THE DEMOGRAPHY, BREEDING BIOLOGY AND MANAGEMENT OF TWO MULLET SPECIES (PISCES : MUGILIDAE) IN THE EASTERN CAPE, SOUTH AFRICA.

Dissertation

Submitted in Partial Fulfilment of the
Requirements for the Degree of

DOCTOR OF PHILOSOPHY

of Rhodes University

by

ANTON BOK

November 1983

ERRATA

p. 14. para. 3, line 3 : for '*faciformis*' read '*falciformis*'.

p. 16, Table 2, Site C : for '98,2' read '98,3'.

p. 27, para. 1, line 2 : for 'river' read 'rivers'.

p. 32, Table 7: for 'Ca co_3' read 'Ca CO_3'.

p. 33, line 7: for '*Eichlornia*' read '*Eichhornia*'.

p. 41, Table 13: insert '(‰)' after salinity.

p. 42, Table 14: for 'secchi disc (om)' read 'secchi disc (cm)'.

p. 56, last line : for 'trophical' read 'tropical'.

p. 56, para. 3, line 4 : for 'turbulance' read 'turbulence'.

p. 82, para. 3, line 8: insert 'the' before 'von Bertalanffy'.

p. 141, para. 2, line 4: for 'that' read 'than'.

p. 157, para. 1, line 7: for 'Kesikamma' read 'Keiskamma'.

p. 172, last line: for 'egg' read 'eggs'.

p. 173, second line: for 'preadapted' read 'pre-adapted'.

p. 175, para. 2, line 5, for 'vittelogenic' read 'vitellogenic'.

p. 177, line 4: for 'our' read 'out'.

p. 203. Table 65: for 'MAR' read 'MAR (mean annual run-off)'.

p. 210, line 5: for '(1983b)' read '((Marais 1983b)'.

p. 221. para. 2, line 4: for 'this' read 'the'.

p. 229. Table 69: for 'Chuluminae' read 'Chulumna'.

p. 230, Table 69: for 'Kariga' read 'Kariega'.

p. 231, para. 4, line 5: for 'is' read 'in'.

p. 257. line 21: for 'Wooten' read 'Wootten'.

FRONTISPIECE

The freshwater mullet, *Myxus capensis*, endemic to the south and south-east coast of southern Africa

TABLE OF CONTENTS

ACKNOWLEDGEMENTS

Many people assisted in various ways during the course of this study and their help is gratefully acknowledged.

I wish to thank P.B.N. Jackson who initiated this study and assisted throughout in many ways, R. Winterbottom and M.N. Bruton for supervision and particularly T. Hecht and M.N. Bruton for critically reading the drafts and offering useful advice during the final stages of this thesis. I am also grateful to the following: T. Tómasson for useful discussions and advice, P. Skelton for information on mullet distribution and useful discussions, I. Gaigher for constructive advice, R. Stobbs for help in the field and preparing the scale photographs, R. Cross for the electron micrographs and M. Davies and P. Coetzee for help in the field. The Director of the J.L.B. Institute of Ichthyology is thanked for the use of equipment during various stages of this study.

This study was completed under the auspices of the Director of the Cape Department of Nature and Environmental Conservation, and the material support of this Department is gratefully acknowledged.

I also wish to thank the many staff members of the Cape Department of Nature and Environmental Conservation who assisted in the many long hours of field work under often extreme climatic conditions, in particular W. Monakali, B. Mitani, M. King, A. Fogarty, H. van Schoor, K. Reynolds and T. Kate.

Thanks are due to the many riparian farmers, too numerous to name individually, who granted permission to work on their land and for their hospitality and assistance.

The support and encouragement from my parents, even before this study was initiated, are greatly appreciated.

Special thanks are due to my wife, Jill, whose support has made this thesis possible. She acted as field assistant, typed all the drafts, prepared some of the figures and gave unselfish and enthusiatic support during all stages of this study. This thesis belongs to her too and is dedicated to Steven and Nina.

ABSTRACT

Aspects of the life history of *Myxus capensis* which were likely to be most affected by man-induced habitat changes, were studied in the eastern Cape. *Myxus capensis* was found to be specialized for a catadromous life history. The fry migrate into freshwater reaches of rivers within a few months of being spawned at sea and return to an estuarine or marine environment when maximum size has been attained and large energy reserves necessary for spawning have been accumulated. *Myxus capensis* penetrates considerable distances up eastern Cape rivers and although present in the upper reaches of some estuaries, is only common in freshwater-dominated systems.

Myxus capensis has adapted its life history style in a number of ways to overcome the constraints associated with the spatial separation of the freshwater feeding areas and the marine spawning grounds in a region prone to droughts and erratic river flow. Research on the more estuarine-dependent *Mugil cephalus*, which is also found in the freshwater reaches of eastern Cape rivers, enabled useful comparisons to be drawn. As the latter species is not dependent on a freshwater phase in its life cycle, it is subject to different selection pressures. This comparative approach gave insights into the adaptive significance of the life history tactics of *Myxus capensis*.

Myxus capensis displays a number of life history tactics characteristic of migratory fish species which are thought to increase population fecundity by increasing the number of large females and hence maximizing egg production. These include a sex ratio in favour of females, faster female growth, females remaining longer in the freshwater feeding areas and reaching a larger ultimate size.

Possible adaptations to the periodic isolation of the feeding and spawning areas include: (i) the development of ripe gonads only in estuarine or marine areas when access to the spawning grounds is ensured; (ii) year-round spawning and hence recruitment which enables the erratic floods to be used at any time for downriver spawning migrations and reduces the chances of total recruitment failure due to short-term adverse environmental conditions and (iii) a relatively wide range of size and age at first (and final) sexual maturity (2+ to 5+ years); this tends to ensure successful reproduction and recruitment in spite of a series of poor years, as well as dampen population fluctuations after long periods of isolation in fresh water.

The dependence of *Myxus capensis* on the freshwater reaches of eastern Cape rivers makes this species vulnerable to man-induced habitat changes. The erection of barriers to migration has cut off large stretches of suitable habitat and almost completely eliminated *Myxus capensis* from certain rivers. This detrimental effect has been largely responsible for the recent inclusion of this species on the *Red Data* list of endangered fish species in South Africa.

This study demonstrated the considerable fisheries potential of both mullet species and this should ensure that their conservation and wise utilization be given high priority. Management proposals include: (i) the netting and lifting of *Myxus capensis* over barriers to migration; (ii) the construction of fish ladders when feasible and (iii) the artificial propagation of this species to enable large-scale stockings of existing man-made impoundments as well as natural habitats to be carried out. It is predicted that the life history characteristics of *Myxus capensis*, which evolved in response to an erratic freshwater environment, should ensure that when man-induced habitat changes are rectified, this species will again flourish in eastern Cape rivers.

CHAPTER 1. INTRODUCTION

The Mugilidae have a worldwide distribution and often form a major component of the ichthyofauna of inshore and estuarine habitats in many parts of the world (Thomson 1966; Oren 1975) including southern Africa (Smith 1949). Being large consumers of detritus and benthic micro-organisms, mullet fulfil an important role in the flow of energy through the ecosystems they inhabit and are consumed by a wide variety of top predators (Odum 1970; Blaber 1980; Whitfield 1980c).

Mullet also have considerable economic importance and exploitation of wild populations forms the basis of fisheries in several countries (Thomson 1966). In South Africa, the relatively small mullet fishery with an annual catch of 1 500 - 2 000 metric tons (mainly *Liza richardsoni*), is largely confined to inshore marine areas west of Cape Agulhas (de Villiers 1976). As mullet are low on the food chain and are efficient secondary producers of protein, they also have considerable potential for aquaculture (Oren 1975). In order to both optimize the management and exploitation of wild populations and improve existing culture methods, considerable research has recently been undertaken on this important family of fishes in many countries. There is consequently an extensive literature on the Mugilidae, particularly on the most widespread species, *Mugil cephalus* (see e.g. Thomson 1966; Pillay 1972; Oren 1981).

Numerous research programmes on the Mugilidae have been undertaken in the eastern Cape (Masson & Marais 1975; Marais 1976, 1980, 1981, 1982, 1983a & b; van der Horst 1976; Marais & Erasmus 1977; van der Horst & Erasmus 1978, 1981; Marais & Baird 1980; Lasiak 1983) and in Natal in South Africa (Wallace 1975a & b; Wallace & van der Elst 1975; Blaber 1976, 1977; Blaber & Whitfield 1977; Whitfield & Blaber 1978a & b, 1979; Whitfield 1980a & b). All the above investigations were confined to inshore or estuarine mullet populations, although two of the 14 mullet species found in southern Africa are known to enter fresh water (Thomson 1966).

Myxus capensis (appropriately called the "freshwater mullet") is endemic to the south and south-east coast of South Africa (Smith 1949) and is found in the freshwater reaches of coastal rivers throughout its range (Crass 1964; Jubb 1967) (Fig. 1). In the past it was considered to be common in the eastern Cape and Smith (1937) stated that this species:

> "Occurs in most of the freshwaters of the coastal region of the eastern Cape, plentiful not far from Grahamstown".

Information on the presence of *Mugil cephalus* in fresh water in southern Africa was until recently very limited. Neither Smith (1937) nor Jubb (1967) in their works on freshwater fishes of the eastern Cape and southern Africa respectively, mentioned that this species penetrates into fresh water. More recent reports record that *Mugil cephalus* penetrates into the freshwater reaches of rivers in the western Cape (Louw 1968; Gaigher *et al.* 1978) and in Natal (Pooley 1975; Bruton *et al.* 1978; Pike 1979).

All the above reports of mullet in fresh water are confined to short observational notes or entries in a species checklist. *Myxus capensis* is often the most numerous and largest freshwater fish species in freshwater reaches of coastal rivers in the eastern Cape and is also a locally popular angling species. In addition, *Mugil cephalus* is also common in the lower reaches of some rivers. It is therefore surprising that there was virtually no reliable information on the distribution or basic biology of mullet in freshwater reaches of southern African rivers before the present research programme was initiated in 1975.

This information was necessary as reports were received from fishermen and riparian landowners that *Myxus capensis* was becoming scarcer in the eastern Cape and had completely disappeared from a number of areas where they had previously been plentiful (PBN Jackson pers. comm. 1975). Numerous factors were held to be responsible for this reported decline, but due to ignorance of the biology of the species, particularly its breeding biology, firm conclusions could not be reached. Man-induced habitat changes were, however, strongly suspected as being a major factor.

In brief, the main reasons for this study on *Myxus capensis* were:

(i) the unknown and possibly threatened conservation status of this species;

(ii) lack of knowledge of its biology and life history and

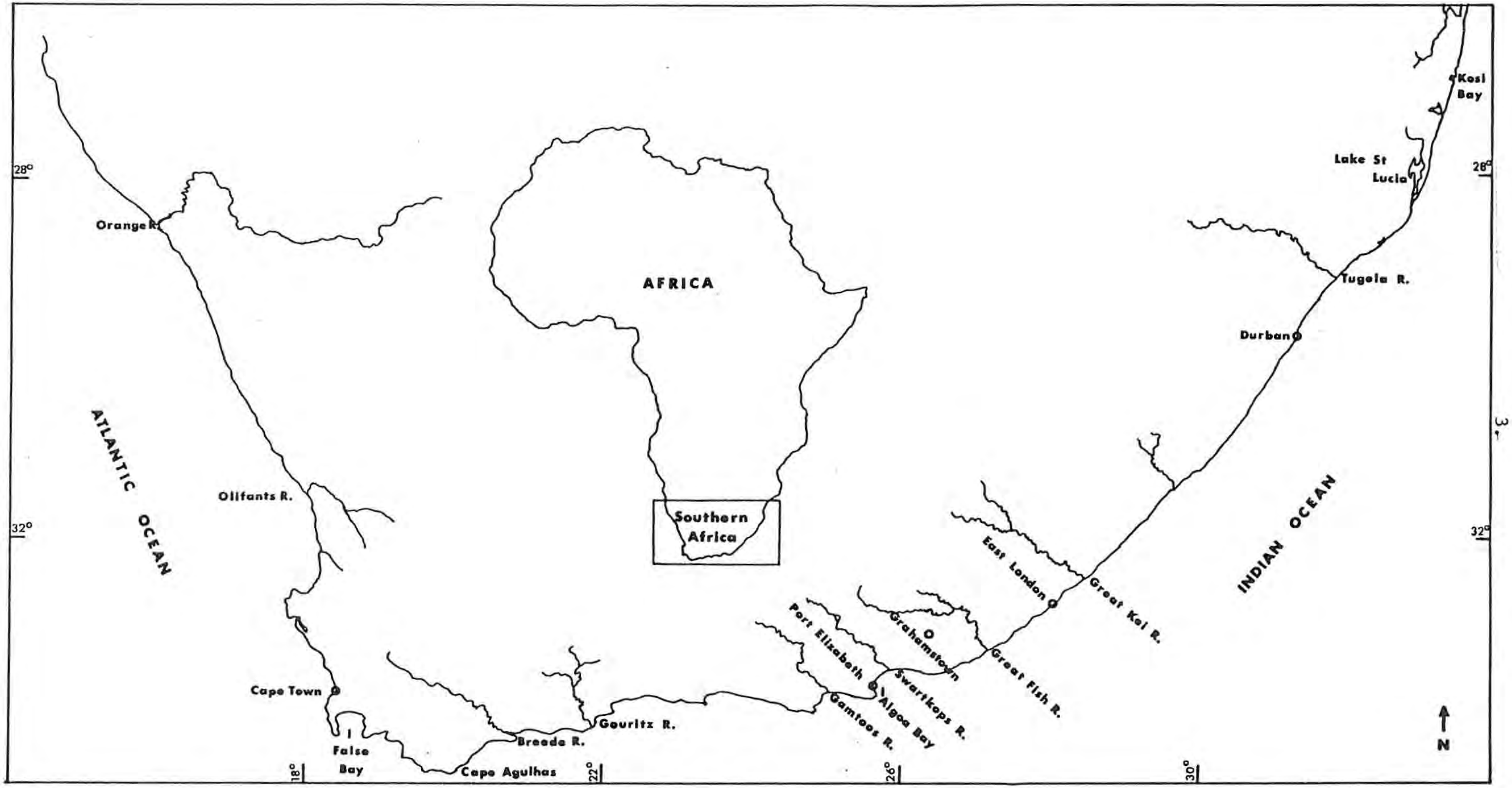


Figure 1. Map of southern Africa showing major rivers from Kosi Bay to the Orange River. The geographical range of *Myxus capensis* extends from Kosi Bay to the Breede River.

(iii) its possible value in freshwater fisheries. *Mugil cephalus* was included in this study mainly for comparative purposes as it co-exists with *Myxus capensis* in estuarine and freshwater habitats in the eastern Cape and the biology of *Mugil cephalus* has been extensively studied in southern Africa and many other countries (see above). In addition, *Mugil cephalus* is considered to be particularly suitable for culture purposes because of its rapid growth, large maximum size, high quality flesh and wide temperature and salinity tolerances (Thomson 1966; Oren 1971).

Research emphasis was therefore placed on those aspects of the life history of both mullet species which were likely to be affected by man-induced changes, namely breeding biology, movements and migrations, relative abundance and demography. Feeding studies were not included in this investigation as detailed research on the feeding ecology of these species has been carried out in the eastern Cape (Masson & Marais 1975; Marais 1976; Marais & Erasmus 1977) and in Natal (Blaber 1976, 1977; Blaber & Whitfield 1977; Whitfield & Blaber 1978a & b; Whitfield 1980a & b). The above research, as well as food and feeding studies on *Mugil cephalus* in other countries (e.g. Brusle 1981), indicated that both *Mugil cephalus* and *Myxus capensis* are sufficiently flexible in their trophic ecology to feed successfully under a variety of conditions. This indicates that man-induced habitat changes may have less impact on the feeding ecology of these species than on those aspects of the ecology chosen for study.

The specific objectives of this study were therefore:

(i) to gain a thorough understanding of the life history of natural populations of *Myxus capensis*;

(ii) to assess the response of the fish populations to natural biotic and abiotic constraints in the environment;

(iii) to assess the degree of dependence of *Myxus capensis* and *Mugil cephalus* on freshwater habitats and compare their life history strategies;

(iv) to assess the effects of man-induced habitat changes on the distribution and conservation status of *Myxus capensis* in the eastern Cape;

(v) to investigate the aquaculture as well as angling potential of each

species under local conditions and
(vi) to recommend conservation measures and management proposals for the utilization and conservation of these species.

This study therefore represents an attempt to relate the life history characteristics of a fish species to its biotic and abiotic environment, and to demonstrate the impact which some man-induced changes have had on their life cycle. The co-existence of two closely related species showing different levels of specialization for a catadromous life history, indicated that useful comparisons of life history tactics may be possible. Few such comparative studies have been attempted as normally too many variables must be considered to make such comparisons meaningful (Mann & Mills 1979). The mullet populations of the eastern Cape therefore provided an unusually good opportunity to answer ecological questions which have rarely been addressed before.

CHAPTER 2. THE STUDY AREA

A. TOPOGRAPHICAL AND BIOTIC CHARACTERISTICS OF THE SAMPLING AREAS.

The Kowie River

From its source in the hills south of Grahamstown, the Kowie River meanders approximately 94 km between steep, often thickly vegetated valleys (Valley Bushveld type vegetation) before entering the Indian Ocean at the town of Port Alfred (33° 36' S, 26° 54' E) (Fig. 2). The main tributary, the Bloukrans River, drains Grahamstown and flows through the Belmont Valley before joining the Kowie 58 km from its mouth. The only other tributary of note, the Lushington River, flows into the Kowie River 32 km from the mouth. The Kowie is a "reservoir-type" river comprising large, deep (often >5 m) pools separated by shallow, stony runs. The river bed varies from sandy mud and detritus in the large pools to stones and boulders in the shallow runs. Apart from a high weir erected at the head of the estuary (see below) there are at least eight smaller weirs across the freshwater reaches. The farming practices in the Kowie catchment consist mainly of pineapple production and stock farming (Heydorn & Grindley 1982).

The tidal effect is apparent for 21 km and the permanently open mouth is guarded by two breakwaters which extend out through the surf zone. The upper estuary is 30 - 60 m wide, 2 - 6 m deep and forms extensive meanders. In these reaches the banks are fairly steep with a narrow intertidal zone of less than 10 m (Day 1981). In the middle and lower reaches the estuary broadens out to 80 - 150 m with extensive mud flats in the vicinity of the "Bay of Biscay", approximately 1 - 2 km from the mouth. Water depth in the middle and lower reaches is about 3 m, increasing up to 8 m on the bends (Heydorn & Grindley 1982).

There are dense areas of *Phragmites australis* along the margins of the upper reaches of the estuary as well as beds of *Zostera* and *Ruppia spiralis* (Day 1981). The large freshwater pools above the estuary are usually fringed by *Phragmites australis* as well as *Typha capensis*, while *Potamogeton* spp. and *Nymphaea caerulea* are found in the shallower areas of the large pools.

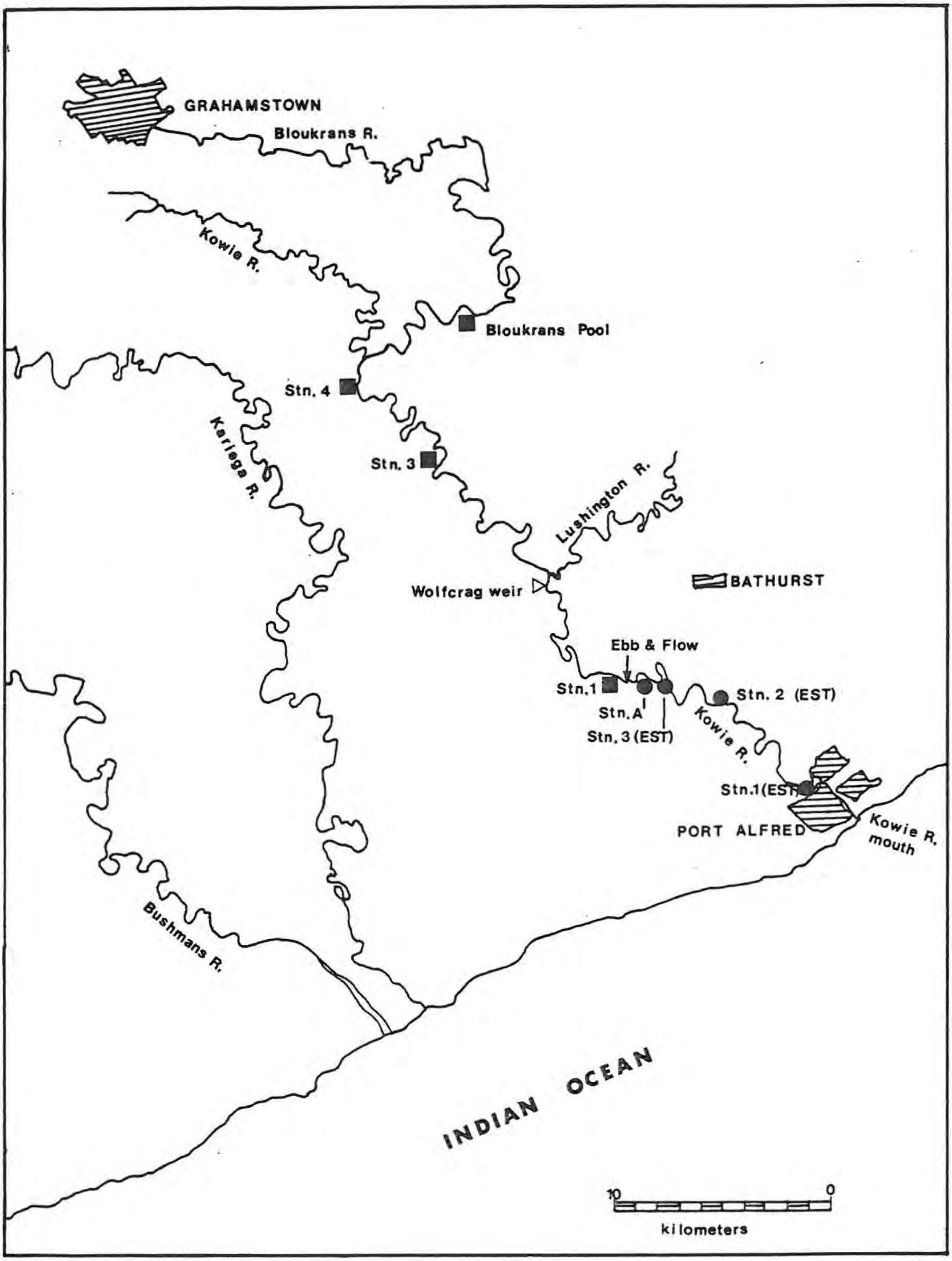


Figure 2. Map of Kowie River system showing the netting stations. (EST = estuary).

Netting sites.

Gill netting in the upper estuary was undertaken 19 km from the mouth (Station A, see Fig. 3) from 1975 to 1977. In addition, during a 13 month (Jan. 1981 to Jan. 1982) gill netting programme, regular netting took place 2 km, (Station 1), 12 km, (Station 2) and 17 km from the mouth (Station 3)(see Fig. 2).

In the freshwater reaches regular gill netting took place at the following three sites:

(i) Station 1. A large pool immediately above the head of the estuary, from which water is drawn for the Port Alfred domestic supply (Fig. 4). In 1976 this pool was dammed by a weir which was severely damaged by floods in 1979. A further weir was built later that year a short distance upstream. This pool is just under one kilometer long, has a maximum depth of 6,5 m and is 20 - 50 m wide.

(ii) Station 3. This station comprises two large adjacent pools on the farm "Luembe", 27 - 29 km from the head of the estuary. The lower pool (Station 3a) is approximately 500 m long, up to 50 m wide and 4,3 m deep (Fig. 5). Station 3b, about one kilometer upstream, is dammed by a 1,5 m weir and is approximately one kilometer long and between 20 - 50 m wide.

(iii) Station 4. This comprises two large pools, approximately 32 km (Station 4b) and 36 km (Station 4a) from the head of the estuary. Station 4a, on the farm "Wesley Wood" (Fig. 6) is approximately 500 m long, up to 4,6 m deep and between 20 - 60 m wide. Station 4b (Fig. 7), on the farm "Brighton", is approximately 400 m long and 20 - 50 m wide.

To obtain growth data, mullet fry were stocked into a pool (70 m long, 40 m wide and 5,5 m deep) in the Bloukrans River (Bloukrans Pass pool) about 47 km from the head of the Kowie estuary (Fig. 8).

Although over 95% of the gill net catches in the freshwater reaches consisted of *Myxus capensis* and *Mugil cephalus*, other species such as the eastern Province rocky (*Sandelia bainsii*), large-mouth bass (*Micropterus salmoides*), Cape moony (*Monodactylus falciformis*) and (in the lower reaches) Mozambique tilapia (*Oreochromis mossambicus*) were occasionally

Figure 3. The upper reaches of the Kowie estuary, 19 km from the mouth (Station A).

Figure 4. The "Ebb & Flow" of the Kowie River showing the old damaged and the new weir and Station 1 on upstream (RH) side of photo. Note low water level after 16 months of no flow.

Figure 5 . Kowie River Station 3a, *ca* 27 km from the head of the estuary. Note low water level after 16 months of no flow.

Figure 6 . Kowie River Station 4a, *ca* 36 km from the head of the estuary. Note low water level (see above).

Figure 7 . Kowie River Station 4b. Note gill net diagonally across pools and overhanging riverine vegetation.

Figure 8 . Bloukrans Pass pool on Bloukrans River, *ca* 10 km upstream of its junction with the Kowie, below the Grahamstown - Port Alfred road.

caught. The traps and seine nets sampled a number of other fish species not usually caught in the gill nets. The fish species other than mullet which were caught in the freshwater reaches of the Kowie River during this study, as well as an indication of their distribution and abundance, are listed in Table 1.

Table 1. The distribution of fish species caught during this study in the Kowie River. a = absent; r = reported as present by farmers or fishermen; p = present, but very few caught; p+ = fairly common; and p++ = abundant.

Species	Head waters	Upper middle	Middle section	Lower middle	Just above ebb & flow	Ebb & flow area
Sandelia bainsii	r	p++	p++	p	a	a
Barbus pallidus	p++	p++	p++	p++	p	a
Barbus anoplus	p++	p	a	a	a	a
Gilchristella aestuarius	a	p++	p++	p+	p+	p++
Oreochromis mossambicus	a	a	a	a	p	p
Monodactylus falciformis	a	a	a	a	p++	p+
Glossogobius tenuiformis	p	p++	p++	p++	p++	p++
Micropterus salmoides	a	r	p	r	p	a
Anguilla marmorata	r	r	r	r	p	p
Anguilla mossambica	p	p	r	r	p	p
Lepomis macrochirus	a	a	a	a	p	a

The Swartkops River

The Swartkops River enters Algoa Bay about 10 km north-east of Port Elizabeth (33^{o} 51' S, 25^{o} 38' E)(Fig. 9). The main tributary, the Elands River joins the Swartkops about 37 km from the mouth. The tidal limit of the estuary is marked by a low causeway 16 km from the mouth. There are three dams in the upper reaches. The Groendal Dam on the Swartkops River, about 50 km from the mouth, supplies water to Uitenhage, while

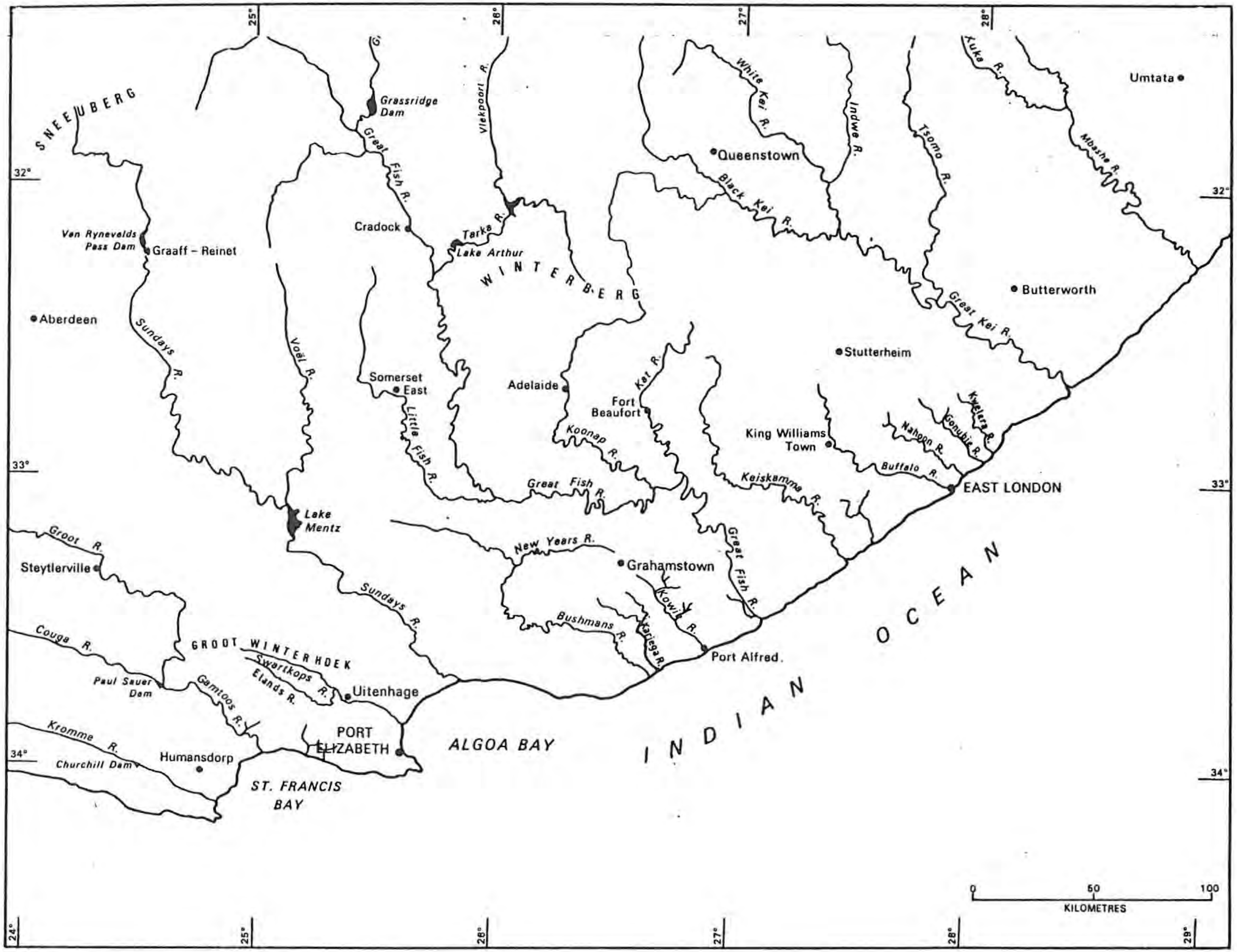


Figure 9. Map of the eastern Cape coastal area showing the major rivers from the Great Kei to the Kromme rivers.

the Bulk and Sand river dams, on two major tributaries of the Elands River, supply water to Port Elizabeth. Although larger than the Kowie River, the Swartkops is also a "reservoir-type" river with large deep pools containing sediments composed of mud and detritus connected by shallow stony runs. The pools are fringed with *Phragmites australis* and the reaches below Uitenhage are infested with *Eichornia crassipes* which can cover over 70% of the water surface during long periods of low river flow. Periodic floods flush this exotic weed out of the system as well as devastate the marginal vegetation.

Sampling sites.

After initial surveys to determine the extent of the upstream penetration of mullet and their abundance in various parts of the river, sampling was restricted to two areas:
(i) Station 1. A single large pool (*ca* 750 m long, 80 - 100 m wide and 2 m deep) situated 1 kilometer above the head of the estuary, immediately upstream of a cement causeway (Fig. 10).
(ii) Station 2. This station comprised a series of four pools situated in the lower Elands River, between 1 - 9 km upstream of its junction with the Swartkops River. The topography of these pools is typified by the pool shown in Fig. 11 . The maximum depth of these pools varied from 3 - 5 m, the length from 200 - 500 m and the width 40 - 70 m.

Virtually no other fish besides mullet were caught in the gill nets set in these areas of the Swartkops River, apart from the occasional common carp (*Cyprinus carpio*), *Micropterus salmoides* and *Monodactylus faciformis*.

The Great Fish River

The Great Fish River mouth enters the Indian Ocean 25 km north-east of Port Alfred (33^{o} 30' S, 27^{o} 08' E).(Fig. 9). The tidal effect extends 16 km from the mouth to Kaffir Drift, although saline water usually penetrated less than half this distance upstream during the study period. The upper reaches of the estuary are shallow due to extensive siltation. In this area depths at low tide are <1 meter and the estuary is 40 - 75 m wide. The middle and lower reaches are also shallow (1 - 3 m) and 100

Figure 10. Swartkops River Station 1, *ca* one kilometer above the head of the estuary. Recent floods had flushed out *Eichornia crassipes* and devastated marginal vegetation.

Figure 11. Swartkops River Station 2. A pool in the Elands River, *ca* one kilometer above its junction with the Swartkops River.

- 150 m wide (Fig. 12). The upper and middle reaches are fringed with beds of *Phragmites australis* which are periodically devastated by floods. (Fig. 13). No other aquatic vegetation is found in this river.

The freshwater reaches above the head of the estuary consist of shallow (usually <2 m) sand-bank type pools with a substrate of muddy sand (Fig. 14). Marginal vegetation is limited due to the scouring effect of flood waters which are known to rise over 10 m (Day 1981).

Sampling sites.

Regular gill netting took place at three sites in the estuary 0,5, 3,0 and 7,0 km from the mouth, which were considered to represent the lower, middle and upper reaches of the estuary according to salinity criteria. Several sites in the freshwater reaches from Kaffir Drift to Double Drift (110 km) were sampled using both seine and gill nets at 3 - 4 month intervals during the study period. For comparative purposes the freshwater reaches were divided into the lower (Kaffir Drift to Hunts Drift - 27 km) and upper reaches (Hunts Drift to Double Drift - 83 km).

The indigenous cyprinid, *Labeo umbratus*, usually dominated the catches in the freshwater reaches of the Great Fish River, particularly above Hunts Drift. The relative abundance of *Labeo umbratus*, mugilids (*Myxus capensis* and *Mugil cephalus*) and *Cyprinus carpio* in gill net catches at three sites in the "upper" sampling area is given in Table 2 .

Table 2 . The relative abundance of fish caught in gill nets upstream of Hunts Drift in the Great Fish River during this study.

Site	Dist. from estuary (km)	Total catch (n)	% of total catch		
			L. umbratus	Mugilidae	*C. carpio*
A	27	994	90,0	6,0	4,0
B	77	857	89,3	9,1	1,6
C	110	3 019	98,2	0,9	0,8

Figure 12 . The mouth of the Great Fish River during flood conditions. Note low salinity flood-waters extending well out to sea.

Figure 13 . The middle and upper reaches of the Great Fish estuary. Note muddy colour of water and excessive siltation.

Figure 14 . Seine netting site on farm "Sportvale", 10 km from the head of the Fish estuary. Note shallow, sandbank-type topography and limited marginal vegetation.

B. CLIMATE AND HYDROLOGY

Myxus capensis is endemic to the south and east coast of South Africa from the Breede River (Gaigher *et al.* 1978) to the Kosi Lake system (Blaber 1978) (Fig. 1). The climate in this region ranges from warm temperate in the south to sub-tropical in the north. Mean daily maximum and minimum air temperatures range from 13,7 - 19,9° C at Cape Agulhas to 17,5 - 25,4° C at Cape St Lucia (Weather Bureau 1954). In the extreme south-westerly regions of the species range over 80% of the annual rainfall occurs in winter. The southern Cape coastal region (seaward of the Cape Fold Mountains), from about Mossel Bay to the Great Fish River mouth, has rainfall more or less equally distributed through the year, while summer rainfall becomes progressively more predominant towards the eastern coastal regions of this species' range (Weather Bureau 1957). The inland catchment areas of the larger rivers draining the Great Escarpment along the south and south-east coast (such as the Gamtoos, Sundays, Great Fish, Great Kei) lie in summer rainfall areas with bimodal rainfall peaks in spring and autumn (Weather Bureau 1957).

The annual rainfall in the catchment areas of rivers inhabited by *Myxus capensis* varies from over 1 000 mm in the Cape Fold Mountains and Drakensberg, to less than 400 mm on the Great Escarpment. In addition, this rainfall is often erratic, especially in the eastern Cape where droughts and floods are not uncommon. The erratic rainfall in this area is reflected in the river flow:

> "The flow in most of the eastern Cape rivers is normally very irregular" (Heydorn & Grindley 1982).

The unpredictable nature of the water flow in the rivers inhabited by *Myxus capensis* may have extremely important disruptive effects on the catadromous life cycle of this species (see below). A closer look at the hydrology of these rivers is therefore warranted.

As this study concentrated on mullet populations found in the Swartkops, Kowie and Great Fish rivers, the discussion of rainfall and hydrology will be largely restricted to these three rivers. The former two rivers have their catchments in the intermediate mountains of the Cape Fold Belt (Winterberg and hills around Grahamstown respectively), while the Great Fish River extends well inland with major tributaries originating on the Great Escarpment. These three rivers, which lie within the centre of the natural range of *Myxus capensis*, are representative of two of the three major river types found in the eastern Cape (Skelton 1980). Only the small coastal rivers, which have limited freshwater reaches suitable for mullet, are not represented.

The Swartkops River has a catchment area of 1 370 km^2 and mean annual runoff of 84 $m^3 \times 10^6$ (Noble & Hemens 1978). The natural river flow of this system has been altered by the construction of the Groendal Dam in the upper reaches of Swartkops itself and the Bulk and Sand River dams in the catchment area of the main tributary, the Elands River. Although there are limited data on natural flow patterns of this system, general trends are apparent. Marais (1976) analysed the flood characteristics at the Groendal Dam from 1938 - 1976 and found no fixed patterns. Floods were found to occur in most months of the year and at irregular intervals. In a report on the rainfall in the Swartkops River catchment, the Port Elizabeth City Engineer (P.E.C.E 1974 from Marais 1976) concluded that the rainfall is fairly evenly distributed over the year, but with a tendency for a large proportion to fall over a few consecutive days. Periods of low rainfall, during which the Swartkops and Elands rivers stop flowing and consist of a series of disconnected pools, appear to be fairly common. From October 1972 until March 1974, for example, there was no spillway discharge from the Groendal Dam and little or no flow in the Elands tributary (Directorate of Water Affairs flow records, pers. comm. 1981).

The Great Fish River, with the second largest catchment (30 427 km^2) in the eastern Cape after the Gamtoos River, has a mean annual runoff of 479 $m^3 \times 10^6$ (Noble & Hemens 1978). In 1975 the natural flow of the Great Fish River was augmented by the transfer of Orange River water via the Orange-Fish tunnel to the upper reaches of the Great Fish River. Before this date, however, the natural flow was probably not seriously modified by man. In spite of its large catchment, the flow in the Great Fish River can be highly variable. During the 21 year period from October 1952 to September 1973 the flow at Carlisle Bridge remained low and even stopped completely for extended periods (Table3). However, periods of low flow seldom exceeded six months and never continued for over 12 months. High floods are also common and on five occasions during the above 21 year period, the mean annual runoff was exceeded in a single month (Directorate of Water Affairs flow records, pers. comm. 1983).

Table 3. The number of times the observed monthly runoff of the Fish River (at Carlisle Bridge) remained below three threshold levels for various time periods during the 21 years from October 1952 to Sept. 1973. The threshold runoff values of 2,6, 1,3 and 0,26 $m^3 X 10^6$/ month are approximately equivalent to 1,0, 0,5 and 0,1 m^3/S mean daily flows respectively. (Directorate of Water Affairs flow records, pers. comm. 1983).

Time period (months)	No. of times the monthly runoff remained below		
	2,6 X 10^6 m^3	1,3 X 10^6 m^3	0,26 X 10^6 m^3
1 - 2	5	8	6
3 - 4	10	14	7
5 - 6	8	6	3
7 - 8	4	3	1
9 - 10	2	1	
11 - 12	1	0	

The Kowie River can probably be considered as representing typical *Myxus capensis* riverine habitat. This study showed that it is populated by large numbers of *Myxus capensis* with a widely ranging age structure. The physical characteristics of this system, with large, deep pools separated by shallow stony runs and with thickly vegetated banks (see above), is typical of the majority of larger coastal rivers in the eastern Cape which originate in the intermediate mountain ranges. Surveys have shown that these systems support large numbers of *Myxus capensis*. Apart from the construction of numerous small weirs, the flow of the Kowie River has been relatively unaffected by man-induced habitat changes. The flow pattern of this system is therefore not only close to the "natural" pattern, but it also probably characteristic of a large proportion of rivers with substantial *Myxus capensis* populations.

The total catchment of the Kowie River is 769 km^2 with a mean annual run-off of 23 m^3 X 10^6 (Noble & Hemens 1978). The upper reaches of the Kowie, as well as its main tributary the Bloukrans River, originate in the hills around Grahamstown, at an altitude of about 600 m. The average rainfall for Grahamstown over the period 1878 - 1950 was 697 mm (Weather Burearu 1954). While $\geq$0.2 mm of rain fell on an average of 92 days per annum, $\geq$10 mm of rain fell on an average of 17 days per year. Rainfall is mainly orographic and Dyer (1937), in describing rainfall in the Albany area, stated that :

> "excessive rainfall in a short period is very rarely experienced" and considered "one to three fairly severe thunderstorms per year over Grahamstown would be considered normal".

However, there is a tendency for a large proportion of the annual rainfall to fall over a few consecutive days, resulting in high floods of short duration.

The biomodal peaks in autumn (March) and spring (Oct./Nov.) in the Grahamstown area are clearly seen in Fig.15 . However, further analysis of rainfall data shows that floods as well as dry spells are liable to occur at any time of the year (Weather Bureau 1954, 1957).

The irregular rainfall pattern is reflected in the erratic flow pattern of the Kowie River as shown during the 13 year period July 1969 to Sept. 1982 (Fig.16). During this time there were a number of dry spells during which the river flow dwindled to a trickle or stopped completely, often for long periods. This is shown by the analysis of the daily mean flow of the Kowie River (from data recorded at Wolfcrags gauging weir, 11 km from the estuary, from October 1969 to September 1981), (Table 4). During these 12 years, the river flow remained low ($<$0,5 m^3/S) for two periods of more than a year, with the longest period being over two years (753 days from January 1972 to February 1974).

In order to ascertain whether the 12 years during which flow records were available were characteristic of longer-term flow patterns, data from synthetic flows for the 59 years from October 1921 to September 1981 were analysed. These data were kindly provided by Mr. A. Görgens

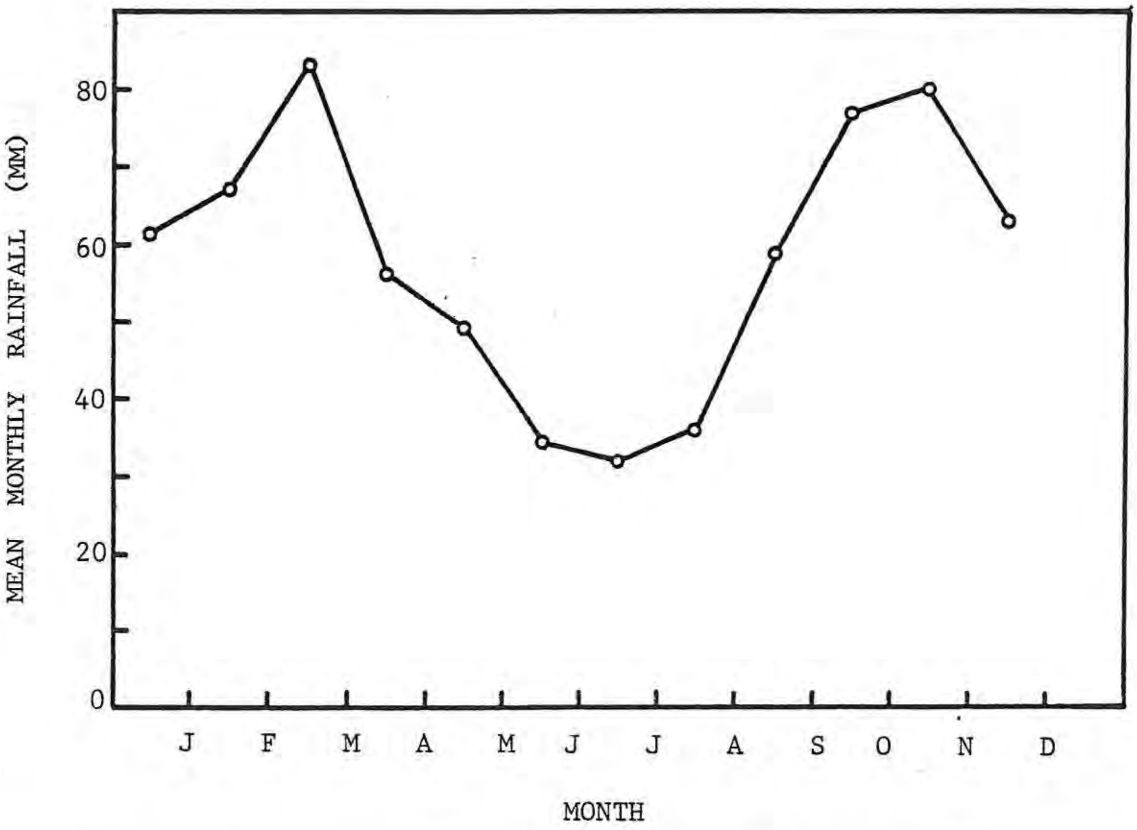


Figure 15. The mean monthly rainfall in Grahamstown over the period 1878 - 1950 (Weather Bureau 1954).

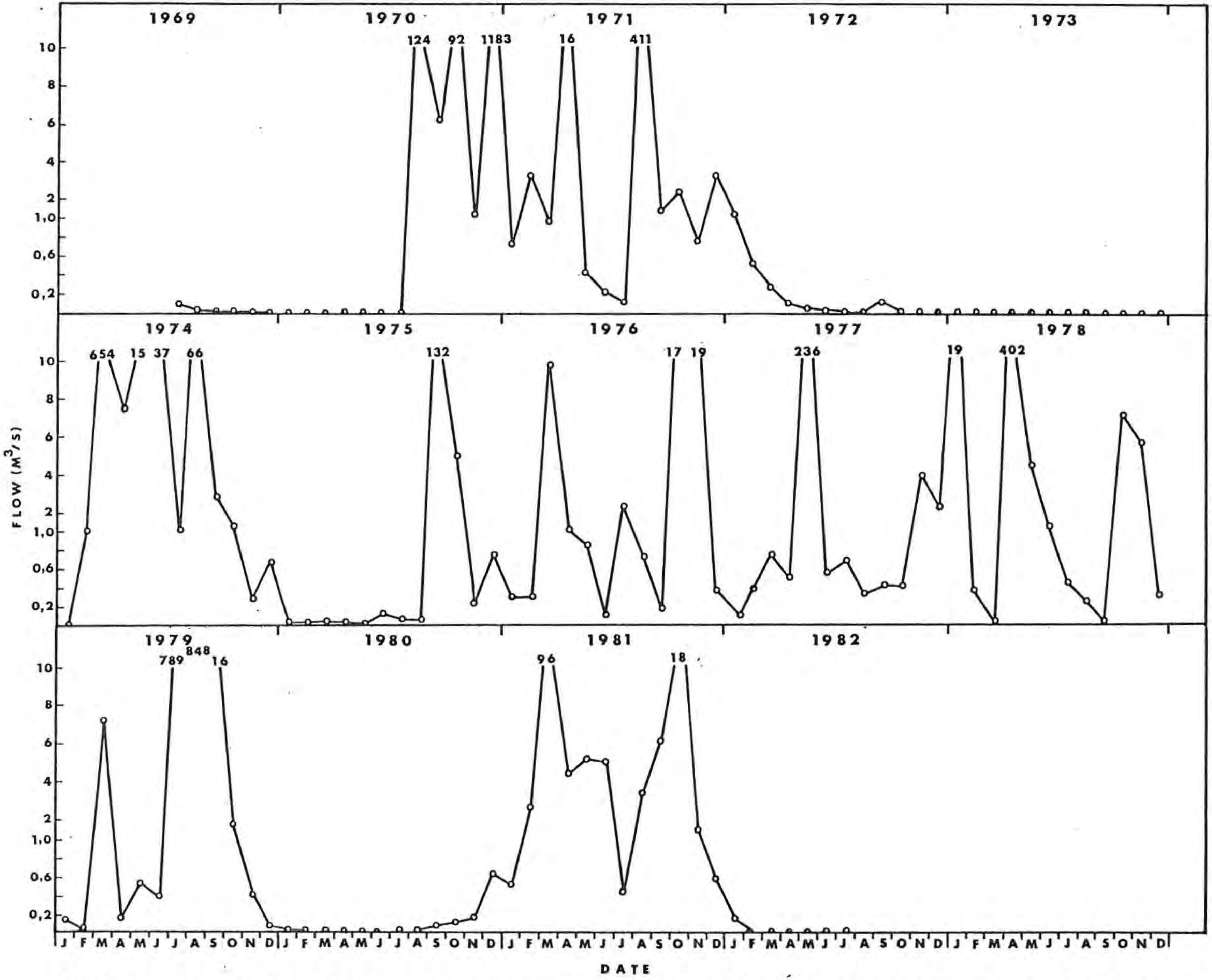


Figure 16. The monthly flow peaks in the Kowie River at Wolfcrag weir from Sept. 1969 to July 1982.

