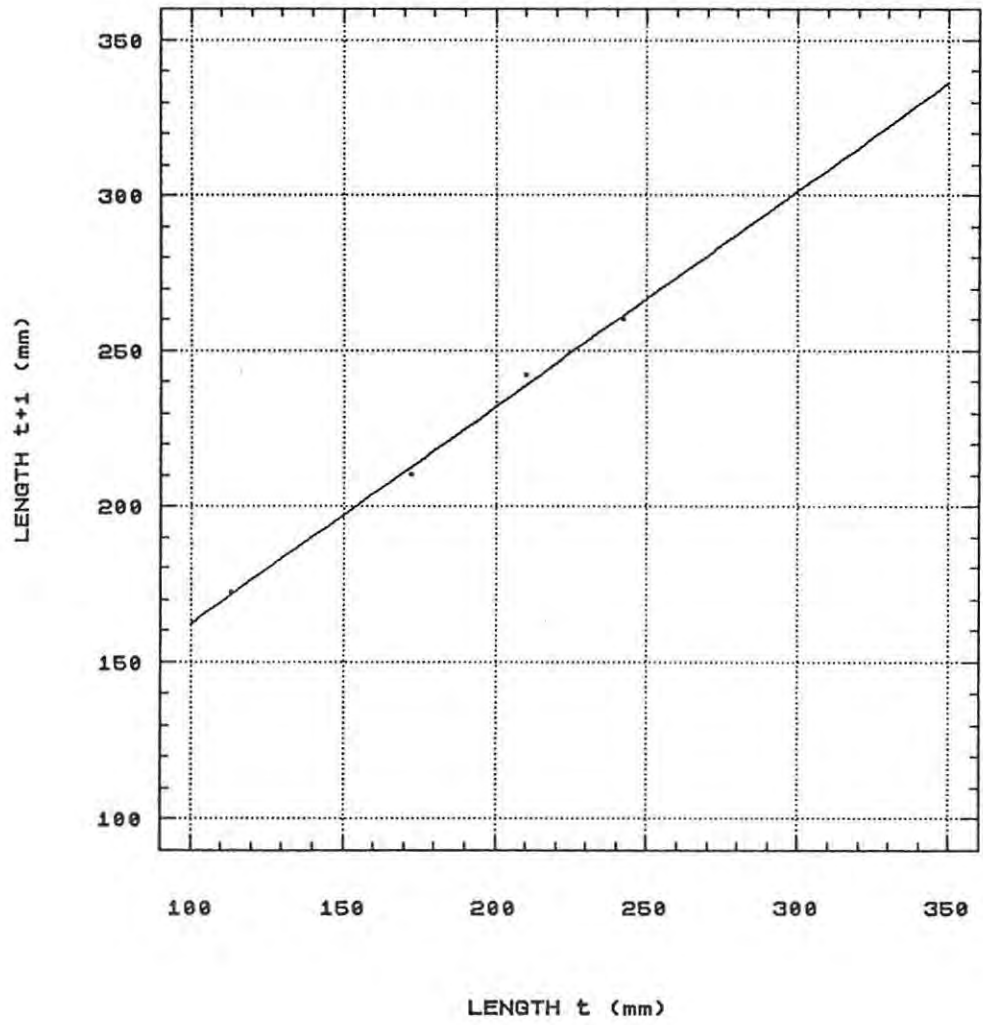


Fig. 41. The Walford plot used to estimate the parameters "K" and Loo in the Von Bertalanffy growth model for the Bradshaw's Mill Dam population.

describing the relationship is given in Table 24 and the resulting fitted curves in Fig. 42. The relationship was checked by firstly correlating standard length to weight directly to obtain a power curve fit (Figs. 43, 44, 45 & 46) and also by using a linear regression of the log:log plot of length on weight.

If the exponent (b) in the relationship:

$$\text{weight} = a \times \text{standard length}^b$$

closely approximates three, this indicates that average growth is isometric, and body form does not alter significantly throughout life. This is the case with all populations studied (Table 25) with the exception of the Rufanes Pool population ( $b = 2,88008$ ). Juveniles from this site were in better than average condition, but adults were in progressively poorer condition as they grew towards maximum size, indicating allometric growth (Fig. 42).

Whilst the exponent "b" can be used to compare "plumpness" (body condition) within a population, it cannot be used to contrast different populations unless the data are pooled. Table 25 indicates that there is variation between the length:weight relationship of the populations studied. Fish from the Mill Farm Dam population show a greater degree of "plumpness" from the early juvenile stage, and retain this state throughout life. Bradshaw's Mill Dam fish show the opposite. The Mill Farm Dam population has a superior weight:length ratio than even the Lake Kariba population (Fig.

Table 25. Statistical data used in the calculation of the relationship of weight to standard length of four populations of O. mossambicus from the eastern Cape

n	b	corr. coef.	intercept	r <sup>2</sup>	a
Bradshaw's Mill Dam 180	3,09433	0,995235	-10,6899	0,99	0,0000227
Mill Farm Dam 119	2,98435	0,985127	-9,91368	0,97	0,0000494
Kowie Lagoon 33	2,96550	0,994879	-10,031	0,99	0,000044
Rufanes Pool 40	2,88008	0,997996	-9,55145	0,99	0,0000526

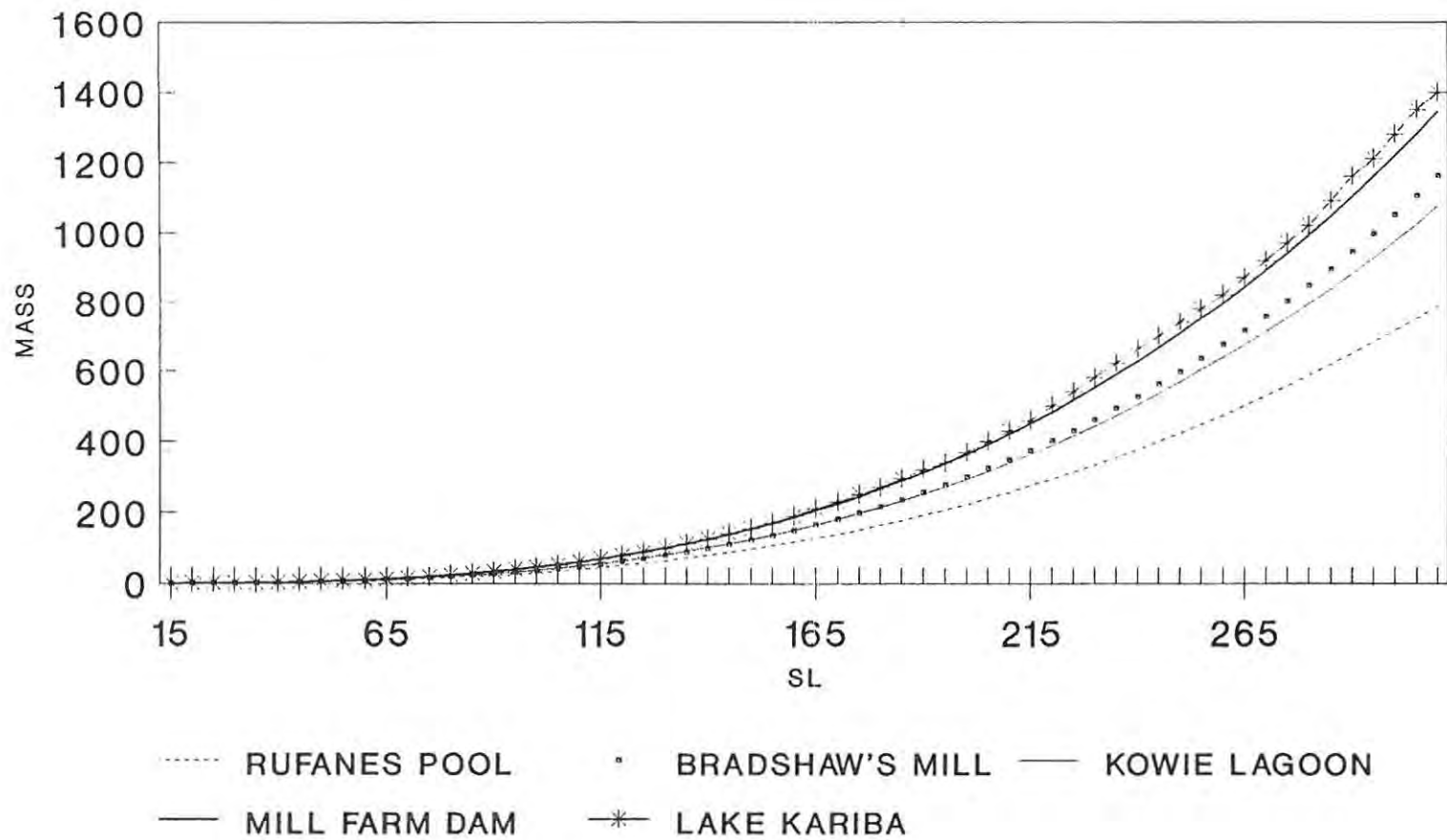


Fig. 42. The relationship between standard length and mass of *O. mossambicus* from the four study sites, and of *O. mortimeri* from Lake Kariba (Balon 1964).

42), up to 140 mm SL. Thereafter the Kariba population comprises individuals which are in slightly better condition than the Mill Farm Dam fish. Bradshaw's Mill Dam has lighter juveniles for their length up to 175 mm SL than the Kowie Lagoon population, but heavier adults. The Rufanes Pool population, although in fair condition for the early juvenile stage up to 50 mm SL, shows evidence of malnutrition in all later stages.

#### Longevity

Significant variations in longevity were recorded during this study (Table 26). These were not in proportion to habitat size but tended to reflect the nutritional status of the lake in terms of food availability to the fish population. Whilst food was not a limiting factor to juvenile fish in Bradshaws Mill Dam, few adult O. mossambicus were recorded over 4 years of age. In the size limited habitat at Rufanes Pool, where individual survival was dependent on density and climatic factors rather than food availability, adults achieved a lifespan of 6 to 10 years. At Mill Farm Dam, where neither food nor density was limiting, a typical lifespan of 6 to 10 years was also recorded. None of the above habitats suffer any significant degree of exploitation, except for occasional recreational angling at Mill Farm Dam on Micropterus salmoides.