Table 4. The number of times the mean daily flow of the Kowie River (at Wolfscrag gauging weir) exceeded the three threshold levels (1,0, 0,5 and 0,1 m^3/S) for various time periods during the 12 years of observed flows from Oct. 1969 - Sept. 1981. (Directorate of Water Affairs).

Time period (Days)	No. of times flow remained below a threshold of		
	1,0 m^3/S	0,5 m^3/S	0,1 m^3/S
1 - 60	22	33	28
61 - 120	7	10	0
121 - 180	5	1	2
181 - 240	0	0	0
241 - 300	0	1	1
301 - 360	2	1	1
>360	2*	2**	1***
	(*478 days & 781 days)	(** 403 days & 753 days)	(*** 508 days)

of the Hydrological Research Unit, Rhodes University, from a computerized mathematical catchment model. Reliable rainfall figures in various parts of the catchment area of the Kowie from October 1921 to Sept. 1981 enabled accurate predictions of the flow of the Kowie River to be made using this model (Görgens 1983, pers. comm.). Analysis of these synthetic flow data showed that the highly erratic flow pattern of the Kowie River, indicated by the 12 years of observed flow data, is also apparent in the longer term data (Table 5). During this 59 year period, there were seven periods of over a year when the predicted flow did not exceed 0,5 m^3/S, with one period during 1923/1925 of over two years (731 days). During 1961 - 1963, a 20 - month period of no flow in the Kowie River just above the estuary was reported by Ninham & Shand (1971, from Heydorn & Grindley 1982).

High floods in the Kowie River are also common. During the 12 - year period from October 1969 - September 1981, the MAR was exceeded in a single month on five occasions (Table 6). The highest monthly flow occurred in August 1979 when over 3 X the MAR was recorded. Floods are likely to occur in virtually any month of the year (Table 6).

Table 5. The number of times the mean daily flow of the Kowie River remained below threshold levels of 1,0, 0,5 and 0,1 m^3/S for various lengths of time. Data were obtained from synthetic flow records computed by Görgens (1983) (see text) for the 59 years from October 1921 to Sept. 1981.

Time period (Days)	No. of times the daily flow remained below		
	1,0 m^3/S	0,5 m^3/S	0,1 m^3/S
0 - 90	151	195	210
91 - 180	27	27	36
181 - 270	10	13	15
271 - 360	8	14	1
361 - 450	7	3	
451 - 540	4	3	2
541 - 630	1		
631 - 720	0		
721 - 810	2	1	
810	1*		

* (1 050 days)

The maximum monthly flow peaks in Fig. 16 clearly show the very rapid "run-down" period, apparently characteristic of these "intermediate" rivers. Flood or high flow conditions witnessed during the study period existed usually for a matter of days rather than weeks. As fish movement, particularly that of large mullet, is probably confined to periods of high river flow, the height and duration of these flow peaks will largely determine the periods of potential fish movement in the river. This aspect is discussed further in Chapter 7 .

In conclusion, the flow pattern of the Kowie River clearly shows that high flow conditions suitable for adult fish movement occur erratically and are of short duration. In addition, long periods of low flow (when fish movement is not possible) are common. At least one such low flow period of more than a years' duration can be expected every eight to ten years.

The unpredictable and erratic nature of the river flow which is characteristic of many of the river inhabited by *Myxus capensis* would be expected to markedly influence the catadromous life history of this species. It was therefore hypothesized at the beginning of this study that *Myxus capensis* has evolved a life history strategy which successfully exploits this erratic and unpredictable environment.

Table 6. The total seasonal flow and date of seasonal peak flow in the Kowie River during the 13 year period October 1969 - September 1982. The "Hydrological Year" is from October to September (Directorate of Water Affairs flow data, pers. comm. 1983).

Hydrological Year	Total seasonal flow	Month of seasonal peak
1969/70	14,1	August
1970/71	102,6	December
1971/72	5,8	October
1972/73	0,2	November
1973/74	87,7	March
1974/75	29,9	September
1975/76	11,1	March
1976/77	28,8	May
1977/78	35,4	April
1978/79	142,7	August
1979/80	2,9	October
1980/81	25,4	March
1981/82	4,6	October

C. WATER QUALITY

The rivers within the distribution of *Myxus capensis* originate from a wide variety of geological deposits, vegetation types and climatic regions. As expected, the water quality and hence ecological suitability of the different river types varies considerably. As the geological composition of the catchment largely determines the water quality of the river draining the area, (Bond 1946), the main geological features of the study area merit discussion.

The two major geological systems found in this area are the Karoo and Cape Supergroups (Fig.17). The mountains of the southern and south-western Cape are formed by the Cape Supergroup and consist of the Table Mountain, Bokkeveld and Witteberg Groups. The Cape Fold mountains of the southern Cape coast, which extend eastwards to near Port Elizabeth, consist mainly of Table Mountain Sandstones (TMS) with the Bokkeveld Group in the valleys (King 1963). Waters draining these mountains are typically minerally deficient and acidic (pH 3 - 6) (Harrison & Agnew 1962; Heydorn & Tinley 1980; Skelton 1980). These soft waters are usually stained from amber to a deep reddish black (termed "Black waters" by Heydorn & Tinley 1980), and are considered to be relatively unproductive and to support a limited fish fauna. The Bokkeveld Formations are primarily of marine origin which yield alkaline waters of high salinity. The Witteberg Group, consisting mainly of quartz sandstones, form low ranges (e.g. hills around Grahamstown) and also yield soft waters.

The Karoo Supergroup includes the Stormberg, Beaufort, Ecca and Dwyka Groups. The latter three groups yield the highly mineralized (chlorides, sulphides) alkaline waters typical of the rivers draining the southern Karoo, such as the Gouritz, Sundays, Gamtoos (Groot tributary) and Great Fish (Noble & Hemens 1978). The larger rivers in Transkei and Natal originate in catchments comprising the Karoo Supergroup. These have a variable dissolved solid content and are generally very turbid (Noble & Hemens 1978).

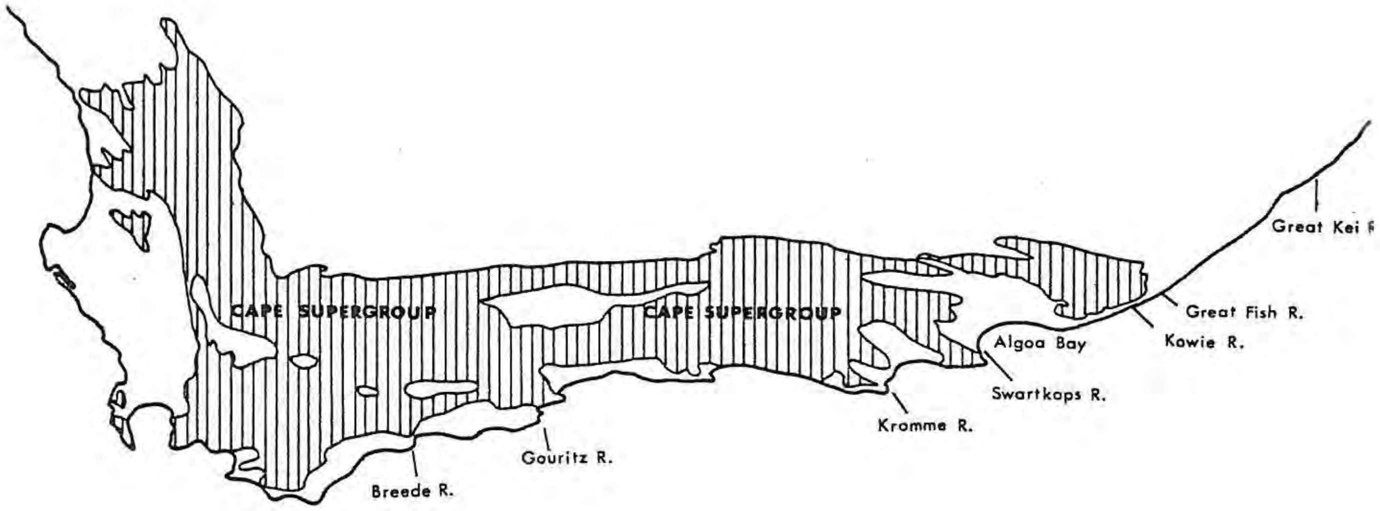
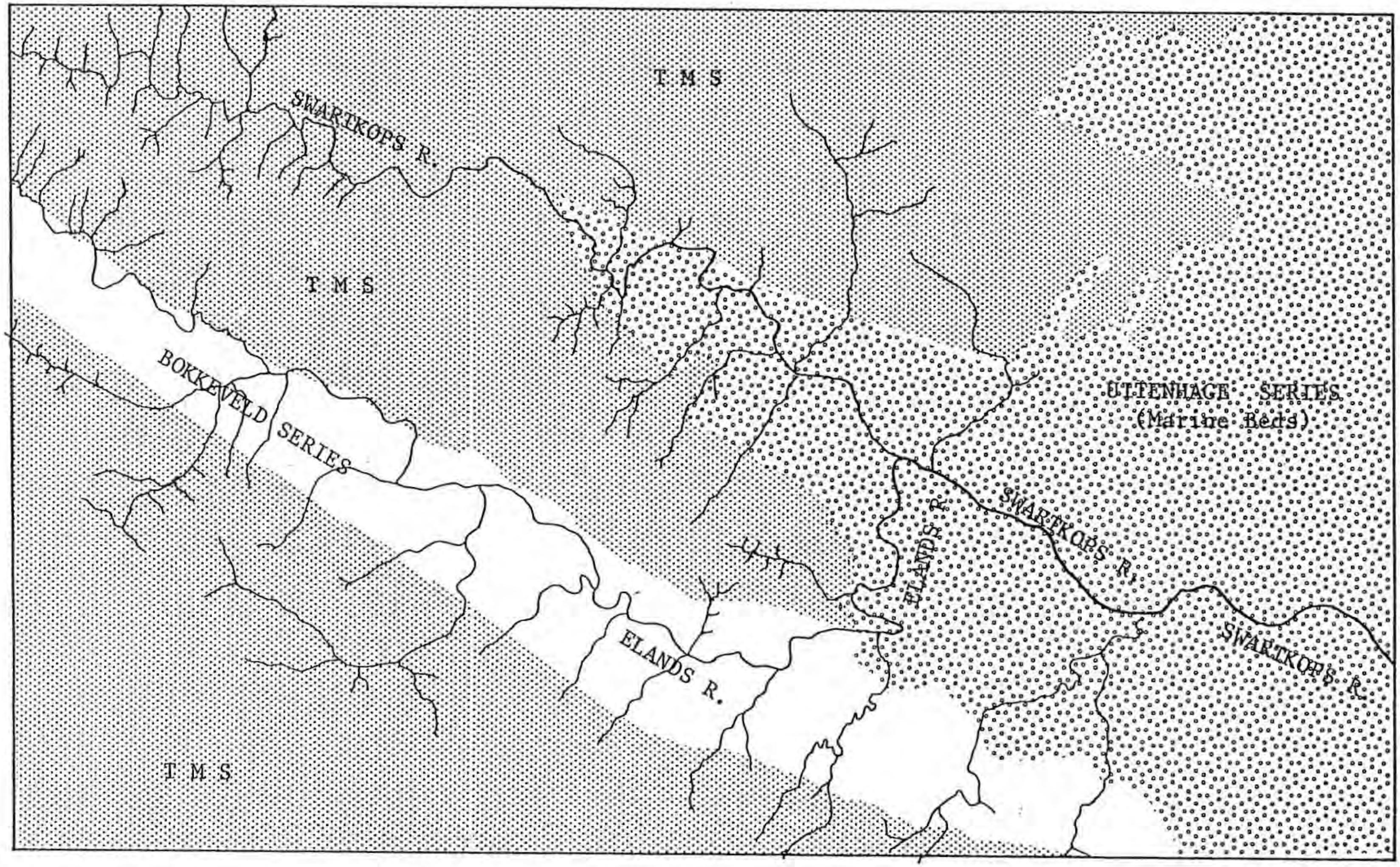


Figure 17. The extent of the Cape Supergroup in the Cape coastal area. (Modified from Heydorn & Tinley 1980).

The Swartkops River

The upper reaches of the Swartkops River drain the Great Winterhoek Mountains which consist mainly of TMS (Fig. 18). As shown in Table 7, water from the upper reaches (just below Groendal Dam) is acidic (pH 6.1), is stained a clear dark reddish-brown and has a low alkalinity, i.e. typical mildly acidic "Black water" of Noble & Hemens (1978). The lower reaches of the Swartkops River pass over the marine beds of the Uitenhage Group which raises both the alkalinity and the pH, as seen from the water quality data from sites 1 and 2 (Table 7). The upper and smaller side tributaries of the Elands River also drain areas of TMS. In this region pH values of 6,1 - 6,4 were commonly found (Table 7). However, the main Elands River bed runs over an outcrop of Bokkeveld shales until it encounters the marine beds of the Uitenhage Group approximately 10 km from its junction with the Swartkops (Fig.18). This increases the mineral content and raises the pH.

The mixing of the water draining these different geological groups appears to account for the highly variable pH values recorded from the waters of the Elands River (Table 7). The pH changes from acidic in the upper reaches to alkaline in the lower reaches of the Elands River. This change is presumably due to the presence of TMS in the upper catchment, resulting in the soft, acidic water of the upper tributaries. However, the alkalinity, mineral content and pH increase progressively as the water flows downriver over the Bokkeveld Shales and the Uitenhage Group of the main river bed. The high mineral content of the water of the lower Elands River is shown by a conductivity reading of 2 600 micro mhos/cm recorded in November 1975 at a point one km before its junction with the Swartkops River. The conductivity in the upper Swartkops (5 km below Groendal Dam) at this time was only 300 micro mhos/cm. A chloride level of 1 500 ppm was recorded in the lower Elands River during a low flow period (Aug. 1975), while the Swartkops itself had a chloride level of 850 ppm just above the head of the estuary. The "diluting" effect of soft water from the upper Swartkops River would account for the lower chloride level of the latter reading.



estuary
4 km

Figure 18 . The main geological formations of the upper catchments of the Swartkops and Elands rivers. The arrow indicates the furthest recorded penetration of *Myxus capensis*. TMS = Table Mountain Sandstone.

Table 7. The pH and alkalinity at various sites in the Swartkops River System. SR = Swartkops River, ER = Elands River.

Site		Distance from estuary (km)	pH mean (range)	Alkalinity (ppm Ca co_3) (mean/and range
No.	River			
1	SR	2	7,8 (6,8 - 8,2)	167 (75 - 240)
2	SR	5	8,0	
3	SR	28	6,5	
4	SR	34	6,1	21
5	ER	22	7,6 (6,8 - 8,4)	101 (25 - 240)
6	ER	23	8,2 (8,0 - 8,3)	75
7	ER	26	7,8 (6,8 - 8,3)	25 (22 - 28)
8	ER	28	6,7 (6,4 - 7,0)	
9	ER	30	8,2	28
10	ER	35	7,0	
11	ER	38	6,7	42
12	ER	upper*	6,1 - 6,4	

* water from the Bulk and Sand river dams in the upper Elands River catchment (data from Port Elizabeth Municipality City Engineer).

Water tests carried out soon after floods in this system indicated that the soft, acidic waters of the upper catchment tend to replace the more alkaline water in the lower river under flood conditions. For example, a major flood occurred in both the Elands and Swartkops rivers in February 1977. During this flood the Elands peaked at 9,11 cumecs on 21-II-1977 and 1 X 10^6 m^3 of water was released from Groendal Dam during February 1977. pH readings taken 22 days after this flood peak were by far the lowest recorded in the lower Elands River (6,4 at site 8) and lower Swartkops (6,8 at site 1). The lowest pH values at sites 9 (6,8) and 11 (6,8) in the Elands River were recorded on 25 May 1977, soon after a flood in this river which peaked at 9,83 cumecs on 9 May 1977. The acidic, unproductive waters of the upper reaches of both the Elands and Swartkops rivers may have an important influence on the distribution of mullet in this system. This aspect is further discussed in Chapter 7.

The Swartkops River receives large imputs of organic effluents in the form of treated sewage and wool washery and tannery effluents from Uitenhage (Day 1981). Although the pollution load in the Swartkops River is high, no fish kills were witnessed during the course of this study. The aritificially high level of nutrients is considered by Jacot Guillarmod (1974) to be largely responsible for the prolific growth of water hyacinth (*Eichlornia crassipes*) in the Swarkops River below Uitenhage.

Water temperatures in the Swartkops River, recorded at 20 cm depth between 08h00 and 10h00 at the time of netting operations, were found to vary between 11° C in winter and 23° C in summer .

The Kowie River

The main geological formations of the Kowie and surrounding area are shown in Fig. 19 . The mainstream of the Kowie River flows through a wide band of shale and sandstone of the Bokkeveld Group which follows the south-easterly course of the river to the coast. The headwater tributaries of the Kowie River drain ridges of Quartzitic Sandstone of the Witteberg Group. This could account for the minerally deficient nature of the water in the upper reaches of the Kowie, as shown by the low conductivity and chloride levels at the Mt. Pleasant site, some 72 km from the head of the estuary (Table 8). The Bloukrans tributary drains Quartzitic Sandstone of the Witteberg Group as well as Grahamstown Silcrete (Alexandra Formation) and deposits of the Dwyka Series of the Karoo Supergroup. At the Bloukrans Pass, some 10 km before its junction with the Kowie, the Bloukrans enters the band of Bokkeveld Shales described above. The mineral content of the water of the Bloukrans was found, as expected from the geological strata of its catchment, to be substantially higher than that of the upper Kowie (Table 8). The gradual increase in conductivity and chloride levels from the upper to the lower reaches of the Kowie is seen in Table 8 . A major source of high salinity water in the lower reaches of the Kowie is the Lushington River (also appropriately called the Brak River) which enters the Kowie River 11,5 km from the head of the estuary.

The lowest dissolved solid concentrations shown in Table 8 were recorded during or soon after flood conditions when low salinity, upper catchment

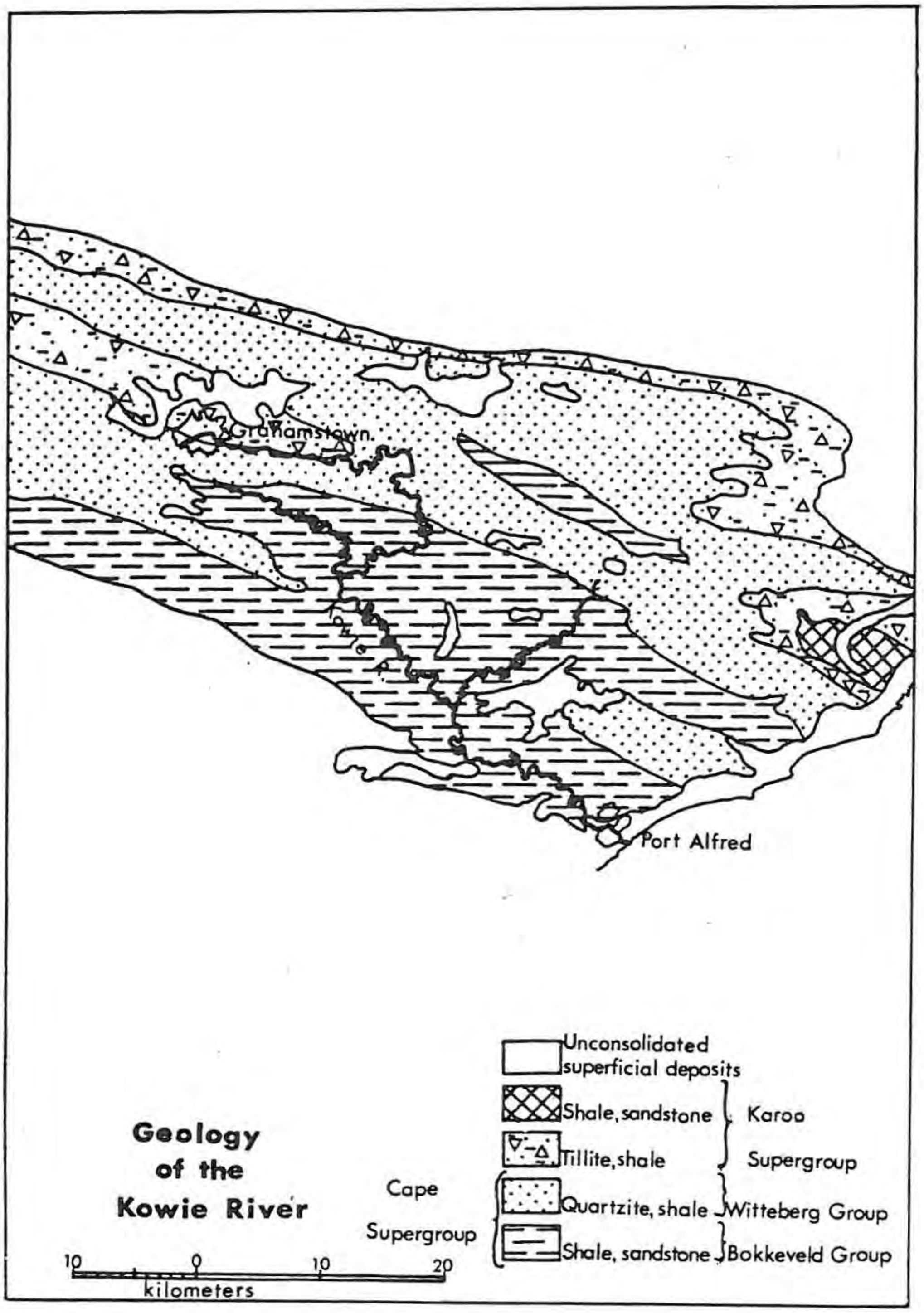


Figure 19. Geology of the Kowie River.

Table 8. The results of chemical analysis of water at various sites in the Kowie River system from July 1974 - Sept. 1975. K = Kowie River; B = Bloukrans River; L = Lushington River. Data given as mean and/or range.

Site	Dist. from estuary (km)	Conductivity (micro MHOS/cm)	n	Chlorides (ppm)	n	Turbidity (J.T.U.)	n	Sulphates (ppm)	n
Mt. Pleasant (K)	72	443 (240 - 550)	6	107 (38 - 200)	6	(2 - 310)	2	15	1
Luembe (K)	26 - 28	2 817 (940 - 4 200)	7	595 (175 - 850)	8	(5 - 12)	2	(78 - 80)	2
Penny's Drift (K)	11	3 057 (1 160 - 5 500)	8	695 (250 - 1 300)	7	(28 - 280)	2	120	1
Station 1 (K)	0,5	4 097 (1 280 - 5 500)	7	983 (250 - 1 250)	6				
Ebb & Flow (K)	0	14 032 (1 240 - 46 500)	9	2 964 (250 - 11 500)	9	(12 - 500+)	3		
Above Sewage (B)	92	(3 100 - 3 300)	2	500 - 525	2	70	1	250	1
Bloukrans Pass (B)	47	1 919 (480 - 2 600)	9	330 (75 - 500)	9	(3 - 500)	2	75	1
Lushington Bridge (L)	29	4 294 (520 - 6 800)	7	921 (100 - 1 500)	7	4 - 500+	2	170 - 180	

flood waters tend to flush out the system. During periods of low river flow, continuous seepage of high salinity water in the catchment as well as evaporation result in the high salinities recorded in the mainstream. Organic pollution of the Bloukrans tributary from Grahamstown urban runoff and via the Grahamstown sewerage works has been observed. DO tests in October 1974 revealed low DO levels (<30% saturation) above the sewerage outfall, but self-purification was rapid and DO levels >75% saturation were found 3 - 4 km further downstream (Bok unpubl. data). The Kowie River is considered to be unpolluted with respect to metals (Watling & Watling 1982, from Heydorn & Grindley 1982).

The high pH (mean 8,2) and alkalinity (mean 139 - 185 ppm Ca CO_3) values of the waters of the Kowie River indicate a fairly high production potential (Table 9). The water is usually clear with mean secchi disc transparency ranging from 71 - 103 cm and maximum values up to 250 cm. Light penetration is limited however, as the water is stained a deep clear brown by organic matter. Algal blooms were not observed at any time. The lowest secchi disc transparency values were taken during floods and indicate an increased sediment load under these conditions. However, the Kowie River normally carries a relatively low silt load (South Africa, Department of Agricultural Technical Services 1975, from Heydorn & Grindley 1982). Even when in flood, secchi disc values in the Kowie are normally greater than from turbid rivers such as the Great Fish during low flow conditions.

Table 9. The pH, alkalinity and secchi disc transparency taken at various netting stations in the Kowie River. Water tests were usually carried out between 08h00 - 10h00.

Station	Distance from head of estuary (km)	pH			Alkalinity (ppm Ca CO_3)			Secchi Disc transparency (cm)		
		mean	(range)	(n)	mean	(range)	(n)	mean	(range)	(n)
1	0,5	8,2	(8,0-8,6)	(17)	185	(104-255)	(17)	71	(30-130)	(13)
3	26 - 28	8,2	(7,8-8,4)	(9)	142	(89-210)	(9)	99	(25-250)	(9)
4	33 - 37	8,2	(7,8-8,4)	(19)	139	(75-218)	(18)	103	(35-250)	(13)

As water temperatures at the three sampling stations in the Kowie River were very similar, the data were combined and are shown in Table 10. A temperature range of 19,5° C was recorded between the upper (28,0° C) and lower (8,5° C) extremes.

Table 10. The monthly water temperatures of the Kowie River (Stns 1, 2 & 3 combined) recorded during the three year study period (1975 - 1978). Temperatures were recorded at 20 cm depth between 08h00 - 12h00 using a mercury thermometer.

Month	Temperature (°C)		n
	Mean	(Range)	
January	24,4	(21,0 - 28,0)	5
February	24,3	(23,0 - 25,5)	5
March	21,6	(19,0 - 25,0)	8
April	20,8	(18,0 - 23,0)	12
May	15,8	(13,0 - 20,0)	14
June	12,4	(8,5 - 16,0)	11
July	11,6	(10,5 - 13,0)	5
August	12,9	(11,0 - 15,0)	11
September	15,9	(13,0 - 20,0)	10
October	19,8	(17,5 - 22,0)	8
November	18,6	(17,5 - 21,0)	4
December	23,1	(22,0 - 24,0)	4

DISSOLVED OXYGEN (DO) IN THE KOWIE RIVER

During discussions with riparian landowners along the Kowie River, indirect evidence of fish deaths caused by anoxic water conditions came to light. For example, in February 1974, when the Kowie River began flowing after being stagnant for 22 months (Fig. 16), a large-scale mullet kill was witnessed on the farm 'Luembe', some 25 km from the head of the estuary (John Tyson, pers. comm. 1975). The water at the time was reported to be "black and foul-smelling", possibly indicative of anoxic conditions.

Subsequent investigations showed that, when river flow was too low to facilitate mixing, very low DO concentrations existed in the deeper waters of large pools (Table 11). The reduced DO levels occurred in summer as well as winter, when no marked thermocline existed. SCUBA diving observations showed that large amounts of organic detritus (largely of vegetable origin) accumulated on the bottom of these large, deep pools. The microbial decomposition of this material is probably responsible for the lowered DO levels found in the deeper water layers. The 2° C increase in water temperature from a depth of 2 m to 5 m (bottom) in Bloukrans Pool recorded in July 1980, (Table 11) is probably a result of this microbial activity.

It is postulated, therefore, that the sudden mixing of surface and bottom water layers in these pools, as occurs when the river floods after a long drought, could reduce the DO throughout the water column to lethally low levels. Such an effect would probably be more severe if it occurs in summer because of increased microbial activity at higher temperatures and the probable development of a thermocline which would inhibit oxygen transfer to the deeper layers. It is possibly significant that the fish-kill reported above occurred when an extended drought was broken in summer. In contrast, when the Kowie River began flowing in July 1983, after being stagnant for 18 months, surface DO levels recorded 11 km upstream of the ebb and flow, within 24 hours after the river had resumed flowing, were close to saturation (94%).

A drop in DO oxygen in the Kowie River during flooding may also be due to the imput of allochthonous organic material caused by heavy rain in the well-vegetated catchment areas. This phenomenon has been reported to occur in Lake Nhalange, a deep (*ca* 27 m), brackish ($3 - 5^{\circ}/oo$) coastal lake forming part of the Kosi system in Maputaland (Allanson & Van Wyk 1969). The DO levels in deeper waters of this lake fell from 88 to 18% saturation after flooding rivers brought organic material into the lake. The above authors considered that the oxidation of this allochthonous organic matter was responsible for the marked drop in DO in the deeper waters which occurred after flooding.

Table 11. The dissolved Oxygen (DO) at various depths in three deep pools in the Kowie River system. Measurements were taken with a Hach Test Kit (*) and a YSI portable oxygen meter (**) (see text).

Locality	Date	Depth (cm)	Temp. (^{o} C)	DO (ppm)	% Satn.	River flow (cumecs)
Bloukrans Pass Pool (Bloukrans R.)	13-III-75*	10	23	9	100	no flow
		185	22	7	80	
		280	22	5	57	
		370	21	0,4	4	
		550	20	0,2	2	
	23-VII-80**	15	10	11,1	99	no flow
		100	9,5	10,6	94	
		200	9,0	10,6	92	
		300	9,5	6,2	55	
		350	9,8	5,0	45	
		400	10,0	0,8	7	
		500	11,0	0,7	6	
Station 1 (Kowie R.)	10-IX-80**	15	15,2	10,2	98	0,1
		100	14,5	10,2	97	
		200	14,0	9,8	92	
		300	13,9	9,2	87	
		400	13,5	8,6	80	
		500	13,5	5,0	47	
		600	13,2	2,6	24	
		650	13,0	1,4	13	
Station 4 (Kowie R.)	30-I-76*	10	24,0	8,0	95	no flow
		450	19,4	<1,0	<10	

Great Fish River

The minerally enriched, highly alkaline and turbid nature of the Great Fish River, as expected from waters draining the Karoo Supergroup of the Great Escarpment, is shown in Table 12. As there were no marked differences in water quality between the various sites sampled, all water quality data were combined. During periods of low flow the water in the Great Fish River has a green-brown colour, indicating high algal concentrations. The high productivity of this water is indicated by the very dense populations of the moggel (*Labeo umbratus*) (Chapter 3). Water temperatures varied between 9° C in August to 28° C in February.

Table 12. Water quality data from the lower Great Fish River (Kaffir Drift to Double Drift) recorded during the period June 1975 - Feb. 1978. Data given as the mean and/or the range in brackets.

Temp. (^{o} C)	Secchi Disc (cm)	pH	Alkalinity (ppm $CaCO_3$)	Chlorides (ppm Cl)	Conductivity (micro MHOS/ cm)
9,0 - 28,0	13 (10 - 15)	8,5 (8,2 - 8,7)	296 (233 - 382)	500	3 150 (3 100 - 3 200)

Kowie and Great Fish estuaries

The natural mean annual runoff (MAR) of the Great Fish River is over 20 X that of the Kowie River (see above). In addition, in 1975 the flow in the Great Fish River was augmented by Orange River water via the Orange-Fish tunnel. The main stream and upper tributaries of the Great Fish River traverse the soft, easily eroded Beaufort sediments of the Karroo Supergroup. Coupled with man-induced soil erosion on a large scale in the catchment, this results in the very turbid, silt-laden waters characteristic of the Great Fish River. The Kowie River, on the other hand, under "normal" flow conditions, is clear and even when flooding has secchi disc readings higher than the Great Fish River under low flow conditions (see above). The substantial differences in the amount and quality of the freshwater inflow into the Kowie and Great Fish estuaries is reflected in the salinity (Table 13) and secchi disc readings (Table 14).

Lowered salinities were recorded throughout the Great Fish estuary during most of the study period. The tidal influence in this system reaches Kaffir Drift 16 km from the mouth (pers. observations). However, only once (December 1982) during the study period were surface salinities >5°/oo (15°/oo) recorded at Station 3, seven km from the mouth. The water at Station 3 was completely fresh at both high and low tide on nine occasions during the monthly gill netting surveys which were conducted over a two-year period. The mean salinity at Station 2 (11°/oo), only three km from the mouth, indicates the lowered salinity regime in this system (Table 13). According to Day (1981)

> "The basic definition of an estuary demands that it must have a measurable variation of salinity within its banks".

The greater portion of the Great Fish River under tidal influence could therefore be classified as "river mouth" rather than a true estuary according to Day (1981).

Table 13. The salinity at the surface and bottom recorded at the gill netting sites in the Great Fish and Kowie estuaries. The sampling periods were Jan. 1981 - Dec. 1982 and Jan. 1981 - Jan. 1982 in the Great Fish and Kowie estuaries respectively.

River	Stn. No.	Distance from mouth (km)	Surface salinity Mean (range)	Bottom salinity Mean (range)
Great Fish	1	0,5	16 (0 - 35)	27 (0 - 35)
	2	3	11 (0 - 35)	23 (0 - 35)
	3	7	1 (0 - 15)	3 (0 - 18)
Kowie	1	2	26 (9 - 35)	30 (14 - 35)
	2	12	10 (0 - 30)	14 (0 - 27)
	3	17	4 (0 - 18)	3 (0 - 14)

In the Kowie estuary, on the other hand, brackish water normally penetrates to the head of the estuary and the upper reaches are only completely fresh for short periods during and after floods. The Kowie would therefore be classified as a "normal" estuary by Day (1981).

Table 14. The secchi disc transparency at the three gill netting sites in the Kowie and Fish estuaries.

Estuary	Stn. No.	Distance from mouth (km)	Secchi disc (om) mean (range)
Great Fish	1	0,5	54 (3 - 200)
	2	3,0	19 (3 - 40)
	3	7,0	8 (2 - 17)
Kowie	1	2,0	117 (50 - 200)
	2	12,0	63 (25 - 175)
	3	17,0	50 (8 - 100)

The seasonal range in water temperatures at the various stations in the Great Fish and Kowie estuaries are given in Table 15 and reflect the warm temperate climate of the area. Further details of salinity and temperature fluctuations in these two estuaries are given below in Chapter 7.

Table 15. The seasonal range in water temperatures at the sample sites in the Kowie and Great Fish estuaries. The month of recording the extreme value is given in brackets.

Estuary	Stn. No.	Distance from mouth (km)	Temp. range (^{o} C)	
			Maximum	Minimum
Kowie	1	2	26,5 (Jan.)	13,0 July
	2	12	28,0 (Jan.)	11,5 July
	3	17	27,5 (Jan.)	10,5 July
Great Fish	1	0,5	28,5 (Jan.)	12,0 June
	2	3	29,5 (Jan.)	11,0 June
	3	7	30,0 (Jan.)	10,5 July

CHAPTER 3. GENERAL METHODS

Regular data collection was restricted to three eastern Cape rivers, the Kowie, Great Fish and Swartkops. These rivers possess different physical as well as biotic characteristics (Chapter 2) and are thought to adequately represent typical *Myxus capensis* habitat types within the eastern Province. Mainly due to logistic considerations, the Kowie was sampled for both adults and juveniles monthly while the other two rivers were sampled approximately every three to four months. During the course of this study all major rivers in the eastern Cape were surveyed for the presence of mullet. Using the gear described below, these surveys were aimed at establishing the presence of and the point of furthest upstream penetration of mugilids. Different gear was used to sample juveniles and adults.

(i) *Juveniles*:

Regular monthly sampling using 2 and 5 mm stretched mesh seine and dip nets was carried out in shallow areas (<1,2 m deep) at the head of the Kowie estuary from February 1975 to December 1977. Irregular netting for juveniles was also conducted at the heads of the Great Fish and Swartkops estuaries and occasionally in other estuaries of the eastern Cape from 1975 to 1982. Under normal flow conditions, the water was sufficiently clear (except in the Great Fish River) to enable the shoals of mullet fry to be located, pursued and netted by sight. Numerous obstacles such as rocks, submerged logs and aquatic macrophytes did not allow set distances to be netted. Under these conditions catches could not be standardized and no attempt was therefore made to calculate C P U E.

The mullet fry were placed in 5 - 10% formalin and fork lengths (FL) recorded. The smaller fish (<30 mm FL) were identified using a microscope by the characteristic tooth structure of each species, as recommended by van der Elst & Wallace (1976).

Seine netting for fry and larger juveniles (<150 mm FL) was also conducted in the freshwater reaches of the three study rivers using a variety of small meshed (8 - 20 mm stretched mesh) nets. These attempts were usually only successful in the Great Fish River in shallow sand-bank type pools, or below barriers to migration in all three rivers where large numbers of upriver-migrating mullet accumulated. Fish >50 mm FL preferred the deeper (>1 m) water of the larger pools and only entered shallow water when attempting to negotiate barriers to migration. The topography of these pools in the Kowie and Swartkops rivers (Chapter 2) precluded the use of seine nets. Although a variety of other gear was used for sampling these areas (see below), catches of juvenile and sub-adult mullet (*ca* 50 - 150 mm FL) were poor.

(ii) *Adults*:

Freshwater reaches.

Initial attempts at sampling adults in the freshwater reaches of the Kowie and Swartkops rivers with seine nets and cast nets were unsuccessful. This was mainly due to the topography of these areas and the ability of large mullet to avoid such nets. Electrofishing also proved unsuccessful because of the limited areas of shallow (<1 m) water. A number of other methods were used with more success and are described below.

(a) Fish traps:

Large (2 m X 1 m X 1 m) funnel-traps consisting of box-like frames of welded 6 mm iron rods covered with 10 mm "anchovy" mesh netting with a single funnel and 3 - 5 m "wings", were set in strategic positions in suitable pools. Small numbers of mullet, usually less than five over a 24 hour period, were captured in this way. The largest number captured during a "setting" was 20 fish. This gear captured fry as well as large adults with minimum damage and provided the majority of specimens for the tagging programme (Chapter 4). The relatively small catches as well as recurrent damage to the traps caused by clawless otters (*Aonyx capensis*) made this method impractical for regular sampling.

(b) Hook and line.

Local mullet anglers usually use a long flexible rod (without a reel), light line buoyed up by small pieces of cork, a sensitive float (usually a porcupine quill) and a small hook baited with soft-bodied insects such as termites (Order Isoptera). The bait is set 0,3 - 2 m below the surface and when hooked the mullet can be lifted out onto the bank within seconds. This method was used in this study, and, although it is unreliable and time-consuming, a total of 146 fish were captured in this way. The majority of these fish were measured, tagged and then released (Chapter 4).

(c) Gill nets.

This proved to be the most consistently reliable method of sampling fish >150 mm FL. Normally one or two fleets of gill nets, each consisting of seven 10 m sections with stretched mesh sizes of 44, 50, 65, 75, 89, 100 and 115 mm joined in series, were set overnight across large pools. Mullet enmeshed in these nets were frequently attacked and eaten by clawless otters as well as terrapins (*Pelomedusa subrufa*). On occasions over 90% of the gill net catch was too badly eaten to provide reliable information. If sufficient numbers were caught during the first few hours of fishing, the gill nets were lifted to avoid unnecessary wastage of fish. As it was difficult to standardize catches under these circumstances, C P U E was not calculated.

As mullet were often isolated in large pools for long periods during dry spells (see Chapter 7), the regular capture of large numbers would probably markedly affect the population size and structure. To reduce this affect, sampling stations usually comprized large pools or two or three adjacent pools and sample sizes were kept as low as possible. During long dry spells, however, the effects of sampling on the mullet populations may have influenced the catch data.

Regular sampling for adult mullet in the freshwater reaches of the Kowie, Great Fish and Swartkops rivers was initiated in mid-1975 and terminated in January 1978. Additional sampling was carried out in the Great Fish River after January 1978 in order to obtain further information for age and growth determinations. The monitoring of growth of mullet fry stocked into selected areas of the Kowie River continued until August 1982.

Water quality tests were carried out at each gill netting station as well as at various points throughout the freshwater reaches of the Kowie, Swartkops and Great Fish rivers. The parameters measured, methods employed and results of these tests are described in Chapter 2.

Estuaries.

Data from initial sampling in freshwater areas indicated that estuarine and marine areas may constitute important habitats for this species during part of its life history. Sampling for adults was therefore extended to include the Kowie and Great Fish estuaries as well as inshore marine areas. The Swartkops estuary was not included as recent fish surveys (Marais 1976; Marais & Baird 1980) failed to capture any adult *Myxus capensis* in this estuary.

The upper reaches of the Kowie estuary (Station A) were incorporated into the freshwater sampling programme discussed above and similar gill netting gear and effort was used. A further gill netting programme in the Kowie and Great Fish estuaries was initiated in January 1981 in order to obtain further data on the breeding biology of *Myxus capensis* as well as details of this species abundance and distribution in a fresh water-dominated estuary. This gill netting programme continued until January 1982 in the Kowie estuary (13 months) and until December 1982 in the Great Fish estuary (24 months).

Netting took place at monthly intervals at three stations in the lower, middle and upper reaches of each estuary. Salinity was the main criterion taken into consideration when the sampling stations were chosen (Chapter 2). One fleet of multi-filament gill nets consisting of six 10 m sections with stretched mesh sizes of 45, 57, 73, 87, 110 and 150 mm joined in series was set at each station. Netting took place overnight from *ca* 16h00 - 18h00 until 07h00 - 09h00. C P U E was estimated as the number (or weight) of fish caught in each gill net fleet set overnight.

The following water quality parameters were recorded at high and low tide at each netting site at the time of netting: water temperature (surface and bottom) using a hand thermometer; salinity (surface and bottom) using an optical salinometer and water transparency using a 20 cm diameter secchi disc. Bottom water samples were obtained using a Hach oxygen sampling bottle.

Information recorded from the fish

The information was recorded from fresh, unpreserved fish and included FL and (occasionally) standard length (SL); individual fish weight to the nearest gram; gonad weight to the nearest 0,1 g; a visually determined gonadal maturity stage (see Chapter 5) and the designation of a fat index value to each fish. In addition, scales (and initially otoliths) were removed for ageing work. When large samples of mullet were captured, as frequently occurred in the Great Fish estuary, individual measurements were recorded from a representative sub-sample. Further details of the recording of data as well as subsequent analysis are described fully in the relevant chapters.

Water quality analysis

Analyses of chlorides, sulphates, turbidity, conductivity and DO were conducted using a Hach Model DR-EL Water Test Kit. Later in the study (1979) a YSI Model 54 Oxygen Meter was also used. Alkalinity was determined by titration against dilute sulphuric acid using phenolthalein and methol orange indicators and pH was measured to the nearest 0,1 using BDH chemical indicators and comparator discs.

CHAPTER 4 . DEMOGRAPHY

INTRODUCTION

In spite of detailed studies of various aspects of the biology of southern African Mugilidae (see Chapter 1), research on age and growth has largely been neglected. The only published study is that of Wallace & van der Elst (1975) on *Mugil cephalus* in St Lucia. These authors estimated the lengths attained at the end of its first year using length frequency data. Apart from unpublished reports on preliminary age and growth data on *Liza dumerili* and *L. richardsoni* in the Swartkops estuary (Marais 1976) and on *L. richardsoni* in the Berg River estuary (Ratte 1977), no further information on age and growth of southern African Mugilidae is available.

Population structure (i.e. frequency of occurrence of the various age or size classes that constitute a population) can give important information on growth, maximum size, mortality and longevity, as well as the contribution of the various size or age classes to population fecundity. Such data may give insights into aspects of a species migratory behaviour. For example, the females of some catadromous species such as eels (Jubb 1964; Tesch 1977) migrate further upstream and reach a much larger size than males. This characteristic appears to have adaptive significance, and is discussed in Chapter 8 . In addition, a population with a large number of year classes tends to be less vulnerable to breeding or recruitment failure and may reflect an adaptation to an unstable environment (Niksolskii 1969). Population structure, therefore, reflects the relationship between a species and its environment.

Knowledge of the age, growth and population structure of a fish species is therefore fundamental to the understanding of its ecology. In addition, this information is essential for the sound management and conservation of any fish species, especially as man-induced changes often cause changes in population structure as well as abundance. The Mugilidae form a major component of the ichthyofauna of nearly all estuarine systems along the southern African coast (Day 1981) and particularly in the eastern Cape (Marais 1981, 1983a, 1983b; this study). As both rivers and estuaries are becoming increasingly altered and degraded by man (Noble & Hemens 1978), baseline studies on the demography of important estuarine and riverine species deserve high priority. A thorough understanding of natural population fluctuations is needed in order to determine changes due to man's activities. This information will be essential if we are to fully understand the ecological effects of any future man-induced changes to these sensitive systems.

In addition, age structure, growth and longevity reflect a species adaptation (at a life history level) to the natural selection pressures of its environment. *Myxus capensis* is more dependent on a freshwater phase in its life cycle than *Mugil cephalus* and therefore shows adaptations in this regard (Bok 1980). Comparative data on age structure and growth could possibly reveal differences in life history strategies that have evolved in response to differences in selection pressures acting on these two species.

The demography of both *Mugil cephalus* and *Myxus capensis* was therefore studied in some detail in the Kowie, Swartkops and Great Fish river systems.

METHODS

Age determinations are fraught with pitfalls. Bagenal & Tesch (1978) state that "no one can claim his age determinations are infallibly accurate". In a recent review of mullet age and growth studies, Quignard & Farrugio (1981) found that results of different researchers showed little agreement. Although these authors reported that most researchers determined age and growth of mullet by means of scales, they concluded that "this method is rather more difficult to apply in the case of the mullet than is that of the other fish living in temperate water". A common error in these studies was the failure to confirm that the scale marks used for ageing were true annuli, i.e. formed regularly once a year. Quignard & Farrugio (1981) considered that many of the reported differences in mullet growth were possibly due to misinterpretation of annuli rather than to real differences in growth rates.

Scale analysis has, however, been used with apparent success to determine age and growth of *Mugil cephalus* in warm temperate regions by a number of workers (e.g. Kesteven 1942; Thomson 1951, 1957; Broadhead 1958; Cech & Wohlschlag 1975). In addition, examination of scales from known-age *Myxus capensis*, stocked into farm dams at the beginning of this study, showed that clear scale rings were deposited once each year in spring. This indicated their suitability for use in ageing studies. An advantage of using scales to obtain age data, rather than other hard parts such as otoliths or opercular bones, is that the fish do not have to be killed. This is particularly important when tagging and recapture studies are undertaken.

Initial attempts at reading untreated otoliths showed no clear pattern of rings and the extra time and labour involved did not appear warranted in view of the relative ease and apparent suitability of scale analyses. To use age data from otoliths (or any other hard part) to validate scale readings is not strictly valid. Agreement of age readings using different hard parts should not be taken as evidence of a valid time scale, unless at least one of the methods has been validated separately (Bagenal & Tesch 1978). Corresponding marks on both structures could, quite possibly, both suggest a wrong age.

In view of the difficulties experienced by other workers in obtaining valid data on mullet age using scales, three additional methods were used to obtain age and growth data in the Kowie River: (i) length frequency distribution analysis; (ii) sampling of known-age fish previously stocked into the Kowie River and (iii) tagging and recapture studies in the Kowie River. It was assumed that if the ageing technique using scale analysis on *Myxus capensis* scales from the Kowie River was found to be accurate, this technique could confidently be used to estimate the age of *Myxus capensis* from the two other rivers. Age estimates of *Myxus capensis* in the Great Fish and Swartkops rivers were therefore made from scale analysis only. *Mugil cephalus* were aged using scale analysis in all sampling areas, while additional growth estimates were obtained from the Great Fish system using length frequency data.

AGE DETERMINATION FROM SCALES

Description of scales

The main features of a generalized mullet scale are illustrated diagrammatically in Fig. 20 . The scales of *Mugil cephalus* have been described in detail by Kesteven (1942). The description of the annuli given by this author corresponds closely to that found for *Mugil cephalus* in this study. Winter bands of closely spaced circuli, a common feature of annuli of many temperate fish species (Tesch 1971), were not usually observed. Scale rings were recognised as "breaks" in the regular disposition of the circuli caused by fragmentation of circuli and by circuli being more widely spaced. Circuli at the outer edge of the annulus were often "cut-off" by circuli laid down at a slightly different angle; this commonly occurred in the anterior shoulder region. Some of these features are shown in Figs.21 - 23. Criteria used for the recognition of false annuli were similar to those mentioned by Broadhead (1958), namely, that they do not occur on all scales of the fish and cannot be traced completely around the scale.

Myxus capensis scales are feebly ctenoid, although cteni were usually absent from scales of larger fish. The concentric circuli are interrupted in the anterior scale region by 6 - 9 radii. These features are illustrated in Fig.24. Interpretation of scale rings on *Myxus capensis* scales proved to be problematic due to the presence of numerous marks or false rings as well as unclear or weakly defined scale rings. True scale rings were recognised as a band of closely-spaced circuli followed by a band of widely-spaced circuli. Clear spaces formed by fragmentation and irregularity of circuli at the outer edge of the closely spaced circuli were often observed and were most prominent at the anterior shoulder of the scale. True scale rings could be traced continuously around the scale through the anterior, lateral and sometimes posterior fields. False rings, on the other hand, were usually discontinuous and often present on only one or two scales of a fish. "Cutting off", where one circuli appears to cut across several other, as described for *Mugil cephalus* scales by Kesteven (1942), usually occurred to a varying degree in the lateral field of the

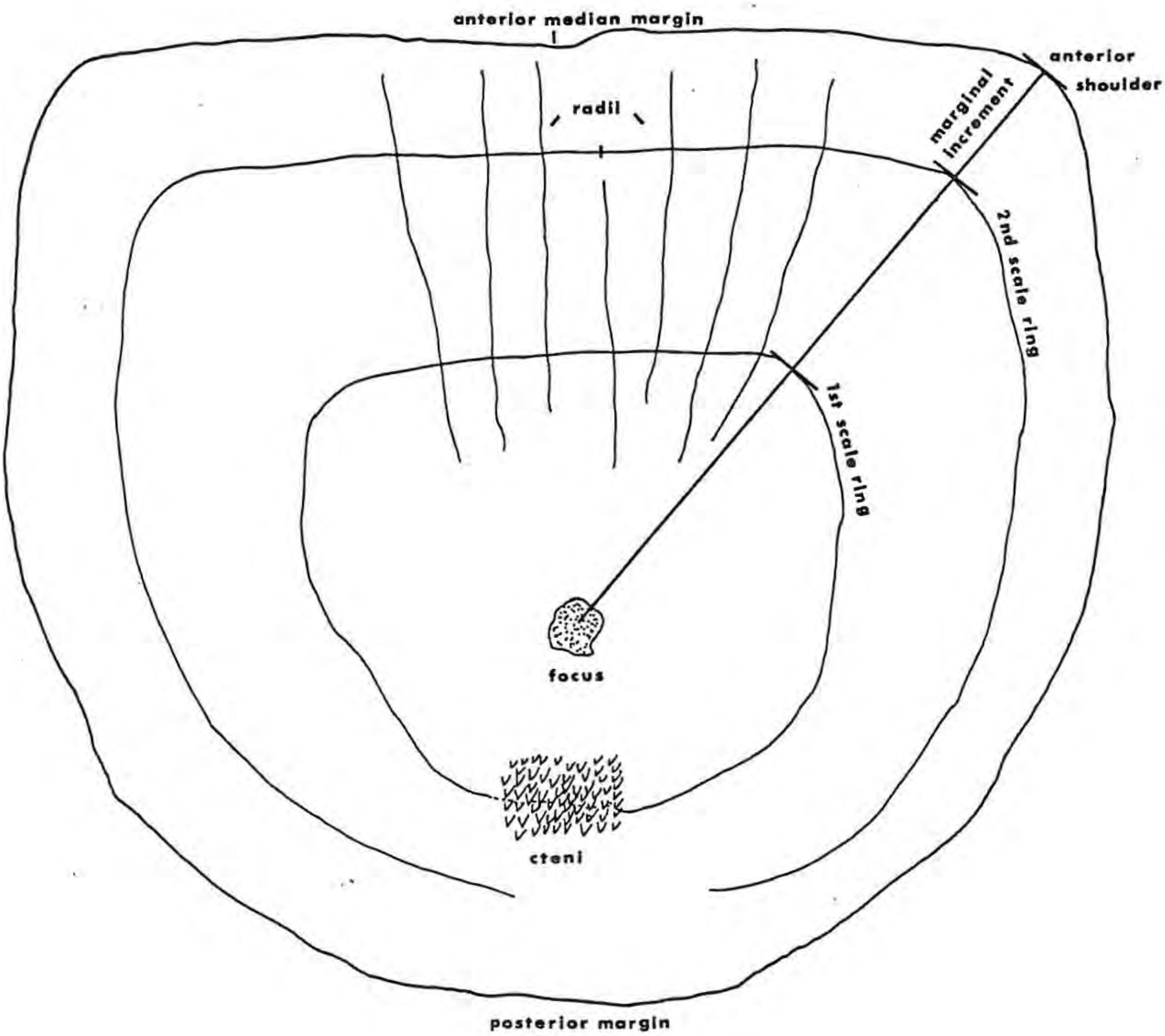


Figure 20. Diagramme of generalized mullet scale showing the various scale features and the measurements recorded.

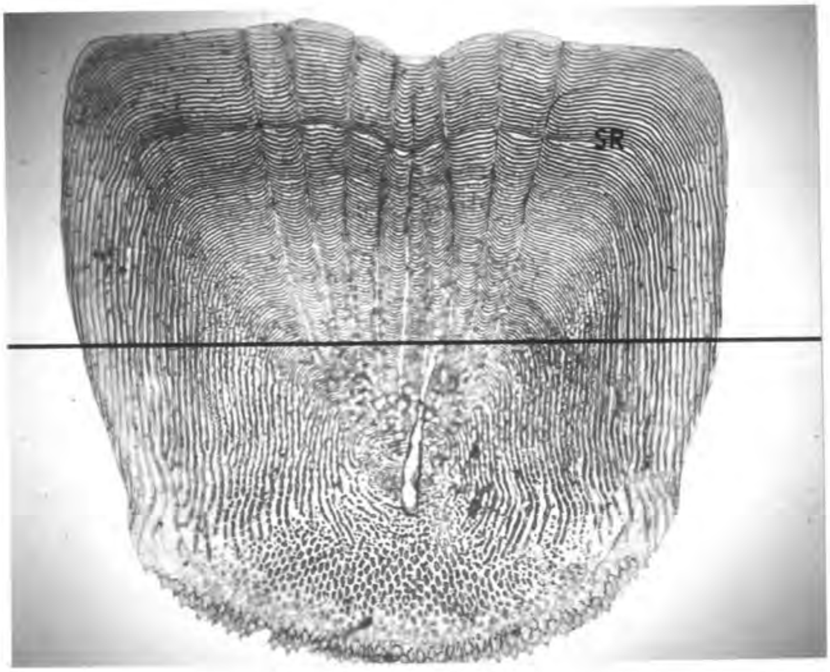


Figure 21. Scale of 1+ year old *Mugil cephalus*, FL 163 mm. Horizontal line is from screen of microfiche reader (48 X). SR = scale ring.

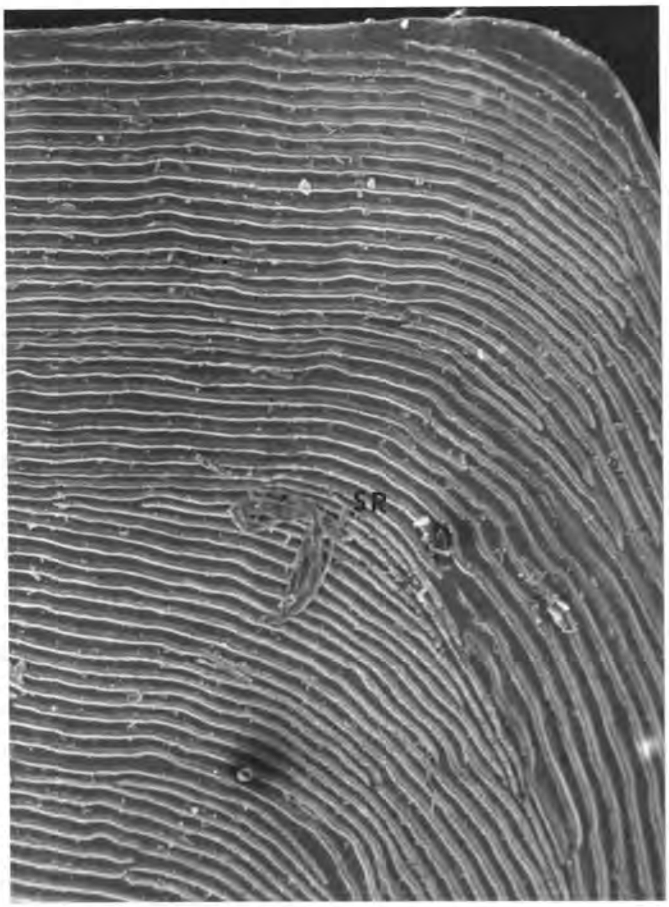


Figure 22. Scanning electron micrograph of anterior portion of *Mugil cephalus* scale showing scale ring (SR). (± 75 X).

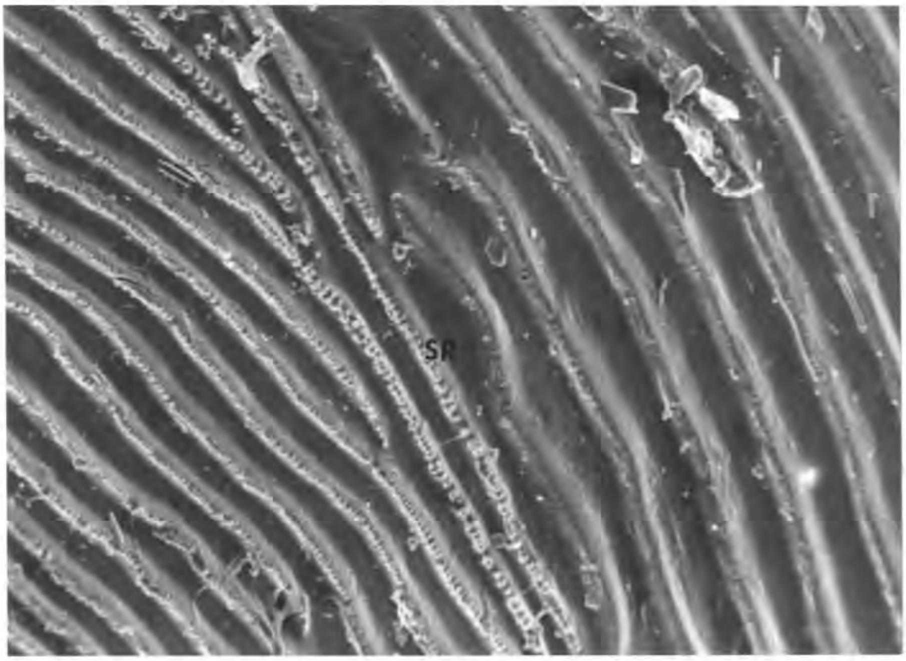


Figure 23. Scanning electron micrograph of scale ring in the anterior shoulder of a *Mugil cephalus* scale (± 150 X). SR = scale ring.

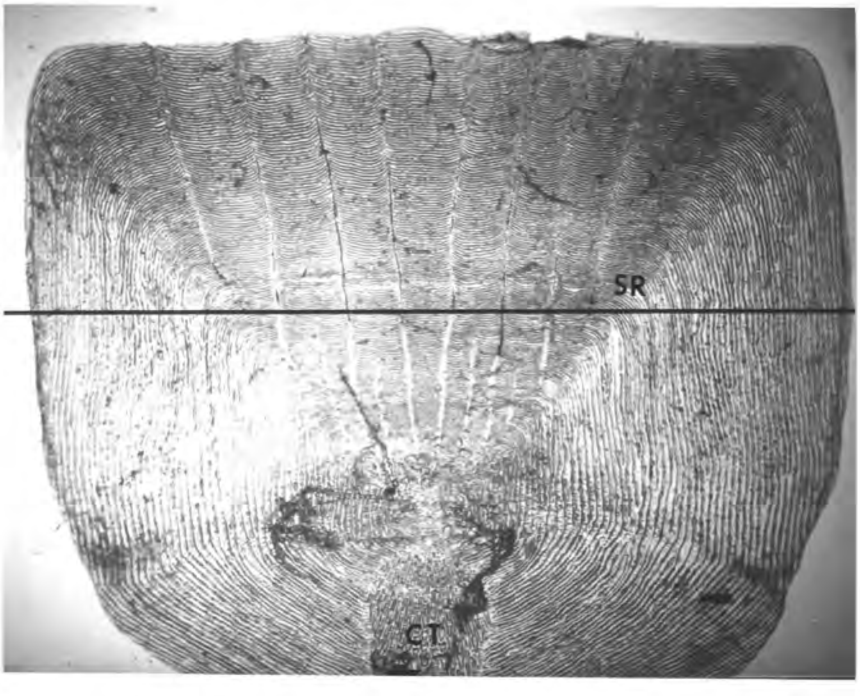


Figure 24. . Scale of 1+ year old *Myxus capensis*, FL 204 mm. 1 = first scale ring; CT = ctenii. Horizontal line is from the screen of microfiche reader.

scale ring. Measurements were taken from the focus to the outer edge of the closely spaced circuli of each annulus.

A further difficulty experienced in analysing scales from both mullet species was caused by the progressive thickening of the centre portion in large scales. This often resulted in the first or second annuli being partly or even totally obscurred in scales of older fish. Similar difficulties have been reported for mullet by a number of authors (Paget 1922 in Hickling 1970; Hendricks 1961; Kennedy & Fitzmaurice 1969; Hickling 1970).

SCALE READING TECHNIQUES

Similar methods were used for analysing the scales of both mullet species. At least six scales from each fish were taken from just above the lateral line and below the anterior edge of the first dorsal fin. Scales from this area were found to be uniformly large and symmetrical. The scales were washed in soapy water and three to eight (usually six) were mounted between glass slides and 'read' using a microfiche reader at 24 or 48 X magnification.

Scale rings were often more clearly defined in the anterior shoulder region. In addition, the anterior median margin tended to be eroded, especially in *Mugil cephalus*. Scale measurements were therefore recorded along the antero-lateral shoulder of the scale, a measuring technique used in other studies on mullet ageing (Broadhead 1958; Chech & Wohlschlag 1975; Grant & Spain 1975a, 1975b & 1975c).

At least three scales from each fish were read and the mean values of the various scale dimensions were calculated. If measurements taken from three scales of a fish differed widely, or true scale rings could not be positively identified, the scales were rejected. In addition, only symmetrical scales with well defined foci were used. The numbers of scales analysed for growth determinations and the percentage rejected are given in Table 16. *Myxus capensis* scales were usually more difficult to interpret than *Mugil cephalus* scales.

TIME OF ANNULUS FORMATION

In order to use scale rings for age determination, it is imperative that the time of formation is known. The size of the marginal increment (distance from the scale margin to the last formed scale ring) will be greatest just before ring formation and smallest immediately after ring formation. The size of the marginal increment was therefore used as an indicator of the recency of ring formation. However, as scale growth decreases with size, changes in the marginal increment of scales were only determined for fish less than two years of age, so as to minimize bias.

Ring formation occurs in *Myxus capensis* during spring (October and November) each year in the Kowie River (Fig. 25). Scale rings were also formed at this time in *Myxus capensis* from the other rivers sampled. Ring formation in *Mugil cephalus* from the Great Fish estuary (Fig. 26), as well as from all the other populations, also occurs in spring (September, October and November). In temperate regions, annuli in fishes are usually formed during periods of slower growth during winter and become apparent when growth resumes in summer (Tesch 1971). *Myxus capensis* and *Mugil cephalus*, in both estuarine and freshwater habitats in the eastern Cape, appear to fit this pattern. In other temperate regions, annulus formation in *Mugil cephalus* also occurs in spring when growth commences after the winter cessation (Thomson 1951). A similar time of annulus formation has been reported for other Mugilidae (Thomson 1957; Kennedy & Fitzmaurice 1969; Hickling 1970).

False rings were common on scales of both *Myxus capensis* and *Mugil cephalus* in this study and may be due to a temporary disruption of feeding intensity during floods. As both species feed mainly on benthic organisms and detritus, turbulance during floods would place this rich upper-benthic food source in suspension and make feeding difficult. In addition, periods of active migration during high river flow are probably also associated with reduced feeding levels. In this regard, Marais (1982) ascribed the virtual disappearance of mullet from the channel-like Sundays estuary after heavy floods, to the removal of the rich surface benthic layer by floodwaters. It is perhaps also significant that in trophical waters, annuli are formed on mullet scales

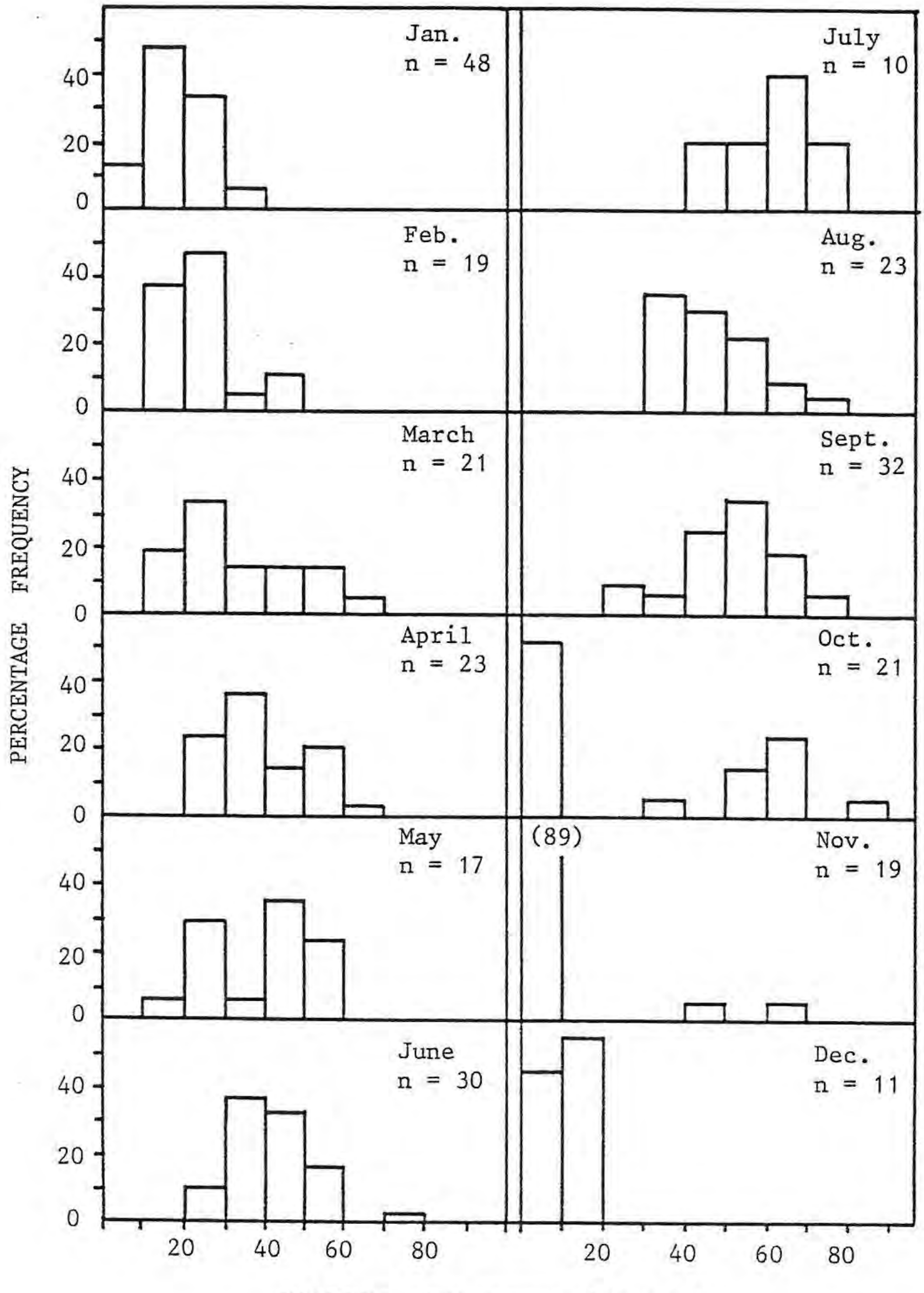


Figure 25. The size of the marginal increment of scales from 284 *Myxus capensis* caught in the Kowie River. Data are from scales with one or two rings only.

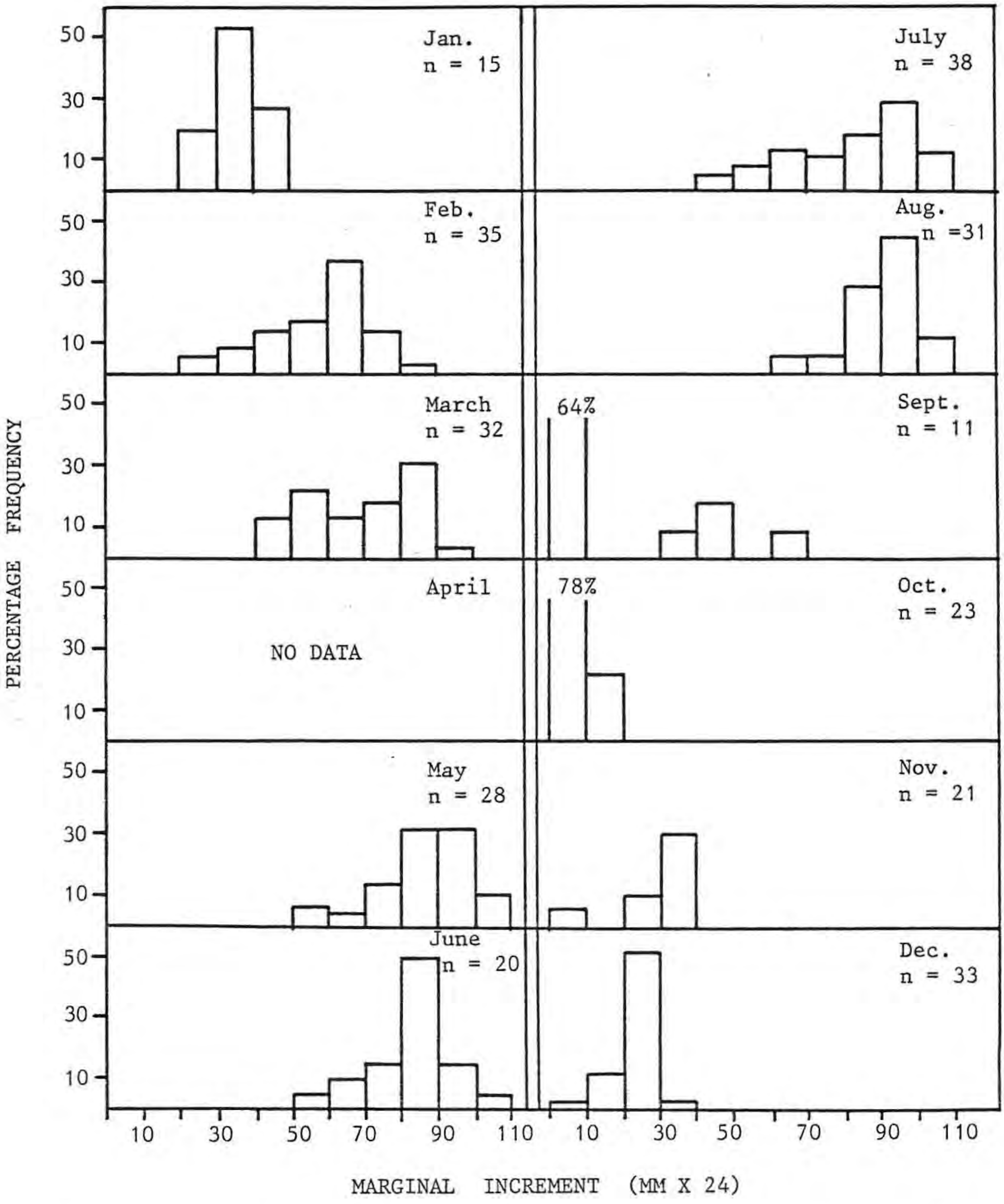


Figure 26 . The size of the monthly marginal increment of scales of *Mugil cephalus* from the Great Fish estuary. Data from 287 fish with scales containing one or two rings only.

during the monsoon periods, when lowered salinities, strong currents and increased turbidity in the estuarine and littoral waters cause major disruptions to benthic fauna and flora (Pillay 1954; Grant & Spain 1975). Similarly, in *Barbus holubi* and *Barbus kimberleyensis* in Lake le Roux, false checks on scales and otoliths were attributed to sudden increases in turbidity during the growing season (Tomasson 1983). The reduced field of vision at this time was thought to adversely effect feeding in these zooplankton feeders.

Table 16. The numbers of fish from which scales were examined and the percentage of rejected scales. (FW = fresh water; EST = estuary).

Species	River System	No. of fish from which scales were examined	% rejected
Myxus capensis	Kowie (FW)	656	30
	Swartkops (FW)	221	30
	Great Fish (FW)	172	27
Mugil cephalus	Kowie (EST)	239	19
	Kowie (FW)	104	25
	Swartkops (FW)	108	25
	Great Fish (FW)	99	9
	Great Fish (EST)	413	8

BACK-CALCULATION OF LENGTHS

In order to back-calculate fish lengths from scale rings, the relationship between fish length and scale radius has to be known. Hile (1970) has suggested that the body scale relationships may differ between populations of the same species. The FL-scale radius relationships of all mullet populations studied were therefore established using least squares regression analysis for the equation : $y = ax^b$, where y = fork length, x = scale radius and b = slope of the regression line. This relationship is curvilinear for both *Myxus capensis* and *Mugil cephalus* from all the study areas (Table 17 and Figs.27 & 28).

Back-calculations were therefore made using Weatherley's (1972) equation:

$$FX = FY \frac{BX^b}{BY^b},$$

where FX = fish length to be determined; FY = fish length at capture; BX = distance from a scale focus to a scale ring; BY = scale radius at capture and b = slope of regression line of fork length on scale radius. Calculations were made using the 'b' values computed for each population (Table 17).

The mean observed length at age, i.e. the FL recorded from fish at the time of ring formation, was also calculated in order to compare these with lengths obtained using the back-calculation technique. The numbers of fish captured at the time of ring formation were, however, limited. Fish captured just prior to ring formation during the minimum growth period in winter, were therefore used to augment the observed lengths at age data.

MATHEMATICAL MODEL OF GROWTH

To enable generalized comparative descriptions of growth of the various mullet populations to be made, the growth data were fitted to the von Bertalanffy (1957) growth model in the form of:

$$L_t = L_\infty \ (1-e^{-K(t-t_o)})$$

where L_t = fork length at age t

L_∞ = maximum theoretical size (asymptotic length)

K = rate at which L_∞ is attained

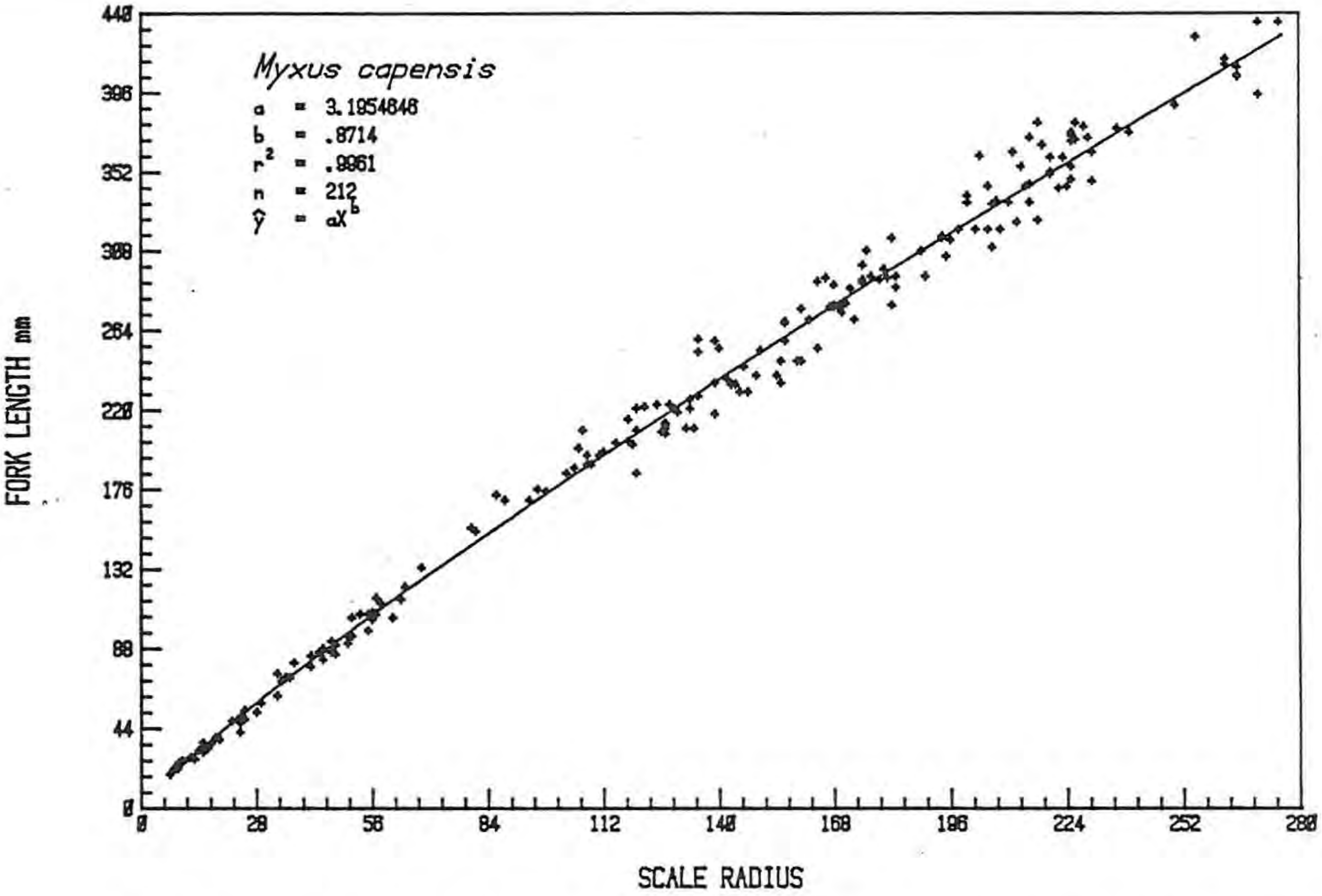


Figure 27 . The relationship between fish length and anterior scale radius (mm X 24) for *Myxus capensis* from the Kowie River.

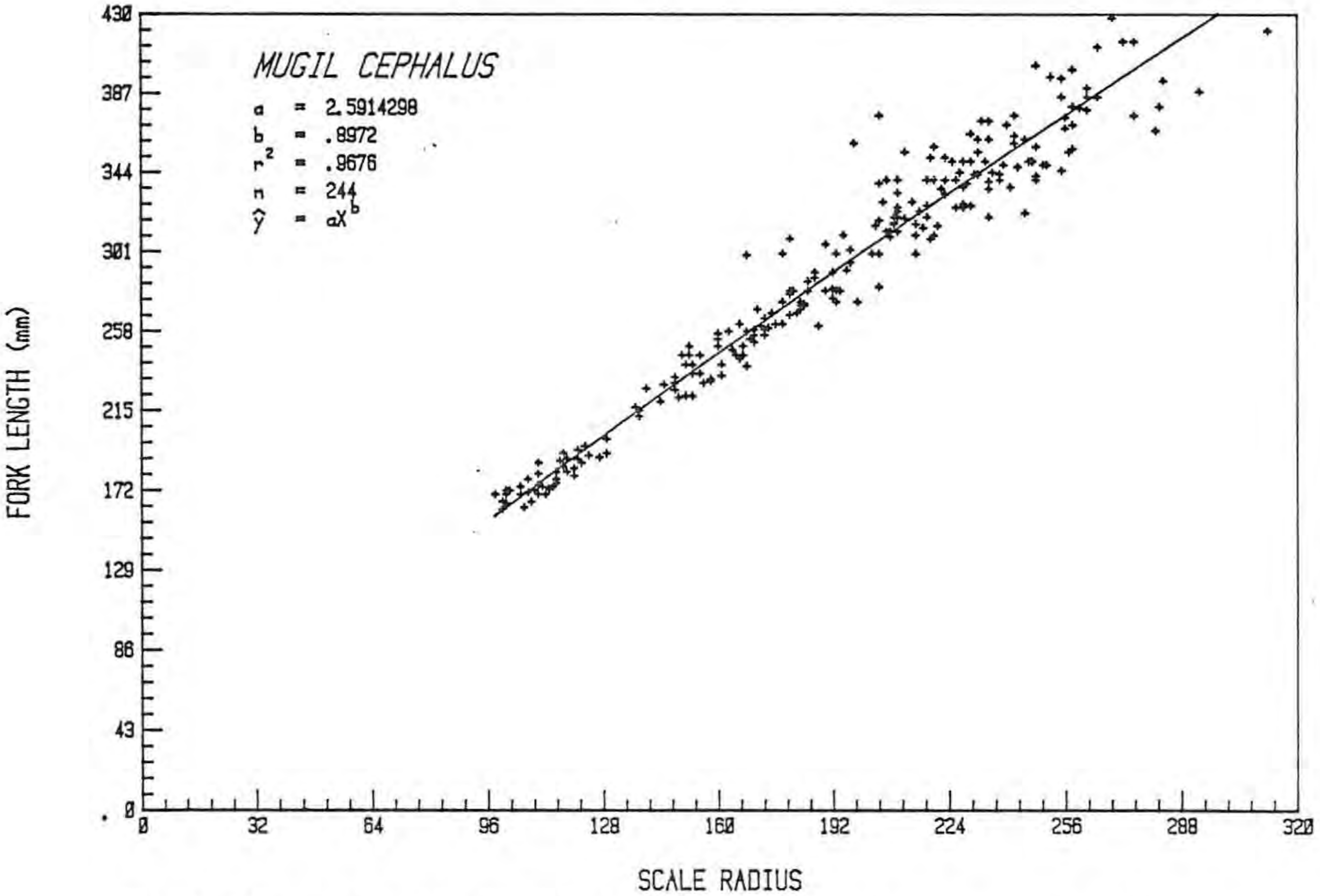


Figure 28 . The relationship between fork length and anterior scale radius (mm X 24) for *Mugil cephalus* from the Great Fish estuary.

t_o = time at which the fish length would theoretically be zero if growth took place according to the above equation.

L_∞ was obtained from a Walford Plot (Walford 1946), at the point where the growth line intersects the 45° diagonal. Due to the oblique intercept of the Walford line with the 45° diagonal, the K and L_∞ values were calculated mathematically using the method of Everhard *et al.* (1975).

The von Bertalanffy growth model implies that growth rate is a constant function of body size alone (Cloern & Nichols 1978), and does not therefore take into account seasonal variations in growth rate. However, in this study the models were constructed using the lengths attained at the end of each growth season, thus ignoring the within season changes in growth rate. The model should therefore be a valid description of annual growth.

Table 17. The relationship between FL and scale radius described by $Y = ax^b$ (where Y = FL (mm) = 'a' constant and 'b' = slope. for *Myxus capensis* and *Mugil cephalus* from the various study areas.

Species	River System	a	b	r^2	n
Myxus capensis	Kowie (FW)	3,1955	0,8714	0,99	212
	Swartkops (FW)	3,0895	0,8778	0,93	158
	Great Fish (FW)	3,1886	0,8724	0,98	125
Mugil cephalus	Kowie (EST)	2,7648	0,8874	0,98	165
	Kowie (FW)	3,1440	0,8543	0,97	87
	Swartkops (FW)	2,9879	0,8818	0,94	80
	Great Fish (FW)	2,7458	0,8858	0,96	78
	Great Fish (EST)	2,5914	0,8972	0,97	244

GROWTH RATE FROM LENGTH FREQUENCY DISTRIBUTION

Due to size selectivity of gill nets, length frequency data must of necessity be viewed with caution. However, the extended period over which the fish were sampled as well as the wide range of gill net mesh sizes used (see Chapter 3), does allow some interpretation of modal progressions of length frequencies.

The extended spawning period as well as the migratory behaviour of *Myxus capensis* (Bok 1979), suggests that length frequency analysis for growth estimates would be of limited value. However, the extended periods of low flow common in the Kowie River effectively 'trap' the mullet in large pools (see Chapter 7). During these periods regular sampling and length frequency analysis can reveal information on growth, without recruitment or emigration altering the size distribution of the fish. Sampling of *Myxus capensis* in rivers other than the Kowie was too irregular to enable length frequency analysis to reveal useful information on growth.

Mugil cephalus has a comparatively short spawning period, with a pronouned peak over 2 - 3 months. Length frequency data should therefore be suitable for obtaining information on age and growth.

GROWTH RATE FROM PREVIOUSLY STOCKED FISH OF KNOWN SIZE AND AGE

Growth of most fish species can fluctuate widely depending upon environmental conditions (Weatherly 1972). The growth of mullet stocked into man-made impoundments may therefore differ considerably compared to natural populations in riverine areas. Comparison of such data for *Myxus capensis* and *Mugil cephalus* in the eastern Cape (Chapter 6) with those of natural populations in this study, may therefore be of little value. However, conditions in parts of the Kowie River appeared suitable for the stocking of known age and size fish and the subsequent monitoring of growth.

Two areas in the upper Kowie River were therefore stocked with juvenile mullet of known age and size which had previously been captured in freshwater at the head of the Kowie estuary:

Site A. A large pool at Station 4a (described in detail in Chapter 2). Regular sampling at this site had established the presence of only a few mullet below 250 mm FL. It was assumed, therefore, that the growth of stocked mullet fry could be followed, using length frequency analysis, for up to two years before "mixing" with naturally occurring stocks would occur. This site was stocked with 3 000 *Myxus capensis* on 1-IX-1979.

Site B. A large pool 100 m downriver of the Grahamstown-Port Alfred road bridge over the Bloukrans River, 47 km upriver from the head of the estuary. Mullet had previously been plentiful in this area, but had recently disappeared due to the erection of a high weir eight km downriver which effectively prevents upriver migration (Bok 1980). This site was stocked with about 1 300 *Myxus capensis* fry on 1-IX-1979.

GROWTH RATE FROM TAGGING AND RECAPTURE

External tags, such as those used in this study, can cause a reduction in growth rate (Bagenal & Tesch 1978). Growth data obtained using this technique should therefore be evaluated with caution. However, as tagging can only retard growth, estimates of growth rates from tagged fish can be used to confirm that growth rates obtained from other techniques are not overestimates. Thus, if growth estimates from tagging are similar to those obtained from other methods, it is unlikely that the latter growth estimates are too high.

The tagging programme concentrated on *Myxus capensis* in the Kowie River as this was the most intensively sampled river. In addition, the Kowie River is a popular mullet fishing river. Contacts with riparian farmers as well as local mullet fishermen were fostered and maintained to ensure that the capture of tagged fish were reported.

Juvenile mullet, about 50 - 100 mm FL, were tagged with Floy FTF fingerling tags inserted immediately anterior to the first dorsal fin. However, initial feasibility studies on mullet tagged in this way and kept in aquaria for observation, were discouraging. Although both Malachite green and Terramycin ointment were applied to the tag wound, over 90% of tagged fish developed chronic fungal (*Saprolegnia sp.*) infections due to the effect of handling. Tagging of fish <100 mm Fl was therefore abandoned.

Mullet >100 FL were tagged with Floy FD 67 anchor tags. The T-bar of the tag was inserted through the dorsal rays near the front of the first dorsal fin and terramycin ointment applied to the wound. Only undamaged fish captured in traps or by hook and line were tagged. The procedure of recording the FL using a measuring board, weighing the fish (in a foam-lined dish) to the nearest gram and inserting the tag, usually took less than one minute. A total of 228 *Myxus capensis* were tagged and released in the Kowie River in this way.

POPULATION STRUCTURE AND LENGTH-WEIGHT RELATIONSHIPS

As mentioned in Chapter 3 , gill netting proved to be the most practical and consistent method of sampling in nearly all areas. The population structure obtained using this method may therefore be biased by inadequate or selective sampling in spite of the range of gill net mesh sizes used. However, as the same gill netting gear was used to sample all the study areas, valid comparisons between these catches could be drawn. On occasions large numbers of mullet < 150 mm FL were caught using seine nets and traps (see Chapter 3). Details of data recorded from the captured fish are given in Chapter 3 .

As size at first sexual maturity in these mullet was roughly 250 mm FL for *Myxus capensis* and 300 mm FL for *Mugil cephalus* (Chapter 5), fish below and above this size were considered to be juveniles and adults respectively. The length-weight relationship in the form of body-weight (g) = aFL^b mm for juveniles and adults (sexes considered separately) were calculated for each mullet population by least-squares regression analysis.

Age-length key

In order to obtain an approximate estimate of the age distribution of the various mullet populations, an age-length key was constructed as described by Ricker (1975). Using the lengths at age data obtained from scale analysis (e.g. Table 23), the percentage of each age among fish of a given length group was calculated. Each mullet population as well as males and females were considered separately. This age-length key was then used to convert the total length frequency distribution of the various mullet populations to age distribution.

An important requirement when constructing an age-length key is that the data are from a representative sample of fish from the population being aged (Ricker 1975). The requirements as stipulated by Ricker (1975) were met. Scale samples were taken in the field so as to ensure that scarce age groups of the catch were adequately represented, i.e. a fixed sub-sampling method was used. This method is recommended by FAO (1981), as opposed to using a random sub-sample when constructing an age-length key.

RESULTS AND DISCUSSION

Myxus capensis

AGE DETERMINATION FROM SCALES

The back-calculated lengths at age from scales as well as the observed lengths at age for *Myxus capensis* from the Kowie, Swartkops and Great Fish rivers are given in Tables 18 - 22.

In both the Kowie and Swartkops rivers the observed lengths at age data agree fairly closely with the back-calculated data. In the Great Fish River, insufficient numbers of suitable fish were sampled to give reliable observed lengths at age data.

As *Myxus capensis* is thought to spawn virtually all year round (Chapter 5) , fish spawned in the middle of the growth season would be expected to have intermediate lengths at time of annulus formation. A shoal of such intermediate-sized fish were seine netted 11 km upriver from the Kowie estuary in January 1978. These fish ranged from 80 - 120 mm FL at the time of capture and possessed one newly formed annulus on their scales. Back-calculation showed that the annuli had formed when the fish were about 50 - 80 mm FL, i.e. about half that of average length at age one. These fish had therefore probably been spawned approximately midway through the previous growth season.

Table 18 Mean back-calculated fork lengths (mm) at age for male and female *Myxus capensis* from the Kowie River obtained from scale measurements. 95% confidence intervals are given in brackets.

No. of rings at capture	No. of fish	Length at age 1	2	3	4	5
				Males		
1	15	125 (8,6)				
2	70	137 (4,9)	236 (7,3)			
3	48	132 (5,1)	225 (8,8)	285 (6,2)		
No. of fish	133	133	118	48		
Mean FL		134 (3,2)	231 (5,6)	285 (6,2)		
Length increment			97	54		
				Females		
1	22	126 (15,0)				
2	75	134 (5,0)	239 (8,1)			
3	49	136 (5,6)	242 (8,1)	306 (7,6)		
4	9	146 (13,7)	252 (14,4)	324 (11,1)	369 (9,2)	
5	5	175 (30,7)	270 (33,3)	333(29,8)	378 (21,0)	412 (6,1)
No. of fish	160	160	138	63	14	5
Mean FL		135 (3,7)	242 (5,5)	311 (6,4)	372 (9,4)	412 (6,1)
Length increment			107	69	61	40
				Sexes Combined		
No. of fish	293	293	256	111	14	5
Mean FL		135 (2,5)	237 (3,9)	300 (4,5)	372 (9,4)	412 (6,1)
Length increment			102	63	72	40

Table 19. Observed lengths at age of *Myxus capensis* from the Kowie River (for details of calculation see text). 95% confidence intervals are given in brackets.

Age	Mean fork length (mm)						Sex Comparison (t-test)
	Male	n	Female	n	Sexes combined	n	
1					112(8,2)	7	
2	207(8,6)	10	218(6,3)	19	214(5,2)	29	N.S. P >0.05 t=1,88
3	280(15,7)	14	300(13,0)	12	289(10,3)	26	N.S. P >0.05 t=1,92
4	313(10,6)	15	360(5,3)	14	336(5,8)	29	Sig. P <0.01 t=7,34
5			395(16,7)	4	395	4	

Table 20. Average back-calculated fork lengths (mm) at age for male and female *Myxus capensis* from the Swartkops River obtained from scale measurements. 95% confidence intervals are given in brackets.

No. of rings at capture	No. of fish	Length at age 1	2	3	4
			Males		
1	16	143 (11,8)			
2	37	130 (6,1)	220 (8,7)		
3	6	127 (12,0)	219 (18,4)	279 (19,2)	
4	1	121	201	278	315
No. of fish	60	60	44	7	1
Mean FL (mm)		131 (5,1)	219 (7,7)	279 (19,2)	315
Length increment			86	60	36
			Females		
1	10	145 (16,1)			
2	38	128 (9,2)	225 (14,6)		
3	30	135 (8,2)	229 (7,9)	297 (7,2)	
4	16	121 (10,3)	210 (11,8)	283 (12,7)	333 (15,2)
No. of fish	94	94	84	46	16
Mean FL (mm)		131 (1,3)	223 (7,1)	292 (6,4)	333 (15,2)
Length increment			92	69	41
			Sexes Combined		
No. of fish	154	154	128	53	17
Mean FL (mm)		132 (3,6)	222 (5,4)	290 (5,9)	332 (15,2)
Length increment			90	68	42

Table 21. Observed lengths at age of *Myxus capensis* from the Swartkops River (males and females) from scale readings (for details of estimation see text). Sample size (n) is given in brackets.

Age (yrs)	Mean FL mm Male (n)	Female (n)	Both Sexes (n)
1		too few caught	
2	233 (5)	231 (5)	232 (10)
3	273 (15)	285 (13)	279 (28)
4		348 (21)	

Table 22. The mean back-calculated fork lengths (mm) at age obtained from scale analysis for male and female *Myxus capensis* from the Great Fish River. The 95% confidence intervals are given in brackets.

No. of rings at capture	No. of fish	Length at age 1	2	3	4
			Males		
1	10	132 (15,5)			
2	15	130 (8,1)	215 (9,1)		
No. of fish	25	25	15		
Mean FL (mm)		131 (7,8)	215 (9,1)		
Length increment (mm)			84		
			Females		
1	9	134 (12,4)			
2	46	127 (4,9)	216 (8,4)		
3	10	125 (12,4)	199 (16,1)	263 (16,1)	
4	6	141 (8,0)	216 (8,0)	310 (8,0)	357 (8,0)
No. of fish	71	71	62	16	6
Mean FL (mm)		129 (3,9)	213 (4,0)	280 (13,1)	357 (8,0)
Length increment			84	71	73
			Sexes combined		
No. of fish	96	96	77	16	6
Mean FL (mm)		129 (3,6)	214 (5,6)	284 (9,8)	357 (8,0)
Length increment			85	70	73

Table 23. The length distribution of *Myxus capensis* from the Kowie River for different scale annuli.

FL (mm)	Scale annuli						
	1	2		3		4	5
		male	female	male	female	female	female
41 - 60	2						
61 - 80	4						
81 - 100	17						
100 - 120	20						
121 - 140	4						
141 - 160	3						
161 - 180	5						
181 - 200	13						
201 - 220	34	5	4				
221 - 240	16	11	11				
241 - 260	7	7	5	1			
261 - 280	1	15	8		2		
281 - 300		25	18	8	1		
301 - 320		14	23	23	8		
321 - 340		1	5	12	9		
341 - 360			8	2	17		
361 - 380					11	3	
381 - 400						3	2
401 - 420						3	3

In general, however, the variation in the lengths at age data of *Myxus capensis* calculated from scales is not excessive (Table 23). A possible explanation may be that although *Myxus capensis* spawns throughout the year, a pronounced spawning peak normally occurs in spring. As this is the time of annulus formation, these fish will form their first annulus after a full season's growth. In addition, fish spawned in autumn or winter will show limited growth before the following spring and should therefore form their first ring close to the scale focus. As mentioned earlier, the progressive thickening of the central portion of the scale can obscure growth rings close to the focus. Also, annulus formation was never observed in *Myxus capensis* <40 mm FL (Table 23). It is possible, therefore, that scales from fish spawned in the autumn and winter (a period of about six - eight months) could be read as being one year old in their second spring. However, as limited growth is thought to take place in these "extra" months, (see below), the size of these 1+ year old fish would be similar to that of the true 12 month old fish. This effect, combined with the peak spawning in spring, probably reduces the variation in lengths at age expected to result from a prolonged spawning. For practical purposes, therefore, the time of annulus formation (spring) can be taken as effectively coinciding with the "birthday" of *Myxus capensis*.

As the back-calculated values are based on more complete data, age estimates using this method were used when comparisons with the three other ageing techniques were made.

GROWTH RATE OF *MYXUS CAPENSIS* FROM LENGTH FREQUENCY DISTRIBUTION

Gill net catches revealed reasonably clear information on growth only at stations 3 and 4 in the Kowie River. As each station consisted of two large pools, adjacent to each other but usually effectively separated in terms of fish movement, the length frequency data from each pool were considered separately (Figs. 29 to 34).

Estimates of the modal progressions of fork lengths extracted from Figs 29 - 34 are given in Table 24. The comparatively rapid growth in summer compared to winter is seen in the data from stations 4a and 4b. Winter growth in length was estimated at 2,5 and 1,3 mm per month respectively, while summer growth was estimated at 7,5 and 5,6 mm per month respectively. Water temperatures in the Kowie River dropped below 13° C in June, July and August (see Chapter 2). It is probable that growth ceases during these months and takes place at very reduced rates during the slightly warmer "winter" months of May, September and October when the average water temperatures ranged from 15,8° C to 19,8° C (Chapter 2).