Table 24. Statistical data used in calculating von Bertalanffy growth curves

<u>von Bertalanffy equation parameters:</u>				<u>Analysis of variance:</u>		
Loo	L +1 t	t o	K	Corr. coefficient	Std. error.	r <sup>2</sup>
Mill Farm Dam						
(males)						
406,254	71,1428+0,82488L	-3,1541	0,19252	0,978	11,702	0,96
	t					
(females)						
347,758	108,9+0,686851L	-1,2723	0,37564	0,914	24,119	0,83
	t					
Bradshaw's Mill Dam						
(males)						
317,351	83,3576+0,736388L	-0,5778	0,306	0,962	18,946	0,93
	t					
(females)						
242,299	146,098+0,397035L	-0,2488	0,92373	0,732	25,887	0,54
	t					
Rufanes Pool						
(both sexes)						
383,387	53,2268+0,861167L	-1,7744	0,1495	0,945	27,446	0,89
	t					
Kowie Lagoon						
(both sexes)						
267,520	90,2268+0,662729L	-0,3273	0,4114	0,936	15,996	0,88
	t					

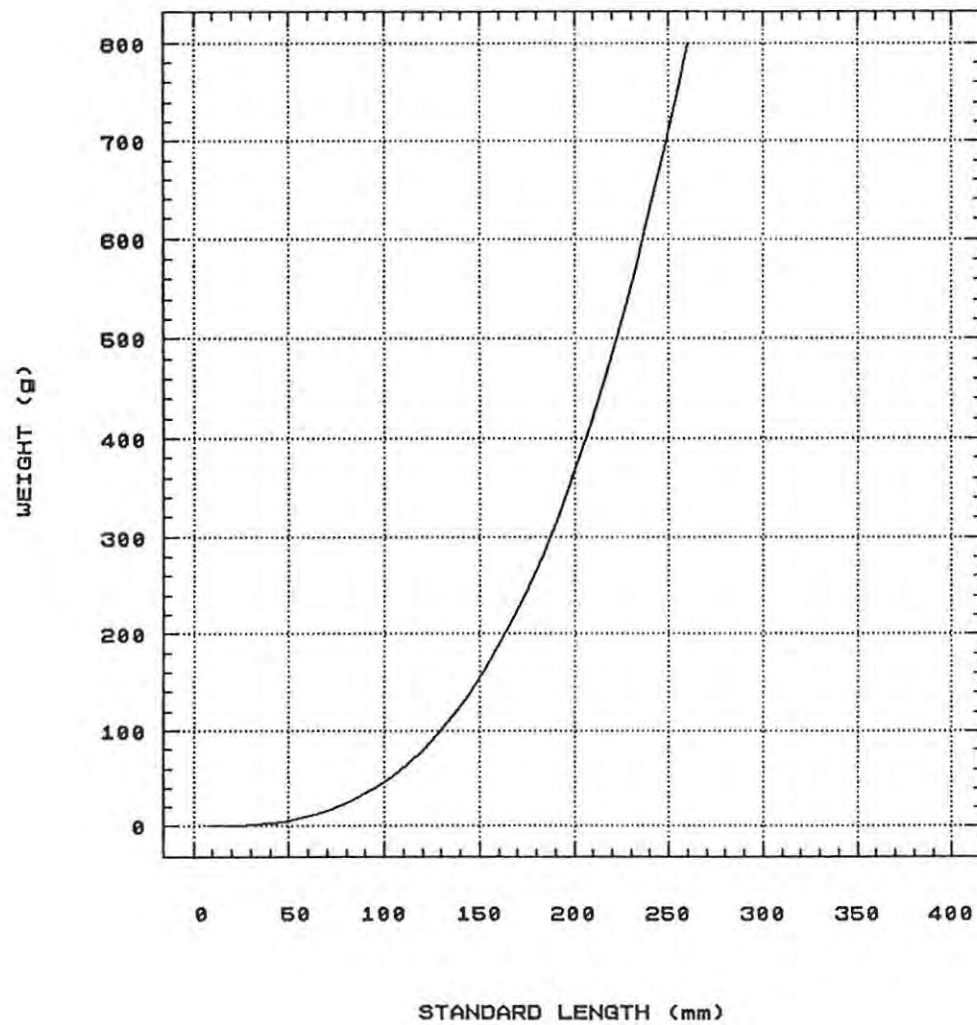


Fig. 43. The relationship of mass to standard length for the Mill Farm Dam population.

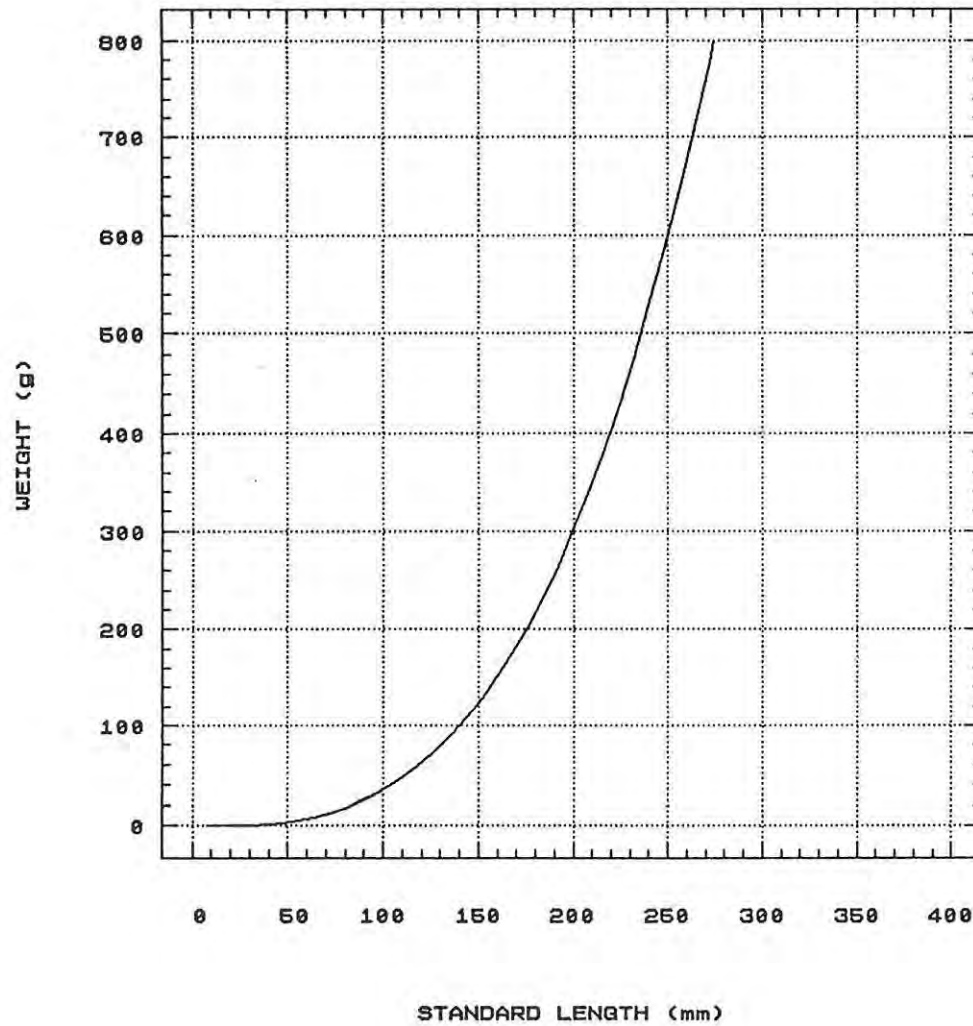


Fig. 44. The relationship of mass to standard length for the Bradshaw's Mill Dam population.

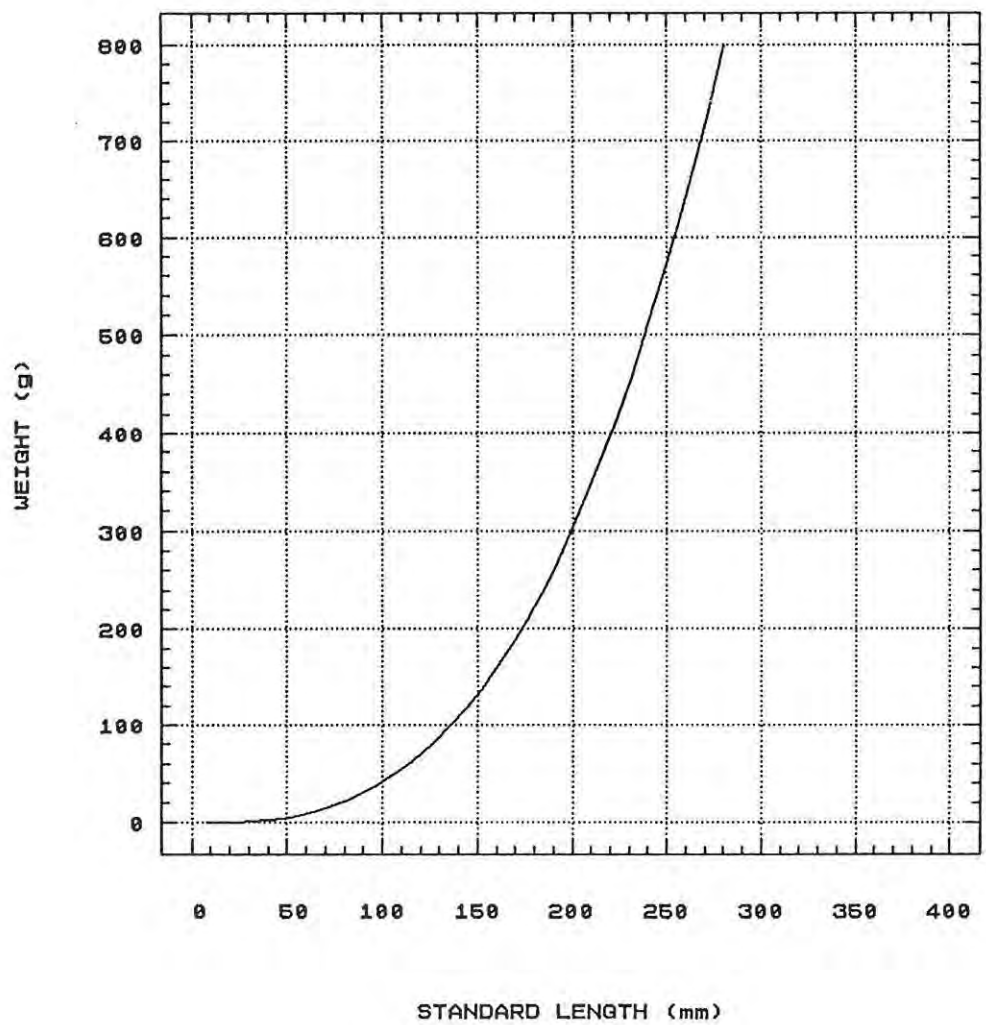


Fig. 45. The relationship of mass to standard length for the Rufanes Pool population.

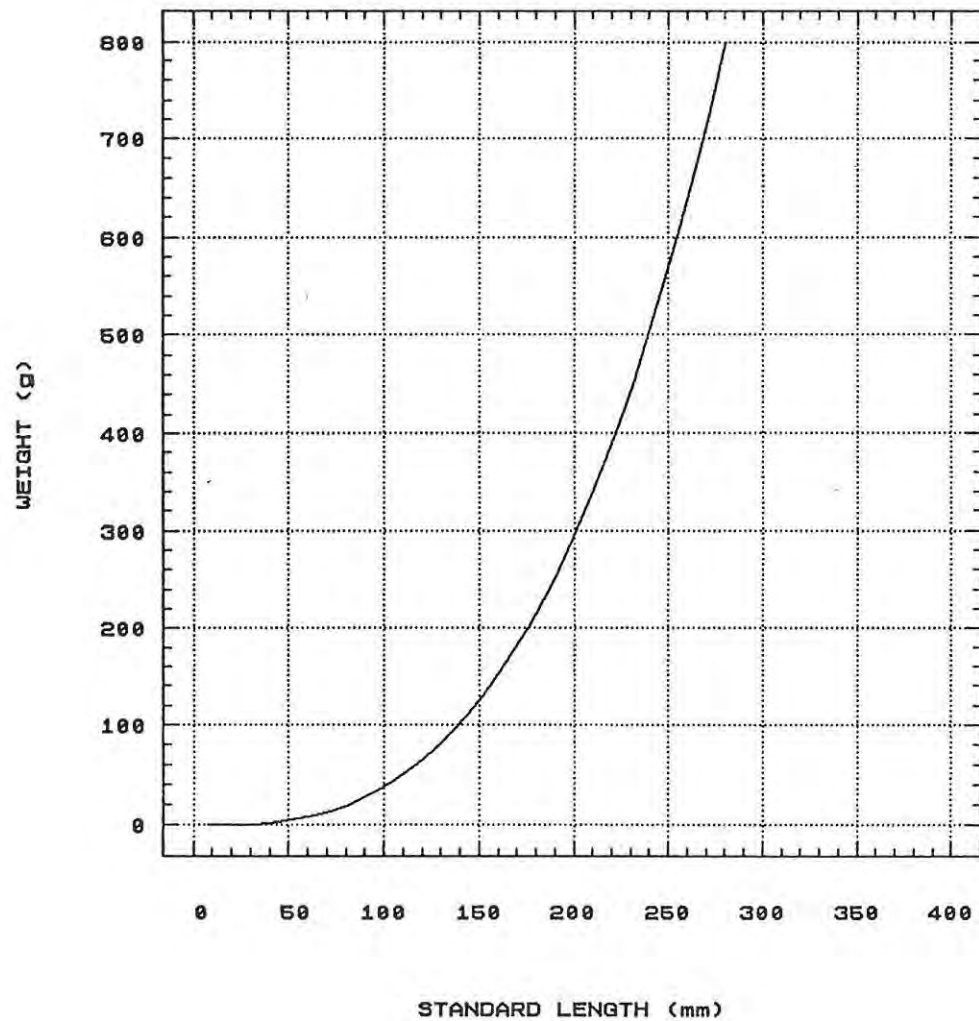


Fig. 46. The relationship of mass to standard length for the Kowie Lagoon population.

Table 26. Typical lifespan of O. mossambicus in the study sites

Bradshaw's Mill Dam	4 years
Kowie Lagoon	6 years
Rufanes Pool	10 years
Mill Farm Dam	10 years

Table 27. The relative proportions by age groups of the O. mossambicus populations of two lakes in the eastern Cape

Age	1+	2+	3+	4+	5+	6+	7+	8+	9+	10+
Bradshaw's Mill Dam										
%	78,5	11,7	7,4	1,8	0,6					
Mill Farm Dam										
%	23,4	28,0	15,9	11,2	7,5	5,6	5,6	1,9	0	0,9

The populations of O. mossambicus from Bradshaw's Mill Dam and Mill Farm Dam were compared to examine their respective age structures (Table 27). These two sites were selected for comparison because of their distinct biotic and abiotic contrasts, and because the same gear (gill nets) was used for sampling at both sites, thereby reducing selectivity or sampling bias.

In Bradshaw's Mill Dam over 90 % of the population consisted of fish under the age of 2 + years. As growth was relatively slow, the bulk of this population therefore comprised small fish. In Mill Farm Dam, the proportions of the total population were less concentrated in the younger age groups: only 51 % of the population was younger than 2 + years, and a further 27,1 % was aged 3 + to 4 + years. A significant proportion of the population (21,5 %) consisted of fish aged

over 5 + years, with the maximum typical lifespan being between eight and ten years. The size compositions of the two populations indicates a lower recruitment rate at Mill Farm Dam, and possible evidence of poor recruitment during the spawning year of the 1 + cohort which is under-represented in comparison to the 2 + cohort. This could have resulted from later maturity as a natural response to improved environmental conditions.

### Discussion

Ring formation due to seasonal influences on behaviour would be expected to become less distinct in habitats nearer the equator and at low altitudes where temperature fluctuations are less acute and water temperatures do not fall below levels at which feeding and growth are inhibited (Fryer & Iles 1972). At high altitudes, and near the extremes of the natural range of this species, climatic factors severely influence the annual cycle of growth and reproduction, and "check" marks would be expected to be distinct on scales and otoliths, as they were in this study. In more tropical habitats where seasonal variations are less marked, rings may result from other factors such as peak spawning periods which may cause reduction in growth, with consequent checks on scales and otoliths (Garrod 1959). Thus Le Roux (1967) found evidence of only one distinct annual ring in populations from Transvaal reservoirs at high altitudes with low winter temperature and marked seasonality. Similarly Hodgkiss & Man

(1977a) reported the formation of one annual ring in the (low) temperature stressed population of Plover Cove Reservoir in Hong Kong, near the northern limit of survival. In tropical waters the hypothesis that scale rings are related to breeding activity rather than seasonal fluctuations in the environment has been suggested (Holden 1956, Garrod 1959, Bruton & Allanson 1974). This view is supported here, as in these habitats cessation of peak breeding activity is not followed by a decline in water temperature to levels which reduce active feeding by Oreochromis species, as is the case at high altitudes or low latitudes near the range limit (this study).

Cochrane (1986) notes that for the first three years O. mossambicus lays down one annual ring in Hartbeespoort Dam. This water body experiences heavy winter mortality of juvenile fish. Why two annual rings should be formed after 3+ years of age in this environment is not known.

The formation of rings by juvenile fish at times other than October/November was not observed during this study. Holden (quoted in Garrod 1959) suggests that juveniles may lay down indistinct rings that are discrete from "breeding" rings. My observations during this study suggest that very small juveniles found with an apparent juvenile ring are the result of late season spawns which have survived the winter but with little opportunity for growth before October/November. Such fish caught at this time of year are usually the smallest of their age class.

It would be reasonable to assume that populations of the same species would have similar growth rates in similar habitats within the same climatic and geographic area. If it is assumed that the populations of O. mossambicus studied in the Kowie River catchment originated from the same genetic stock, then variations in environmental conditions must be responsible for the differences in growth rate and body condition shown among the four populations. These environmental factors lead to the following characteristics in the Mill Farm Dam population which are not collectively shared by the other populations studied:

1. Very rapid juvenile growth
2. Rapid and sustained adult growth to a large body mass (2100-2400 g)
3. Good body condition compared to the other populations
4. Long life
5. Less variation in growth rate between males and females

The very rapid growth and good body condition of the Mill Farm Dam population can be compared to closely-related populations from large stable lakes such as Lake Kariba (O. mortimeri) where they thrive and reach a large maximum mass (3,5 kg., Kenmuir 1983). Similar growth rates and body condition have been recorded for the O. mossambicus from Nyamithi pan on the Phongolo floodplain (Bruton 1979). This is in contrast to the other three populations studied where the average length:weight ratio indicates relatively poor condition.

Bruton & Allanson (1974) and Bowen (1979) suggested that the stunted growth and poor body condition of O. mossambicus in L. Sibaya result partially from a combination of poor quality food available in the habitat selected by adults, and early maturity. The latter was indicated by Hecht & Zway (1984) as possibly being responsible for poor growth in the stunted population of the Klein Tshipise Hot Spring, where overcrowding depleted food resources. However in the Matiovila Hot Spring, food in the form of detritus was abundant and did not therefore act as a growth-limiting factor, although the fish were still stunted. Elevated water temperatures (27 to 36,7<sup>o</sup> C) throughout the year led to a potential ability to breed throughout the year, although the resultant increase in density did not lead to exhaustion of the available food resources. Fryer & Iles (1972), however, argue that a correlation between size, growth rate and availability of food is not always easy to demonstrate, and the plasticity shown by tilapia species is affected by more than mere food alone. In the small habitat, Rufanes Pool, benthic samples were found to be rich in diatoms and detritus which, according to Bowen (1982), can fulfill the nutritional requirements of tilapia. This depends on the ratio of digestible matter (diatom frustule contents and bacteria) to undigestible matter, which was not determined in this study. Despite this, growth was slow compared to (the larger) Mill Farm Dam which was also rich in detritus and diatoms.

Garrod (1959), working on the growth of Oreochromis esculentus in Lake Victoria, collected few fish over eight years of age, although occasional specimens of 10 yrs were caught. He also noted that very old fish were only found in specific areas (in the case of Lake Victoria, outside the Kavirondo Gulf) indicating that longevity is environmentally rather than genetically influenced in this habitat, although this may be affected by exploitation. Le Roux (1961), reporting on the growth of O. mossambicus in some Transvaal impoundments, found widely varying growth rates and longevity: large fish were not necessarily old (as also noted by Garrod 1959) and longevity ranged between 5 and 11 years for the different lakes examined.