Faster female growth is also indicated by data from station 4b (Fig. 33 and Table 24) where the length frequencies for each sex are given separately. The female fish grew 4,1 mm/month compared to 2,3 mm/month for males over a period of a year. The years growth of male fish estimated from the modal progression of lengths at station 4b(290 - 315 mm FL), corresponds closely to the growth estimated using back-calculation for three to four year old male fish from the Kowie River (285 - 315 mm FL). The length frequency data of female growth over a year (315 - 360 mm FL) is similar to the back-calculated value for three to four year old fish (311 - 372 mm FL). A close agreement in growth estimates using length frequency analysis and back-calculation from scale data, is therefore apparent.

GROWTH RATE OF *MYXUS CAPENSIS* IN THE KOWIE RIVER FROM PREVIOUSLY STOCKED FISH.

The capture of the previously stocked *Myxus capensis* during the first year after release proved problematic. Small-meshed gill nets were not available

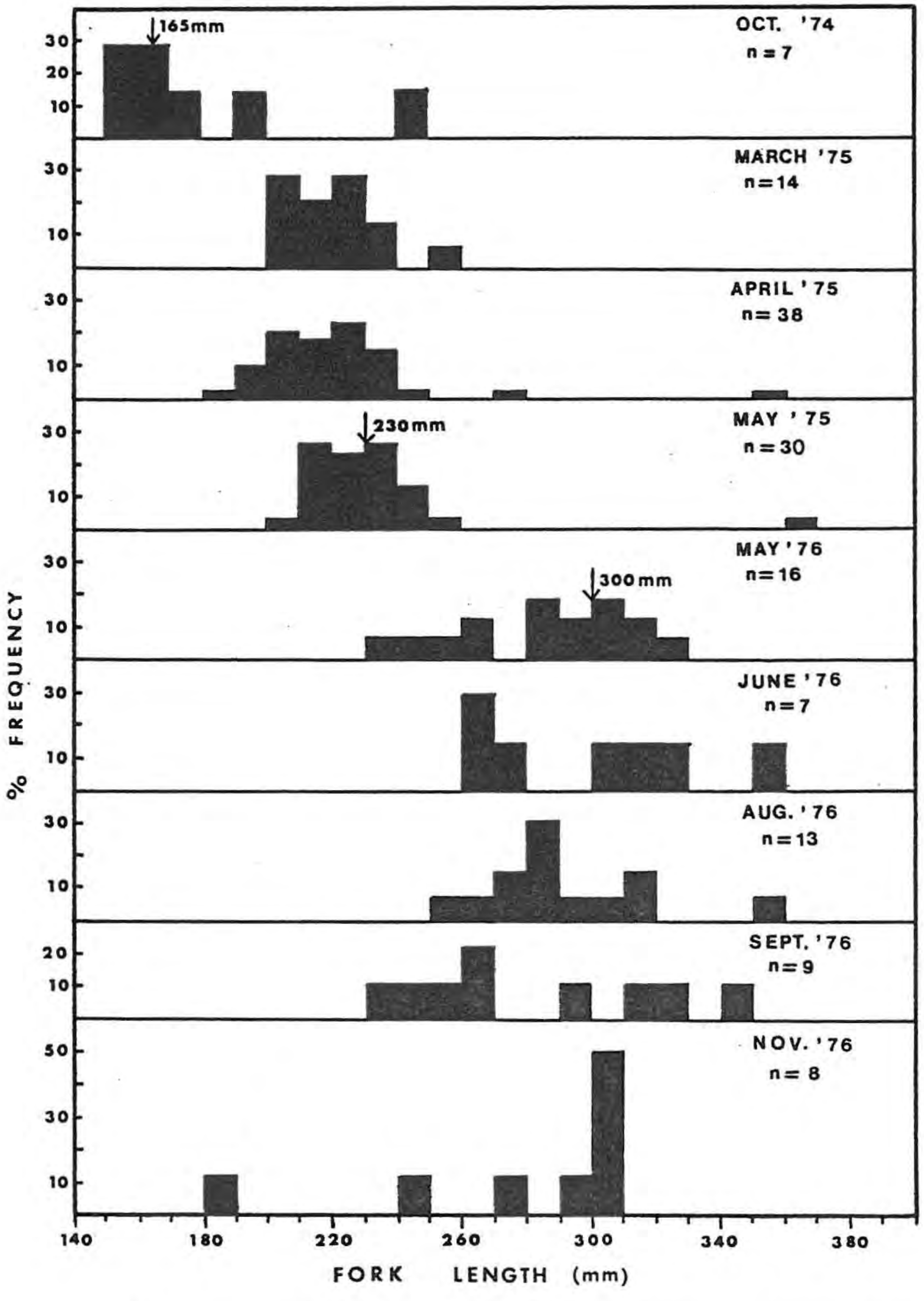


Figure 29. The length frequency distribution of *Myxus capensis* caught in gill nets at station 3a in the Kowie River.

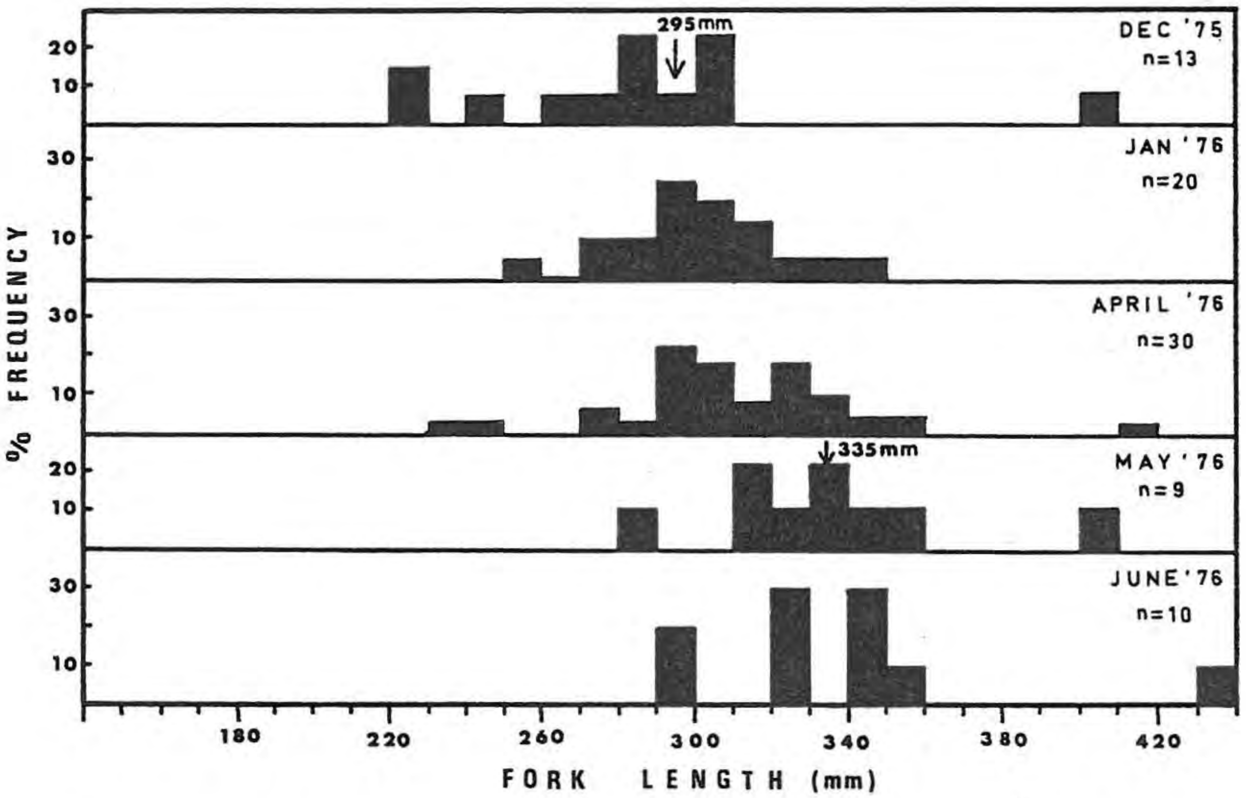


Figure 30. The length frequency distribution of *Myxus capensis* caught in gill nets at station 3b in the Kowie River.

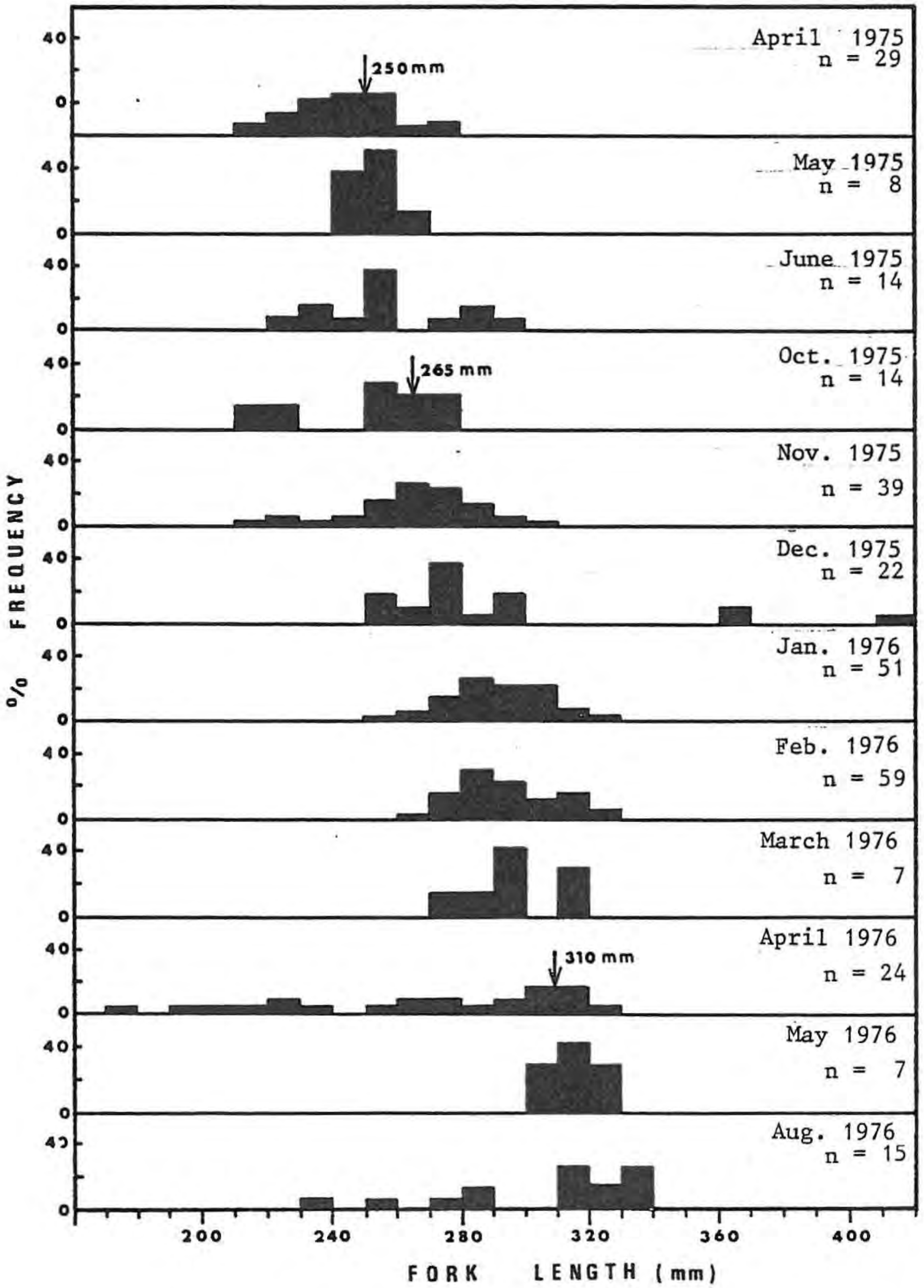


Figure 31. The length frequency distribution of *Myxus capensis* caught with gill nets at station 4a in the Kowie River.

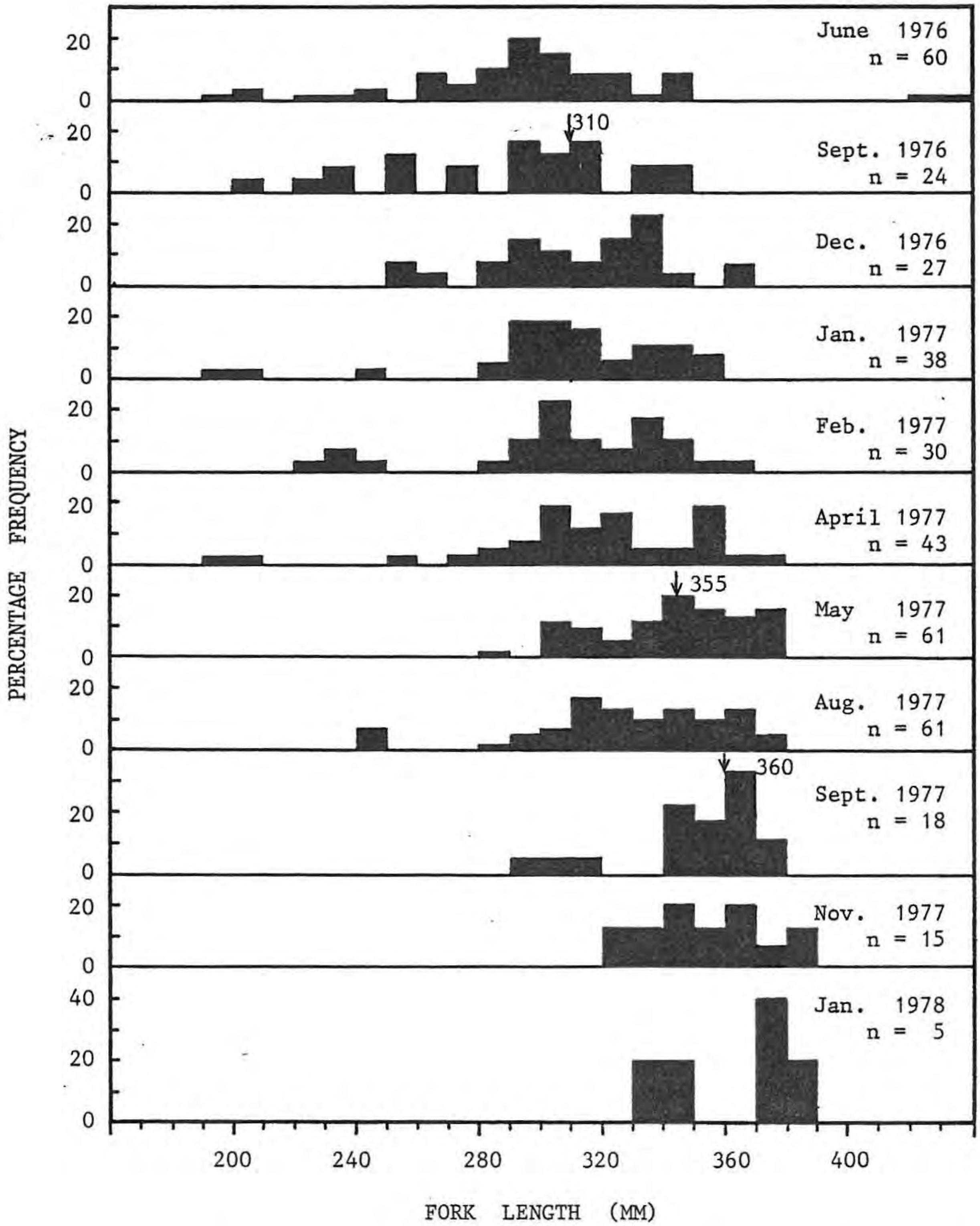


Figure 32. The length frequency distribution of *Myxus capensis* at station 4b in the Kowie River over the study period.

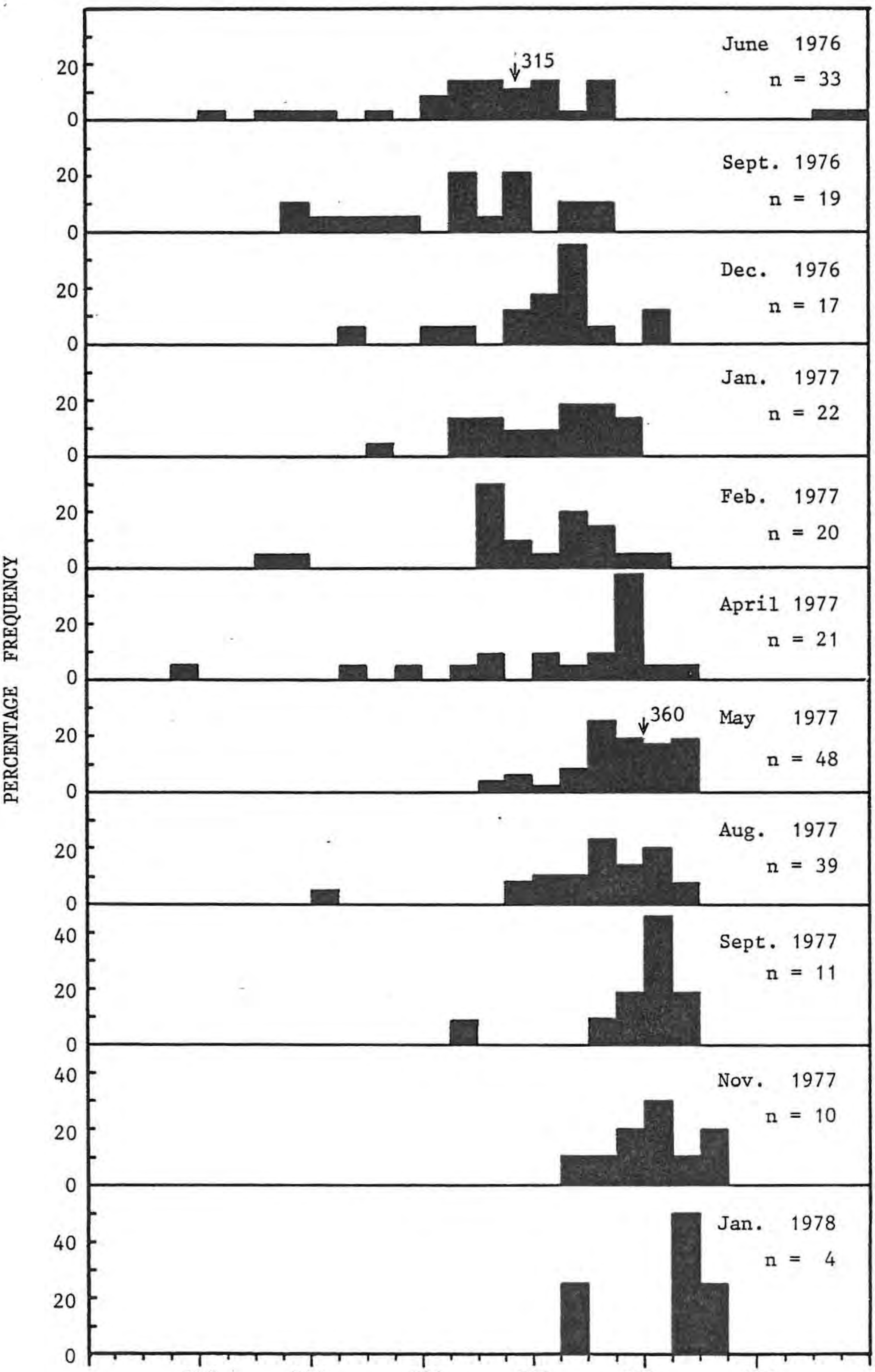


Figure 33. The length frequency distribution of female *Myxus capensis* at station 4b in the Kowie River over the study period.

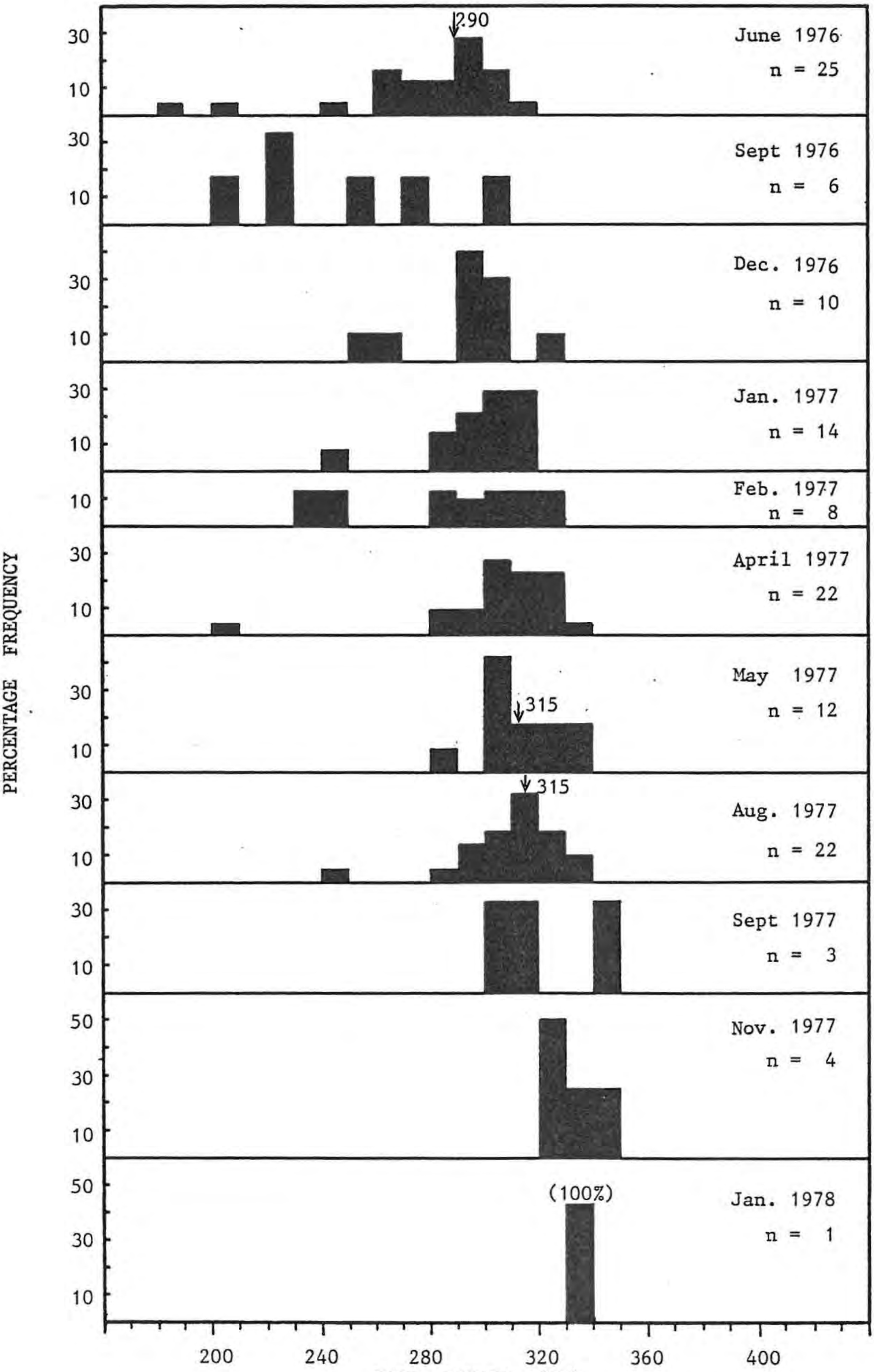


Figure 34. The length frequency distribution of male *Myxus capensis* at Station 4b in the Kowie River over the study period.

Table 24. Estimates of the modal progressions of fork lengths of *Myxus capensis* caught using gill nets in four pools in the Kowie River. The data were extracted from length frequency graphs (see Figs. 29 - 34).

Stn.	Time period	No. of months	Season	Modal progression of FL (mm)	Total growth (mm)	Growth (mm/per month
			Sexes combined			
3 (a)	Oct '74-May '75	7	summer	165 - 230	65	9,3
	May '75-May '76	12	whole year	230 - 300	70	5,8
	Oct '74-May '76	19	2 summers & 1 winter	165 - 300	135	7,1
3 (b)	Dec '74-May '76	5	summer	295 - 335	40	8,0
4 (a)	April '75-Oct '75	6	winter	250 - 265	15	2,5
	Oct '75-April '76	6	summer	265 - 310	45	7,5
	April '75-April '76	12	whole year	250 - 310	60	5,0
4 (b)	Sept '76-May '77	8	summer	310 - 355	45	5,6
	May '77-Sept '77	4	winter	355 - 360	5	1,3
	Sept '76-Sept '77	12	whole year	310 - 360	50	4,2
			Females			
4 (b)	June '76-May '77	11	whole year	315 - 360	45	4,1
			Males			
4 (b)	June '76-May '77	11	whole year	290 - 315	25	2,3

and sampling with seine nets and traps had limited success. During the second and third growth season, however, when the fish were large enough to be captured in gill nets (>about 150 mm FL), larger numbers were caught.

To facilitate comparisons with growth data obtained from scales, sampling was carried out in winter when growth had ceased and just prior to ring formation. The results are summarized in Table 25. At Site A, the fish grew from an initial mean size of 31 mm FL to mean lengths of 122 and 250 mm FL at the end of the first and second growth seasons, respectively. At Site B, the fry at stocking formed a modal peak at 30 - 40 mm FL. These fish attained mean lengths of 240 and 323 mm FL at the end of their second and third growth seasons, i.e. at ages two and three years respectively (Table 25).

Table 25. The mean lengths at age of *Myxus capensis* in the Kowie River as determined from scale back-calculation and length frequency distribution of stocked fish. The 95% confidence intervals are given in brackets.

Locality	Method of growth estimation	Estimated length (FL mm) at age 1	2	3
All areas	scales	135 (2,5)	237 (3,9)	300 (4,5)
Site A	length frequency	122 (8,4)	250 (4,9)	
Site B	length frequency		240 (4,9)	323 (4,9)

The mean size of females at site B after three years growth (330 mm FL) was found to be significantly larger ($p < 0.01$; $t = 396$; DF = 30) than that of male fish (313 mm FL). However, there was virtually no difference in the mean size of females (240 mm FL) and males (241 mm FL) at site B after two years growth. In general, there is close agreement between the growth data obtained from scale back-calculation and from the growth of the stocked fish (Table 18).

GROWTH RATE OF *MYXUS CAPENSIS* IN THE KOWIE RIVER FROM TAGGING AND RECAPTURE DATA.

Only seven out of a total of 228 (3,1%) tagged mullet were recaptured. In two fish, a male and a female, the period between tagging and recapture was

Table 26. Tag-recapture data for *Myxus capensis* in the Kowie River.

Tagged data			Recapture data			Period before recapture (days)	Movement		Growth			Seasons
Date	Length (mm)	Weight (g)	Date	Length (mm)	Weight (g)		Km	Direction	Total (mm)	mm/30 days	g/ day	
8-XII-75	293		30-I-76	297	367	43	0		4	2.8		SP & S
26-X-75	258		18-XII-75	268		53	0		10	5.7		SP & S
15-IX-75	265		30-I-76	275	285	75	0		10	3.9		SP & S
17-VI-75	259	217	8-XI-75	265		144	0		6	1.2		W/SP
20-V-75	234	157	8-XI-75	248		172	10	upstream	14	2.4		W/SP
8-IV-75	230	134	22-IV-76	303	345	379	10	upstream	73	5.8	0.56	one year
28-III-75	204	96	30-IV-77	304	399	764	6	upstream	100	3.93	0.40	two years

SP = spring; S = summer; W = winter

sufficiently large to give long-term growth data (Table 26). Both the female fish, which grew from 230 - 303 mm in 379 days, and the male fish, which grew from 204 - 304 mm in 764 days (Table 26), showed close agreement to growth estimated from scale back-calculation. These data therefore indicate that growth estimates of *Myxus capensis* using scale analysis are not too high.

DESCRIPTION OF GROWTH

The close agreement of the age estimates from scale analysis with those of all the other techniques, confirms the validity and accuracy of the former method. As the data from scale back-calculation were more complete than observed lengths at age data, estimates using the former method were used for further descriptions of growth.

The values of the von Bertalanffy growth equation, calculated for *Myxus capensis* from the various rivers, are given in Table 27. The values t_o for both males and females are all close to 0. In addition, the correlation coefficient (r^2) for the Walford regression of length at age t + 1 against length at age t varied between 0,97 and 1.00, indicating a good fit. A typical Walford plot of male and female *Myxus capensis* is given in Fig. 35 . The above findings indicate that the growth data obtained from scale analysis are well described by von Bertalanffy growth equation (Everhard *et al.* 1975). The close agreement between the lengths at age data obtained from the two methods for *Myxus capensis* from all study areas is shown in Table 28.

Table 27. The values of the constants in the von Bertalanffy growth model and the correlation coefficients from the Walford plot as fitted to the lengths at age data of *Myxus capensis* from the various study areas.

River	Sex	L_∞	K	t_o	r^2
Kowie	females	521	0,316	0,055	1,00
	males	353	0,585	0,182	1,00
Swartkops	females	431	0,373	0,027	1,00
	males	389	0,416	-0,006	1,00
Great Fish	females	521	0,269	-0,019	0,97

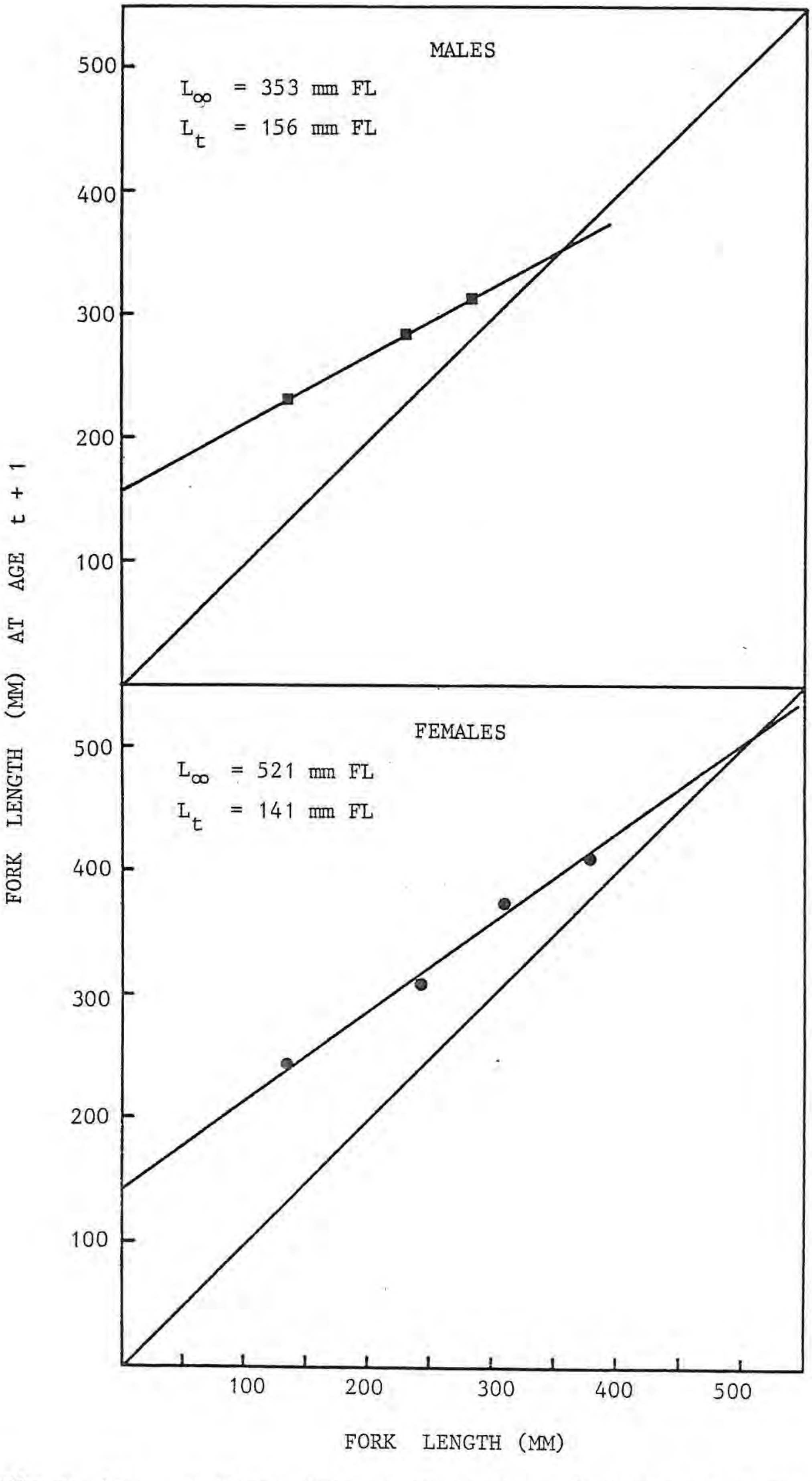


Figure 35 . Walford plots of *Myxus capensis* (male and female) from the Kowie River. Data are from back-calculation using scales except at age four in the male fish, where the observed length at age was used.

Table 28. The lengths at age (mm FL) of *Myxus capensis* from the various study areas from scale analysis and using the von Bertalanffy growth equations (Table 27).

Length at age	Kowie River				Swartkops River				Great Fish River	
	Males		Females		Males		Females		Females	
	Back Calc.	Von Bert.	Back Calc.	Von Bert.	Back Calc.	Von Bert.	Back Calc.	Von Bert.	Back Calc.	Von Bert.
1	134	134	135	135	133	132	131	131	129	125
2	231	231	242	239	219	219	223	225	213	220
3	285	285	311	316	278	277	292	289	284	288
4	313*	315	372	371	315	315	333	333	357	344
5		332	412	412		340		364		386
6		341		441		357		385		418
7		345		463		368		399		443

* calculated from observed length at age data

The von Bertalanffy growth model describes an asymptotic curve, ie. an initial period of rapid growth followed by a progressive decline in growth rate with age. This trend is shown in the lengths at age data for *Myxus capensis* from all study areas (Table 28 , Fig. 36). In female fish from the Kowie and Great Fish rivers however, the growth in length of 2+ and 3+ year old fish are very similar, but thereafter declined markedly. Annual weight increments are highest in the second year in male fish, but highest in the third and fourth year in females (Table 29 and Fig. 37).

Female fish were found to grow faster than males from an age of two years and older in the Kowie River (Table 28, Fig. 36). Student t tests showed these differences in length to be significant in the second year ($p < 0,01$; $t = 2,734$; $DF = 254$) and third year ($p<0,01$; $t = 4,61$; $DF = 109$). Scales from male fish from the Kowie River with four or more annuli were not analysed in this study. The substantially faster somatic growth of females compared to males in the Kowie River is shown in Fig. 37 . This trend of faster female growth also occurs in the Swartkops River but here the growth differences were not statistically significant. The absence of male fish with more than two annuli in the Great Fish River precluded any attempt at comparing sexual differences in growth in this river. The higher growth coefficient (K) and lower L_∞ values of the males (Table 27) are characteristic of the sex that matures earlier at a smaller size (Kingsley 1980). The data on breeding biology (Chapter 5) are in agreement with this supposition.

The length frequency distributions of male and female *Myxus capensis* from the various study areas show that female fish predominate in the larger size classes in all populations (Figs. 38 & 39). This could be attributed to the faster growth of the female fish. However, increased mortality of larger males or earlier downriver migration of males would also result in a predominance of females in the larger size classes.

As shown by the age structure of the various *Myxus capensis* populations (Fig. 40), as well as the relative frequency of males and females in the various age groups (Table 31), the relative numbers of males decline in the older age groups. This indicates that earlier downriver migration (or increased mortality) of males, particularly in the Swartkops and Great Fish rivers (Table 31 & Fig. 40), also contributes to the predominance of females in the larger size classes.

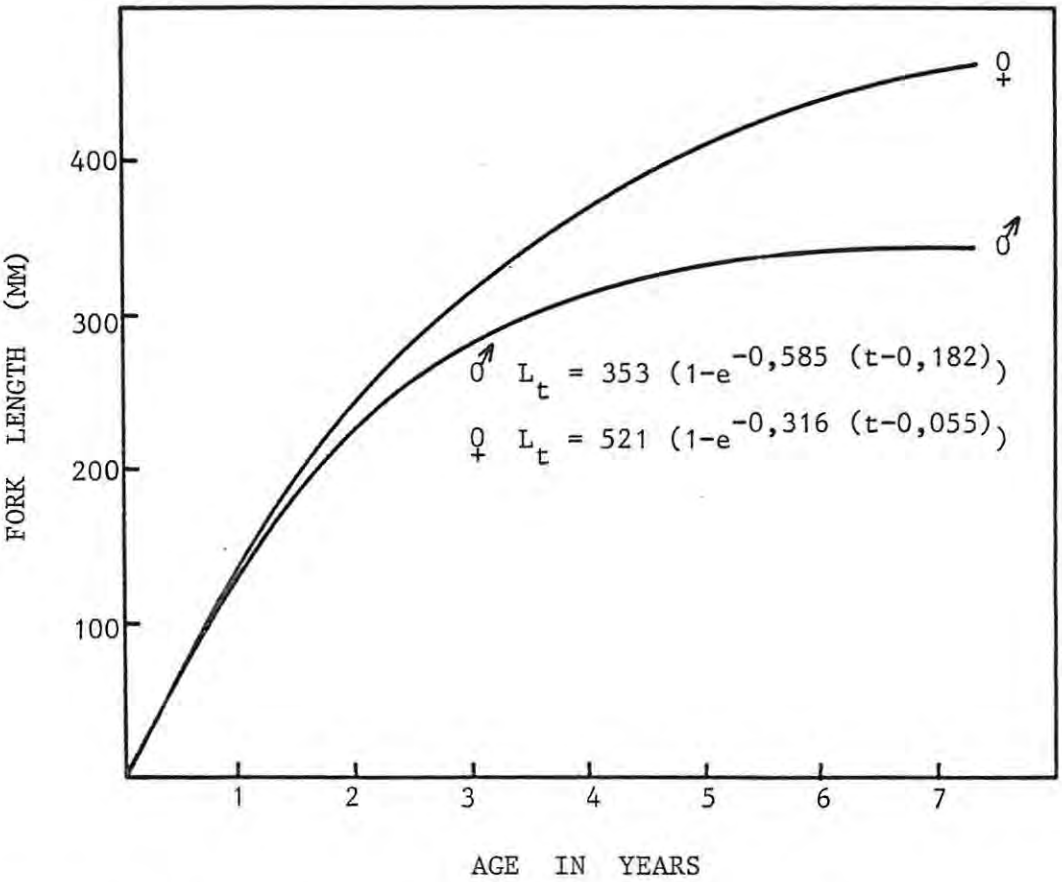


Figure 36 . Growth in length of male and female *Myxus capensis* from the Kowie River calculated from the von Bertalanffy growth equations.

Table 29. The weight at age and annual weight increments (g) of *Myxus capensis* from the three rivers studied. Weight values calculated from von Bertalanffy lengths at age data converted to weight using the length : weight relationships given in Table 30.

Age (yrs)	Kowie River				Swartkops River				Great Fish River	
	Males		Females		Males		Females		Females	
	Weight	Incre.	Weight	Incre.	Weight	Incre.	Weight	Incre.	Weight	Incre.
1	25		25		29		29		21	
		122		138		103		115		110
2	147		163		132		144		131	
		180		278		169		186		194
3	327		441		301		330		325	
		121		320		153		217		263
4	448		761		454		547		588	
		80		325		130		205		275
5	528		1 086		584		752		863	
		47		283		102		166		264
6	575		1 369		686		918		1 127	
		21		246		72		124		241
7	596		1 615		758		1 042		1 368	

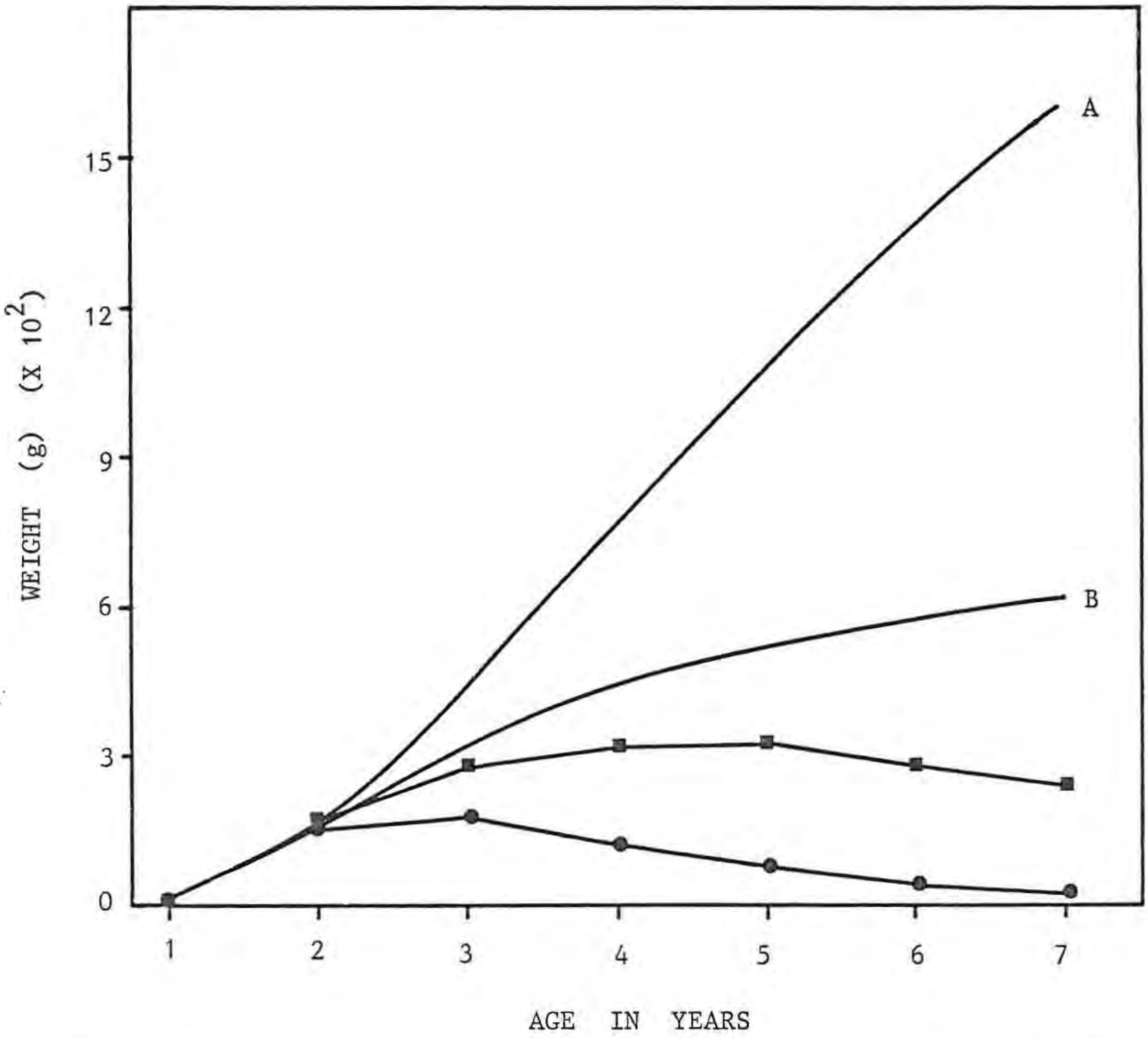


Figure 37. The somatic growth of female (A) and male (B) *Myxus capensis* from the Kowie River, calculated using the von Bertalanffy growth equation (see text). The annual weight increments for females (squares) and males (circles) are also given.

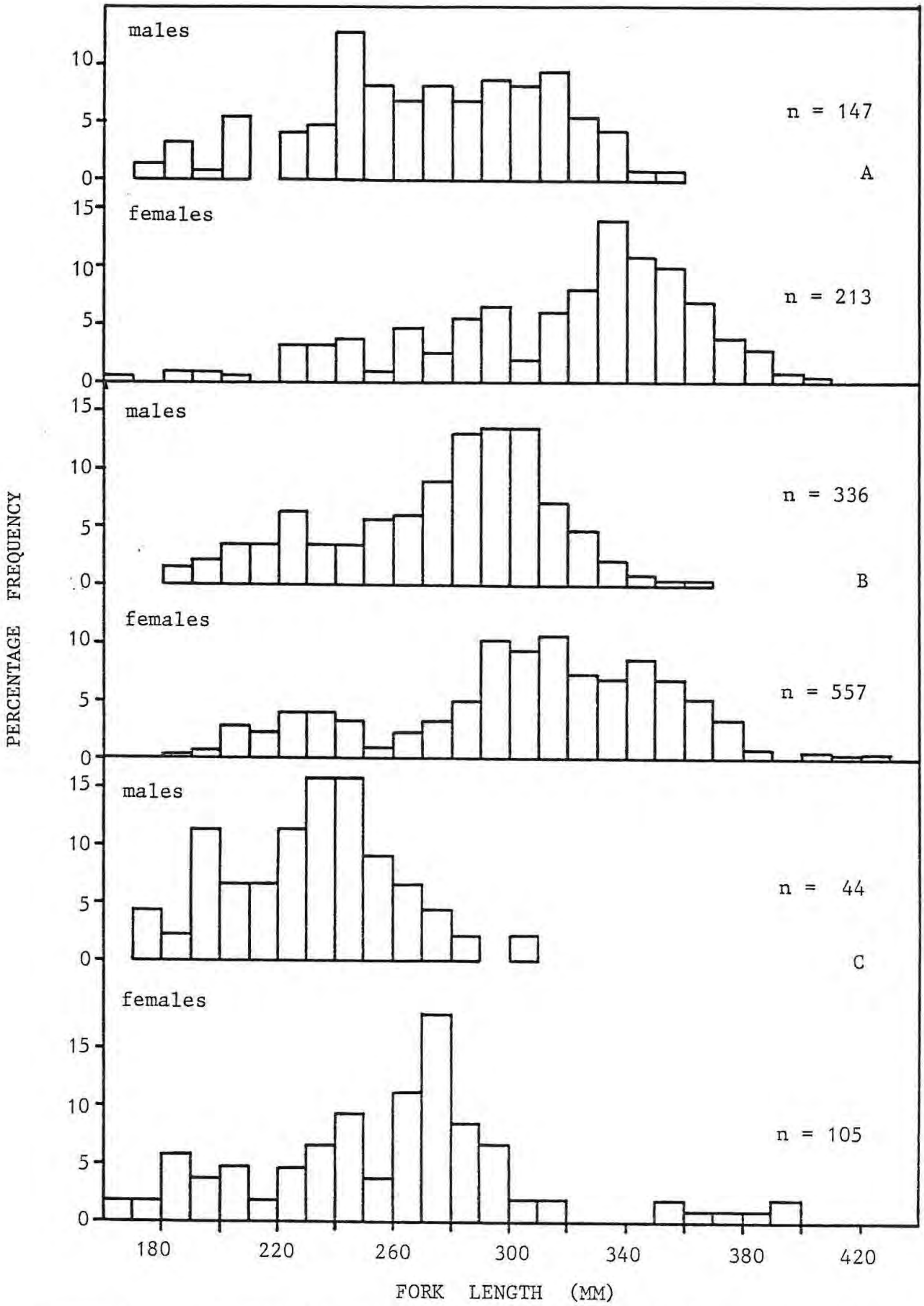


Figure 38 . The length frequency of male and female *Myxus capensis* from the freshwater areas of the Swartkops (A), Kowie (B) and Great Fish (C) rivers.