In the thermally harsh environment of Plover Cove Reservoir (Hong Kong) (Hodgkiss and Man 1977) few fish over four years of age were recorded, but the authors suggest that was also influenced by illegal fish poaching. Hecht & Zway (1984) showed that the stunted population of O. mossambicus (maximum length 105 mm SL) in the Matiovila Hot Spring consisted of short-lived individuals which rarely exceeded five years in age. In the nearby Luphephe-Nwanedzi impoundment an age of nine years was attained, coupled with good growth rates (Hecht 1980).

The longevity of O. mossambicus in the eastern Cape follows the general pattern described in the above examples, in that an increasing degree of environmental harshness results in a

shorter than expected lifespan. Habitats with favourable feeding and living conditions such as Mill Farm Dam, enable the fish to attain an age typical of the maximum recorded for this species elsewhere.

## Reproduction

### Introduction

Most tilapias have the well-known capacity, often deplored by aquaculturalists, to reproduce at a small size when they are environmentally stressed (Fryer & Iles 1972, Trewavas 1983). It has been suggested that this precocious reproductive ability is hormonally induced as a response to stress, and may have a survival value (Noakes & Leatherland 1977). This study investigated the breeding biology of O. mossambicus over a range of habitats, and suggests that environmental variations between habitats within the same catchment of a river system (at locations in close proximity) are the cause of the highly variable phenotypic plasticity of this species.

The following hypothesis was tested: that increasing environmental harshness would lead to the following suite of reproductive characteristics in the distinct populations:

- (1) Longer spawning season
- (2) Earlier sexual maturity, at a smaller size
- (3) Increased fecundity
- (4) Smaller eggs
- (5) Lower individual survival of the more numerous offspring
- (6) Shorter sexually active lifespan of the adults due to shorter longevity
- (7) Decreased parental investment in nestbuilding

The reproductive biology of O. mossambicus in the eastern Cape was therefore investigated to test this hypothesis.

## Methods

Gonads from a size range of fish collected from different habitats were examined for stage of development and classified according to the scale of Nikolski (1969). Development was plotted against standard length and mass, and the point calculated at which 50 % of the population became mature, for males and females separately, and for the population as a whole. The onset of maturity was taken at a gonad maturity index of III and above (after De Silva 1986).

Fecundity was examined by removing the ripe gonads from mature females of varying mass and counting the ova likely to be spawned in the next brood. O. mossambicus has often been reported as having ova of differing size in the gonads (Aravindan & Padmanabhan 1972, Hodgkiss & Man 1978) due to their ability to spawn as frequently as every 30 to 40 days (Baerends & Baerends van Roon 1950, Vaas & Hofstede 1952, Bohrer 1953, Bruton & Bolt 1975), and therefore only the larger ova were included. The number of ripe ova in the gonads may exceed the number likely to be spawned at any one time, and some apparently ripe ova may be re-absorbed by the cells of their follicle (Aravindam & Padmanabhan 1972). In this study fecundity was taken to mean the total number of eggs per clutch. Clutch size was therefore re-examined by counting the number of newly spawned eggs (examined up to 48 hours after spawning) held in the buccal cavity of females.

Egg dimensions were assessed by examining 25 randomly selected eggs from the ripe gonads (stage V) of 39 individual fish and using a compound microscope and scale graticule to measure the longest and shortest diameter. Mean egg size was compared between populations using a Students t test.

Spawning frequency under natural conditions was assessed by noting the occurrence of the following events in various habitats:

- (1) The date of annual commencement of nestbuilding activity by males.
- (2) First occurrence of fry, either in the buccal cavity of netted females, or free-swimming as newly released juveniles (about 3 weeks of age according to Bruton & Boltt 1975).
- (3) Last recorded presence of fry in buccal cavities, or free-swimming.
- (4) Cessation of territorial behaviour by males.
- (5) Monthly measurements of mean gonad maturity indices of adult fish.

#### Experimental manipulation of fecundity

The results of observations on feeding, growth and longevity suggested that the environmental conditions in Bradshaw's Mill Dam were more harsh than in Mill Farm Dam. The effect of food quantity on the reproductive performance of O. mossambicus was therefore tested under artificial conditions. Spawning frequency under controlled conditions was tested under food-abundant and food-deprived conditions. All other environmental

conditions remaining equal between replicates. One brood of juvenile O. mossambicus (mean mass 60 g) was divided into two groups of 50 siblings and raised in separate 3500 l circular plastic tanks with recirculated and filtered water. One replicate was fed commercial trout feed for three months at 10 % body mass per day to simulate good feeding conditions, and the other replicate fed at a rate of 1 % for one month, and thereafter 0,5 % body mass per day to retain the fish in poor condition. Two males and six females were randomly selected from the growing tanks and placed in 1500 l breeding tanks with a sandy substrate. Water temperature fluctuated between 25 and 31<sup>o</sup> C. The females (each individually tagged with numbered Floy tags) were checked at two-day intervals for eggs in the buccal cavity. These were removed, counted and measured, and the clutch number and mean egg size recorded against the tag number of the parent. The female fish was then returned to the same tank.

## Results

### Mean size at maturation

Whilst none of the four populations investigated showed signs of maturing at an age comparable with that described by Elliot (1955, 3,5 months in brackish water ponds in Hawaii) or at a length as small as that described by Hecht & Zway (1984, 35 mm SL in Matiovila Hot Spring), substantial variations were observed (Tables 28, 29 & 30).

Table 28. Reproductive data for four populations of O. mossambicus from the eastern Cape. (m = males, f = females, n = sample size)

Site	n	Age at maturity (years)	SL at 50% maturity (mean)	Mass at 50% maturity (mean)	Typical clutch size (at SL)	Spawning season (months)	Reproductive lifespan (years)
Rufanes Pool							
(m)	78	1+	110	40	376	5	6 - 7
(f)	94	1+	118	49	(87 - 232)		6 - 7
Bradshaw's Mill Dam							
(m)	120	2+	168	170	1394	5	2 - 3
(f)	87	2+	186	239	(215 - 245)		2 - 3
Kowie Lagoon							
(m)	126	3+ (?)	223	410	2662	4	6 - 7
(f)	97	3+ (?)	212	345	(245 - 275)		6 - 7
Mill Farm Dam							
(m)	41	2+	265	842	3113	3	6 - 7
(f)	27	2 - 3+	263	820	(205 - 350)		6 - 7

Table 29. A comparison of the standard length at onset of maturity between male and female O. mossambicus from the four populations studied (M = males, F = females).

Population	SL at 50 % maturity M/F	Sample size (n) M/F	Significant difference between sexes	(t statistic) (P probability)
Bradshaw's Mill Dam	168/186	20/11	Yes	t = 4,703 P = > 0.001
Kowie Lagoon	223/212	17/22	Yes	t = 2,820 P = > 0,01
Mill Farm Dam	265/263	11/10	No	t = 0,528 P = < 0,20
Rufanes Pool	110/118	10/9	Yes	t = 2,639 P = > 0,02

Female fish with gonads containing ripening ova (stage III-IV) varied from 85 mm to 385 mm SL between habitats. The smallest mature fishes from the Mill Farm Dam population were similar in length to the largest recorded specimens from the Bradshaw's Mill Dam population (Table 28). The Kowie Lagoon population matured at a length greater than the early maturing Rufanes Pool and Bradshaw's Mill Dam populations, and at an age of 3+ years. However, as the sample size from this site was biased in favour of large adults because of catch selectivity, it is likely that the onset of maturity occurs at a smaller size and at 2+ years of age, similar to that of the Bradshaw's Mill Dam population. The Rufanes Pool population contained the smallest mature fish of the four sites, with the onset of maturity taking place at lengths between 90 and 130 mm SL. As this population was not stunted in size, large mature adults of both sexes (270 to 286 mm SL) were also present. The majority of fish from this site matured during the first year of life.

Table 30. The sizes of the smallest sexually mature O. mossambicus observed in the four populations studied in the eastern Cape (Gonad maturity index = > II).

Site	Sex	Standard length (mm)	Mass (g)	Sample size (n)
Rufanes Pool	males	85	26	11
	females	87	25	15
Kowie Lagoon	males	60	7	62
	females	145	117	51
Bradshaw's Mill Dam	males	102	40	47
	females	104	41	25
Mill Farm Dam	males	145	154	30
	females	214	404	20

The Mill Farm Dam and Kowie Lagoon populations matured at a length of over 70 % of the mean maximum for their respective populations (Table 31). This is typical of African cichlids living in large lakes (Iles 1971). The Rufanes Pool population showed clear evidence of early maturity at both a small size and young age (Table 28), and at under 50 % of mean adult length (Table 31).

Differences of mean standard length at maturity between the sexes, and between populations, were tested by means of a Students t test for paired statistics. The results showed a significant difference of length at maturity between males and females ( $P = > 0,02$ ) for each population with the exception of that of Mill Farm Dam (Table 29). Each population was then compared with the other three, and length at maturity (for each sex) was found to be significantly different between populations ( $P = 0,01$ ).

#### Discussion - age at maturity

##### Bradshaw's Mill Dam

The relationship between the gonadal development rate of this population and standard length is almost linear. Sexual maturity of 50 % of the population occurs at a mean length of 175 mm SL. As the growth of males is faster than that of females, sexual development occurs at an earlier age in males. For this population first maturity occurs during the third summer of life when the males are between 20 and 24 months of

Table 31. Standard length at onset of maturity (GMI = 2 II) as a percentage of maximum length for O. mossambicus from the four sampling sites. (standard length in mm.)

Site	SL at 50%	Mean maximum	Sample	SL at maturity
	maturity	SL	size (n)	as % of maximum length.
	Male/female	Male/female	Male/female	Male/female
Rufanes Pool	110 / 118	281 / 250	78 / 94	39,1 / 47,2
Bradshaw's Mill	168 / 186	266 / 246	120 / 87	63,1 / 75,6
Mill Farm	265 / 263	356 / 359	41 / 27	74,4 / 73,3
Kowie Lagoon*	223 / 212	289 / 262	126 / 97	77,2 / 80,9

\* sample biased towards larger specimens due to catch selectivity

age (2+). Females grow more slowly than males and the onset of maturity is delayed until late in the third summer of life at which time they are 22 to 26 months old (2+).

The bulk of this population therefore consists of immature fish, as mortality rates of 3+ and 4+ age fish are high (Table 27), and lifespan is limited to 4 to 5 years. The reproductive lifespan is therefore limited to 2 to 3 years compared to 6 to 7 years for all the other populations studied.

Although the length at maturity is small, the population in this habitat could not be called early maturing when compared to other populations occurring in harsh environments. In Lake Sibaya Bruton & Bolt (1975) reported the size at first maturity to be 100 mm SL for males and 80 mm for females, at an age of two and one years old, respectively. At the onset of maturity the fish were already small for their age, and the change from directing energy from somatic to gonadal development does not appear to be responsible for the poor growth and low maximum individual size of this population. As survival over an age of 4 years was low, the reproductive lifespan was limited to 2 years for females and 3 years for males.

#### Kowie Lagoon and Rufanes Pool

The sexual development of fish from the Kowie Lagoon follows a similar trend to that in Bradshaw's Mill Dam, although maturity occurs slightly later. The Rufanes Pool population is an example of early maturity due to environmental stress,

and has the characteristics typical of an altricial life-history style. "Altricial" is defined as a trend towards earlier maturation, increased fecundity, smaller eggs and shorter life span (Balon 1979 and 1980, and Noakes & Balon 1982). The reproductive lifespan is long, juvenile mortality is high, and the spawning season is extended. Reproductive output is the highest of that at any of the sites sampled as reflected by the catch-per-unit-effort data for juveniles (Fig. 21). Parental investment in the form of nestbuilding was minimal at Rufanes Pool as nests were rudimentary and the smallest in relation to the size of fish.

#### Mill Farm Dam

The onset of maturity took place at a high average mass (700 to 900 g). For males the first reproductive activity occurred during the third summer of life when fish were between 20 and 24 months of age. Females grew more slowly, and first spawning occurred during the latter part of the third summer for faster growing individuals (2+ years old) or during the fourth summer for slower growing individuals (3+ yrs). All sexually mature fish were large and deep-bodied, unlike the other three populations studied, where small adult individuals were common (Table 30). The short spawning season, relatively low fecundity, high parental investment in nestbuilding and guarding, and late maturity, signify that the environmental conditions are "perceived" by the fish to be "stable" or predictable. Their reaction has been to adopt a more precocial lifestyle. A precocial life-style is defined as a

trend towards delayed maturation, reduced fecundity, larger eggs and increased longevity (Balon 1979 and 1980, Noakes & Balon 1982).

#### Fecundity

It is well known that there is a general relationship between body mass and clutch size in cichlids (Fryer & Iles 1972). It was not possible to obtain a good size range of female O. mossambicus with ripe gonads from each of the sampling sites. This made the analysis of the relationship between clutch size and body mass and length difficult. As larger cichlids produce more ova per clutch than small ones, it was not possible to accurately compare fecundity between the different populations. This was due to the small sample size of female fish with ripe gonads, and the large disparity in size between adult females of different populations, especially those from Mill Farm Dam. Mean egg size also increases with body mass. Egg number was plotted against body length and the resulting relationship is illustrated in Figure 47.

Egg number per unit body mass was also calculated and the results shown in Table 32. The wide standard deviations in mass and the small sample sizes must be considered if the populations are to be compared.

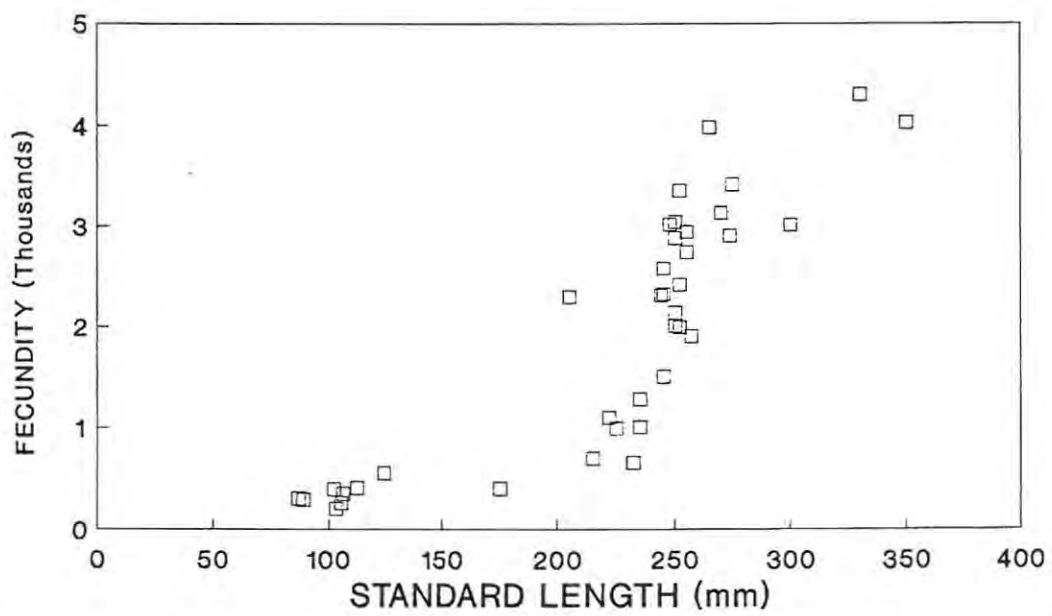


Fig. 47. The relationship between fecundity (brood size) and standard length of *O. mossambicus* in the eastern Cape.

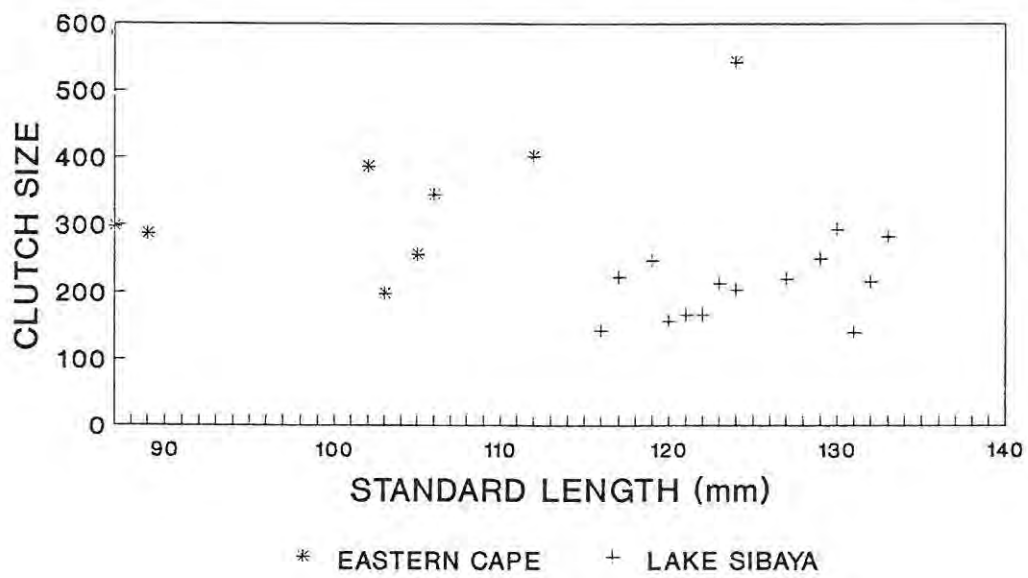


Fig. 48. A comparison between the fecundity (brood size) of small adult *O. mossambicus* in the eastern Cape and Lake Sibaya.

Table 32. The number of eggs per unit body mass in the gonads of O. mossambicus from the four sampling sites in the eastern Cape (SD = one standard deviation)

Site	Sample size	Mean mass (g)	SD	Mean number of eggs per unit mass	SD
Rufanes Pool	10	99,7	125	6,92	3,4
Bradshaw's Mill Dam	8	518	52	2,63	0,9
Kowie Lagoon	11	621	52	4,27	0,69
Mill Farm Dam	9	1055	507	3,32	0,98

Other records of fecundity in this species are given by the following authors, but as these are given in proportion to total length they are not directly comparable (Vaas & Hofstede 1952, De Silva & Chandrasoma 1980, De Silva 1986).

Table 34. Analysis of variance between mean egg size from the four populations of O. mossambicus studied in the eastern Cape. (N/S = no significant difference)

Populations compared	Sample size	t	P
Bradshaw's Mill Dam : Rufanes Pool	18	1,764	0,1
Bradshaw's Mill Dam : Kowie Lagoon	20	0,228	N/S
Bradshaw's Mill Dam : Mill Farm Dam	17	2,401	0,05
Rufanes Pool : Kowie Lagoon	22	1,929	0,1
Rufanes Pool : Mill Farm Dam	19	3,682	0,01
Mill Farm Dam : Kowie Lagoon	21	2,215	0,05

The fecundity of O. mossambicus from the eastern Cape is high in comparison to the Lake Sibaya population (Fig. 48) (Bruton, pers. comm), but similar to the Msinyeni Pan population from the Phongolo floodplain. Egg sizes varied significantly between three of the four populations examined (Table 34). The larger mean egg size of the Mill Farm Dam fish compared with those from the other three populations (Table 33) may be a function of larger body size or more stable environmental conditions than those in the smaller water bodies studied. The Lake Sibaya population (Bruton & Allanson 1974) has a low fecundity and large individual egg size for such small fish. The harsh feeding conditions experienced by adult fish in Lake Sibaya, as reported by Bruton (1979) and Bowen (1976, 1978, 1979) would be expected to give rise to a relatively higher fecundity and smaller egg size than the Mill Farm Dam population where food was abundant.

#### Experimental manipulation of spawning frequency

Experimental results on the effects of environmental harshness (food availability) on fecundity and spawning frequency are summarised in Table 35.

Poor condition, resulting from a "maintenance" ration, appeared to stimulate spawning frequency and increase the number of multiple spawns. Out of a total of six females in each replicate, three "maintenance" diet and two well-fed fish spawned more than four times during the trial period of 133 days.

Table 33. Typical egg lengths from various populations of O. mossambicus. (Egg length is given along the long axis, in mm).