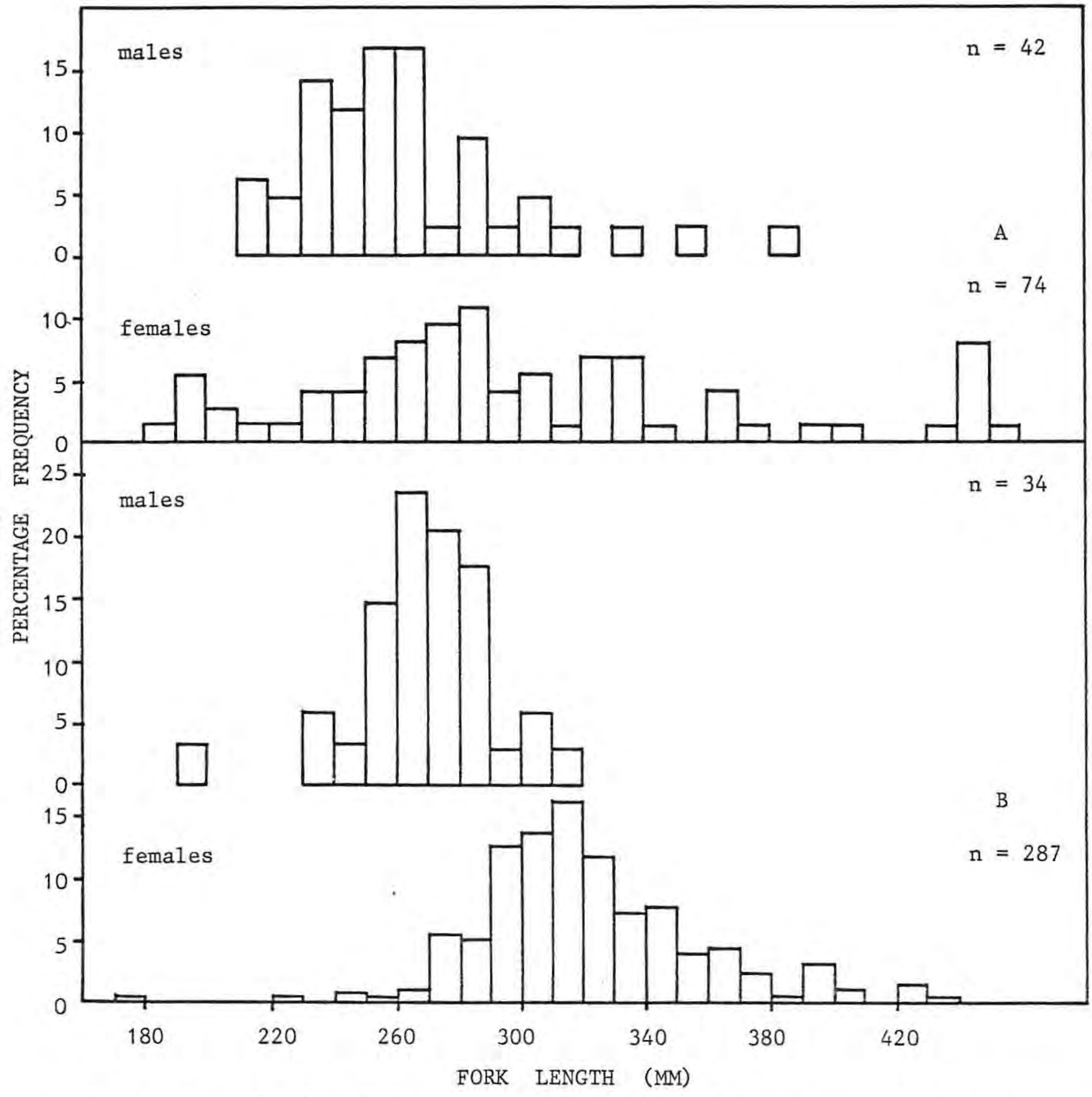


Figure 39. The length frequency distribution of *Myxus capensis* (sexes given separately) from the Kowie (A) and Great Fish (B) estuaries.

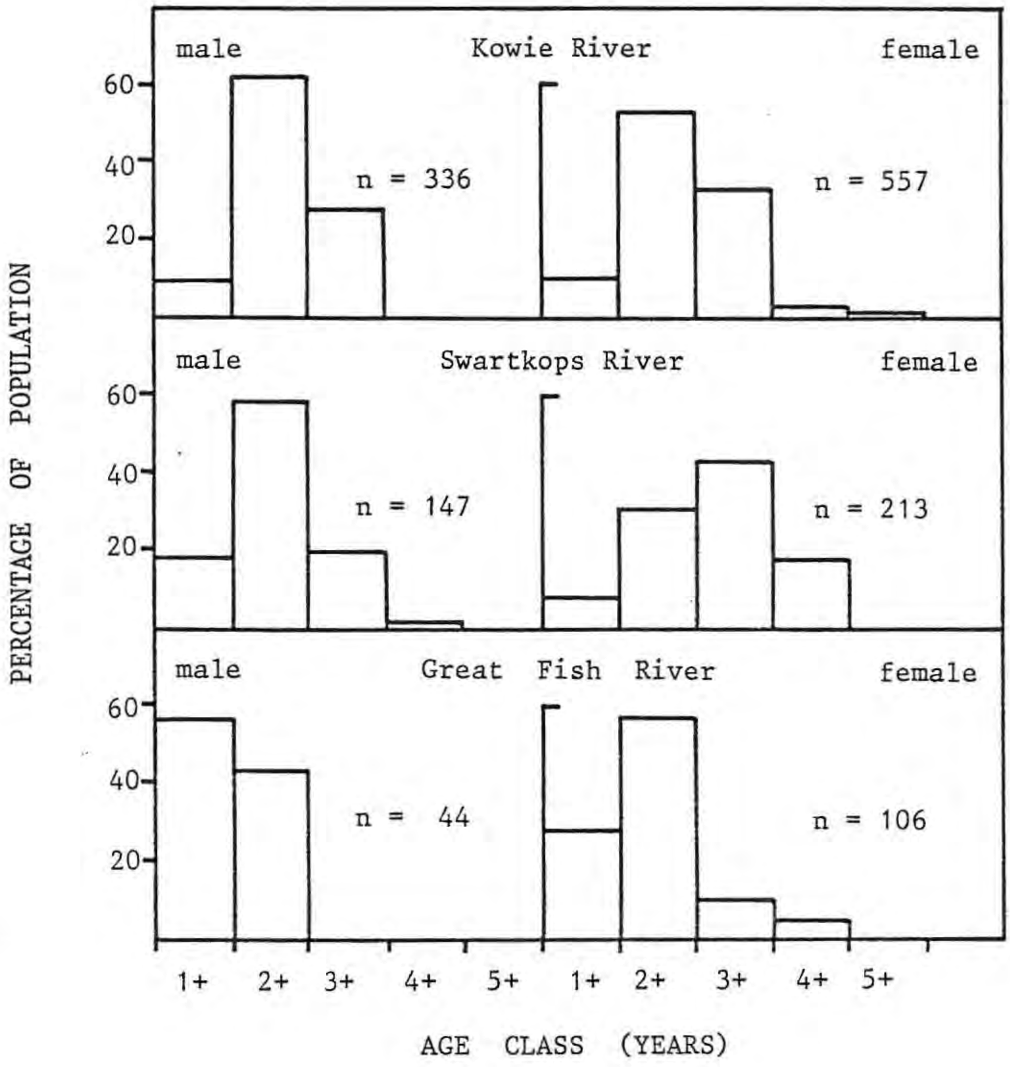


Figure 40. The age structure of *Myxus capensis* in the Kowie, Swartkops and Great Fish rivers, excluding the 0+ year class. Values were calculated using length-age keys (Ricker 1975).

Table 30. The length : weight relationships of *Myxus capensis* from the study areas according to the expression $W = a\ FL^b$, where W = body weight in grams. FL is fork length in mm, and 'a' is a constant and 'b' an exponent.

River	Group	a ($\times 10^{-6}$)	b	r^2	n
Kowie	juveniles (50-150 mm FL)	26,41	2,807	0,984	45
	sub-adults (150-250 mm FL)	7,40	3,088	0,935	256
	females (>250 mm FL)	1,42	3,400	0,972	153
	males (>250 mm FL)	6,30	3,143	0,932	245
	combined (all fish)	3,97	3,215	0,995	275
Swartkops	sub-adults (<250 mm FL)	10,50	3,034	0,878	90
	females (>250 mm FL)	0,57	3,561	0,949	173
	males (>250 mm FL)	2,74	3,290	0,882	94
	combined (all fish)	0,92	3,479	0,980	237
Great Fish	sub-adults (<250 mm FL)	3,30	3,244	0,976	90
	females (>250 mm FL)	1,97	3,341	0,976	60
	males (178-310 mm FL)	1,53	3,392	0,960	47
	combined (all fish)	2,43	3,303	0,988	167

There is evidence from work on other fish species (Alm 1959; Gaigher *et al.* 1978) that individual fish with higher growth rates reached sexual maturity at an earlier age than slow growing fish. If this is true for *Myxus capensis* and results in faster growing males migrating earlier, this would accentuate any sex-related growth differences. However, earlier migration (or mortality) of faster growing older fish would result in Lee's phenomenon (Ricker 1975) where back-calculated lengths at a given age are smaller when calculated from scales of older fish. This tendency is not marked in the data for *Myxus capensis* (Tables 18-22). It appears, therefore, that the observed sex related growth differences are real and not a result of the earlier migration or increased mortality of faster growing males.

The calculated L_∞ value for female fish may be slightly high, as the largest females caught in the Kowie, Great Fish and Swartkops systems (including estuaries) were 69, 83 and 21 mm respectively below the calculated L_∞ values (Table 32). A possible explanation may be that as *Myxus capensis* usually migrate downriver before sexual maturity is reached and do not return (Chapter 5), there is little data available on the older, slower growing fish. This may bias the growth data and result in an overestimation of the asymptotic length. Only two (0,2%) male *Myxus capensis* from the Kowie River system (one each from the river and estuary) were larger than the postulated L_∞ while the largest male from the Swartkops River was 30 mm below the L_∞ value (Table 32).

3

Table 31. The relative frequency of male fish in the various age groups of *Myxus capensis* from the Kowie, Swartkops and Great Fish rivers. Values obtained using age-length keys (Ricker 1975).

Age group	Kowie River		Swartkops River		Great Fish River	
	Total	% male	Total	% male	Total	% male
1+	88	40	45	62	54	46
2+	503	41	154	56	79	24
3+	279	34	121	25	11	0
4+	15	0	40	5	5	0
5+	5	0				

An indication of the potential longevity of both sexes of this species was shown by the capture of two females (480 and 456 mm FL) and one male (425 mm FL) *Myxus capensis* in the Paul Sauer Dam (on the Couga River, a tributary of the Gamtoos system) 14 years after the completion of the 93 m high dam wall. The fish, which showed typical signs of senescence such as marked spinal curvature (Woodhead 1979), had presumably been 'trapped' in the dam on completion of the wall. They were therefore at least 14 years old. This age estimation was confirmed by examination of scales.

The growth rates of male fish in all three rivers studied were very similar (Tables 18 - 22). Female fish from the various rivers showed larger differences in lengths at age (Tables 18-22 ; Table 28; Fig.41), with fish from the Kowie River showing faster growth. However, the growth differences were relatively small, especially during the first three years. The length : weight relationships of fish from the three study areas (Fig.42) are also very similar.

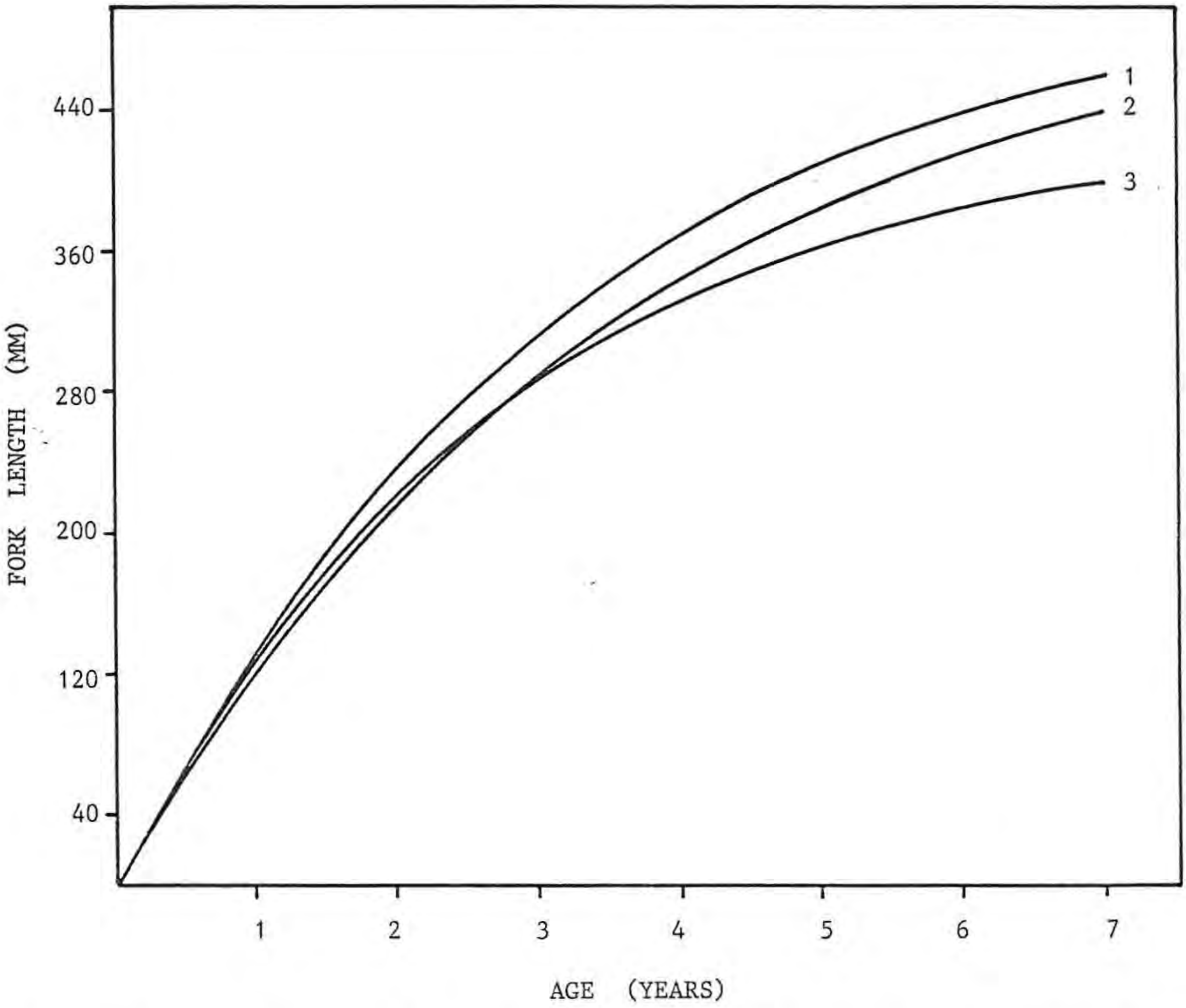


Figure 41. The growth in length of female *Myxus capensis* from the Kowie (1), Great Fish (2) and Swartkops (3) rivers as determined from the von Bertalanffy growth equations (see text).

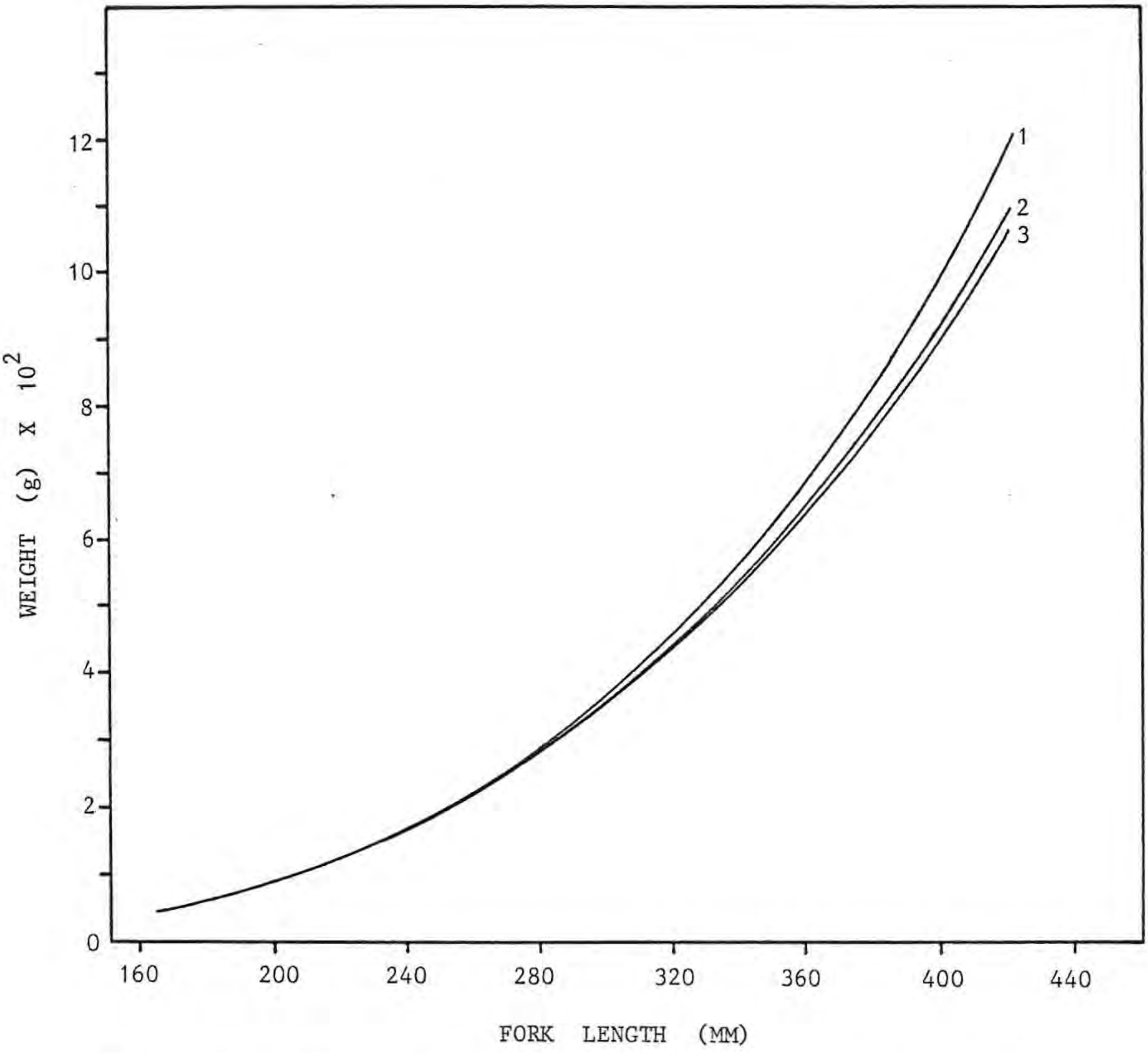


Figure 42 . The length : weight relationships of *Myxus capensis* from the Swartkops (1), Great Fish (2) and Kowie Rivers (3) from length : weight regressions given in Table 30 .

Table 32. Estimates of the ultimate or asymptotic fork lenghts (L_∞) from the von Bertalanffy equations for *Myxus capensis* from the Kowie, Swartkops and Great Fish rivers. The maximum size of *Myxus capensis* caught in these river systems (including the estuaries) are also given.

River System	Sex	L_∞ (mm)	Max. length caught (mm)
Kowie River	male	353	370
	female	521	435
Kowie estuary	male		385
	female		452
Great Fish River	female	523	396
Great Fish estuary	male		320
	female		440
Swartkops River	male	389	359
	female	431	410

MUGIL CEPHALUS

AGE DETERMINATION FROM SCALES

The back-calculated and observed lengths at age for *Mugil cephalus* from the various study areas are given in Tables 33 - 39. Sufficient observed lengths at age data were available only from the Kowie and Great Fish estuaries (Tables 34&38 resp.) and agree fairly closely with the back-calculated data. In all freshwater areas, *Mugil cephalus* with three or more annuli were rare. Lengths at age three years were therefore estimated from 2+ year old fish caught in mid-winter, at the end of the growth season and just prior to the formation of the third annulus. Sexual differentiation in the field was difficult in fish smaller than about 220 mm FL. In the freshwater areas of the Kowie and Great Fish rivers, where relatively few fish above this size were caught, the lengths at age estimates were therefore calculated from combined data.

Table 33. Mean back-calculated fork lengths (mm) at age (yrs) for *Mugil cephalus* from the Kowie estuary. Sexes are given separately and combined. 95% confidence intervals are given in brackets.

No. of rings at capture	No. of fish	Length at age 1	2	3	4
			Males		
1	26	147 (11,2)			
2	48	145 (5,1)	230 (6,8)		
3	4	131 (35,3)	209 (44,1)	283	
No. of fish	78	78	52	4	
Mean FL		145 (5,1)	228 (6,8)	283 (28,4)	
Increment			83	55	
			Females		
1	17	158 (15,2)			
2	36	147 (6,9)	236 (9,2)		
3	11	140 (14,2)	232 (15,4)	307 (15,4)	
4	2	117	208 (23,6)	266 (1,4)	340 (8,3)
No. of fish	66	66	49	13	2
Mean FL		148 (5,8)	234 (7,0)	301 (12,0)	340 (8,3)
Increment			86	67	39
			Sexes combined (plus unsexed fish)		
No. of fish	177	177	116	22	2
Mean FL		145 (3,5)	228 (4,6)	293 (9,2)	340 (8,3)
Increment			83	65	47

Table 34. The observed mean lengths at age of *Mugil cephalus* from the Kowie estuary (Stn. A). For details of the estimation see text. The sample size (n) is given in brackets.

Age (yrs)	Mean fork length (mm) Male	Female	Combined
1			
2	237 (16)	266 (6)	245 (16)
3	292 (17)	305 (20)	299 (37)

Table 35. The mean fork lengths (mm) at age of *Mugil cephalus* (sexes combined) from the Kowie River (Stn 1). Lengths at age one and two were obtained from back-calculation of scales and at age three from fish with two scale rings caught in winter just prior to the deposition of the third ring. 95% confidence intervals are given in brackets.

No. of rings at capture	No. of fish	Length at age 1	2	3
1	44	123 (5,6)		
2	34	124 (6,1)	193 (6,7)	
3	11			248 (9,5)
No. of fish	89	78	34	11
Mean FL		123 (4,2)	193 (6,7)	248 (9,5)

Table 36. The mean fork lengths (mm) at age of *Mugil cephalus* (sexes separate and combined) from the Swartkops River. Lengths at ages one and two were obtained from back-calculation of scale readings and at age three from observed length at age (see text). The 95% confidence intervals are given in brackets.

No. of rings at capture	No. of fish	Length at age 1	2	3
		Males		
1	41	184 (11,6)		
2	13	203 (23,9)	310 (18,5)	
3	10			365 (14,9)
No. of fish	64	54	13	10
Mean FL		189 (10,4)	310 (18,5)	365 (14,9)
Increment			121	55
		Females		
1	12	208 (27,2)		
2	12	194 (14,7)	302 (7,4)	
3	10			279 (11,1)
No. of fish	34	24	12	10
Mean FL		201 (14,8)	302 (7,4)	279 (11,1)
Increment			101	77
		Sexes combined		
No. of fish	98	78	25	20
Mean FL		192 (8,4)	306 (9,4)	372 (9,2)
Increment			114	66

Table 37. The mean fork lengths (mm) at age of *Mugil cephalus* (sexes separate and combined) from the Great Fish estuary from back-calculation of scales. 95% confidence intervals are given in brackets.

No. of rings at capture	No. of fish	Length at age 1	2	3	4
			Males		
1	90	149 (4,8)			
2	49	153 (6,7)	270 (6,4)		
3	5	160 (21,0)	257 (17,5)	327 (7,9)	
4	2	155 (30,5)	242 (20,8)	307 (6,9)	342 (19,4)
No. of fish	146	146	56	7	2
Mean FL		151 (3,7)	268 (5,8)	321 (5,9)	342 (19,4)
Increment			117	53	21
			Females		
1	56	152 (5,0)			
2	82	163 (5,0)	282 (5,0)		
3	31	160 (9,2)	269 (7,4)	347 (8,1)	
4	3	146 (17,0)	276 (20,4)	348 (14,7)	
No. of fish	172	172	116	34	3
Mean FL		159 (3,4)	278 (4,0)	347 (7,7)	408 (14,7)
Increment			119	69	61
			Sexes combined		
No. of fish	318	318	172	41	5
Mean FL		155 (2,5)	275 (3,3)	343 (6,1)	382 (11,4)
Increment			120	68	39

Table 38. The mean observed lengths at age of *Mugil cephalus* from the Great Fish estuary. Sample size is given in brackets.

Age	Mean fork length (mm)		
	Males	Females	Combined
1			180 (41)
2	275 (40)	276 (37)	275 (77)
3	342 (4)	355 (20)	353 (24)
4			415 (2)

Table 39. The mean fork lengths (mm) at age of *Mugil cephalus* (sexes combined) from the Great Fish River. Lengths at age one and two years were obtained from back-calculation of scale readings and at age three years from observed lengths at age. The 95% confidence intervals are given in brackets.

No. of rings at capture	No. of fish	Length at age		
		1	2	3
1	76	138 (3,6)		
2	4	110 (7,8)	229 (17,6)	
3	3			259 (24,9)
No. of fish	83	80	4	3
Mean FL		137 (3,4)	229 (17,6)	259 (24,9)
Increment			92	30

GROWTH OF *MUGIL CEPHALUS* FROM LENGTH FREQUENCY MODES

Length frequency data from the freshwater areas of the Great Fish River gave clear indications of growth for 0+ and 1+ year old fish. Thereafter, the modal peaks become unclear.

Combined catch data from gill and seine nets for the period 1975 - 1980 (Fig. 43) shows that *Mugil cephalus* grow from 20 - 40 mm FL in September (start of growth season) to 90 - 150 mm FL by March. As growth ceases by about April (see below), this represents slightly less than a full seasons' growth.

Length frequency data obtained using seine nets at a site 10 km upriver from the tidal limit of the Great Fish estuary, from November 1981 to July 1982, gave a clearer indication of growth during the first year (Fig. 44). From a modal FL of 50 - 60 mm in November (about two months after the start of the growth season), the fish reached 130 - 160 mm FL at the end of the first year of growth. The cessation of growth after April is clearly apparent in Fig. 44. These estimates of lengths at one year in freshwater areas of the Great Fish River (130 - 160 mm FL) are similar to the mean obtained from back-calculation from scales, namely 137 mm FL.

Length frequency data of gill net catches of *Mugil cephalus* in the Great Fish estuary from March 1980 to May 1983 are given in Fig. 45. Catches during the winter months (May, June, July, August) of all four years show a distinct modal peak at 250 - 290 mm FL. In addition, a winter modal peak at 160 - 190 mm FL is seen in the catches of 1980 and 1982. As *Mugil cephalus* spawn at sea during autumn and winter and recruit as fry <40 mm FL into this river over the winter months (Chapter 5), these modal peaks probably correspond to the lengths reached after one and two seasons' growth.

The decline and cessation of growth during the autumn and winter months in the Great Fish estuary is apparent in the 1982 length distribution modes (Fig. 45). Little or no growth is seen after March 1982 until September

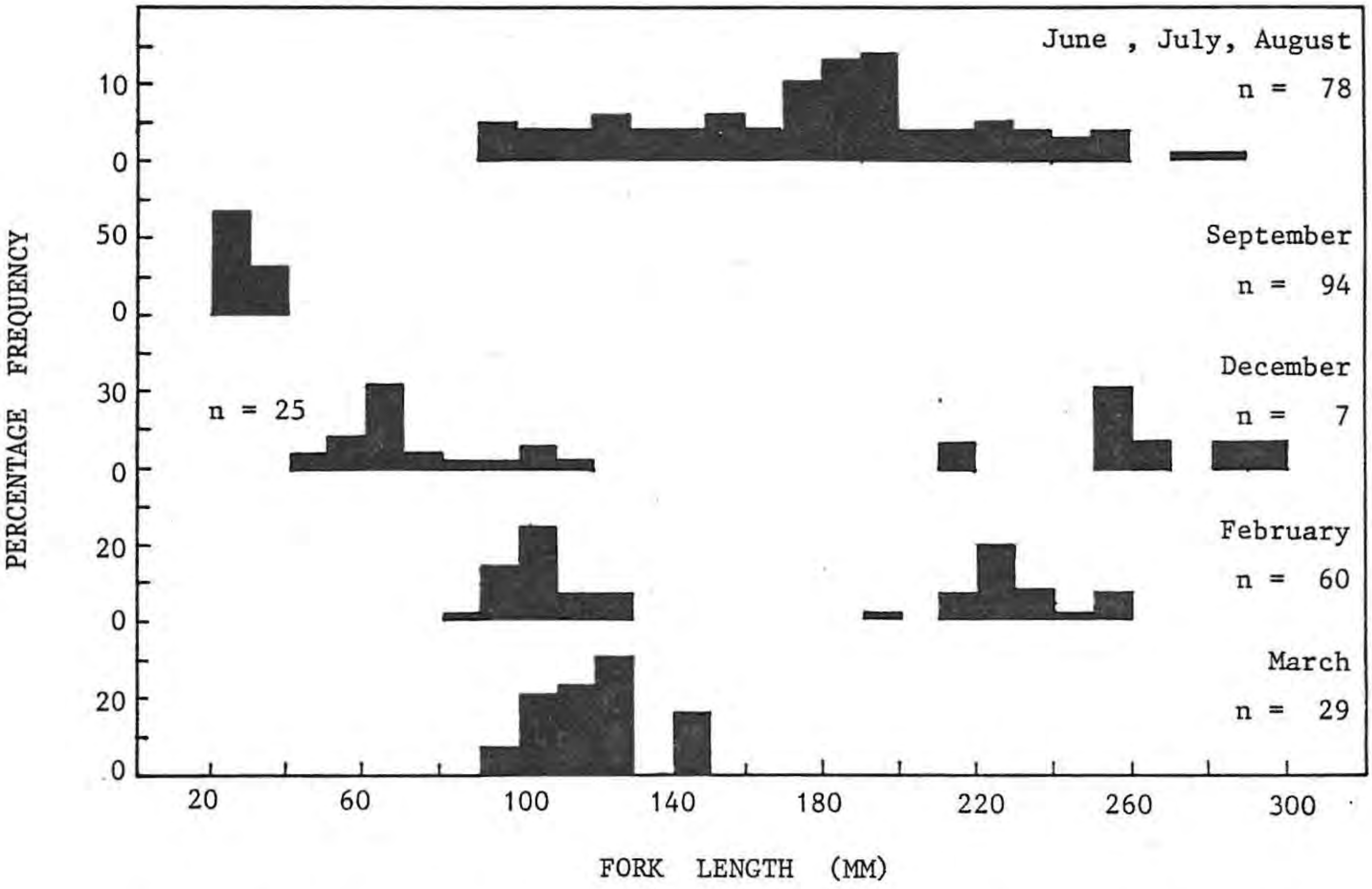


Figure 43. The length frequency distribution of *Mugil cephalus* caught in the Great Fish River from 1975 to 1980. Data are from all areas, with seine and gill net catches combined.

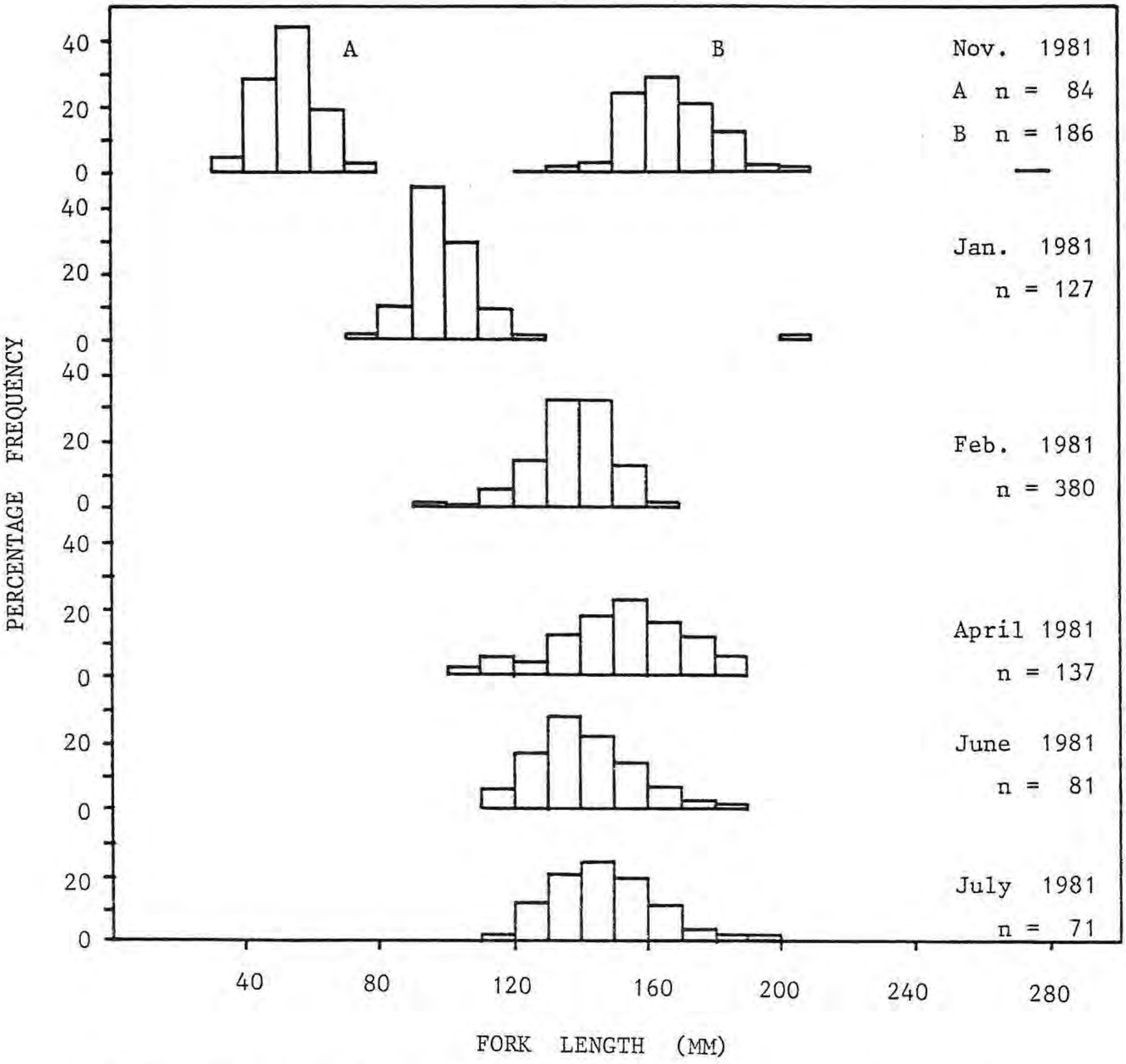


Figure 44 . The length frequency distribution of *Mugil cephalus* caught using seine nets at a single site (farm "Sportvale") in the Great Fish River during the period November 1981 to July 1982.

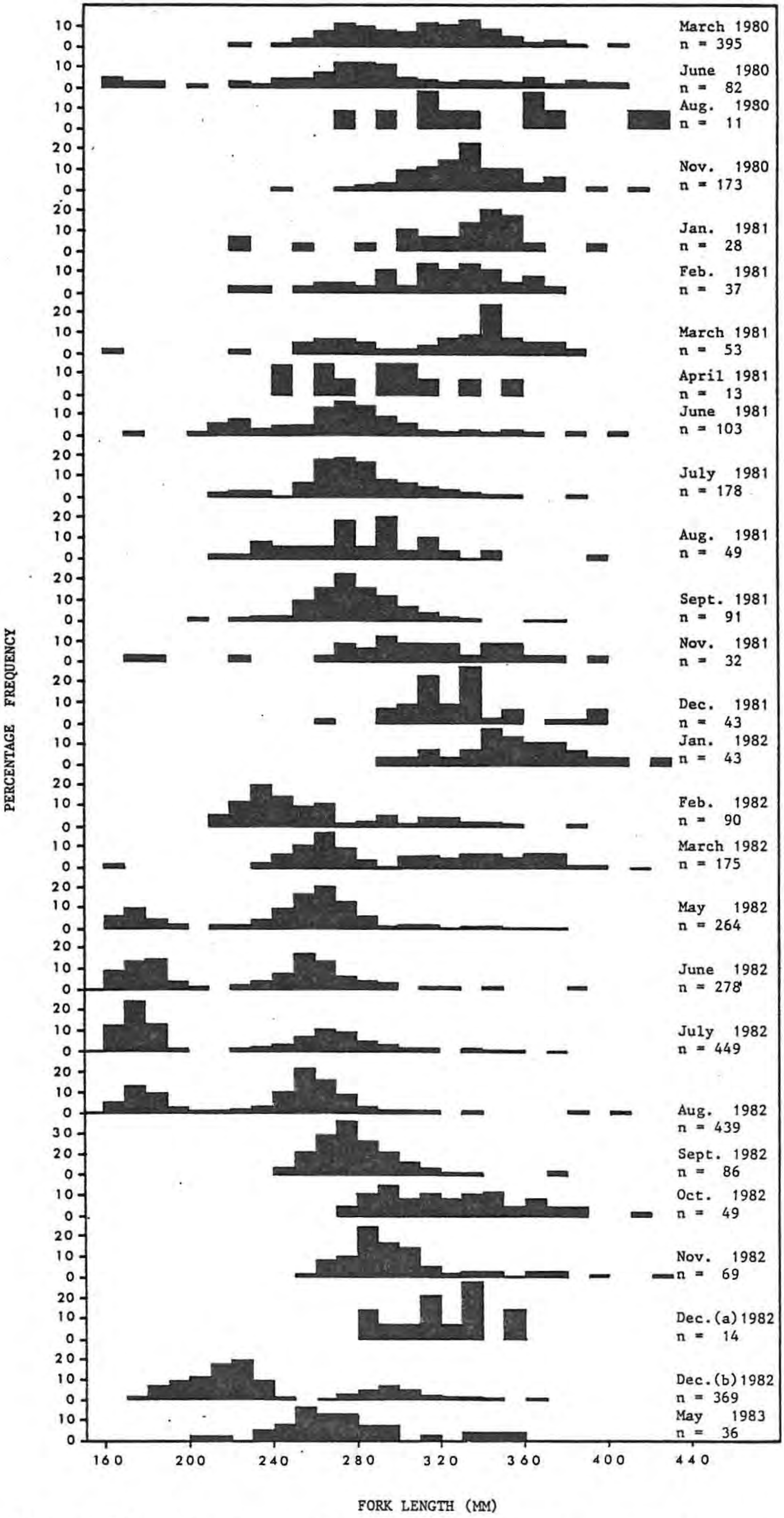


Figure 45. The length frequency distribution of *Mugil cephalus* caught in gill nets in the Great Fish estuary from March 1980 to May 1983.

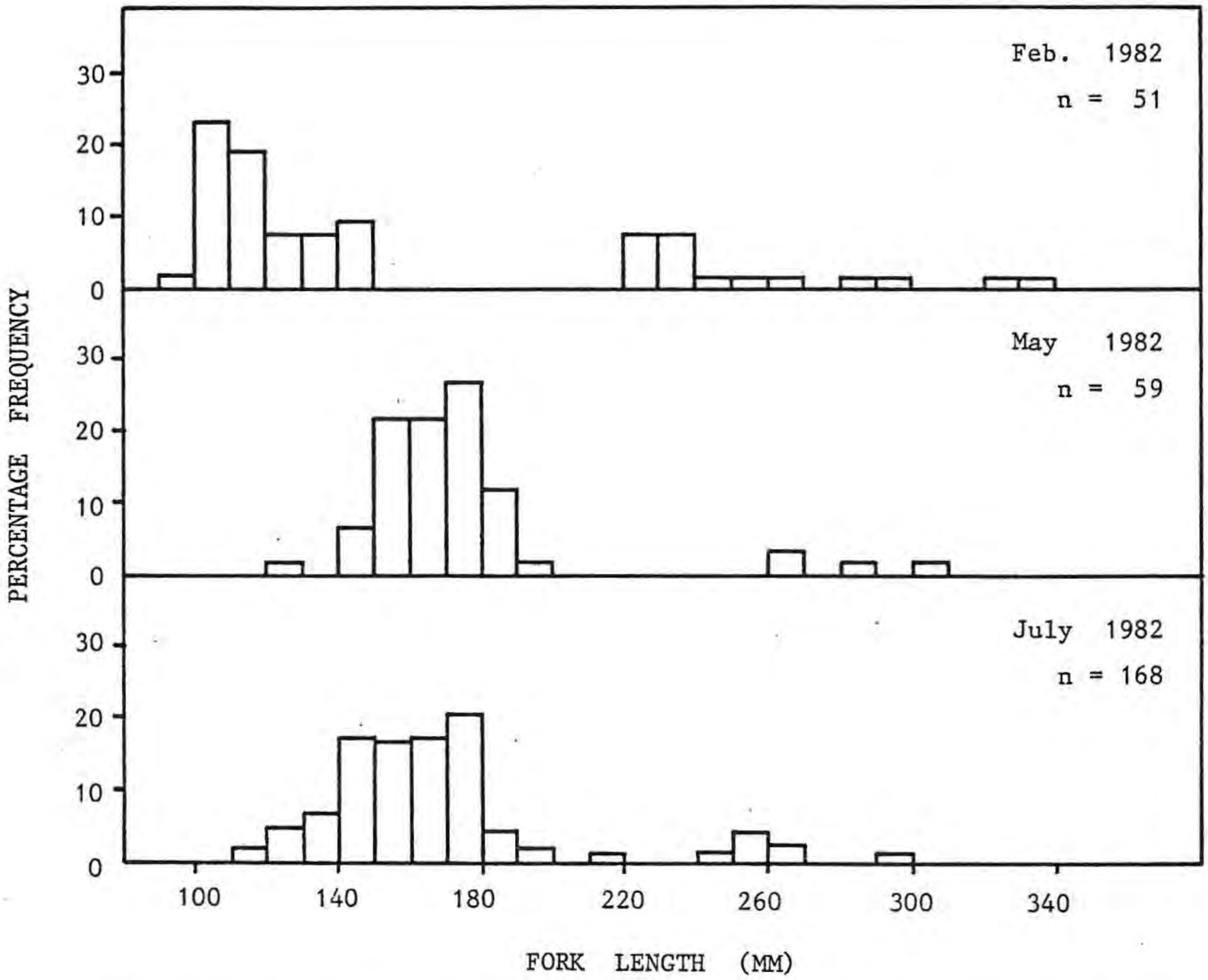


Figure 46. The length frequency distribution of *Mugil cephalus* caught using seine nets in the Great Fish estuary in February, May and July 1982.

1982, a period of about five months. Temperature recordings at Station 3 in the Great Fish estuary showed that water temperatures dropped below 18° C during this five month period (Fig.77; Chapter 7). Growth cessation in winter has also been reported for *Mugil cephalus* in western Australia when temperatures dropped below 16 - 18° C (Thomson 1951).

As mullet below about 160 mm FL were not usually caught in the gill nets used in the Great Fish estuary, the length distribution mode of fish at the end of their first year (160 - 190 mm FL) found using this method could be biased. Seine netting in the upper estuary was therefore carried out in February, May and July 1982 to enable comparisons with the gill net data to be made. As seen in Fig.46, a modal length of 140 - 180 mm FL was found in the seine net catches in winter. Although the modal ranges of fish caught in the different gear at the end of their first year do overlap, the gill nets were apparently sampling only the faster growing first-year fish. In general, however, the length distribution modes at the end of the first year (140 - 190 mm FL) and second year (250 - 290 mm FL) correspond well with the combined mean lengths at age for one year old (155 mm FL) and two year old (275 mm FL) *Mugil cephalus* from the Great Fish estuary as calculated from scales (Table 37).

DESCRIPTION OF *MUGIL CEPHALUS* GROWTH

The lengths at age obtained from scale back-calculation and empirical data from the various study areas were used to calculate the values of the von Bertalanffy growth equations (Table 40). The excellent fit to the Walford plots in all cases (r^2 = 0,99 - 1,0) indicate the data are well described by the von Bertalanffy growth equation (Everhart *et al.* 1975). Because of the low numbers of 2+ and 3+ year old fish sampled in the Great Fish River, growth estimates from this area should be regarded as preliminary.

Table 40. Von Bertalanffy growth equation constants as fitted to the lengths at age data of *Mugil cephalus* from the various study areas. The correlation coefficients (r^2) from the Walford Plot are also given. (FW = freshwater areas; EST = estuary).

River System	Sex	L_∞	K	t_o	r^2
Kowie (EST)	females	439	0,363	-0,135	0,99
	males	393	0,407	-0,131	1,00
	combined	491	0,278	-0,261	1,00
Kowie (FW)	combined	450	0,241	-0,325	1,00
Swartkops (FW)	males	411	0,78	0,218	1,00
	females	625	0,272	-0,439	1,00
	combined	463	0,546	0,017	1,00
Great Fish (FW)	combined	273	1,137	0,390	1,00
	females	520	0,385	0,055	0,99
Great Fish (EST)	males	360	0,821	0,331	1,00
	combined	433	0,565	0,218	1,00

Length increments in all study areas are greatest in the first year and then decline steadily with age (Tables 33 to 39). The typical asymptotic growth in length curves for *Mugil cephalus* from all the study areas, as described by the von Bertalanffy growth model, are shown in Figs.47 and 48. Annual weight increments show a more varied pattern (Table 41 & Fig 49), but generally the largest increments occurred in the 2+ to 4+ year old fish. Male fish from the Great Fish estuary and Swartkops River, however, gained maximum weight in their 1+ year.

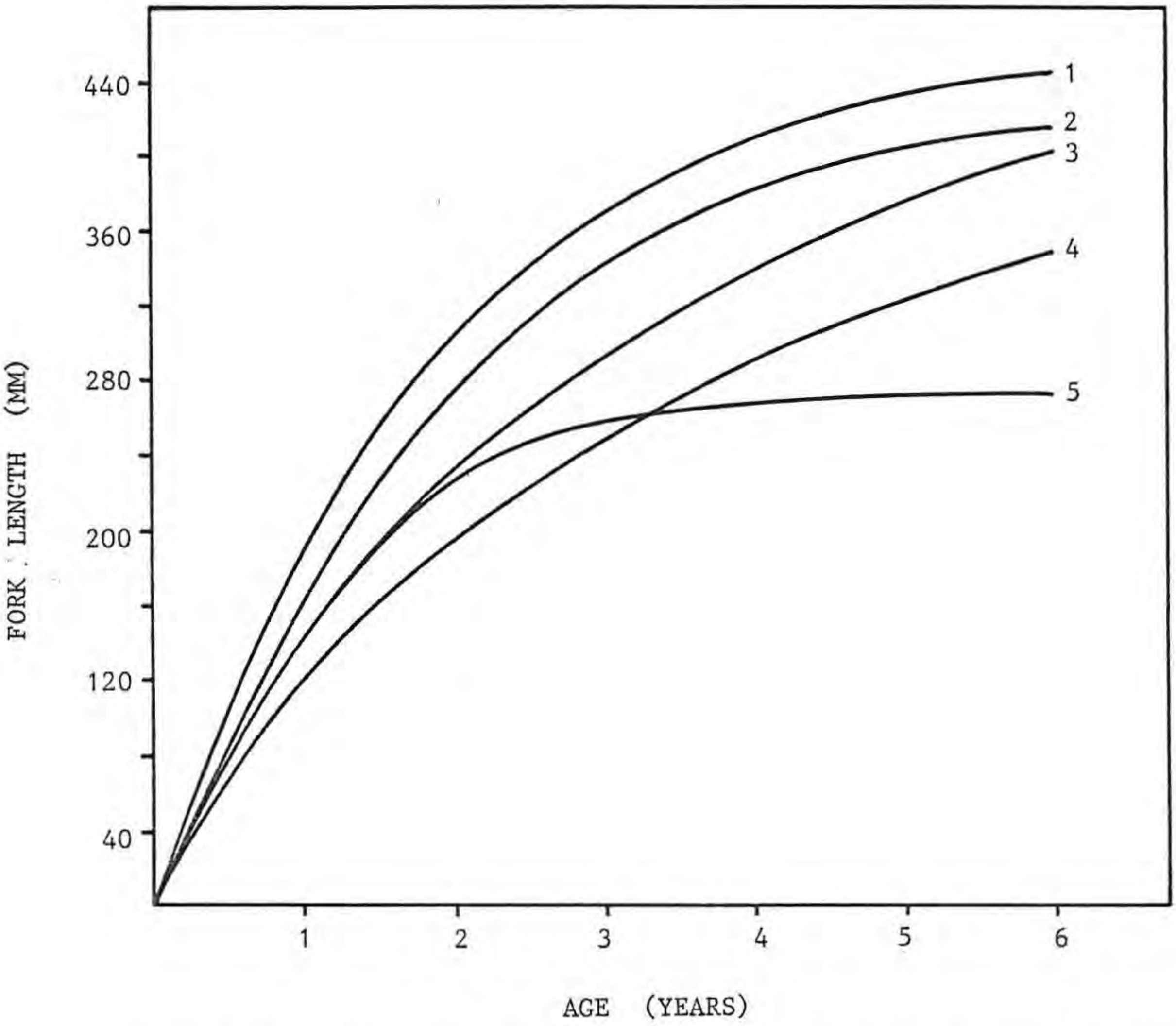


Figure 47 . The growth in length of *Mugil cephalus* (sexes combined) from the Swartkops River (1), Great Fish estuary (2), Kowie estuary (3), Kowie River (FW) (4) and Great Fish River (FW) (5). Data calculated using the von Bertalanffy growth equations (see Table 40).