Site	Mean length	Range	Sample size	Reference
Mill Farm Dam	3,48	3,1-3,8	9	This study
Bradshaw's Mill Dam	2,82	2,4-2,9	8	This study
Kowie Lagoon	2,87	2,4-3,2	12	This study
Rufanes Pool	2,41	2,1-2,7	10	This study
n/a		1,9-2,9		Peters (1963)
n/a		2,0-2,2		Vaas & Hofstede (1952)
n/a	3,0			Chako & Krishnamurti (1954)
n/a		1,9-2,6		Fishelson (1966)
n/a	3,0			Aravindan & Padmanabhan (1972)
n/a		2,7-3,0		Trewavas (1983)
Sri Lankan dams		1,8-2,7		De Silva (1986)
Lake Sibaya		3,0-3,5		Bruton (1979)

As expected, at the start of the trial the well-fed fish were significantly heavier in mass than those kept on a maintenance diet ( $t = 2,976$   $P = > 0,02$ ), and consequently egg-number per clutch was greater. The results between the two replicates are directly comparable as all fish were siblings, and the mean length of each was within the standard deviation of the other. Brood size was highly variable (as was spawning frequency per individual) and could have been influenced by behavioural factors in the small artificial habitat. Brood size from the group held under the "maintenance" diet was significantly larger than that from the well-fed group ( $t = 9,235$   $P = > 0,001$ ). No trend towards repetitively small or large broods per individual female was significant, although brood-size per individual fish increased with successive spawns. Egg-size was not significantly different between well-fed and poorly-fed fish ( $t = 0,541$   $P = < 0,20$ ). Therefore the trend was towards more, but similar-sized eggs when food availability was limited.

The results are inconclusive in that only one factor (food availability) was tested, whereas in the natural habitat a combination of factors, stimulated by food availability, is likely to influence reproductive performance. Another influencing factor could be poor feeding by the fish in both replicates during the trial. Bruton & Boltt (1975) report that O. mossambicus involved in reproductive activities feeds little, or not at all, and this was experienced during the 133 days of the experiment. The reduced feeding would have

caused a loss of some definition between the two groups, especially as there was no significant difference in condition factor at the start of the test. The well-fed group did not gain either length or mass, whereas the poorly fed group gained an average 7,17 mm SL and 2,5 g mass, having a nutritional deficit to make up. The lack of growth in the well-fed group indicates that supplementary feeding was not utilised by fish that are in reasonably good condition, but benefits fish in poor condition.

Table 35. The reproductive performance of sibling O. mossambicus under conditions of varied food availability. One standard deviation in brackets.

	"Maintenance" diet	Well fed
Mean SL (mm) of female		
at beginning of experiment	143 (7)	148 (12)
at conclusion of experiment	150 (9)	148 (11)
Variation	+7 (4)	0 (8)
Mean mass (g) of female		
at beginning of experiment	108 (19)	113 (29)
at conclusion of experiment	111 (22)	112 (20)
variation	+3 (5)	-1 (18)
Mean clutch size	410 (336)*	577 (419)*
Mean egg diameter		
long axis	2,72 (0,1)	2,73 (0,12)
short axis	2,00 (0,09)	2,04 (0,05)
No. of spawns	18	15
Mean no. of broods		
per individual female	3	3
Maximum no. of broods		
per individual female	5	5
Multiple spawnings (4 or more)	3	2
Total egg production	8 894*	10 991*
Length of trial (days)	133	133
(25/10/1988 - 7/3/1989)		

\* In a few cases, where the number of eggs mouthbrooded was very low, indicating infertility or loss, the total was not included in the calculation of mean clutch size.

The culture conditions can be contrasted to the less harsh and more predictable conditions with which the fish have evolved in their natural environment. In both replicates the response was to turn to a distinctly altricial reproductive lifestyle, with high fecundity, high spawning frequency (a mean of three, and maximum of five broods during 133 days), and poor or nil growth during the trial.

#### Spawning season and frequency

Table 28 indicates the length of the breeding season for the various populations based on regular observations of nesting, territorial behaviour by males, mouthbrooding by females and the presence of free-swimming fry. Under natural conditions the spawning season in the eastern Cape varies from 3 to 5 months between habitats, and usually commences in late November or when minimum water temperatures exceed 18° C.

Natural spawning frequency has been described for Lake Sibaya by Bruton & Bolt (1975), who found that the brooding period lasts 20 to 22 days, and by Lombard (1959, "2 to 3 weeks"). Vaas & Hofstede (1952) and Bohrer (1953) suggest that the spawning interval may be as frequent as every 30 to 40 days under aquarium conditions. Bruton & Bolt (1975) record a 36 day interval for Lake Sibaya, and Crass (1964) a 6 to 7 week interval.

Results from O. mossambicus from the eastern Cape which were spawned under artificial conditions (ponds) indicate that up

to five broods per female may be spawned during a 133 day period. This suggests that adult females may mouthbrood almost continuously over this period, although under experimental conditions the eggs were removed from the mouth 1 to 2 days after spawning. Removal of eggs from mouthbrooding cichlids is known to stimulate spawning (Impson 1988). Assuming that the incubation cycle lasts approximately 10 to 12 days (Baerends & Baerends-van Roon 1950, Hickling 1950) and parental care of the fry a further 10 days, and allowing a week between each cycle (Bruton 1973), then between three and five broods may be produced each breeding season in various habitats in the eastern Cape.

#### Nest building

Colonies of nest-guarding males fitted the pattern described by Fryer & Iles (1972) and Bruton & Bolt (1975). However, unlike Lake Sibaya where the chosen substrate for nest construction was open sand, in the eastern Cape O. mossambicus preferred to build nests amongst Potamogeton pectinatus and avoided open water substrates (Fig. 26 & 27). At Mill Farm Dam, where P. pectinatus growth is dense, males were observed to uproot the plants in order to excavate circular depressions in the dense vegetation. Nests at this site varied in diameter from 30 to 75 cm and were located at depths from 50 to 75 cm only (Table 36). Only at Kowie Lagoon were nests seen at depths as great as 100 cm. This is in contrast to other reports, where nests were observed at depths as great as 6 m

Table 36. The diameter and depth of O.mossambicus nests from populations within the study area, and Lake Sibaya (Bruton 1979). (n = nest sample size, est. = estimated diameter, - = data not available)

Site	Nest diameter (cm)	Water depth (cm)	Length of male (mm SL)	Mass of male (g)
Rufanes Pool (n = 5)	30 - 50 (est.)	30 - 50	112 - 295	68 - 950
Bradshaw's Mill Dam (n = 8)	25 - 45	30 - 50	164 - 280	165 - 738
Kowie Lagoon (n = 14)	40 - 90	40 - 100	223 - 300	410 - 1068
Mill Farm Dam (n = 34)	50 - 75	50 - 75	257 - 385	708 - 2464
Lake Sibaya (n = -)	20 - 185	41 - 850	mean 170	-

(Bruton 1973). The nests constructed at Mill Farm Dam were the most carefully built and maintained, being symmetrical with a smooth clean base following the removal of a "column" of P. pectinatus from the nest base to the water surface, i.e. macrophytic vegetation did not overhang the nests (Fig. 26). At Bradshaw's Mill Dam nests were simple excavations made in very shallow water (30 to 50 cm) and were often cluttered with Typha capensis stems and other detritus. Many nests from this lake were not symmetrical, and were not clearly defined. At Rufanes Pool, turbidity hindered the observation of nests, although simple dish-shaped excavations could be felt by wading in the shallows.

At Mill Farm Dam, nests were grouped together at distances from 2 to 12 m apart over a shoreline length of 30 to 50 m. During two years of visual observations, only two such "arenas" were noted, while isolated nests were scattered at intervals around the littoral, always in association with P. pectinatus growth (Fig. 18). As this plant growth was often very thick around the nests, and formed beds extending up to 80 m without open water, it is not known how adult O. mossambicus males find females in breeding condition. Most females were caught or observed to be in relatively deep water (2 to 3 m) along the edge of Potamogeton banks, and were generally only found amongst macrophytes whilst mouthbrooding. Diving in the vegetation indicated that the nests were surrounded by a "wall" of plants that obscured all possibility of visual sightings of females from the nest area. The high

density of juveniles in the highly turbid Rufanes Pool also suggests that poor visibility does not hinder reproductive success. This contrasts with the situation reported by Bruton & Boltt (1975) in Lake Sibaya where O. mossambicus females cruising within sight of the male nesting territories were attracted to the nests by the males' breeding displays.

#### Reproduction - general discussion

O. mossambicus is capable of maturing at three and a half months of age under adverse or aquarium conditions (Elliot 1955). Early maturity at a small size is not always a result of small habitat size, although small water bodies such as pools or isolated hot springs are likely to suffer wider ranging physico/chemical variations than large lakes, with resultant stress if these conditions approach the tolerance limits of the species. In investigating the thermally stressed population in the Matiovila Hot Springs, Hecht & Zway (1984) noted that the largest fish collected was a male of 105 mm SL, and the smallest female with ripe ovaries was 35 mm SL at an age of one year. This is small for a natural population of this species and is indicative of a dwarf population. From the nearby Luphephe Nwanedi reservoir, an environment more favourable for growth, sexual maturity was attained at an average length of 140 mm and 2+ years of age. Under some conditions this species can delay first breeding until the summer of the third year of life (2+ age group) at which time the fish have attained a larger mass if feeding conditions are

good (Balon & Coche 1974). The abiotically harsh environment of Lake Sibaya has led to an early maturing and precocious breeding population (Bruton & Boltt 1975). This population consists largely of small adult fish in poor condition which are denied use of the food-abundant terraces due to the shallow depth and threat of predation.

In some habitats lack of space for nestbuilding may limit spawning success to larger and more aggressive individuals, and smaller males may be unsuccessful in establishing territories and repulsed into deeper water (as reported by Bruton & Boltt 1975 in Lake Sibaya). This would be particularly true of small water bodies, or littoral zones where the gradient is so steep that suitable depths for reproductive behaviour (nestbuilding) are limited.

The characteristics typical of altricial life styles, as described for tilapias by Noakes & Balon (1982), would be expected to occur in unstable or harsh habitats. These are taken to be habitats which undergo unpredictable and near cataclysmic physico-chemical changes, or cyclical fluctuations such as flooding, which are interrupted, for example, by Man's regulation of river-flow. "Stability" is not taken to mean a lack of fluctuations in the physical environment, e.g. in water level. Tilapias have evolved under riverine conditions (Fryer & Iles 1972, Greenwood 1974) and have adapted to fluctuating water levels and flooding at certain times of the year. If lacustrine habitats fluctuate in a cyclical pattern,

tilapias may retain the ability acquired by their riverine ancestors to successfully utilise these habitats. In the case of Lake Sibaya, which is abiotically harsh for tilapias, Bruton & Boltt (1975) suggested that the retention of these adaptive characteristics has meant that the colonisation of a shallow lake with a fluctuating littoral has been within their capabilities. In other natural populations, reproduction tends to be seasonal and closely tied to seasonal fluctuations in temperature and water level (Lowe-McConnell 1975), although lacustrine tilapias may breed irrespective of flooding in tropical waters (Lowe-McConnell 1982, Stallard et al. 1986).

Growth may be adversely affected by the onset of maturity if reproductive behaviour consumes most of the energy available to the fish from the food that is ingested. This may be the case in Bradshaw's Mill Dam where growth rates decrease sharply after the onset of sexual maturity. In a similar way, the Lake Sibaya population of *O. mossambicus* examined by Bruton (1973) and Bowen (1982) suffered from extreme adult malnutrition due to poor quality food in the preferred habitat of adults. This resulted in a rapid decline in growth rate after maturity, poor body condition, and a switch to an altricial life style, with the onset of maturity at 43 % of maximum length. This compares remarkably well with the Rufanes Pool population which matures at 39,8 to 47,2 % of the maximum standard length of adults (Table 31). Although Rufanes Pool is shallow and rich in food for the fish, abiotic factors such as low temperature, high turbidity, fluctuating water level and

very small habitat size make this a harsh environment for the tilapias, which have adopted a more altricial suite of life-history characteristics. The bulk of the population is short lived with only a small proportion attaining more than 3+ years of age. Mean clutch size is relatively large, egg size is only 69 % of that of the more precocial Mill Farm Dam population, parental investment in nestbuilding is small, and the spawning season is extended.

The variations in egg size between the four populations are clear indicators of the effects of environmental harshness on the reproductive output of tilapias. In the Mill Farm Dam population, somatic growth after maturity is not reduced to the extent of the other populations, because of the favourable feeding conditions which prevail throughout most of the lake basin for adults and juveniles alike. This enables the fish to rapidly attain a large body mass which directly influences fecundity (larger gonads with more gametes and therefore a larger clutch size) and individual egg-size, as suggested by Lowe-McConnell (1982). It is also significant that both the growth rates and maximum mass attained by males and females are less distinct between the sexes than at any of the other three sites.

The depth at which O. mossambicus builds nests may be dependent on substratum material, slope, turbidity and the bathymetry of the lake. The depths recorded during this study are similar to those observed in Sri Lankan reservoirs by De

Silva (1983, 1985a) but generally shallower than those recorded by Bruton & Boltt (1975) and Bruton (1979). Nest dimensions are roughly proportional to the size of the male, although this could not be tested statistically. It is interesting to note that the nests constructed by male O. mossambicus of 1500 to 2000 g in Mill Farm Dam were generally smaller than those made by the largest males (300 to 400 g) from Lake Sibaya, which measured up to 185 cm in diameter (Bruton 1979). The continual extension and re-modelling of nests by precociously breeding males in some waters was possibly hindered in Mill Farm Dam by the thick plant growth, which must also reduce visual interaction between males, and between males and females. The largest nests in Lake Sibaya were on extensive sandy terraces (Bruton 1979). In contrast to the findings of Bruton (1979) and De Silva & Chandrasoma (1980), nest size at Mill Farm Dam was independent of water depth. This may have been due to the lack of small breeding males as all breeding adults were large and deep-bodied, and suitable nesting substrates were freely available.

Spawning frequency may be influenced by the prevailing physico-chemical environmental conditions, irrespective of body condition of the fish at the time. O. mossambicus have been shown to spawn readily whether in good or poor condition. Bruton (1973) indicated that the poorly nourished adults in Lake Sibaya may spawn as often as four or five times, or at least two broods per season (Minshull 1967). Spawning frequency was related to rising or declining lake level, which

could either enhance or hinder spawning success. De Silva (1985a), working on a 2662 ha lake in Sri Lanka, suggested that fluctuations in lake level could influence reproductive output to such an extent that the standing stock as exploited by a commercial fishery could be affected three years later. It is generally accepted that large stable lakes and rivers which undergo predictable cycles are less suitable for repetitive spawning than environmentally harsh, fluctuating habitats like small dams and pools.

The hypothesis that fecundity should increase with increasing environmental harshness could not be fully tested in this study by examination of wild populations due to the wide variations in adult fish length and mass between populations, and small sample sizes. If the number of broods per spawning season is taken as an indicator of annual fecundity, then the Rufanes Pool and Bradshaw's Mill Dam populations are more fecund due to the large total number of eggs spawned by individual females per year. One female fish from the latter population may raise four to five broods of a mean size of 1394 per season, 5575 to 6970 eggs in total. The larger females from Mill Farm Dam, may brood more eggs per clutch (a mean of 3113), but spawn once or twice only per season, totalling 3113 to 6226 eggs annually. The total population fecundity however is higher at Bradshaw's Mill Dam due to the earlier maturity and the greater density of adult fish. If the clutch size of females from Bradshaws Mill is regressed against standard length ( $r = 0.68$ ,  $n = 8$ ), and extrapolated to

the mean length of Mill Farm Dam females, then the former is the more fecund.

In summary, the Mill Farm Dam population has the precocial reproductive traits expected from large, stable lakes or rivers, whereas the other three populations generally follow an increasingly altricial reproductive life style due to the "harshness" in their size- or food-restricted habitats. The reproductive characteristics of the different populations conform to the predicted reactions to harsh or benign environmental conditions which formed the hypothesis for this study.

## GENERAL DISCUSSION

The populations of O. mossambicus examined during the course of this study displayed a wide variety of life-history characteristics. It was not part of this study to examine the early life-history stages, and observations were limited to juveniles and adults only, subsequent to the formation of the definitive phenotype. Studies of the early life-history of O. mossambicus are required to establish the epigenetic effects of varying egg size and yolk quality. Experimental manipulation of the phenotype by varying food quality, sibling density and parental condition may have a significant effect on epigenetic events such as age at first maturity which could be of benefit to aquaculture as suggested by Noakes & Balon (1982).

Much of the literature which examines the varying life-history forms of tilapias concentrates on the intergeneric and interspecific rather than the intraspecific variability. For example, Lowe-McConnell (1982) compares the relative colonising success of T. zillii (a guarder) with O. leucostictus (a bearer) in dams in Uganda. However, there are a number of studies examining distinct populations of O. mossambicus which can be used for comparison (Le Roux 1961, Bruton 1973, 1979, Bruton & Allanson 1974 Bruton & Boltt 1975, Hodgkiss & Man 1977a & b, 1978, Hecht & Zway 1984, Cochrane 1984, 1985, 1986, De Silva 1985 a & b, 1986, De Moor et al 1986). The widely varying phenotypes of O. mossambicus described in these diverse populations often reflect similar

responses to the same environmental cues (e.g. food availability and depth), as found in the eastern Cape.

The availability of abundant, good quality food in the form of diatom-rich detritus and its associated periphyton (as described by Ruttner 1966 and Bowen 1976) would appear to be the key factor in determining the life-history path followed by *O. mossambicus* during its life span. In very small habitats such as isolated hot springs (Hecht & Zway 1984) and riverine pools (Rufanes Pool, this study) space may become more influential on the life-history style than food availability. The results from the Rufanes Pool population suggest that abundant food in the form of diatoms, bacteria and periphyton may stimulate growth and longevity, but this is tempered by physico-chemical factors such as habitat size, low temperature and water level fluctuations. A few adults may achieve a large mass and long life, but the population as a whole remains distinctly altricial in its characteristics (high juvenile mortality, early maturity, high reproductive output, short lifespan).

Mill Farm Dam supports a population with predominantly precocial characteristics, compared to the altricial life style expressed in Bradshaw's Mill Dam and Rufanes Pool. This is almost certainly due to the favourable ecological conditions for good growth therein: benthic samples of detritus were rich in diatoms compared to those from Bradshaw's Mill Dam; the entire lake area is accessible to the

fish for feeding, reproduction or refuge; and water temperatures are more homothermal than at other sites. As a result the fish are fast growing during both the juvenile and adult phases, and longevity is high. Sexual maturity is delayed, and first spawning takes place at a high individual mass. Spawning frequency is low. This is in spite of apparently "harsh" environmental conditions such as low winter temperatures, and non-cyclical water level fluctuations. These may be accommodated without stress by the physiological tolerances of the fish, due to their adaption in the ancestral form to fluctuating riverine conditions (Fryer & Iles 1972, Liem 1973, and Greenwood 1974). As in Lake Sibaya, the colonisation of a shallow lake with fluctuating level, and therefore "renewed" littoral zone, has been suggested to be a preferred habitat of O. mossambicus (Bruton 1973). In a physical sense the lake at Mill Farm resembles an occasionally inundated floodplain lake, and differs from Lake Sibaya in its high nutrient input and shallow depth.

Tilapias are still-water fish, and typically thrive in floodplain lakes with seasonal climatic regimes and fluctuating water levels (Lowe McConnell 1982). The hot season may not coincide with the time of rising water, but tilapias have evolved breeding strategies independant of flooding. In some systems tilapias experience rising water levels during autumn (the middle and lower Zambesi) (Balon & Coche 1974) and in others during winter (the southern Okavango swamp) (Fox 1976), but remain temperature-dependant spawners. The fish use

the time of rising waters to feed extensively to build up fat reserves, as reproduction takes place largely at the expense of somatic growth. In the eastern Cape, the rapid growth of the young-of-the-year in Mill Farm Dam (which takes place mainly during the cooler months of autumn and early winter), and the spring peak in condition factor, demonstrate the same trend even at the limit of this species' natural range where winter temperatures may be close to lethal. Lowe-McConnell (1958) makes two points that are relevant to growth under conditions of stress:

1. Tilapia living under favourable conditions show little variation in growth rate and final size between the sexes, whereas growth of male tilapia exceeds that of females under harsh conditions.

2. Fish in poor condition (low weight for length) matured at a much smaller size than those in good condition.

Both these factors are clearly demonstrated by the results of this study.

The population from Bradshaw's Mill Dam shares many of the life-history characteristics with the Lake Sibaya population studied by Bruton & Boltt (1975) and Bowen (1976). In this habitat various factors contribute to food quality being limited to adult fish, which as a consequence mature early and grow very little thereafter. The steep underwater profile of the lake, low winter temperatures, the dominance of the

shallows by reeds, and the non-cyclical variations in the physico-chemical conditions would suggest that this is a "harsh" environment for O. mossambicus. As a result the adoption of an altricial life style is to be expected.