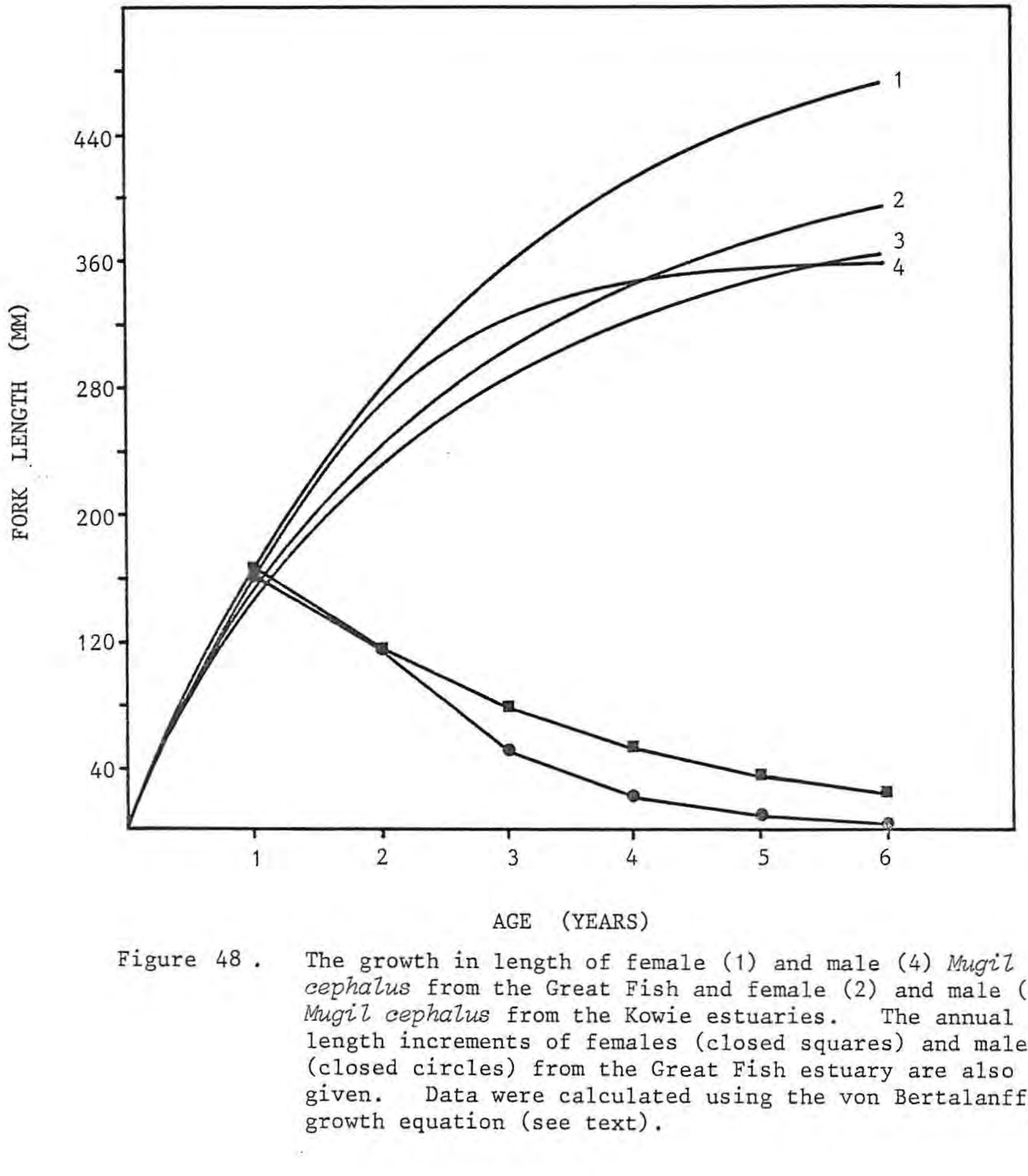


Figure 48 . The growth in length of female (1) and male (4) *Mugil cephalus* from the Great Fish and female (2) and male (3) *Mugil cephalus* from the Kowie estuaries. The annual length increments of females (closed squares) and males (closed circles) from the Great Fish estuary are also given. Data were calculated using the von Bertalanffy growth equation (see text).

Table 41. The weights at age and annual weight increments (g) of *Mugil cephalus* from the various study areas. Values calculated from von Bertalanffy lengths at age data using length : weight relationships given in Table 42.

Age (yrs)	Kowie Est.				Great Fish Est.				Swartkops River				Kowie River		Great Fish River	
	Males		Females		Males		Females		Males		Females		Combined		Combined	
	Wt.	Incr.	Wt.	Incr.	Wt.	Incr.	Wt.	Incr.	Wt.	Incr.	Wt.	Incr.	Wt.	Incr.	Wt.	Incr.
1	44		46		50		57		92		115		28		34	
		118		133		232		241		393		324		77		144
2	162		179		282		298		485		439		105		178	
		141		173		224		390		315		434		116		87
3	303		352		506		688		800		873		221		265	
		176		232		130		380		180		488		135		31
4	479		584		636		1 068		980		1 361		356		296	
		119		187		66		336		87		477		137		14
5	598		771		702		1 404		1 067		1 838		493		310	
		94		153		34		254		50		427		132		4
6	692		924		736		1 658		1 117		2 265		625		314	

Table 42. The length : weight relationship of *Mugil cephalus* from the various study areas from the equation $W = a\ FL^{b}$, where W = weight in grams, FL in mm, 'a' constant and 'b' an exponent. FW = freshwater; EST = estuary.

River System	Fish Group	a X 10^6	b	r^2	n
Kowie (FW)	♂ & ♀ 120 - 310 mm FL	17,7	2,964	0,97	164
(EST)	♂ & ♀ 137 - 300 mm FL	23,40	2,901	0,91	255
	♀ >300 mm FL	2,73	3,289	0,92	78
	♂ >300 mm FL	10,90	3,051	0,89	50
	♂ & ♀ whole range	6,93	3,123	0,98	210
Great Fish (FW)	♂ & ♀ 98 - 282 mm FL	4,52	3,219	0,98	92
(EST)	♂ & ♀ 177 - 300 mm FL	11,02	3,049	0,95	242
	♀ >300 mm FL	6,80	3,142	0,91	143
	♂ >300 mm FL	1,27	3,433	0,85	42
	♂ & ♀ whole range	5,10	3,192	0,99	275
Swartkops (FW)	♂ & ♀ 164 - 300 mm FL	2,20	3,348	0,97	87
	♀ >300 mm FL	10,52	3,071	0,92	90
	♂ >300 mm FL	11,21	3,065	0,89	109
	♂ & ♀ whole range	3,02	3,288	0,99	205

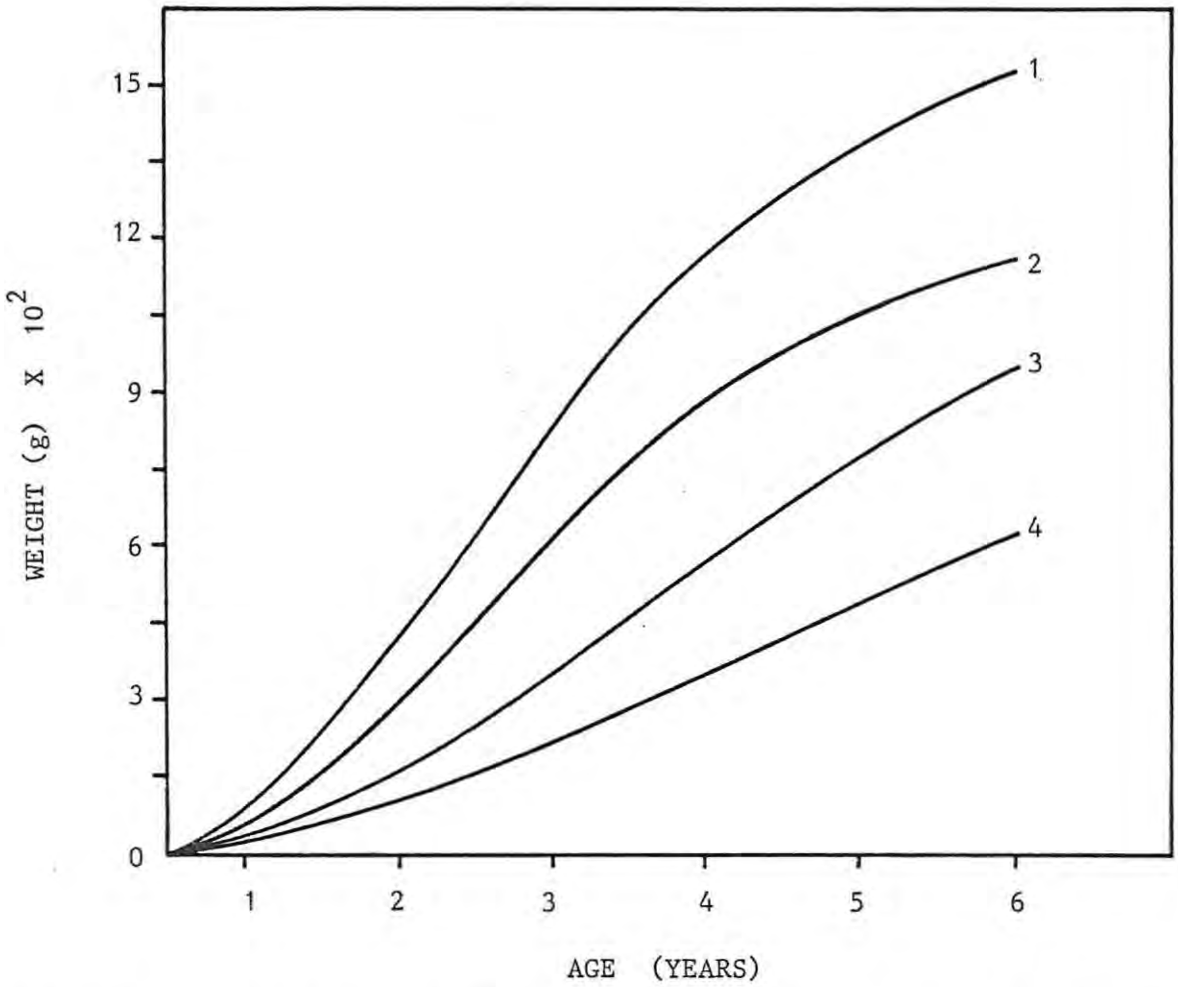


Figure 49. The growth in weight of *Mugil cephalus* (sexes combined) from the Swartkops River (1), Great Fish estuary (2), Kowie estuary (3) and Kowie River (FW) as calculated using the von Bertalanffy growth equations (Table 40).

Female *Mugil cephalus* tended to grow faster than males in all the populations studied. Student t tests carried out on all back-calculated lengths at age data, however, showed these differences to be significant only in the Great Fish estuary. Here differences in lengths at age were significant at age 1 ($p<0,01$; $t = 2,982$; $DF = 316$), age 2 ($p<0,01$; $t = 2,760$; $DF = 170$) and age 3 ($p<0,01$; $t = 2,933$; $DF = 39$). These sexual growth differences in length are seen in Fig. 48 and the larger differences in weights at age in Table 41 . For example, at four years of age, females are heavier than males by 105 g in the Kowie estuary, 432 g in the Great Fish estuary and 381 g in the Swartkops River. These sexual growth differences are reflected in the higher K and lower L_∞ values for male fish (Table 40).

The large sexual growth differences, as extrapolated using the von Bertalanffy equation for older fish (Table 41), appear to be realistic. In *Mugil cephalus* isolated in impoundments in the eastern Cape, sex-related growth differences were even larger than those postulated for older fish in Table 41, (Chapter 6). Female *Mugil cephalus* from a freshwater impoundment (Amanzi Dam) were on average 45 mm FL (517 g) and 70 mm FL (1 001 g) larger than the males after three and four growth seasons, respectively.

Other studies on natural populations of *Mugil cephalus* also revealed that female fish grow slightly faster than males after the third year (Kesteven 1942; Thomson 1951; Broadhead 1958; Chech & Wolschlag 1975, Grant & Spain 1975).

The population structure of *Mugil cephalus* from the various study areas, as determined by gill net catches (Figs. 50 &51), indicate that females predominate in the larger size classes. The numbers of both sexes dropped markedly at the end of the second year, with relatively few fish surviving to age 3+ (Table 43 & Fig. 52). There is no marked tendency for females to live longer than males. The predominance of females in the larger size classes therefore appears to be related largely to their faster growth rate.

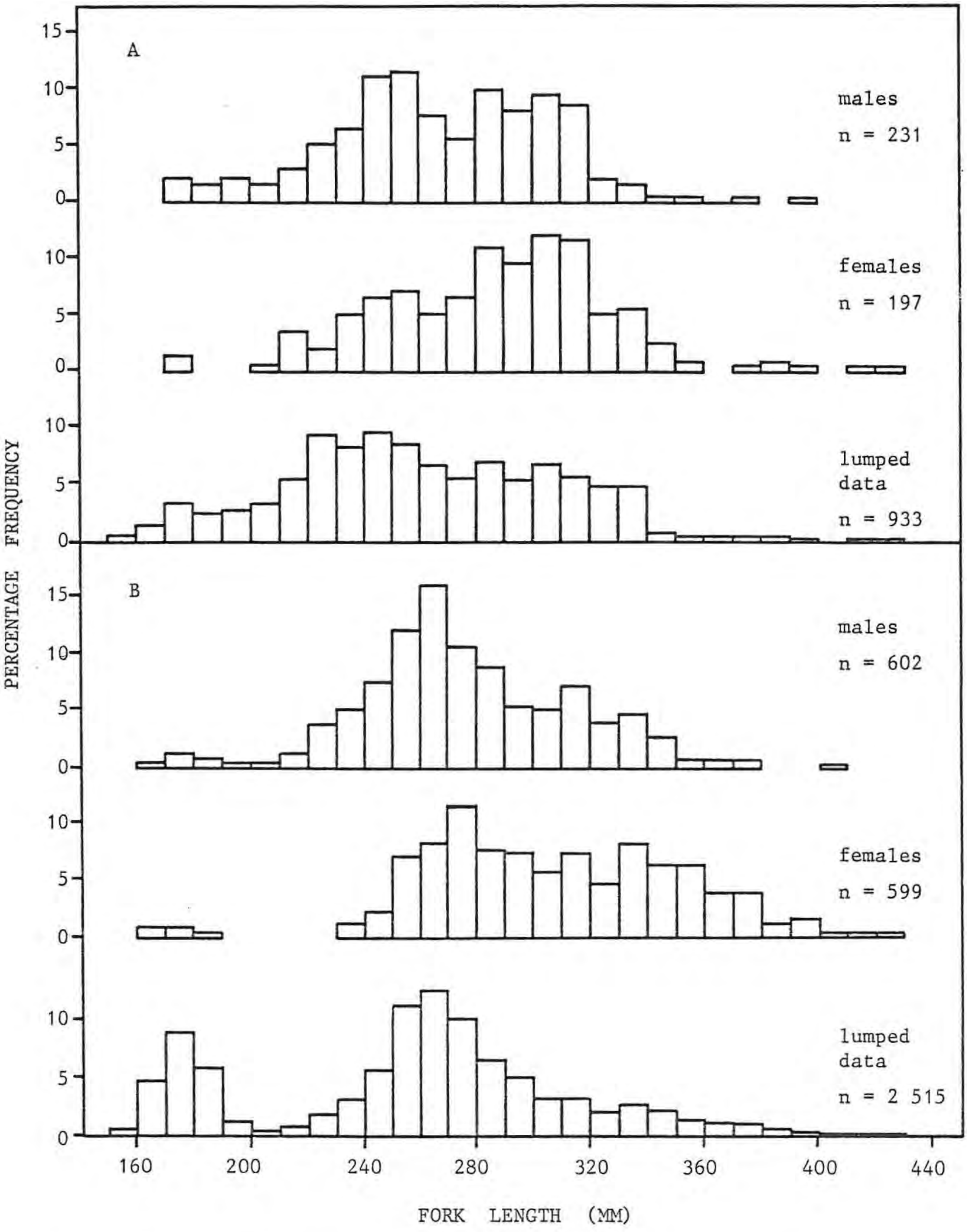


Figure 50. The length frequency distribution of *Mugil cephalus* from the Kowie (A) and Great Fish (B) estuaries. Data for males and females are given separately; lumped data includes unsexed fish.

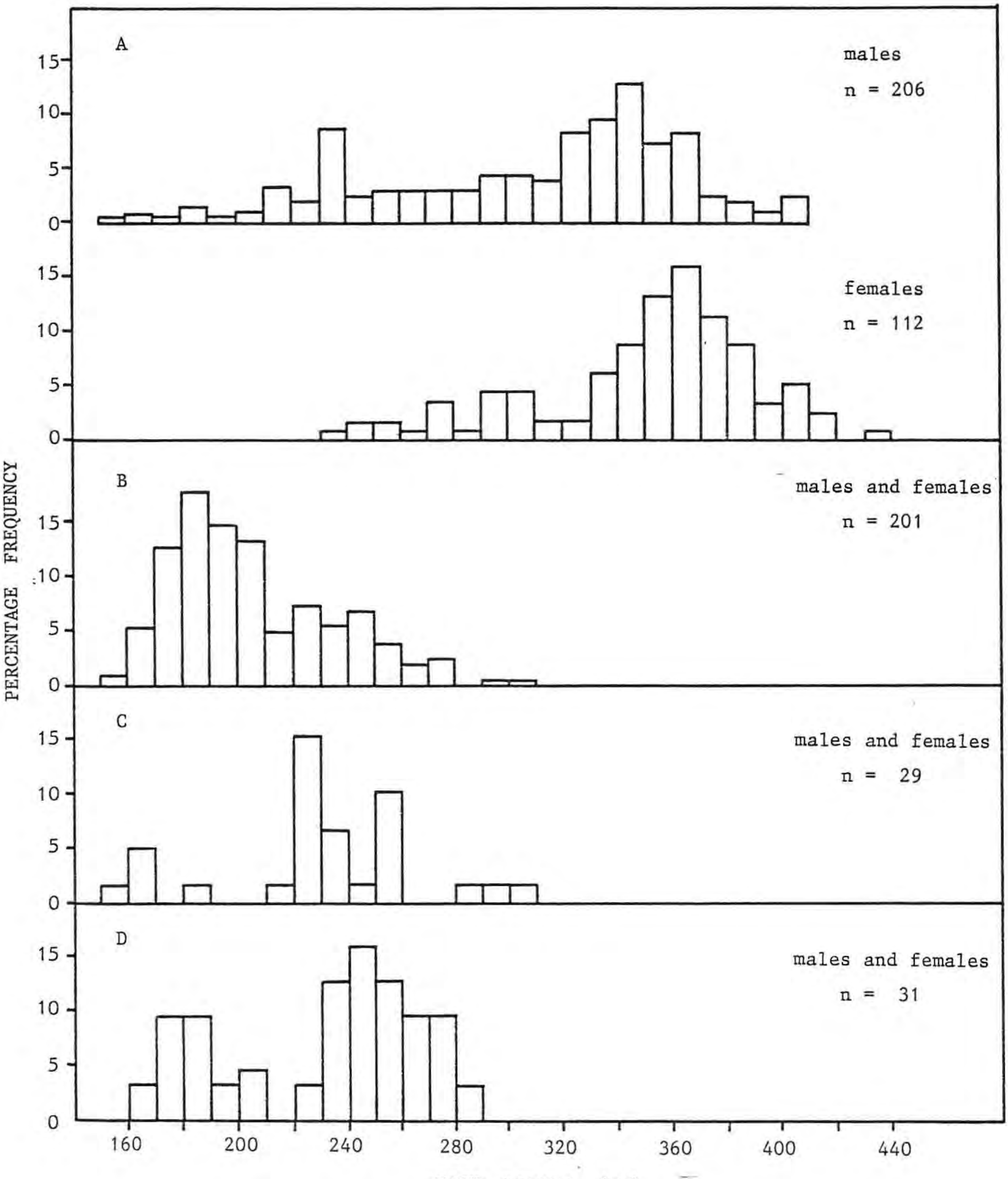


Figure 51. The length frequency distribution of *Mugil cephalus* from the Swartkops (A), Kowie (B), Great Fish (C) and Bushmans (D) rivers.

Table 43 . The relative frequency of male fish in the various age groups of *Mugil cephalus* from the study areas based on age structure determined using age-length keys (Ricker 1975).

Age	Kowie estuary		Great Fish estuary		Swartkops River	
	Total	% male	Total	% male	Total	% male
1+	133	55	621	62	183	72
2+	244	55	468	41	130	54
3+	40	43	100	16		
4+	4	0	12	58		
5+						

In the freshwater areas no 3+ year old fish were captured (Fig. 52). Large scale downstream migration to estuarine areas in preparation for spawning is probably responsible for the absence of older fish in freshwater areas.

As the size of sexual maturity of *Mugil cephalus* from this area is about 300 mm FL (Chapter 5), it is probable that the majority of these fish spawn in their 2+ and 3+ years. The sudden increase in mortality at these ages may therefore have resulted from the stress associated with spawning.

There was a tendency for back-calculated lengths at a given age to be smaller when calculated from older fish in both the Kowie and Great Fish estuaries (Tables 33 & 37). This so-called Lee's phenomenon (Ricker 1975) could be due to biased sampling, with relatively more slower-growing older fish being caught, or increased natural mortality of the faster growing fish. As faster growing *Mugil cephalus* have a tendency to mature at an earlier age (Brusle 1981), it is possible that faster growers suffer greater mortalities associated with an earlier spawning. In addition, if faster growing fish in freshwater migrate downriver before slower growers, this could partly explain the comparatively slower growth rate recorded in *Mugil cephalus* from the freshwater areas of the Great Fish and Kowie rivers.

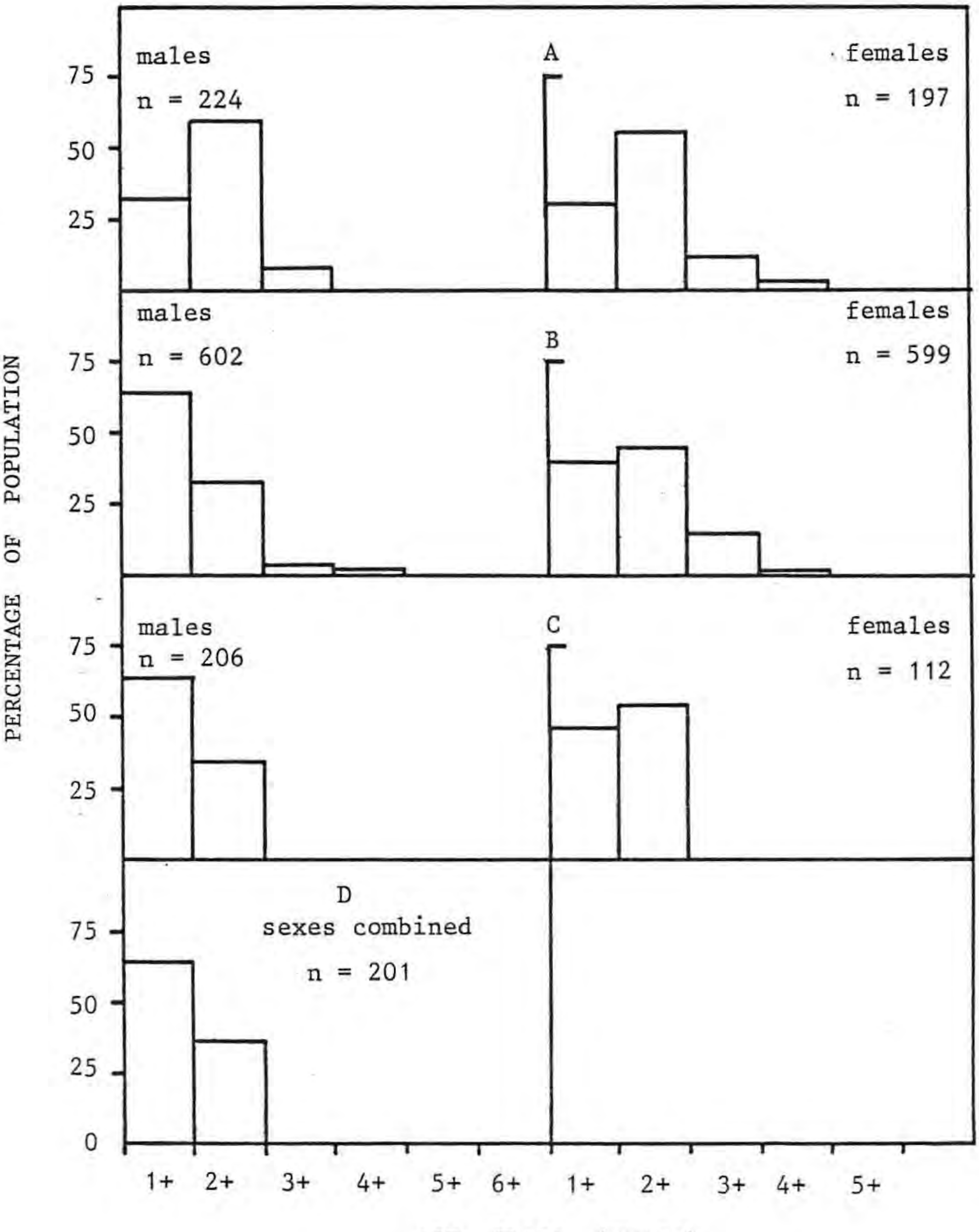


Figure 52. The age structure of *Mugil cephalus* in the Kowie (A) and Great Fish (B) estuaries and in the Swartkops (C) and Kowie (D) rivers. The 0+ year classes are excluded. Values were calculated using length-age keys (Ricker 1975).

Mugil cephalus from the various study areas show marked growth differences in both length (Fig. 47) and weight (Fig. 49 & Table 41). For example, using combined growth data, the mean mass at three years of age in the Swartkops River is 850 g, in the Great Fish estuary, 630 g, in the Kowie estuary, 349 g and the Kowie River, 221 g. These differences in growth rates of *Mugil cephalus* from the various areas, are also reflected in the length : weight relationships (Fig. 53). The highest ratio was found in the Swartkops River, followed by the Great Fish and Kowie estuaries. The condition or "fatness" of the various populations is therefore positively related to the growth rate.

The rapid growth of *Mugil cephalus* in the Swartkops River is probably related to the fact that the fish were almost exclusively found in the lower reaches where highly eutrophic conditions prevail (Chapter 2).

Experimental work on mullet growth in fertilized and unfertilized ponds (Bok, unpubl. data) as well as in farm dams at low stocking densities (Chapter 6) has shown that *Mugil cephalus* is able to increase growth rates markedly under favourable conditions in freshwater areas. The growth rate in the Swartkops River is higher in the first two years than that recorded by various researchers for natural populations of this species in various parts of its range, including tropical areas (Table 44). The higher growth rate of *Mugil cephalus* in the Great Fish compared to the Kowie estuary occurred in spite of the very much higher densities of mullet in the former estuary (Chapter 7). The highly favourable conditions for growth and survival of *Mugil cephalus* in the Great Fish estuary are probably related to the relatively large inflow of nutrients and organic matter into the system from the Great Fish River (Chapter 2).

Substantial differences in growth of various mullet populations have been reported from adjacent estuaries in Florida (Broadhead 1958) and in western Australia (Chubb *et al.* 1981). In both these areas, however, some correlation with temperature differences are indicated, as faster growth occurred in the estuaries situated in the lower latitudes. The close proximity of the Great Fish and Kowie estuaries and the similarity in water temperatures (Chapter 2), however, argue against climatic factors being responsible for the observed growth differences.

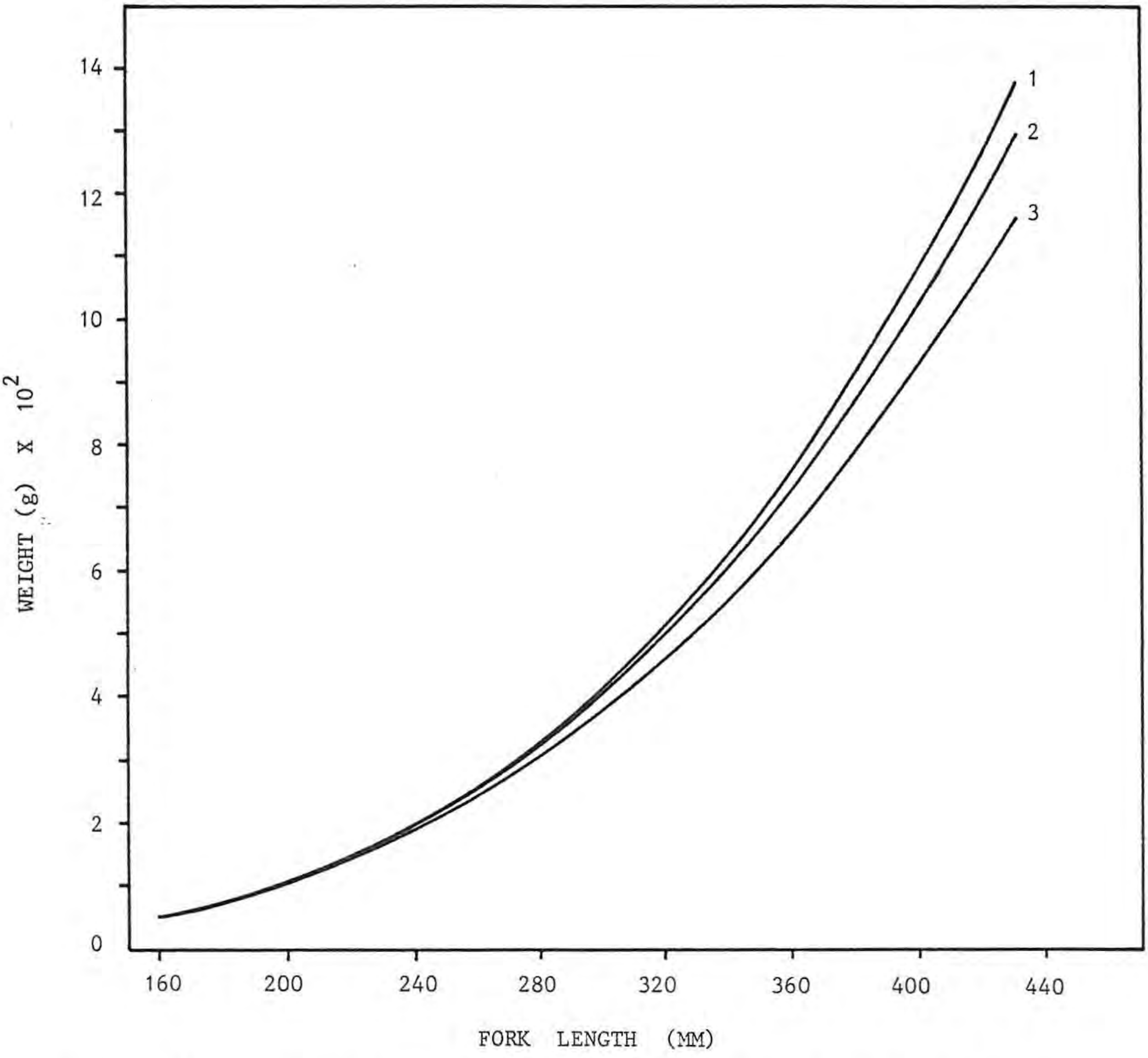


Figure 53. The length : weight relationship of *Mugil cephalus* from the Swartkops River (1), Great Fish estuary (2) and Kowie estuary (3), calculated from length : weight regressions in Table 42.

Table 44 Mean length at age of *Mugil cephalus* from various localities. Lengths are converted to fork lengths using regression equations given by Wallace (1975a).

Fork length (mm) at age (yrs)						Ageing method	Locality	Source
1	2	3	4	5	6			
155	275	343	382			scales	Great Fish estuary	This study
145	228	293	340			scales	Kowie estuary	This study
123	193	248				scales	Kowie River	This study
192	306	372				scales	Swartkops River	This study
137	229	259				scales	Great Fish River	This study
192 *(178 - 205)						length frequency	St Lucia system	Wallace & van der Elst (1975)
149	231	317	397	477	537	scales	Aust. (east temperate)	Kesteven (1942)
150	240	340	380	420		length frequency	Aust. (west temperate)	Thomson (1951)
140	245	336	405	467	505	scales	Aust. (west temperate)	Thomson (1951)
155	285	378	444	491	524	scales	Aust. (north tropical)	Grant & Spain (1975)
183 *(159 - 198)						length frequency	Aust. (west temperate)	Chubb *et al.* (1981)
	171	253	333	426	503	otoliths	Sea of Marmora	Erman (1959)
65	161	241	329	380		otoliths	Bosphorus	Erman (1959)
166	246	318	384	426	451	scales	Italy	Morovic (1954, in Thomson 1963)
150	219	264	303	335		scales	South Texas, USA	Cech & Wohlschlag (1975)
142	207	263				scales	Pensacola, Florida	Broadhead (1958)
134	207	271				scales	Apalachicola, Florida	Broadhead (1958)
175	258	307				scales	Cedar Keys, Florida	Broadhead (1958)
178	269	319				scales	Homosassa, Florida	Broadhead (1958)
167	229	290	385	464		scales	Mahanadi, India	Thakur (1967)
Mean 153	233	301	371	432	504			
(range) (65 - 198)	(161 - 306)	(241 - 378)	(303 - 444)	(335 - 491)	(451 - 537)			

* = range.

In the St Lucia system in Natal, Wallace & van der Elst (1975) found that *Mugil cephalus* reach fork lengths of 108 - 143 mm by March and postulated a size at the end of the first year of 178 - 205 mm FL. However, this may be an overestimate as these authors did not allow for the probable growth decline during the autumn and winter months. More rapid mullet growth in St Lucia is likely, however, because of the higher water temperatures and longer growth period in this system compared to the more temperate eastern Cape estuaries.

In general, the growth of *Mugil cephalus* in the Kowie and Great Fish estuaries over the first two years is similar to that found in other areas, particularly that reported by Kesteven (1942) and Thomson (1951) from estuaries and inshore waters in climatically similar parts of south-western and south-eastern Australia (Table 44). In the third and fourth year, however, mullet growth in the Kowie estuary is comparatively slower.

The paucity of *Mugil cephalus* larger than 400 mm FL in both the Kowie and Great Fish estuaries has also been reported from other eastern Cape estuaries (Marais & Baird 1980; Marais 1981, 1983a, 1983b).
The presence of large *Mugil cephalus* in Natal estuaries, particularly in St Lucia where specimens 400 - 640 mm predominated in catches (Wallace, 1975a), may be related to both faster growth and greater longevity of this species in these more sub-tropical systems. Age and growth data of *Mugil cephalus* from the latter areas are, unfortunately, not available.

GENERAL DISCUSSION

The finding that the growth rate of *Myxus capensis* from the Swartkops River is similar to fish from the other two rivers (at least during the first two or three years), is in contrast to the finding that *Mugil cephalus* grows substantially faster in this highly enriched river compared to its growth elsewhere. In addition, the growth rates of *Myxus capensis* stocked into a number of water bodies, including fertilized and unfertilized freshwater fish ponds, were remarkably similar, unlike those found for *Mugil cephalus* (Chapter 6 ; unpublished data). It is possible that growth (particularly the upper limit) during the first year may be genetically fixed in *Myxus capensis*. This would be an unusual trait as most fish species (such as *Mugil cephalus*) are able to show dramatic increases in growth rates under favourable conditions.

A possible explanation may be that (as discussed in Chapter 7) small (50 - 120 mm FL) *Myxus capensis* have a superior ability to negotiate rapids during low flow conditions compared to larger fish. Small size may therefore be an advantage during its first year when this species spends much of its energy on migrating upriver. If this is true, then unlike most other fish species, rapid growth in its first year would be disadvantageous and would therefore be selected against. *Mugil cephalus*, on the other hand, which is not dependent on a freshwater habitat and hence migratory ability, has developed the potential to greatly increase its growth rate from an early age under favourable conditions.

In general, the growth rate of *Myxus capensis* compares favourably with other mullet species (excluding *Mugil cephalus*) from various parts of the world, with only species from tropical and sub-tropical areas showing faster growth (Table 45).

The possible significance of sex-related growth differences, population structure, age composition etc., will be further discussed in relation to the breeding biology in Chapter 5 and will be only briefly mentioned here.

Faster female growth was found in both mullet species, but the predominance of females in the larger size classes is more marked in *Myxus capensis*. This is probably due to the majority of female *Myxus capensis* undergoing their downriver spawning migration at a greater age. In both species an increased proportion of large females in the population is probably a strategy to increase population fecundity (see Chapter 5).

The absence of *Mugil cephalus* older than 2+ years in freshwater areas of rivers and the low numbers of 3+ and older fish in estuarine areas, is in contrast to that found for *Myxus capensis*. The importance of a large number of age classes, particularly a wide range of ages at first sexual maturity, may be related to the stability of a species' environment (Nikolskii 1969). In the eastern Cape, the unpredictable and erratic river flow means that the estuaries present a more stable habitat with fewer constraints to a marine spawning species than the freshwater reaches of the rivers. A large number of age classes would therefore be advantageous for a catadromous species such as *Myxus capensis*. This aspect is discussed further in Chapter 5 .

Table 45 Growth of *Myxus capensis* and other mullet species from various localities. Measurements given as fork lengths unless specified.

Species	Length (mm) at age (years)					Ageing method	Locality	Source
	1	2	3	4	5			
Myxus capensis	135	237	300	372		scales	Kowie River	This study
Myxus capensis	132	222	290	332		scales	Swartkops River	This study
Myxus capensis	129	214	284	357		scales	Great Fish River	This study
Liza richardsoni	62	129	181			otoliths	Berg River estuary	Ratte (1977)
Aldrichetta forsteri	110	180 - 190	240 - 250	290 - 320	320 - 350	scales	western Australia	Thomson (1957)
Aldrichetta forsteri	136 - 154					length frequency	Swan-Avon, Australia	Chubb *et al.* (1981)
Aldrichetta forsteri	70	140	210	260	310	otoliths	south Australia	Harris (1968)
Valamugil seheli	139	265	357	424	473	scales	Queensland, Aust.	Grant & Spain (1975)
Liza vaigiensis	84	210	310	388	450	scales	Queensland, Aust.	Grant & Spain (1975)
Liza aurata	**116					length frequency	Gulf of Marseilles	Albertini-Berhaut (1978)
Liza aurata	*120	210	260	300	360	unspecified	Black Sea	Nikolskii (1961)
Liza aurata	*210	280	330	360	410	unspecified	Caspian Sea	Nikolskii (1961)
Liza aurata	*113	183	300			unspecified	Adriatic Sea	Serbetis (1939, in Nikolskii 1961)
Liza aurata	*112	174	217			unspecified	Gulf of Glascony	Arné (1938, in Nikolskii 1961)
Liza aurata		***107	187	242	265	scales	southern England	Hickling (1970)
Liza ramada		***118	202	264	296	scales	southern England	Hickling (1970)
Liza ramada		181	210	234	272	unspecified	Gulf of Glascony	Arné (1938, in Hickling 1970)
Crenimugil labrosus		*** 90	161	246	263	opercula	southern England	Hickling (1970)
Crenimugil labrosus		125	169	214	251	scales & otoliths	Irish waters	Kennedy & Fitzmaurice (1969)
Crenimugil labrosus	*160	230	270	290	320	unspecified	Caspian Sea	Nikolskii (1961)
Crenimugil labrosus		236	305	366	422	scales	Mediterranean	Erman (1959)
Crenimugil labrosus		*155	233	324	383	unspecified	Mediterranean	Morovic (1963, in Hickling 1970)
Crenimugil labrosus		*175	260	327	387	scales	Mediterranean	Rossignol (1951, in Hickling 1970)
Mugil curema	203	288	327	345	353	length frequency	E. Virginia, USA	Richards & Castagna (1976)

* unspecified; ** standard length; *** total length

CHAPTER 5. BREEDING BIOLOGY

A. BREEDING BIOLOGY OF *MYXUS CAPENSIS*

INTRODUCTION

Prior to the present study there had been no detailed investigation of the breeding biology of this species, and available knowledge was both meagre and conflicting. Crass (1964) summed up existing knowledge with the statement:

> "Large numbers of small eggs are produced, but where they are laid is unknown".

Riparian landowners and mullet fishermen claim that *Myxus capensis* breed in the freshwater areas of eastern Cape rivers. The evidence usually cited is the appearance of "mullet fry" in freshwater areas during periods of drought when the rivers consist of isolated pools, which precludes recruitment from salt water. If substantiated, these observations would be significant, as most (if not all) Mugilidae appear to spawn only in a marine or brackish water environment (Eckstein 1975, Nash & Koningsberger 1981).

As outlined in Chapter 2 , the topography and flow regime of rivers in the study area are such that fish movement within the rivers is largely restricted to short periods during floods. Combined with the erratic and unpredictable rainfall and hence riverflow of the area, this effectively means that adult fish in fresh water have only limited and erratic access to saltwater areas for spawning purposes. This may be a disadvantage, as reproduction of fishes in temperate regions is characteristically cyclic, so as to take advantage of the most favourable phases of the environmental cycle (Scott 1979). Considering the above arguments, spawning in freshwater would therefore hold advantages for this species.

An important aspect of this study was therefore to investigate the reproductive strategy of *Myxus capensis* which has evolved to ensure successful reproduction in spite of the difficulties created by its catadromous life-history.

Myxus capensis has a threatened conservation status (Skelton 1983) and, in addition, is suitable for stocking into inland waters to increase the angling and fisheries potential (Chapter 6). The implementation of stocking programmes for conservation or fisheries management purposes would require large numbers of young fish. Research on the artificial propagation of *Myxus capensis* was therefore incorporated into this study. Lack of suitable facilities, however, curtailed the induced spawning aspect of this research. A major problem encountered in this work proved to be the availability of sexually mature broodstock fish. This is a prerequisite for the success of any artificial propagation research and is a serious obstacle in mullet spawning work (Nash & Koningsberger 1981). The results of preliminary research on the capture and maintenance of *Myxus capensis* broodstock are therefore included.

METHODS

AREA SAMPLED

Initially, sampling was restricted to the freshwater reaches of the rivers, except in the Kowie where regular netting was carried out in the upper reaches of the estuary. Initial results however, indicated that *Myxus capensis* migrate to an estuarine or marine spawning ground. The sampling programme was therefore extended so as to include regular sampling in all areas of the Kowie and Great Fish estuaries. Netting was also conducted at irregular intervals in the inshore marine zone, off a sandy beach adjacent to the mouth of the Great Fish River.

MATURATION STAGES

The gonads of all fish caught were examined and subjective gonadal maturity stages, similar to those of Nikolskii (1963), were allocated (Table 46). The testes showed little macroscopic development and the various maturation stages were often difficult to distinguish accurately. Analysis of sexual development therefore concentrated on female fish. It is reasonable to assume, however, that for successful spawning the sexual development of male and female fish are synchronized (Scott 1979).

Table 46. Gonadal maturation stages of male and female *Myxus capensis* as modified from Nikolskii (1963).

Stage I Immature

Ovaries and testes small, thread-like, grey to whitish, often difficult to distinguish between the sexes. Gonosomatic index (GSI - below) $<0{,}5$.

Stage II Resting or inactive virgin

Ovaries small, transluscent grey-red or opaque red bags; single eggs not visible to the naked eye. Female GSI <1, usually $<0{,}5$. Testes small and white.

Stage III Active

Ovaries opaque orange-yellow, rapidly increasing in size, with length over 1/2 body cavity; granular whitish eggs visible to the naked eye. Female GSI 0,5 - 3. Testes slightly enlarged and whiter.

Stage IV Ripe (see Fig. 53).

Ovaries fill most of body cavity; ova yellow, opaque and tightly packed. Female GSI >3. Testes enlarged and white with length 2/3 of body cavity. Sexual products not extruded when light pressure applied, although viscous milt may be extruded if firm pressure is applied.

Stage V Ripe-running

Ova transluscent, separate and enlarged, females have distended body cavity with GSI usually >10, but variable. Testes similar in appearance to Stage IV. Male GSI up to 1,5, variable. Sexual products of both sexes extruded when light pressure applied.

Stage VI Spent

Ovaries large, deflated, bloody sacs with few large, opaque eggs remaining. Female GSI <3, variable. Males difficult to distinguish macroscopically from Stage IV, no milt extruded when light pressure applied to abdomen.

The six developmental stages of the ovaries used in this study correspond roughly to the five stages of oogenesis of *Mugil cephalus* ova based on histological studies by Kuo *et al.* 1974 (Table 47). Ova diameters of *Myxus capensis* were obtained from ova preserved in 5% formalin. Stage II of this study is approximately equivalent to the primary oocyte and yolk vesicle stage while Stages III and IV are approximately equivalent to the yolk globule stage. Stage V and VI correspond roughly to the ripe and atretic stages respectively.

Figure 53. Stage IV (Ripe) ovaries of *Myxus capensis*.

Table 47. The macroscopic ovarian developmental stages (with the corresponding ova diameters) of *Myxus capensis* used in this study and the five general stages of oogenesis of *Mugil cephalus* ova (Kuo *et al.* 1974).

This Study			Kuo *et al.* 1974		
Stage		Ova diam.	Stage		Ova diam.
No	name	(μm)	No	name	(μm)
II	Inactive	220	1	Primary oocyte	12 - 170
III	Active	200 - 380	2	Yolk vesicle	170 - 210
IV	Ripe	340 - 660	3	Yolk globule	200 - 700
V	Ripe-running	680 - 880	4	Ripe	
VI	Spent	300	5	Atresia	

GONOSOMATIC INDEX

The unpreserved ovaries were weighed to the nearest 0,1 g in the field and the gonosomatic index (GSI) calculated using the formula:

$$\text{GSI} = \frac{\text{gonad weight} \times 100}{\text{total fish weight}}$$

The weights of the testes tended to be very small in relation to body weight. Even in matured and ripe-running specimens the testes usually weighed less than 1 g. GSI values of male fish were therefore not routinely recorded, apart from a sample of ripe-running and spent fish captured in the sea.

FECUNDITY

To determine the absolute fecundity of *Myxus capensis*, ovaries in stage IV of gonadal development were preserved in Gilson's fluid or 10% formalin for at least three months to facilitate hardening of the eggs and separation from the ovarian tissue. The gonads were split longitudinally and shaken at irregular intervals. After hardening, the ovarian tissue was separated from the eggs by means of forceps and repeated rinsing with tap water. A random sample of eggs was then placed in a petri-dish and egg diameters measured to 0,01 mm using a dissecting microscope with a micrometer eye-piece. The eggs were then dried for at least 12 hours in an oven at 60 - 70° C. To ensure equilibrium of the moisture content between the eggs and the air during weighing and counting, the eggs were kept in the weighing room for about 12 hours after oven drying, before being weighed to the nearest 0,1 mg. At least three subsamples of over 500 eggs were weighed and counted and the total number of eggs per fish was calculated by proportion for each subsample. The final fecundity was calculated as the mean of the replicate subsamples. Differences between replicates were small, with the coefficient of variation never greater than 2,8% (mean = 1,23; n = 21).

RECRUITMENT OF FRY

Information regarding spawning seasons can also be obtained from the time of recruitment and size distribution of fry. If the age of fry when first captured is known, the time of spawning can be estimated. Sampling for mullet fry was therefore carried out at monthly intervals at the head of the Kowie estuary and sporadically in other estuaries from Maitland (33° 59' S, 25° 18' E) to Nahoon (32° 58' S, 27° 56') (Fig. 9). The fry were captured using 2 mm and 5 mm (stretched mesh) seine and dip nets, placed in 5 - 10% formalin and measured to the nearest mm at a later date. The smaller specimens were identified by the characteristic tooth structure of each species (van der Elst & Wallace 1976) with the aid of a dissecting microscope.

MAINTENANCE OF MULLET BROODSTOCK IN SEA WATER

Large *Myxus capensis* were captured by means of gill nets set across pools in the freshwater reaches of the Kowie River. The nets were constantly serviced from a boat and the captured fish carefully released into a landing net by cutting away the restraining mesh of the gill net. The fish were then placed into floating holding cages or plastic containers. By working carefully, most fish captured in this way were undamaged apart from possibly loosing a few scales.

Adult fish caught in freshwater were successfully acclimated to 100% sea water (35°/oo salinity) over periods of as little as four to 12 hours. During rapid acclimation, fish were initially placed in approximately 50% sea water for at least an hour and then placed into approximately 75% sea water for a further hour. Finally, the salinity was steadily increased to 90 - 95% sea water over the remaining two hour period before the fish were transferred into pure sea water. As broodstock need to be in an advanced stage of gonadal development for induced spawning to occur, the gonadal development of the fish acclimated to sea water was determined at intervals. This was done by either inserting a canula into the oviduct and sucking out a few eggs (Kuo *et al.* 1974), or by sacrificing the fish and dissecting out the gonads. Adult *Myxus capensis* were held in the following three systems:
(i) *Holding cages in Kowie Lagoon.* Two large (3 x 2 x 1.5 m) cages, constructed from knotless multifilament nylon mesh (200 mm stretched mesh) over a wooden frame, were placed on the substrate in about 2 m of water in the lower East Bank Lagoon (area *ca* 1 ha) adjacent to the

Kowie estuary. This lagoon is situated about one kilometer from the estuary mouth and connected via a shallow channel to the larger Blue Lagoon lying nearer the mouth. Both lagoons have limited contact with the main channel of the estuary via a number of seepage points in the stone berm separating the lagoons from the estuary itself. The salinity of these lagoons (30 - 40%) approximated that of sea water.

The stocking density in these cages varied between 2 - 6 fish per cage. The fish were occasionally fed trout pellets, but relied mainly on natural food.

(ii) *Large outdoor aquarium.* Four adult *Myxus capensis* (two males and two females), captured in fresh water in the Kowie River, were transported in 200 l plastic drums to the Oceanarium at the Port Elizabeth Museum. During the four hour journey the fish were acclimated to 90% sea water before being transferred (on 6 April 1977) into a 9 m diam. x 1.5 m deep outdoor aquarium containing filtered sea water in the Oceanarium complex.

(iii) *Closed circuit seawater system.* Adult mullet were kept in two circular 800 l asbestos tanks (sealed with inert Epidermix paint) fed by sea water recirculated through a biological filter. The whole system of *ca* 3 000 l was housed in a constant environment laboratory in the J.L.B. Smith Institute of Ichthyology, Grahamstown. Individual mullet were kept in this system for over 12 months. Food in the form of fresh or frozen *Daphnia* and trout pellets was given daily. Various trials in which the light regime and water temperatures were altered to simulate change from summer to winter conditions for these parameters were carried out on these fish.

RESULTS

GONADAL MATURATION

In spite of regular monthly sampling for adult fish at various freshwater sites in the Kowie River over three years, no *Myxus capensis* beyond gonadal maturation stage III were caught. The limited sexual development in fresh water was also found in mullet caught in all the other rivers sampled. The most advanced gonads from fish caught in fresh water were opaque-orange or red in colour with a maximum ova diameter of 240μm. Maximum GSI values of ovaries from these mullet did not exceed 0.80 (Table 48).

No spent fish were found among the 451 adult females examined from the Kowie River. Only one spent fish was sampled in freshwater during this study - a female, 435 mm FL, caught 10 km upstream of the ebb and flow in the Great Fish River on 23 February 1982. It appears, therefore, that very few fish return to freshwater areas after spawning.

The gonads of *Myxus capensis* captured in the estuaries showed the whole range of gonadal maturation stages, except stage V. Far more "active" females were found in estuarine compared to freshwater areas (Table 48). Although no ripe-running fish were found in the estuaries, fish on the verge of spawning as well as recently spent fish were captured (Fig. 54). The degree of gonadal development of females at station 3 (upper reaches) and station 1 and 2 (lower reaches) of the Great Fish estuary were very similar (Fig. 54). The highest GSI value recorded in the Great Fish estuary was 12,8 (gonad mass of 58,0 g), although GSI values rarely exceeded 10. In the Kowie estuary, the highest GSI value recorded was only 2,7, but this relatively low figure could be due to inadequate sampling.

Ripe-running *Myxus capensis* were only captured in the sea during this study. A total of 42 male and seven female fish with gonads in maturation stage V were captured using seine nets in water less than 2 m deep in the surf zone off a beach within 1 km of the mouth of the Great Fish River. The highest GSI value recorded from four ripe-running females captured in this area was 15,9 (mean ± S.D. = 13,6 ± 2,8). This GSI value may be lower than the true maximum GSI value, as eggs were flowing freely from specimens at capture and substantial numbers of eggs could have been lost during netting. This supposition is supported by subsequent fecundity determinations of these ripe-running fish, which were markedly lower than expected.

Most (89%) of the 47 male fish captured in the surf off the Great Fish River beach were ripe-running or partly spent. The testes from these fish were, however, relatively small. The highest GSI value recorded

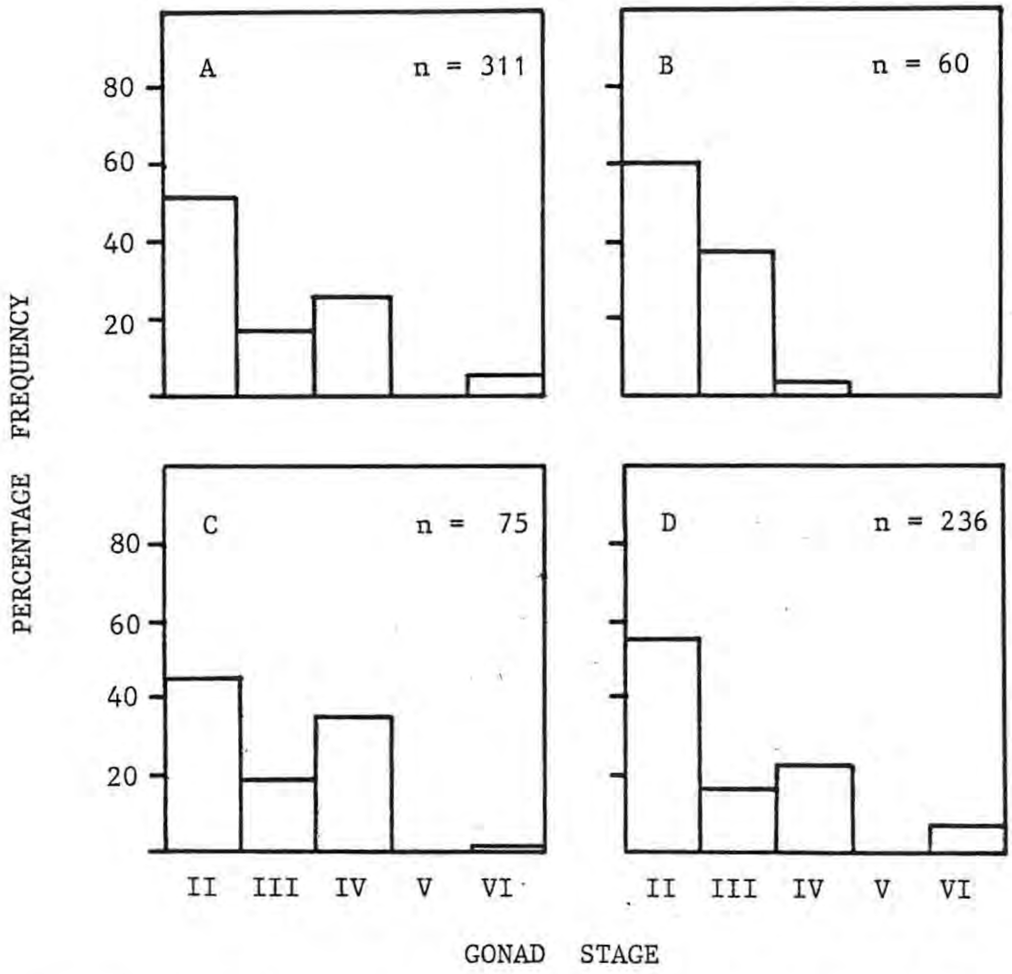


Figure 54. The frequency of occurrence of each gonad stage of adult female *Myxus capensis* captured in the Great Fish estuary (all stations combined) (A) and Kowie estuary (B). Data from the Great Fish estuary are given separately for stations 1 and 2 combined (C) and station 3 (D).

Table 48. The gonadal development of adult female *Myxus capensis* (FL >250 mm) from the various freshwater, estuarine and marine areas sampled. Gonads termed "active" are those in developmental Stage III and above.

Area	Locality	Total number caught	% with "active gonads"	Maximum GSI
Kowie R.	freshwater	451	13,3	0,73
	estuary	60	40,0	2,70
Great Fish R.	freshwater	65	6,2	0,77
	estuary	311	47,3	12,77
Swartkops R.	freshwater	185	31,4	0,68
Surf zone	Great Fish River beach	14	71,4	15,9

was only 1,34 and the largest testis mass, 2,3 g. Although loss of milt during capture may have reduced the mass of the testes, it appears unlikely that the GSI of spawning male *Myxus capensis* increases above a value of about 2,0.

SPAWNING SEASON

RECRUITMENT OF FRY

The monthly catches of *Myxus capensis* at the head of the Kowie (Fig.56) and various other eastern Cape estuaries (Fig.56), show that large numbers of fry (15 - 40 mm FL) are present almost all year round. Larger numbers of smaller fry (< 30 mm FL) were usually caught in spring (September, October and November) and large-scale capture and stocking operations (Chapter 6) were usually most successful at this time. A virtual all year recruitment of *Myxus capensis* fry, with more intensive recruitment in spring, is therefore indicated.

SEASONALITY OF GONADAL MATURATION

The seasonal occurrence of "active" gonads in adult female *Myxus capensis* in freshwater areas of the Swartkops (Fig.57) and Kowie rivers (Fig.58) indicates an extended breeding season as female fish with "active" gonads were found during all months of the year. There was, however, an indication of slightly higher gonadal activity during autumn and winter.

The occurrence of adult females with active gonads from both the Kowie and Great Fish estuaries during the various seasons of the year are shown in Fig. 59 . There was no marked difference in seasonal gonadal development of females in the upper, freshwater reaches and the lower, more saline reaches of the Great Fish estuary. The GSI values (means, standard error and ranges) of active female fish caught at station 3 in the Great Fish estuary over the study period are given in Fig. 60 .

These data show that the ovaries are active during all months of the year and that spawning appears to take place during all four seasons. Unlike the results from fish captured in freshwater, there is no indication of any seasonal peak in gonadal maturation in females captured in either

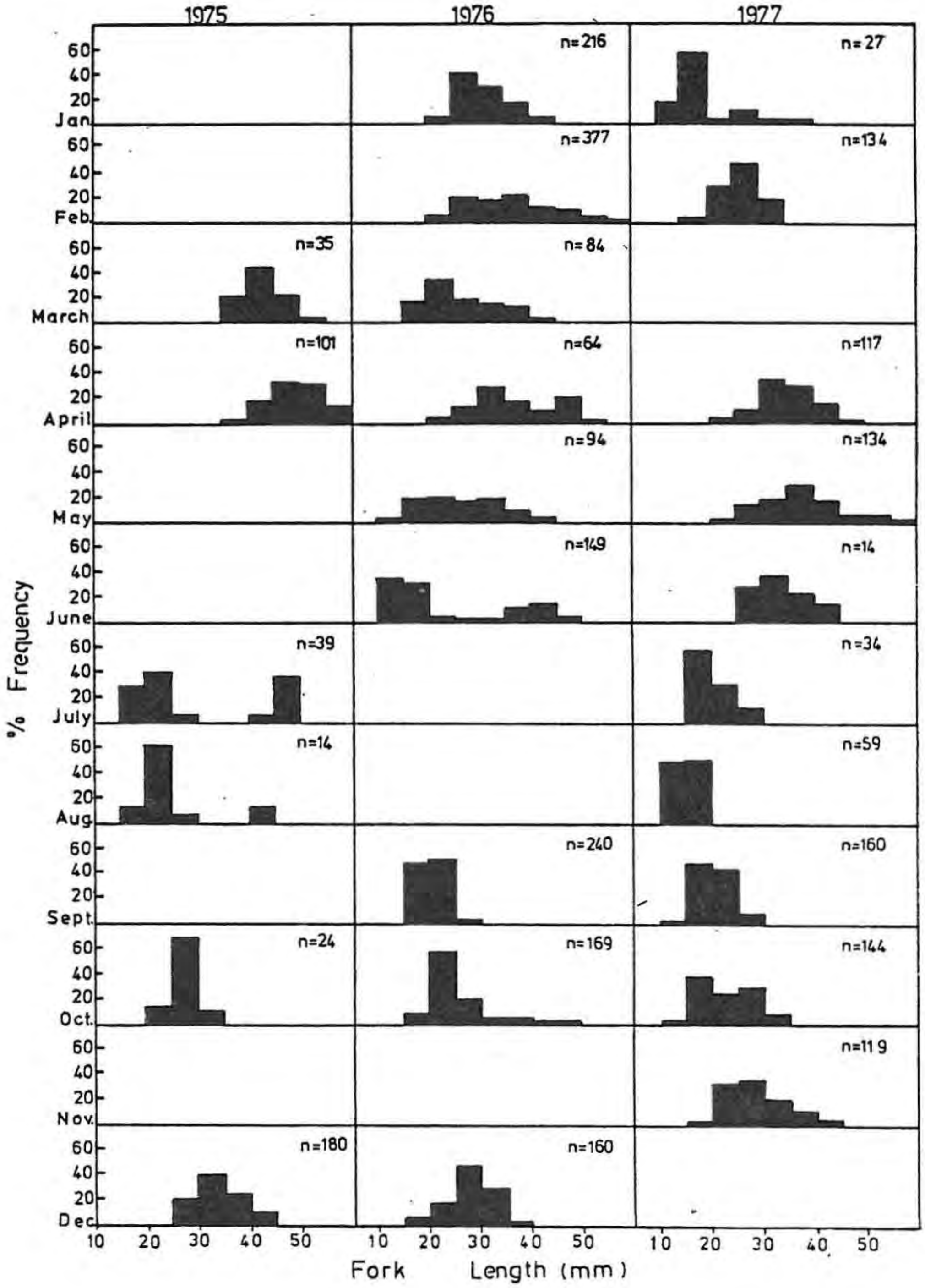


Figure 55 . The length frequency distribution of *Myxus capensis* fry caught at the ebb and flow of the Kowie estuary.

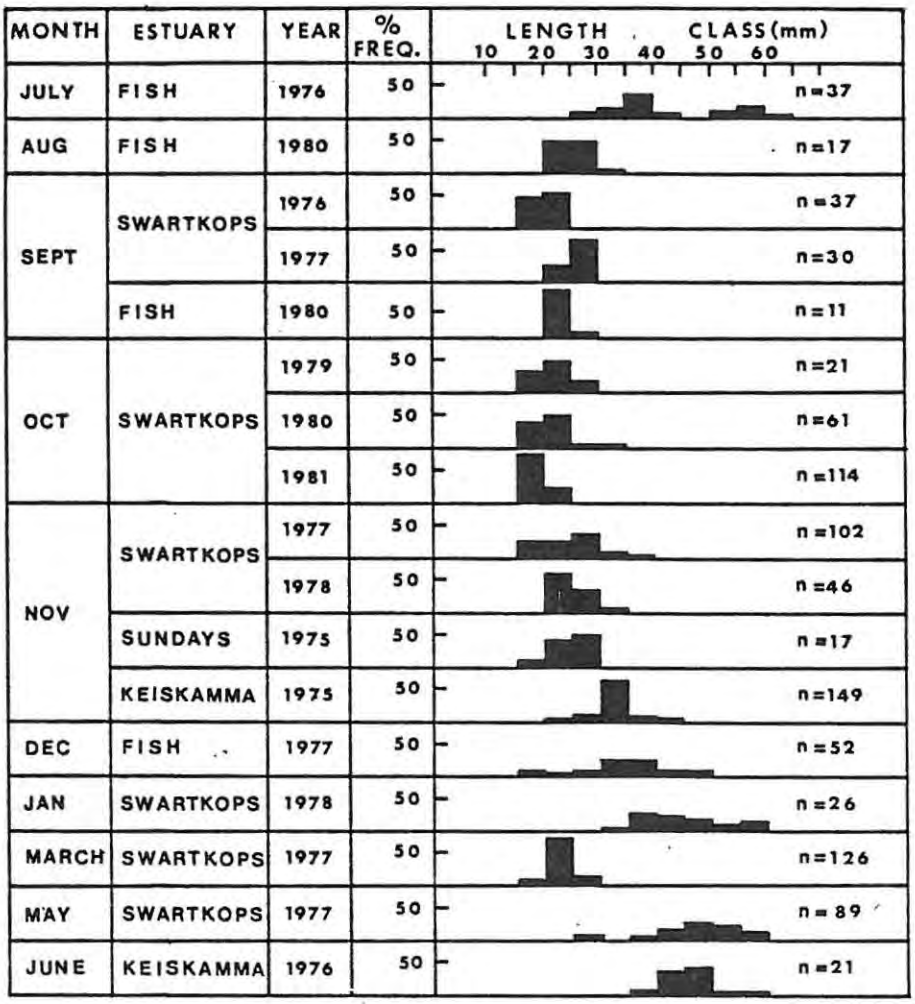


Figure 56 . The length frequency distribution of *Myxus capensis* fry caught at the heads of various eastern Cape estuaries during 1975 - 1981.

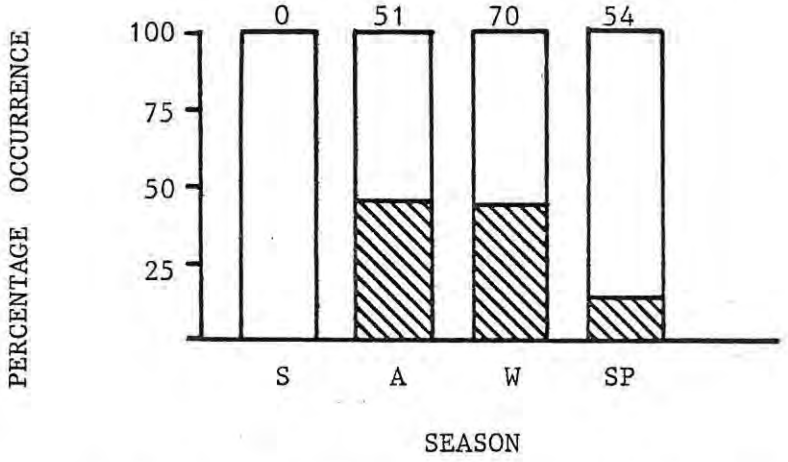


Figure 57. The occurrence of adult female *Myxus capensis* with "active" ovaries (cross-hatched) during the four seasons in the Swartkops River. S = summer, (December, January and February), A = autumn (March, April and May), W = winter (June, July and August), SP = spring (September, October and November). Numerals indicate sample size.

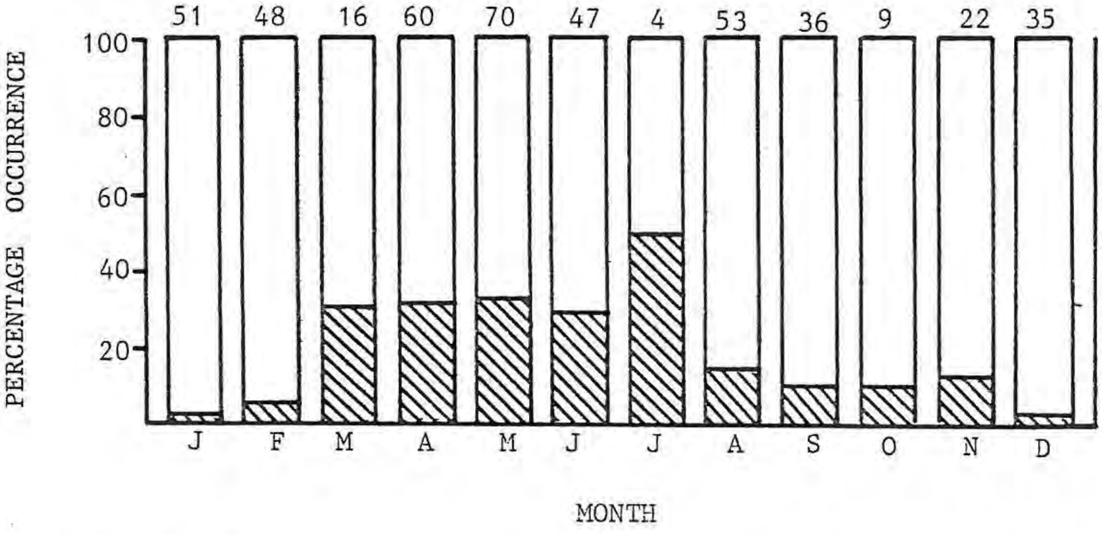


Figure 58. The occurrence of adult female *Myxus capensis* with "active" gonads (cross-hatched) in monthly catches from the freshwater reaches of the Kowie River. Data for 1975 - 1977 combined. Numerals indicate sample size.

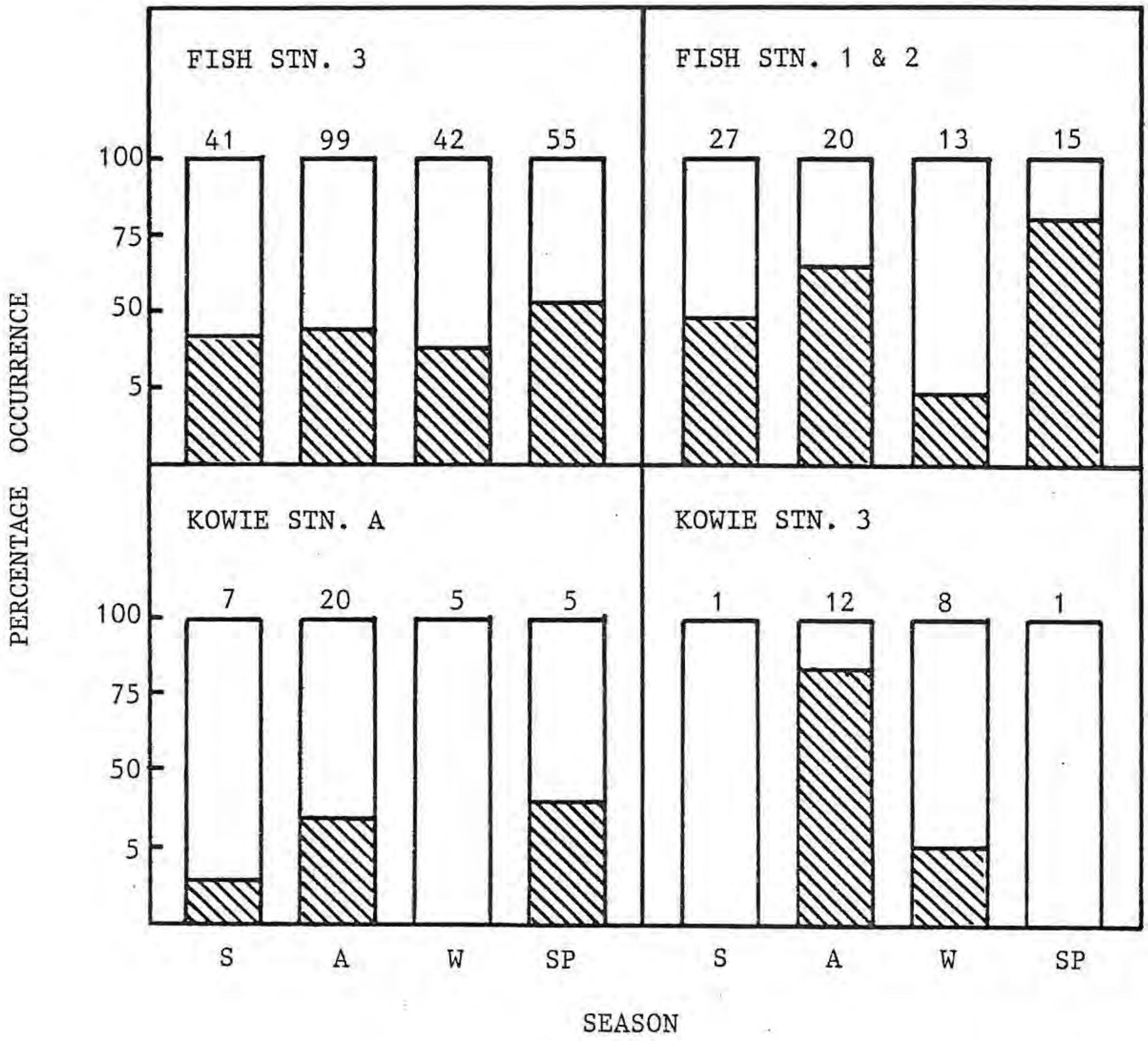


Figure 59. The percentage occurrence of adult female *Myxus capensis* with "active" gonads (cross-hatched) in the Great Fish and Kowie estuaries during the four seasons of the year. Numerals indicate sample size.

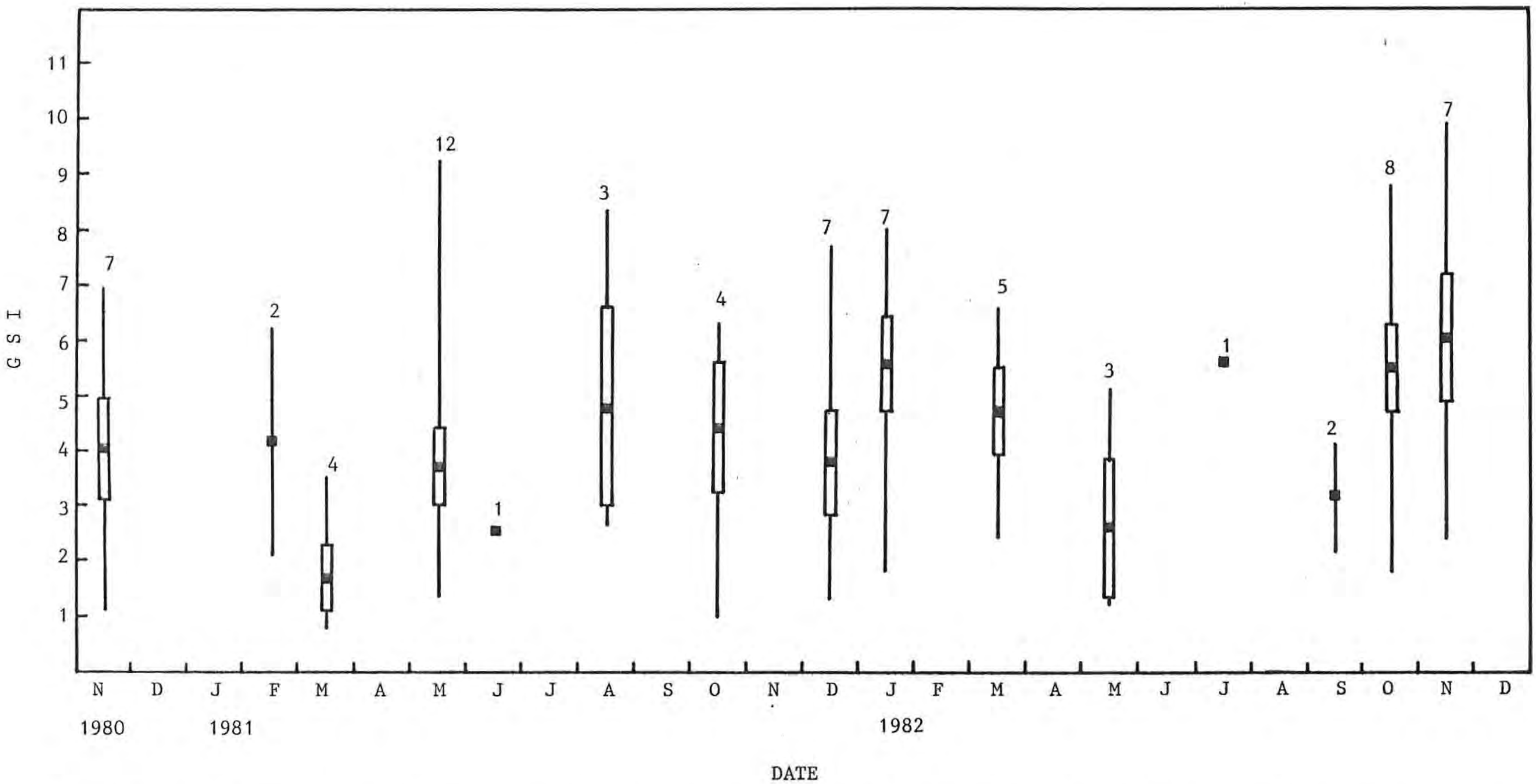


Figure 60. The gonosomatic index (GSI) of female *Myxus capensis* with "active" gonads caught at station 3 in the Great Fish estuary. The data are given as means (squares) ± standard errors (rectangles) and ranges (vertical lines) of monthly catches. Numerals indicate sample size.

the Great Fish or Kowie estuaries (Fig.59).

Regular sampling in the surf zone off the Great Fish River beach was not possible because of the rough surf conditions which usually prevail along this exposed stretch of coast. Unsuccessful netting was therefore probably more a reflection of ineffective sampling that the absence of fish. Ripe-running *Myxus capensis* were netted on four separate occasions off this beach, twice in spring (November) and twice in autumn (April).

SIZE AT SEXUAL MATURITY

The virtual absence of fish with spent gonads in freshwater areas and low numbers caught in the estuarine areas, as well as the short life span of *Myxus capensis* (see Chapter 4), indicate that the vast majority of females spawn only once. It can reasonably be assumed, therefore, that when sexually active fish are captured (particularly in fresh water), sexual maturity is occurring for the first time.

The length frequency distribution of sexually active *Myxus capensis* caught in the freshwater and estuarine areas studied (Fig.61) show a wide range of size classes containing sexually active fish. This variation in size of sexually active fish (equivalent to size at first maturity) and the absence of a specific spawning season, argues against the feasibility of determining the median size at first maturity, i.e. length at which 50% of the sample captured during the spawning season, is sexually mature.

The smallest sexually active female examined measured 268 mm FL. The limited gross morphological changes in maturing testes in fresh water and estuaries did not allow an accurate estimate of size of first maturity of male fish in these areas. The capture of 42 ripe-running males in the marine zone (see above), however, enabled such an estimate to be made. The modal length of these ripe-running male fish was 250 - 280 mm FL with the smallest measuring 216 mm FL (Fig.62). This indicates that males become sexually mature at a smaller size (up to 50 mm) than females.

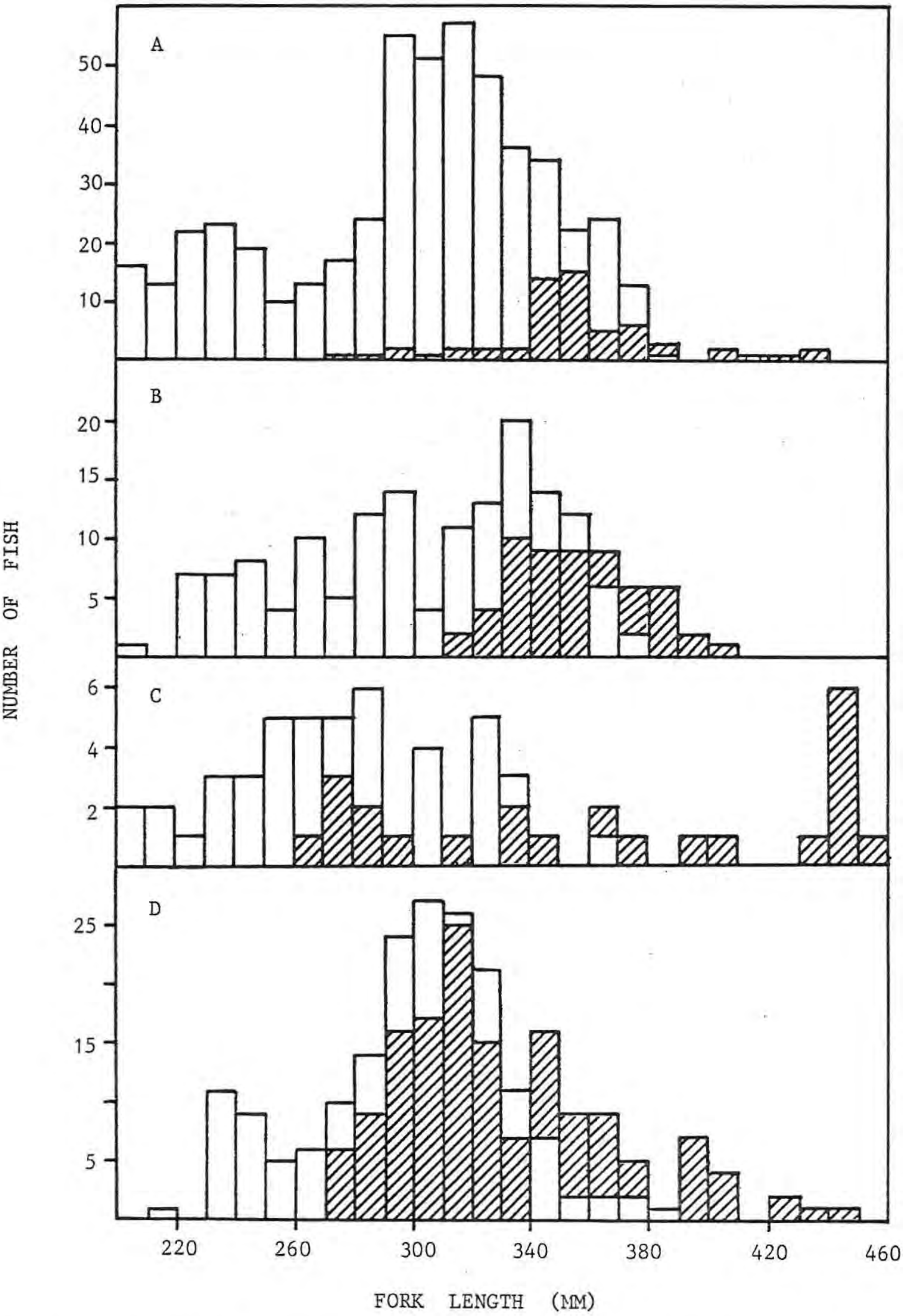


Figure 61. The length frequency of sexually active (cross-hatched) and sexually inactive (open) female *Myxus capensis* of FL 200 mm caught in the freshwater areas of the Kowie (A) and Swartkops (B) rivers and in the Kowie estuary (C) and Great Fish estuary (D).

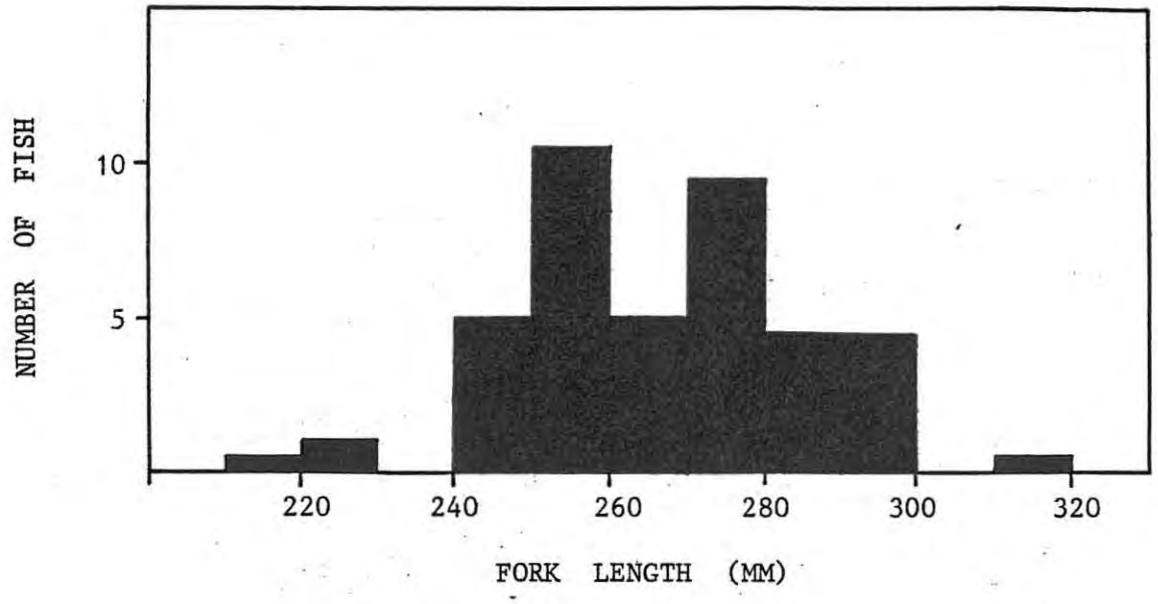


Figure 62. The length frequency of ripe-running male *Myxus capensis* caught in the surf-zone off the Great Fish River mouth beach.

OVA DIAMETERS

Size-frequency analysis of ova from mature and ripe-running ovaries showed there were two distinct size classes (Fig. 63). Large, yellow yolk-filled eggs of uniform size constituted the bulk of the ovaries, while a relatively insignificant (by weight) amount of small, (< 220μm), white, yolkless eggs were also present. The large yolky eggs are thought to represent the eggs in the final stages of development, (the tertiary yolk globule stage; Kuo *et al.* 1974), prior to spawning. The uniform size of these yolky eggs, indicates that individual female mullet are single spawners and probably shed all their eggs over a short period of time.

THE RIPE EGG

Immediately after the capture of ripe-running *Myxus capensis* in the surf off the Great Fish River beach on 16-IV-1981, yellow transluscent ova were stripped from two females into a dry plastic container and mixed with milt obtained from two ripe-running male fish caught in the same haul. After stirring with a small amount of sea water, the eggs were placed in plastic buckets containing continuously aerated sea water and transported *ca* 100 km back to Grahamstown. These eggs were slightly negatively buoyant but were kept in suspension by the water currents created by aeration. The eggs were observed for 48 hours during which time the water temperature varied betweem 16,4 - 19,0^{o} C. Although embryogenesis of most of these eggs was initiated, development did not proceed to beyond the embryonic disc stage.

These eggs (measured 6 hours after fertilization) were spherical and transparent, with diameters from 0,84 - 0,92 mm (mean ± S.D. = 0,88 ± 0,02, n = 16) and usually contained one, rarely two, oil droplets. These oil droplets varied from 0,24 to 0,32 mm (mean ± S.D. = 0,30 ± 0,03, n = 14) in diameter.

SEX RATIO

In all fresh water and estuarine areas there is a large imbalance in favour of females, which dominate among the larger size groups (Fig. 64).

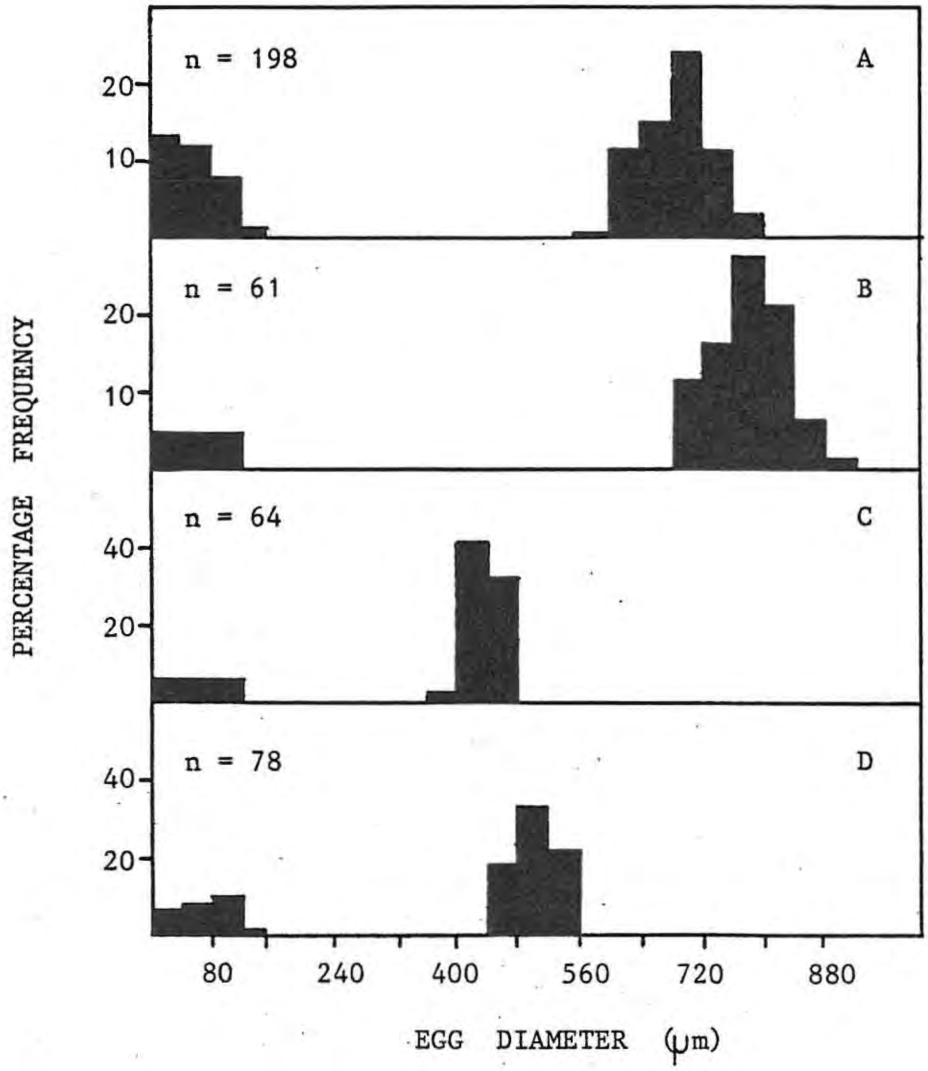


Figure 63. The size frequency of ova from two ripe-running (A & B) and two ripe (C & D) *Myxus capensis* ovaries.

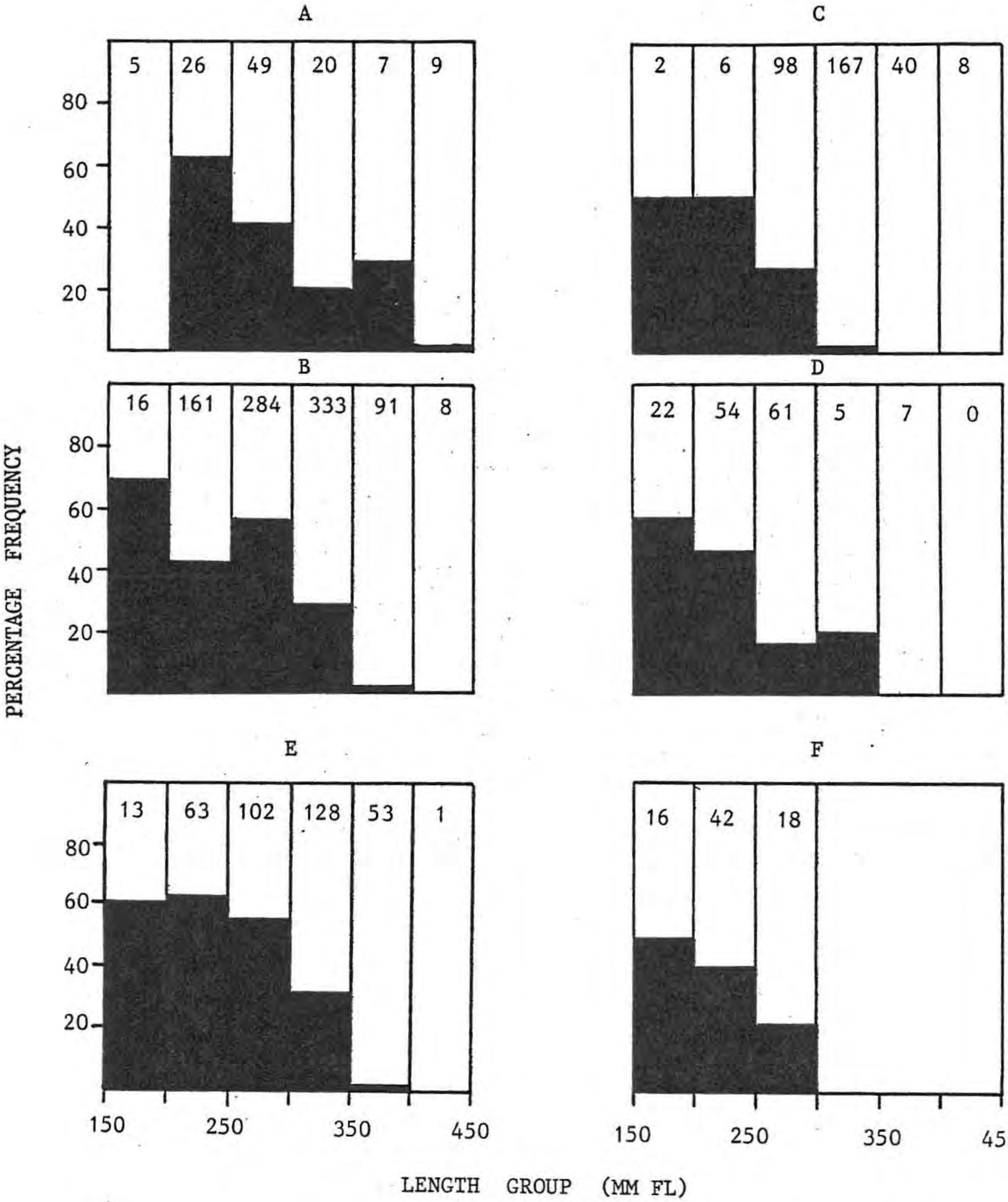


Figure 64. The sex ratios (males ■ , females □) of different size classes of *Myxus capensis* captured in the Kowie estuary (A), Kowie River (B), Great Fish River (C), Great Fish estuary (D), Swartkops River (E) and Bushmans River (F). Numerals indicate total numbers in the size classes.

It is interesting to note that males constituted 77% of a sample of 60 fish netted in a single haul in the surf off the Great Fish River beach, while males only formed 11% of the 321 adult *Myxus capensis* netted in the Great Fish estuary.

FECUNDITY

Egg counts were carried out on ovaries in developmental stage IV, which contained yolk-filled eggs of uniform size. The absolute fecundity determinations therefore adhere to the definition of Bagenal (1978) as "the number of ripening eggs in the ovary just before spawning". The fecundity of *Myxus capensis* varied from 150 270 eggs in a 280 mm FL female to 509 429 in a 430 mm FL female. Fecundity was related exponentially to length (Fig. 65) and linearly to body weight (w) according to the expressions:

$$\text{absolute fecundity} = 0{,}0127\ \text{FL}^{2{,}8985}\ (r^2 = 0{,}93;\ \ n = 21)$$

$$\text{absolute fecundity} = 510{,}5\ W + 24223{,}2\ (r^2 = 0{,}89;\ \ n = 21)$$

The absolute fecundity of *Myxus capensis* therefore increases as approximately the cube of its length, a common relationship in fishes (Bagenal 1978). The wide range in size of spawning female fish (270 to 450 mm FL) in this (postulated) single spawning species, means that a large female can contribute over four times as much as a small female to the population fecundity. The "fecundity index" for *Myxus capensis*, based on the catch composition from the various sampling sites (Fig. 66), indicates that a wide range of length classes contribute substantially to the total population fecundity.

The relative fecundity of *Myxus capensis*, calculated over the size range of sexually active fish, varied from 632 - 528 eggs/g body weight. However, as Bagenal (1978) points out, comparisons of relative fecundity of various populations or species can be misleading. The differences in the contribution which the gonads make to total body weight, as well as changes in condition of the fish as spawning approaches, argue against the validity of using relative fecundity for comparative purposes.

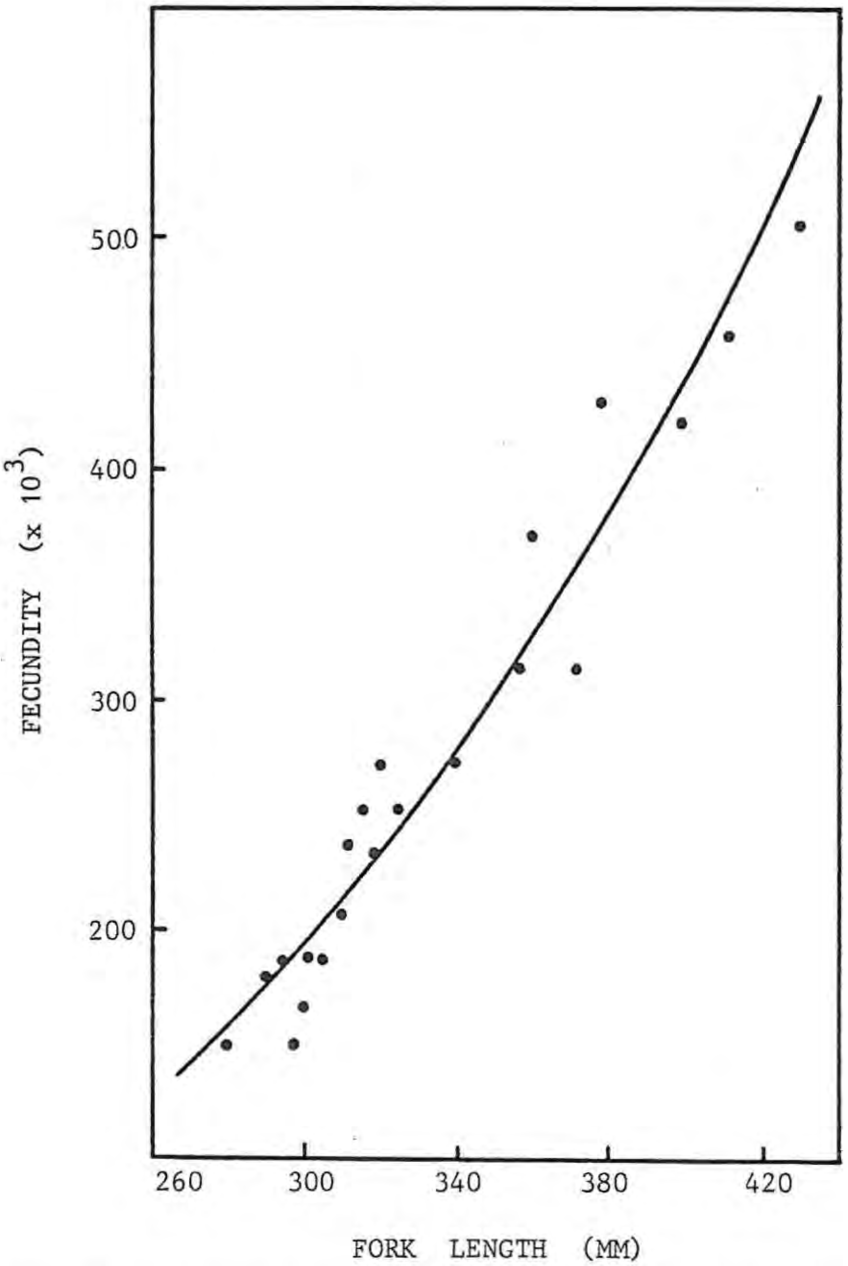


Figure 65. The absolute fecundity related to FL of 21 ripe *Myxus capensis* captured in the Kowie and Great Fish estuaries. Absolute fecundity = 0,0127 FL ^{2,8985} (r^2 = 0,93; n = 21).