The concept of "stable" or favourable environmental conditions resulting in a different suite of life-history characteristics to those under a harsh environment has been well examined for a wide variety of animals, including birds and insects (Bruton 1989). Most animal species have evolved to fill one or the other habitat type, i.e. altricial species are adapted to capricious environments, and precocial species to equable environments. Most species have a degree of phenotypic flexibility, but few can match O. mossambicus for the diversity of habitats it can successfully colonise, and the range of phenotypes expressed. Freshwater lakes, rivers and swamps, brackish estuaries and coastal lagoons, coral atolls and hypersaline desert pools and thermal springs have all been shown to support populations of this species. One indication of the phenotypic plasticity of O. mossambicus is the extent to which it has been successfully translocated to many parts of the world (Courtenay & Stauffer 1984). O. mossambicus has the ability to express some characteristics typical of "K"-selected species under favourable conditions, and yet retains the potential to adopt a more "r"-selected life style should it be exposed to environmental perturbations. Thus the fish has two options: either to display the precocial characteristics with a high investment in each individual

young, or to move towards the altricial mode where nest-building is rudimentary, ova may be smaller although more numerous, and parental care reduced. Whilst parental care in Oreochromis does not (and can not) decline to the extent of purely nest-guarding as in the genus Tilapia, the degree of investment per individual young can be very flexible depending on environmental conditions. This is well described by Lowe-McConnell (1982) for the closely related Oreochromis shiranus chilwae from Lake Chilwa (Malawi) where, due to harsh abiotic conditions, the subspecies is smaller, matures earlier, is more fecund and has an extended breeding season compared to O. shiranus in the stable habitat of Lake Malawi. These characteristics are flexible and may be reversed to some extent during periods when the abiotic conditions in Lake Chilwa are more favourable (Lowe-McConnell 1982).

Phenotypic flexibility extends to the catholic feeding habits of O. mossambicus. During this study the fish were found to feed almost exclusively on benthic detritus, which is similar to the diet Lake Sibaya (Bowen 1979, 1981, 1982) and in various Sri Lankan reservoirs (De Silva 1985a & b). Other workers have found O. mossambicus to have a herbivorous diet, specifically higher plants (Minshull 1969), or feed on a mixture of zooplankton and benthic invertebrates (Le Roux 1956, Le Mare cited in Hickling 1970, De Moor et al. 1986) or an opportunistic diet which may include detrital floc, macrophytes, small fish, periphyton and terrestrial insects (Bruton 1973). The limitation of the eastern Cape tilapia

populations to feeding solely on benthic floc and diatoms does not imply that the available food is of poor quality. The nutritional adequacy of detrital material has been well documented and discussed by Bowen (1979), Pullin (1982), Edwards et al. (1983) and De Silva (1985b). The nutritional limitations experienced by adult O. mossambicus feeding in Lake Sibaya were an indirect result of water depth, which restricted larger fish to deeper water, where their food was mixed with large quantities of indigestible matter. The warm and shallower waters of the terrace areas provided an abundant supply of this food, and were the preferred habitat of the more eurythermal juveniles which were as a consequence in good condition. Bowen (1976) argues that the relationship between food quality and depth that was found in Lake Sibaya is likely to be found in other aquatic ecosystems. Bright sunlight and high temperatures in the shallows and a high nutrient status of the water stimulates the production of diatoms and other organisms utilised by tilapia as food. For this reason the water bodies studied in the eastern Cape should depend less on depth for their food abundance as they are all shallow, and more on temperature gradients, water exchange time, turbidity and the nutrient input. The high habitat preferability index of Mill Farm Dam indicates that all these factors contribute to this being a nutritionally favourable environment for tilapia, similar to the floodplain pans of the Phongolo River where O. mossambicus is equally abundant and fast growing (Bruton 1979). In comparison, the

steeply profiled Bradshaw's Mill Dam environment, with its limited shallow areas and low nutrient status, is best exploited by large numbers of small O. mossambicus which can use the warm but limited shallow areas effectively.

The aspect of cold tolerance needs some comment. Some experimental work on the degree and duration of cold tolerance of O. mossambicus was carried out by Allanson et al (1962), and Allanson & Cross (1970), and field observations were made by Bruton & Taylor (1979) and Blaber & Whitfield (1976) after significant fish kills. Bruton (1973) argues that tolerances in the field can be expected to be narrower than under experimental conditions, and quotes Odum (1971) who suggested that "accessory factor interaction" and the metabolic cost of physiological regulation at extreme conditions may reduce the tolerance limits. Research by Allanson et al (1962) showed that the median lethal temperature for O. mossambicus under experimental conditions was 9,9° C. Under natural conditions in the eastern Cape, it has been shown that even during mild winters, such as experienced during the course of this study, temperatures as low as 9,9° C do occur. As Allanson et al (1962) used juvenile-sized fish for their experiments, and considering that juveniles have higher temperature preferenda than adults, it seems likely that mortalities of juveniles do take place during winter due to cold. However a degree of cold tolerance in adult O. mossambicus from this area seems to be the case, compared to other populations. Bruton & Taylor (1979) describe the mortality of numerous adult O. mossambicus

in the freshwater Lake Bangazi-South (Natal) after five days of water temperatures below 13<sup>o</sup> C, during which time a minimum of 10<sup>o</sup> C was recorded. Temperatures of this order occur regularly in the eastern Cape, and tilapia are likely to have acclimated to these lower temperatures. However, temperature tolerance is generally regarded as the physiological factor controlling the distribution and survival of O. mossambicus in South Africa and most particularly at the range limits (Jubb 1967). Whilst this species may flourish at low altitudes in the eastern Cape, it will not sustain a population in the Grahamstown area, 50 km from the coast at an altitude of about 500 m (pers. obs.). Minimum winter water temperatures in Grahamstown are usually only one to two degrees colder than at Bradshaw's Mill Dam, indicating that even in coastal areas the margin for survival is small.

The growth rate of O. mossambicus under artificial conditions has been experimentally recorded by numerous aquaculture trials. There are only a few detailed records from natural populations which can serve as a comparison to the growth rates from this study (Le Roux 1961, Bruton & Bolt 1975, Hodgkiss & Man 1977a). It is clear that the growth rates observed in the Mill Farm Dam population are very high by even the standards of sub-tropical populations, whereas those in Bradshaw's Mill Dam are more typical of "dwarf" populations such as described by Fryer & Iles (1972), Lowe-McConnell (1982) and Hecht & Zway (1984). The Mill Farm Dam population could be an example of Geist's (1989) "luxury" or "dispersal"

phenotype, living in an especially favourable environment of food abundance. However, this is negated by the reproductive and growth data reported earlier in this study, as fecundity, age at maturity and longevity were contrary to that of the "dispersal phenotype". If the Mill Farm Dam is an example of a "stable benign environment" (Holm 1989), which seems to be the case as evidenced by the growth and longevity of the fish, then the low population density (shown by CPUE) is anomalous. Holm (1989) argues that when a stable benign environment is biologically saturated, it presents the ideal K-selective situation. This population has adopted K-selected characteristics, at the same time retaining a low population density. I have attributed this low density to periodic desiccation of the lake: the 1985 drought reduced the lake to only 15 % of its maximum surface area, and population size declined accordingly. What is surprising is the relatively poor recruitment rate during the summer of 1985/86 when water level was high and breeding conditions apparently ideal.

The rate at which a species can change its life-history pattern (heterochrony) to suit environmental changes towards more predictable or less predictable conditions, is rapid. Certainly some aspects of the phenotype can change within one generation, for example the offspring of deep-bodied and late maturing tilapia if raised under aquarium conditions will mature at a small fraction of the size of that of their parental stock, even if well fed. Thus it was expected that the drought conditions that prevailed in the study area during

1988/1989 would have a marked effect on the life-history characteristics of fish populations such as those in Mill Farm Dam. However the phenotypic characteristics of a population may not be immediately altered as a response to severe environmental change. Vogt (quoted in Geist 1989) found that the phenotype of deer changed progressively over four generations under improved nutritional conditions. This "maternal effect" (Denenberg *et al.* 1962, Denenberg & Rosenberg 1967, Beach *et al.* 1982) is important in terms of the capability of populations (e.g. in Mill Farm Dam) to resist cataclysmic environmental events such as desiccation, which may be short-lived. This population was briefly sampled during April 1989 when the water surface area had decreased to 23 % of full capacity (Fig. 12). Whilst adult *O. mossambicus* had retained their deep-bodied and robust appearance, the shallows were found to have high densities of juvenile tilapia of numerous length groups, which had never been recorded when water levels were high. Despite the continually dropping water level which caused the drying out of tilapia nests, reproductive activity appears to have been stimulated by the deteriorating conditions, whereas during the high water phase in the summer of 1985/86 reproductive output was low. Holm (1989) describes such environments, which are characterised by alternating patterns of benign and adverse conditions as "discontinuous benign environments", wherein biotic saturation is interrupted by mass mortality during the adverse periods. Further investigation into the effects of continued

desiccation at this site could shed light on other aspects of the life-history of the fishes, and the ability of this phenotypically flexible animal to adapt its life-history to the prevailing environment.

For a species living at the climatic extremity of its natural range, the occurrence of altricial life-history characteristics would be expected to predominate. That O. mossambicus manages to display precocial characteristics in an adverse environment suggests that this species could be better described as being A-selected along the lines described by Greenslade (1983). Species that are "adversity selected" retain the ability to shuttle between and combine the characteristics of r- and K-selected strategies, depending on prevailing environmental parameters. It is these species which are truly phenotypically plastic. Whilst O. mossambicus does not have the ability to adjust its life-history style to withstand environmental adversity to the same extent as genera such as Nothobranchius, Ctenopoma and Protopterus, there are reports of it surviving drought by burying itself in the sand of dry river beds until conditions improve (Donnelly 1978 quoted in Trewavas 1983). This species is known to be one of the last to succumb to desiccation of pans on the Phongolo floodplain (Zululand) and one of the first to re-colonise pans after re-filling (White et al. 1984). It is one of the most eurytopic of fishes, and probably one of the most phenotypically plastic and physiologically tolerant vertebrates in the animal kingdom.

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