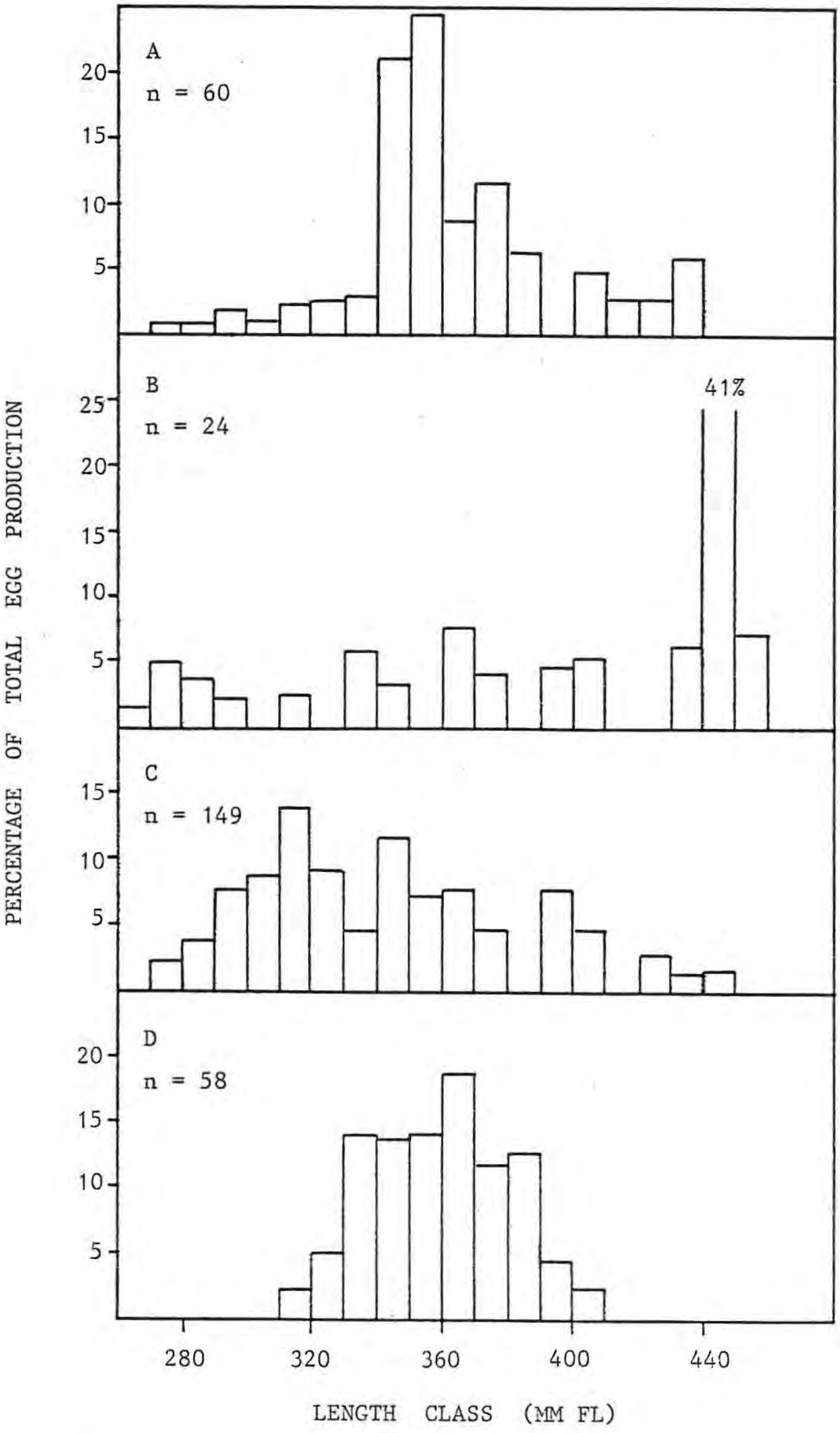


Figure 66. The population fecundity of *Myxus capensis* based on the length frequency of active female fish caught in the freshwater reaches of the Kowie River (A), the Kowie estuary (B), the Great Fish estuary (C) and the Swartkops River (D).

CONDITION

Myxus capensis accumulated fat reserves in the wall of the abdominal cavity. Fish sampled were given a "fat index" on a 5 point scale (0 - 4), with "0" designating fish with no visible fat deposits and "4" the maximum. The occurrence of the allocated fat indices in relation to length in fish from the Kowie River (Fig. 67), shows that significant fat accumulation (values 3 and 4) occurs only in adult fish. The smallest size at which over 50% of the catch have fat indices of 3 or 4, occurred in the size class 240 - 260 mm FL in males and 260 - 280 mm FL in females. Significantly, these size classes correspond to the minimum size at sexual maturity of each sex (see above). This strongly indicates the role these fat deposits play in providing a readily available energy source for the development of gonads as well as for use during the migration downriver for spawning purposes. The relative condition of mullet at various times of the year and at various stages of gonad development was assessed using the formula by Bruton (1979):

$$CF = \frac{\text{Actual weight}}{\text{Expected weight}}$$

where expected weight = $a \times \text{fish\_length}^{b}$

The regression equations of weight on length for the groups under consideration are given in Chapter 4 , Table 30 .

In the freshwater reaches of the Kowie River, the relative condition of subadults (150 - 250 mm FL) is lowest in winter, rising to a peak in spring (Fig.68A). Adult males show little change in relative condition during the year (Fig.68B), whereas adult females show a slight fall in relative condition in winter (Fig. 68C). In the months of April, May and June, sufficient numbers of "sexually active" (i.e. gonad stage III) females (n = 19, 17 and 10 respectively) were caught in these freshwater reaches to enable the relative condition of sexually active and inactive fish to be calculated separately. As shown in Fig 68C, the sexually active fish have a markedly higher relative condition compared to the inactive fish. Ovaries remain small in fresh water, and would therefore have a negligible effect on condition. This indicates that only fish in a relatively good condition (probably due to large-scale fat

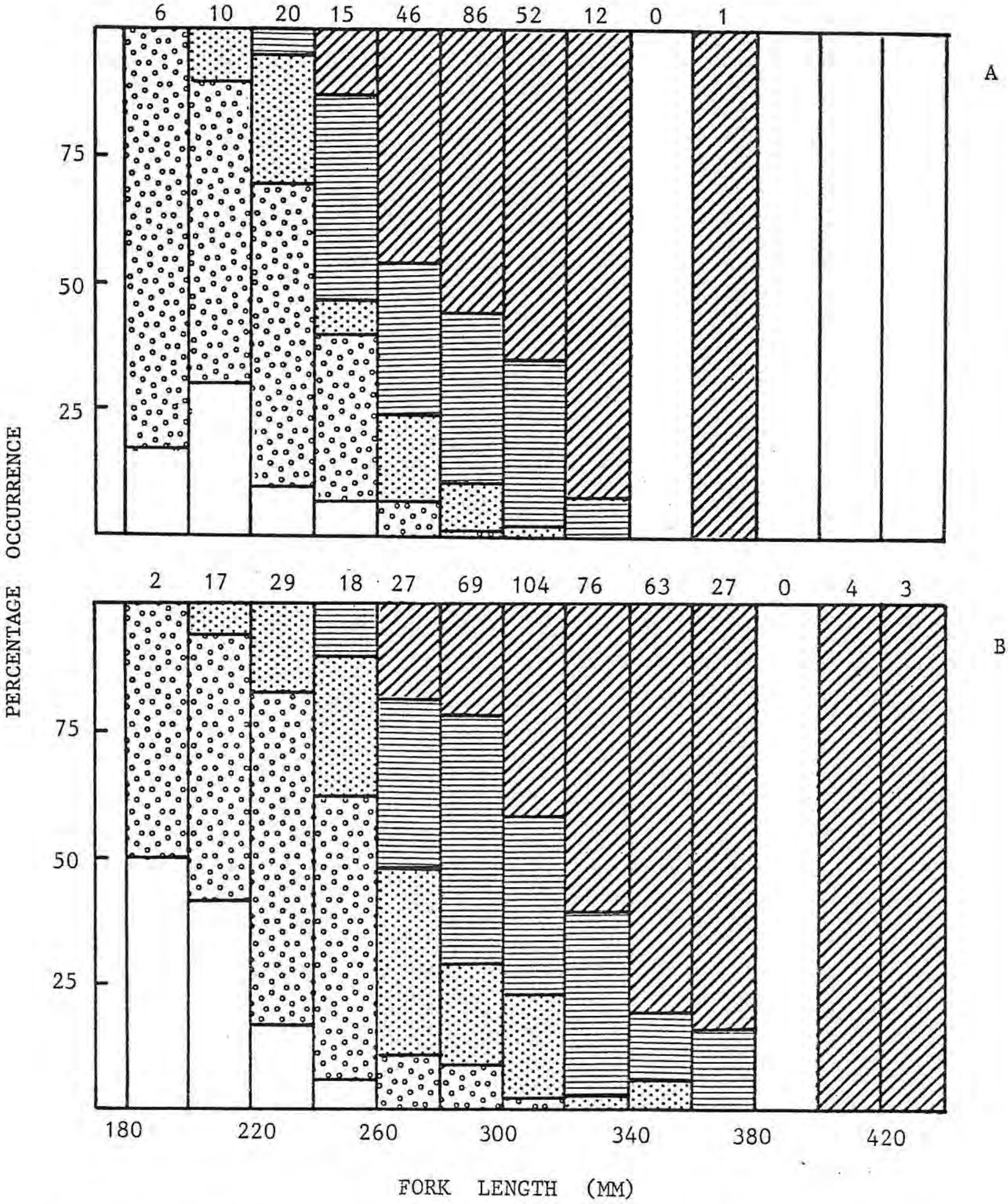


Figure 67. The percentage occurrence of five stages of fat accumulation (see text) relative to length of male (A) and female (B) *Myxus capensis* from freshwater reaches of the Kowie River. The fat index stages are represented as follows: open = stage 0, circles = stage 1, dots = stage 2, horizontal lines = stage 3, cross-hatched = stage 4. Numerals indicate sample size.

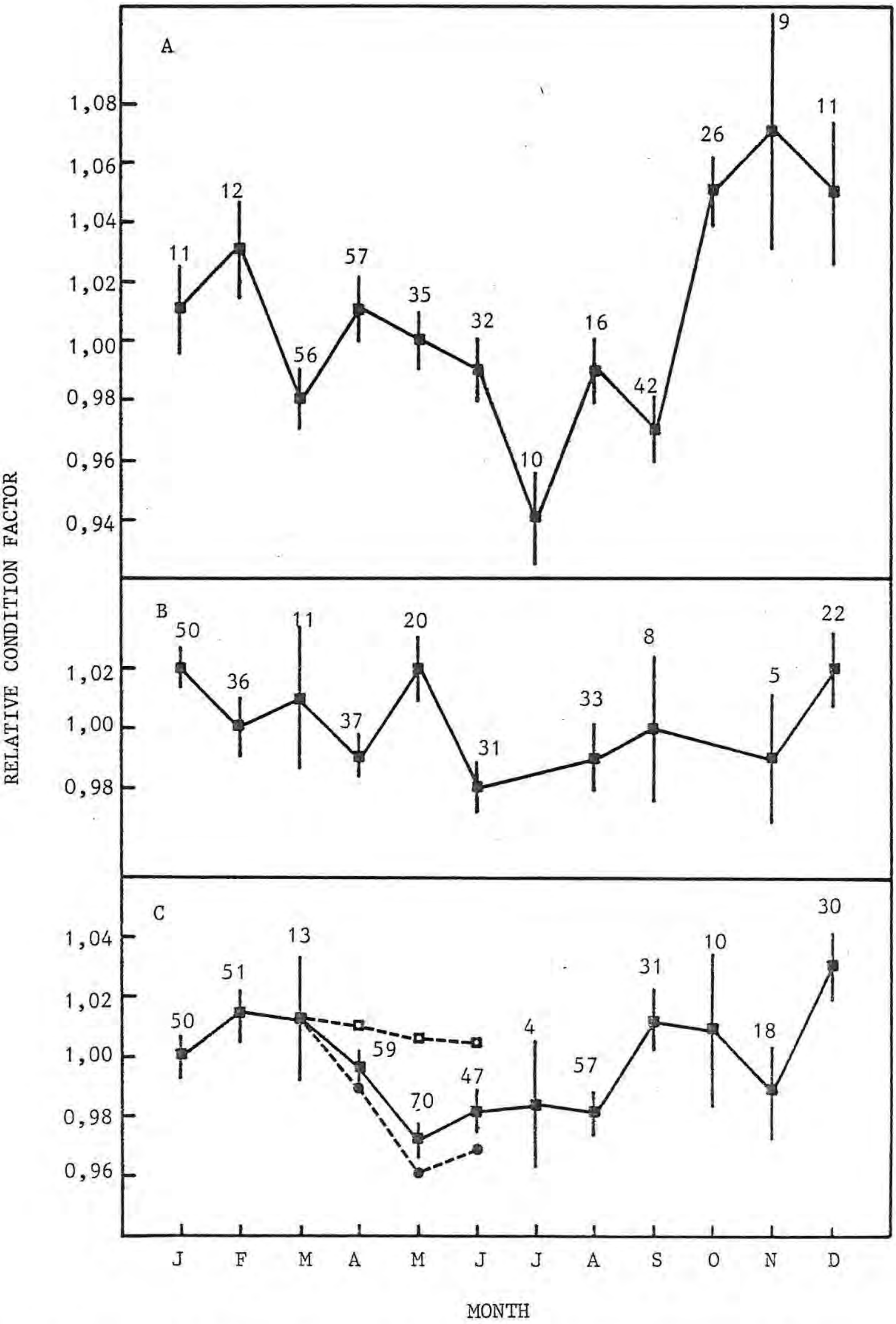


Figure 68. The monthly relative condition of *Myxus capensis* sub-adults (A), adult males (B) and adult females (C) caught in freshwater reaches of the Kowie River. The relative condition of sexually active (open squares) and inactive (closed circles) females are given separately for April, May and June. Data are given as monthly mean (closed squares) and standard errors (vertical lines). Numerals indicate monthly sample size.

deposition) are physiologically "ready" to begin sexual development.

The relative condition of female fish from the Great Fish estuary in relation to the observed GSI values, calculated both with and without ovary weights, are shown in Fig. 69. The relative condition is seen to drop sharply as the ovaries start developing. At GSI values greater than five, the relative condition (with ovaries) stabilizes at the lower level. This decline in condition indicates that the production of the ovaries is at the expense of energy reserves, which are not adequately replaced through feeding.

The relative condition (minus ovaries) of females drop to 0,85 when the GSI rises above 8 (Fig.69). This value corresponds closely with a mean relative condition (minus ovaries) of 0,86 for three ripe-running females captured in the surf, as well as with the mean relative condition (with ovaries) of all spent females captured in the Great Fish estuary, namely 0,88 (S.D. = 0,06, n = 15). The marked loss of condition in these fish emphasises the large metabolic cost of reproduction in female *Myxus capensis*.

The fall in relative condition of ripe male fish is much less than that of ripe females. The mean relative condition (minus testes) of five ripe (stage IV) male fish caught in the Great Fish estuary was 0,96 (S.D. = 0,06), while 35 ripe-running and partially spent males netted in the surf had a mean relative condition of 0,95 (S.D. = 0,06). The lower metabolic cost of reproduction in males is consistent with the large difference in the size of ovaries and testes in ripe fish (see above).

MAINTENANCE OF BROODSTOCK FISH IN SEA WATER

(i) *Holding cages in Kowie Lagoon.*

Individual fish were kept in these cages for over 18 months without showing any indication of gonadal maturation. For example, two female fish (326 and 445 mm FL) stocked on 11-V-1979 and sacrificed on 26-IX-1979 (i.e. over six months later) had gonads in late stage II and GSI values of 0,31 and 0,71 respectively. These two fish were, however, in poor condition (CF = 0,77 and 0,64). A shortage of

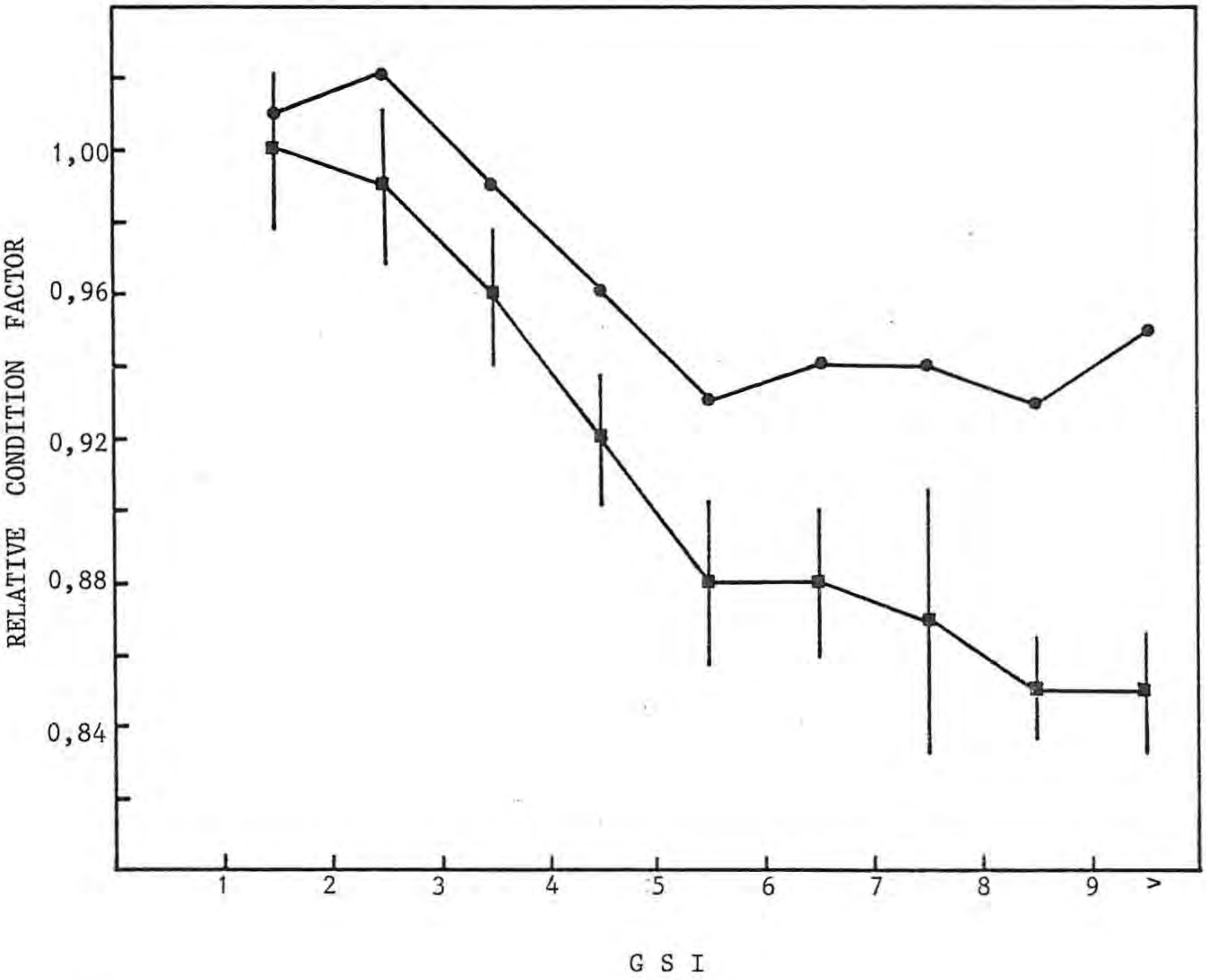


Figure 69 . The mean relative condition factor (see text) of female *Myxus capensis* from the Great Fish estuary, calculated with (circles) and without (squares) gonad weight in relation to the observed GSI values. The vertical bars represent standard errors of the mean.

adequate food probably contributed to the lack of gonad development in the fish held in these cages (see below).

(ii) *Large outdoor aquarium.*

When sampled 50 days after stocking, no ripening of the gonads was evident (Table 49). Again, lack of adequate food (as indicated by low condition factors) could have contributed to this lack of gonadal development.

Table 49 . Details of two male and two female *Myxus capensis* 50 days after stocking into a seawater aquarium at the Port Elizabeth Museum.

FL (mm)	Mass (g)	Sex	GSI	Gonad description	Relative C.F.
342	486	♀	0,66	St. II, yellow, no eggs visible	0,84
350	577	♀	0,59	St. II, yellow, no eggs visible	0,91
329	465	♂	0,21	St. III	0,92
309	334	♂		St. II	0,80

(iii) *Closed-circuit seawater system.*

At no stage did the gonads of mullet kept in this system show any signs of ripening beyond stage II. The largest ova diameters found in female fish after exposure to 100% sea water was 180 μm. These ova were therefore smaller than the ova of "active" mullet caught in freshwater habitats (in the early phase of stage III) which have ova diameters of up to 240 μm.

BREEDING BIOLOGY OF *MUGIL CEPHALUS*

INTRODUCTION

In order to assess the possible adaptive significance of the reproductive strategies of *Myxus capensis*, it was considered useful to draw comparisons with *Mugil cephalus*. Not only do these two mullet species co-exist in both the estuarine and freshwater areas studied, but the biology of *Mugil cephalus* has been extensively studied in many parts of the world. The methods and equipment used to collect the data were identical to those described for *Myxus capensis*.

RESULTS

GONADAL MATURATION AND SEX RATIO

The data obtained on sexual development are limited but indicate that gonadal maturation begins in both sexes at approximately 300 mm FL (Table 50). This finding is similar to those from other studies. Both Thomson (1963), working in southern Australia where climatic conditions are similar to the study area, and Whitfield & Blaber (1978) working in Lake St Lucia, found that sexual development of *Mugil cephalus* occurs only in fish over 300 mm FL (Table 51). Fish larger than 300 mm FL were therefore considered "adults" in this study.

Limited gonadal development occurs in the freshwater reaches of eastern Cape rivers, where a maximum GSI of 1,3 was recorded (Table 50). In these freshwater areas there is a large imbalance in favour of males (Table 50), which is in direct contrast to that found for *Myxus capensis* (above).

Few sexually active and no ripe-running *Mugil cephalus* were found in either estuary. A paucity of ripe-running female mugilids has been reported by a number of authors (Brusle 1981). Although ripe *Mugil cephalus* were found in the St Lucia system, no ripe-running fish were among the 1 814 sexually mature specimens examined by Wallace (1975b). Final sexual maturation, as for *Myxus capensis*, therefore appears to occur at sea. The only ripe-running *Mugil cephalus* caught in this study (a male, 373 mm FL) was seine netted in the surf zone about 1 km from the Great Fish River mouth on 18-V-1982.

Table 50. The gonadal development and sex ratio of *Mugil cephalus* from the various study areas.

River System	Locality	No. caught		ratio males: females	% "Active" adults		Size (mm FL) of smallest active fish		Max. female GSI
		males	females		males	females	male	female	
Swartkops	freshwater	203	109	1:0,5	15	15	316	359	1,3
Kowie	freshwater	59	9	1:0,2	0	0			<1
	estuary	227	181	1:1	19	6	308	344	7,2
Great Fish	freshwater	19	5	1:0,3					<1
	estuary	602	599	1:1	10	6	290	312	

RECRUITMENT OF FRY

The most reliable data on the spawning season of *Mugil cephalus* was obtained from regular monthly sampling for fry over a three year period at the head of the Kowie estuary. The recruitment of fry (15 - 40 mm FL) took place at this site mainly from July to October, with smaller numbers in May, June and November (Fig. 70 ; Bok 1979). Additional fry recruitment data obtained from catches at the heads of the Maitland, Swartkops, Kariega, Great Fish, Kesikamma and Nahoon estuaries, corresponded closely with those from the Kowie estuary (Fig. 71). These data show that recruitment of *Mugil cephalus* fry occurred mainly from July to September in the Great Fish River and from September to October in the Swartkops River. *Mugil cephalus* fry of 15 - 40 mm FL are estimated to be between 3 - 8 weeks old (Anderson 1958; Liao *et al.* 1971). The majority of fry captured in this study were 20 - 30 mm FL, with an estimated age of 4 - 6 weeks. The spawning period of this species along the eastern Cape coast, therefore, appears to extend over the seven month period from April to October, with the peak spawning period during the winter months June, July and August.

CONDITION FACTOR

The monthly relative condition factors (see above) of sub-adult *Mugil cephalus* from Kowie River Station 1 (FL range 120 - 310 mm) and from

Table 51. The length and age at first sexual maturity of *Mugil cephalus* in various localities.

Locality	Length (mm) Males	Length (mm) Females	Age (yrs) Males	Age (yrs) Females	Authority
Florida (NW to NE)	242 - 286	260 - 300	2+	2+	Broadhead (1953 , 1958).
Florida (E)	330	350	2	3	Stenger (1959) from Thomson (1963)
Gulf of Mexico	240	258			Arnold & Thomson (1958)
Black Sea			6 - 7	7 - 8	Nikolskii (1961)
Australia (E)	310	310	3	3	Kesteven (1942)
Australia (W)	310 - 350	310 - 350	3	3	Thomson (1951)
Sea of Marmora	400	415	5	5	Erman (1959) from Thomson (1963)
Med. (Israel)	470	470	3	3	Abraham (1963)
Lake Kinneret		570		2+	" "
Mauritania	390	460	3	3	Brulhet (1975)
Heated effluent - Texas		160		1	Linder *et al.* (1975)
South Africa (St Lucia)	340*(440)	360*(480)			Wallace (1975b) (*Length at which most specimens were sexually mature).
South Africa (St Lucia)	300	320			Whitfield & Blaber (1978)

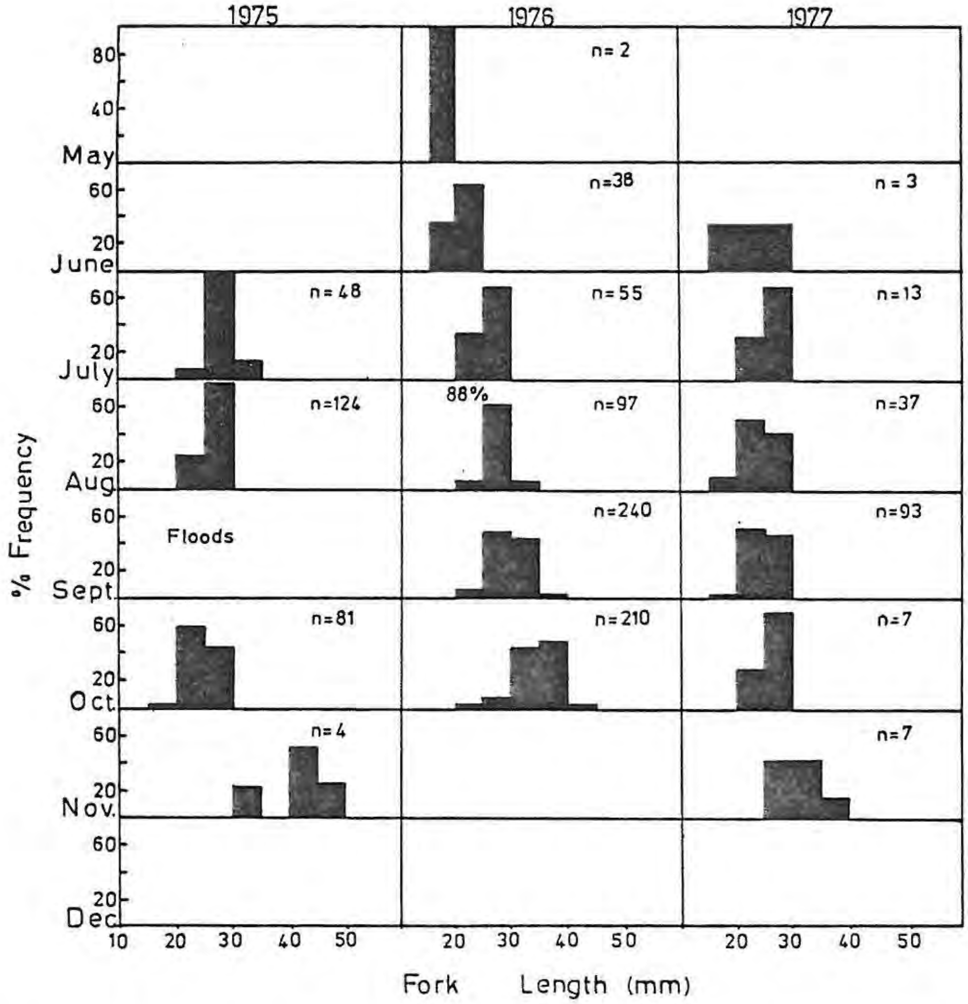
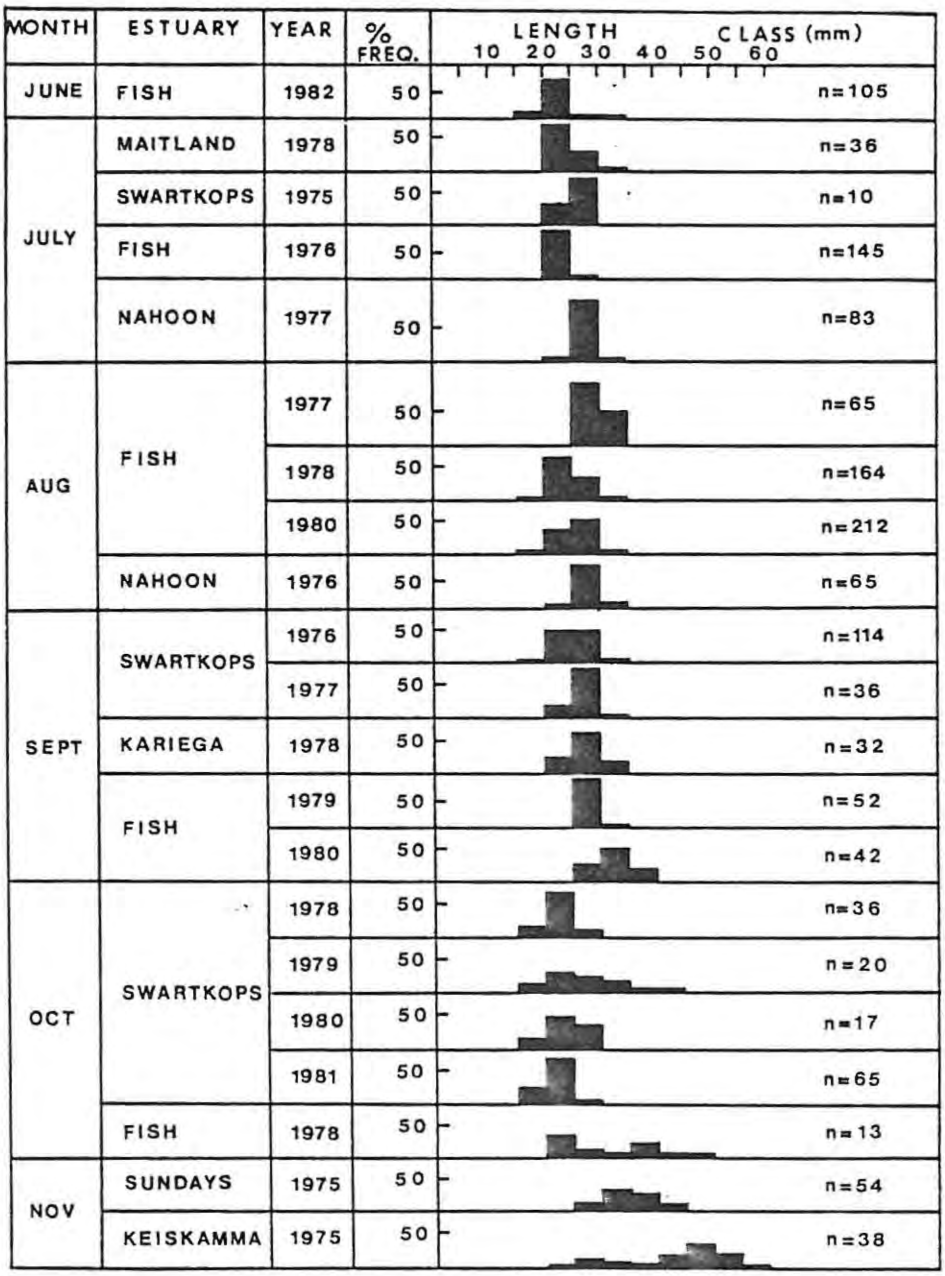


Figure 70. The length frequency distribution of *Mugil cephalus* fry caught at the ebb and flow of the Kowie estuary.



MONTH	ESTUARY	YEAR	% FREQ.	LENGTH CLASS (mm) 10 20 30 40 50 60
JUNE	FISH	1982	50	n=105
JULY	MAITLAND	1978	50	n=36
	SWARTKOPS	1975	50	n=10
	FISH	1976	50	n=145
	NAHOON	1977	50	n=83
AUG	FISH	1977	50	n=65
		1978	50	n=164
		1980	50	n=212
	NAHOON	1976	50	n=65
SEPT	SWARTKOPS	1976	50	n=114
		1977	50	n=36
	KARIEGA	1978	50	n=32
	FISH	1979	50	n=52
		1980	50	n=42
OCT	SWARTKOPS	1978	50	n=36
		1979	50	n=20
		1980	50	n=17
		1981	50	n=65
	FISH	1978	50	n=13
NOV	SUNDAYS	1975	50	n=54
	KEISKAMMA	1975	50	n=38

Figure 71. The length frequency distribution of *Mugil cephalus* fry caught at the heads of various eastern Cape estuaries during 1975 - 1982.

the Kowie estuary (FL range 137 - 299 mm) are shown in Fig. 72. The expected weights were calculated from the following regression equations of mass on length taken from the fish (sexes combined) caught throughout the year:

Kowie River Stn. 1 $M = 0{,}0000177\ FL^{2{,}964}$ (r = 0,97, n = 164)
Kowie estuary $M = 0{,}0000234\ FL^{2{,}901}$ (r = 0,911, n = 255)

The relative condition of *Mugil cephalus*, in fresh water and in the estuary, shows a clear winter decline. In fresh water the relative condition drops lower and takes longer to recover compared to fish in the estuary. This difference could be partly due to the lower mean water temperatures at the freshwater site which remain below 13° C for three months in winter (June, July and August - Table 10). Due to the moderating influence of the relatively warm sea water in winter (14 - 18° C), temperatures in the lower estuary seldom drop below 13° C (Day 1981; Bok unpubl. data).

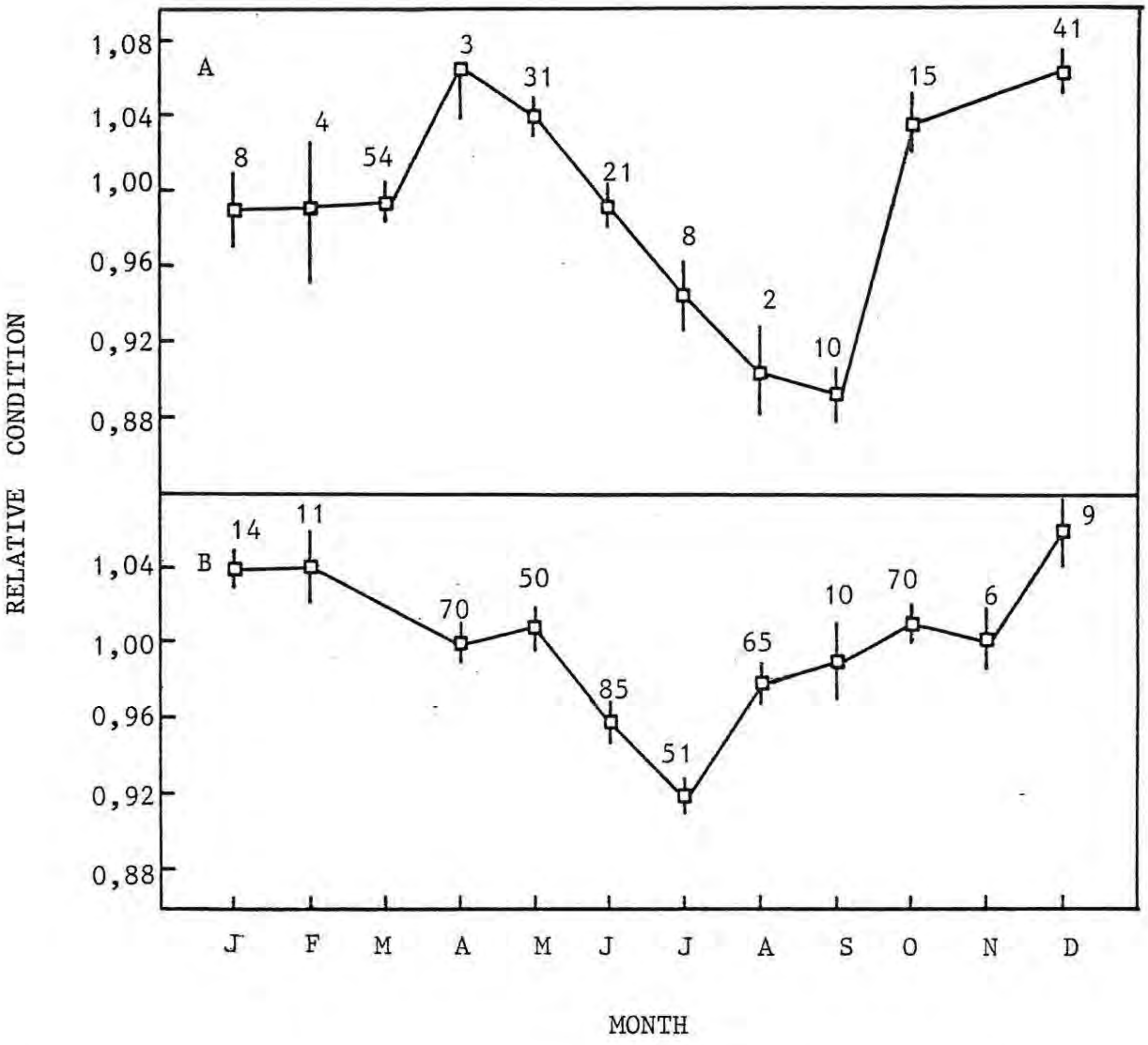


Figure 72. The mean monthly relative condition factor (see text) of *Mugil cephalus* (sexes combined) from the Kowie River Stn. 1 (A) and Kowie estuary (B). Vertical bars represent standard errors, numerals monthly sample size.

GENERAL DISCUSSION

Aspects of breeding biology such as reproductive effort, length of spawning season, size at sexual maturity, life-span of each sex, sex ratio, etc. are all components of a species total life history strategy and reflect the relationship between an organism and the selection pressures of the environment. In this section the possible adaptive significance of the various components of the breeding biology of *Myxus capensis* will be discussed and compared with those of *Mugil cephalus* and other mugilids. A synthesis of the total life history strategy of *Myxus capensis* will be attempted in a separate section.

GONADAL DEVELOPMENT

The very limited gonadal development of *Myxus capensis* in freshwater, where GSI values never exceeded 0,08, has distinct advantages. The risk of isolation in freshwater means that advanced development of gonads in this habitat could be a wasteful expenditure of valuable energy. In addition, fish heavy in roe may be less capable of undertaking a strenuous spawning migration. Maturing freshwater fish tend to display reduced swimming speeds as they become ripe (Blaxter 1969 in Katopodis 1977). Available energy reserves may, therefore, be better utilized for the migration itself. The data from both the Great Fish and Kowie rivers show that marked development of gonads of *Myxus capensis* takes place only after they have migrated to the estuaries, when there should be a clear passage to the marine spawning areas (Table 48).

In contrast to *Myxus capensis*, *Mugil cephalus* undergoes substantial gonadal development in fresh water. In this study, GSI values of up to 1,29 were recorded in female *Mugil cephalus* in the Swartkops River. Four year old female *Mugil cephalus* held in a 8 ha farm dam near Uitenhage (33^{o} 43' S, 25^{o} 30' E) developed ripe ovaries with GSI values up to 3,08 and a maximum gonad mass of 101,5 g (Bok 1983, unpublished data). Five year old *Myxus capensis* from this dam showed only limited gonadal development with GSI values less than 0,6.

In studies elsewhere, very advanced gonadal development of *Mugil cephalus* in freshwater habitats has been reported. Females with gonads which appeared "ripe and ready to spawn" with GSI values of over 12 were found by Shireman (1975) in fresh water in Lake Palourde, Louisiana, USA. Abraham *et al.* (1966) reported GSI values of over 19 in female *Mugil cephalus* which had been stocked into Lake Kinneret in Israel. It is apparent that in spite of the energy loss involved, the development of mature gonads in *Mugil cephalus* confined to fresh water (which have to be subsequently resorbed), appears to be fairly common (Eckstein 1975; Shireman 1975).

In many eastern Cape rivers, *Mugil cephalus* appears to have adapted a strategy different to that of *Myxus capensis* in order to cope with the problem of the adult fish being isolated in freshwater during the spawning season. The catch data from the Kowie, Great Fish and Bushmans rivers (Fig. 51; Chapter 4) show that *Mugil cephalus* >300 mm FL are very rare in the freshwater reaches of these rivers. In these populations, downriver migration to estuarine or marine habitats therefore occurs before the size at first sexual maturity (*ca* 300 mm FL) is reached. The presence of large adult fish in the Swartkops River, in contrast, may be related to the highly favourable conditions for rapid growth which exist in the lower reaches due to enrichment by purified domestic effluent and other organic effluents (Chapter 2).

In Israel (Abraham *et al.* 1966), New Zealand (M^c Dowall 1978) and Japan (Suzuki 1965), adults are reported to be rare in the freshwater reaches of rivers while sub-adults are common. In Australia (Thomson 1966) and the USA (Johnson & Mc Lendon 1970; Shireman 1975) on the other hand, adult *Mugil cephalus* are common in the freshwater reaches of rivers. As the different populations probably undergo migratory strategies best suited to their particular environments, the freshwater zones of many eastern Cape rivers may therefore be relatively unsuitable for this species.

SPAWNING GROUNDS

In a recent world-wide review of mugilid spawning localities Brusle (1981) p. 128, remarks that "Locations of spawning grounds remain controversial." A number of authors have proposed possible spawning sites of South African Mugilidae (Wallace 1975b; van der Horst & Erasmus 1981; Lasiak 1982). Direct evidence is however lacking, and to date there have been no observations of mullet spawning in this region. Apart from the collection of small numbers of *Liza richardsoni* and *Mugil cephalus* eggs in inshore areas off the Cape of Good Hope (Brownell 1979), fertilized mullet eggs or larvae <10 mm have not been collected in southern Africa.

Evidence from this study strongly indicates that *Myxus capensis* spawns at sea. The evidence includes: (i) the absence of substantial gonadal development in freshwater; (ii) the capture of small fry (migrating upstream) only in estuarine or near estuarine areas; (iii) the presence of only ripe and spent (not ripe-running) fish in estuaries and (iv) the capture of fully ripe-running male and female fish only in the marine surf zone.

This study failed to reveal evidence for *Myxus capensis* spawning in inshore marine areas. After the capture of ripe-running males (n = 35) and females (n = four) in a single seine net haul in the surf zone (<2 m deep) about 300 m from the mouth of the Great Fish estuary on 16 April 1981, intensive netting for fertilized eggs and larvae was carried out. Sampling with plankton nets at the site of capture of the adults as well as in the Great Fish River mouth the following day, yielded negative results. Five days later, surface plankton tows were carried out using a boat 300 m to *ca* 3 km offshore of the site where the ripe-running adults had been located. No fertilized eggs or mullet larvae were found. This negative result may, however, indicate a low catchability of the eggs or larvae. SCUBA diving and gill netting 100 - 600 m offshore did not reveal any concentration of mullet.

Salinity fluctuations in inshore areas where the ripe-running fish were captured, were substantial. Intrusion of low salinity estuarine water reduced the salinity during the period described to $25^{o}/oo$ at low tide. In the river mouth itself, salinities ranged from 4 - 35% over the tidal cycle. Salinities below $26^{o}/oo$ are reported to reduce egg survival of *Mugil cephalus* to 10%, compared to 91% survival at $32^{o}/oo$ (Sylvester *et al.* 1975). Although the salinity tolerance of *Myxus capensis* eggs is not known, it seems likely that areas close to river mouths, where lowered salinities are possible, would not be chosen as spawning sites.

The capture of ripe-running *Liza dumerili* in the mouth of the Swartkops

River led van der Horst (1981) to suggest that spawning took place there as well. However, this author conceded that these fish may have been *en route* to the sea to spawn. An inshore marine spawning of mullet was proposed by Wallace (1975b) who found ripe-running *Liza macrolepis*, *L. dumerili* and *Valamugil cunnesius* in the St Lucia estuary. This author proposed that spawning of these mullet and possibly *Mugil cephalus* takes place in inshore areas in the vicinity of St Lucia estuary mouth. However, this area does not appear to be suitable at all times. Whitfield & Blaber (1978) reported that markedly reduced salinities prevailed in St Lucia estuary and adjacent inshore areas during the *Mugil cephalus* spawning months of April and May 1976, such that inshore spawning by *Mugil cephalus* at this time would have been detrimental to the survival of fertilized eggs.

Further evidence in conflict with inshore spawning close to river mouths is the apparent absence of mullet eggs and larvae in the estuarine plankton along the south and south-east coast of South Africa. In spite of intensive monthly sampling over a two-year period for newly hatched fish larvae in the Swartkops estuary (Melville-Smith & Baird 1980), and sampling in the Kromme estuary (Melville-Smith 1981) and the St Lucia system (Wallace & van der Elst 1975), no larval Mugilidae less than 10 mm FL were found in the plankton. If spawning occurs in the vicinity of river mouths, tidal currents would be expected to wash at least limited numbers of eggs or larvae into the estuaries. In view of the vast numbers of mullet fry larger than 15 mm FL in these systems, at a size when they have full control over their movements, it appears that there is only active recruitment of fry into estuaries. The apparent absence of mullet larvae in estuaries on the east and south coast of South Africa therefore strongly indicates a marine spawning beyond the influence of tidal and inshore currents.

During a 28 month sampling period < three km offshore on the Atlantic and False Bay sides of the Cape of Good Hope, Brownell (1979) encountered fertilized eggs of some 40 fish species. Of the two mullet species in the area (*Mugil cephalus* and *L. richardsoni*), only very small numbers of *L. richardsoni* (n = seven) and *Mugil cephalus* (n = 33) eggs were sampled intermittently on both sides of the Cape of Good Hope. In view of the abundance of adults of both mullet species in inshore and estuarine habitats in this region, it appears that the area sampled by Brownell (1979) was only on the periphery of the spawning grounds of both species.

This study showed that *Mugil cephalus* has a well-defined winter spawning period. It is therefore possibly significant that winter sea temperatures approaching the optimum for *Mugil cephalus* spawning (22° C, Liao *et al.* 1972) are only found offshore near the edge of the continental shelf off the eastern Cape coast (Christensen 1981).

In summary, the available evidence on mullet spawning grounds off the south and south east coast of South Africa indicates that spawning occurs >3 km offshore, possibly adjacent to the estuaries, but beyond the influence of tidal or local inshore currents. In view of the lack of factual evidence for the above proposal, a brief review of the literature on mullet spawning grounds is presented below.

In different areas of the world, the spawning grounds of mullet appear to be varied (Brusle 1981). In all instances, however, spawning appears to be confined to oceanic or brackish water. An exception may be *Rhinomugil corsula* which, according to Kurian (1975), "is reported to breed in rivers and enclosed waters". Evidence for this freshwater spawning is unfortunately not presented. A claim of *Mugil cephalus* spawning in fresh water has been made by Johnson & M^{c} Clendon (1970), who found 30 postlarval mullet (28 - 40 mm SL) 192 km upstream from the mouth of the Colorado River. As these mullet were estimated to be about two months old, at an age when fry commonly enter estuaries, the authors proposed that only a freshwater spawning could explain the presence of these postlarvae so far up the Colorado River. The validity of this claim has, however, been questioned by Whitfield & Blaber (1978). From data on the minimum size of recruitment of *Mugil cephalus* fry into estuaries and the swimming ability of postlarval mullet in St Lucia, these authors express the opinion that the Colorado postlarval mullet could quite feasibly be derived from a marine spawning. The present study found small *Myxus capensis* (11 mm FL) and *Mugil cephalus* (16 mm FL) fry approximately 22 km upstream from the mouth of the Kowie River. It appears that efficient use is made of tidal currents to supplement the limited swimming ability of the small fry during their migration up the estuaries.

Published reports of mullet spawning in estuaries in other areas are usually based on indirect evidence such as the capture of ripe-running fish in the estuary. Such evidence is given for the spawning of *Aldrichetta forsteri* in the Avon-Heathcote estuary in New Zealand (Webb 1973) and in the Coorong lagoon in south Australia (Harris 1968). However, more recent evidence from western Australia indicates that *A. forsteri* spawns outside estuaries in marine waters (Chubb *et al.* 1981; Lenanton 1982). Again, the postulated estuarine spawning of *Mugil cephalus* and *Valamugil seheli* in the Bohle estuary in Australia (Grant & Spain 1975a; 1975b) and for *Mugil cephalus ashensis* spawning in the Senegal estuary (Brulhet 1975), is based on inconclusive evidence.

Breder (1940) described what he proposed was spawning of *Mugil cephalus* in a shallow creek off the Florida coast. The described spawning behaviour compares closely with observed spawning behaviour of mullet induced to spawn in aquaria (Nash & Koningsberger 1981). However, no eggs were found by Breder (1940), and Breder & Rosen (1969) state that the proposed spawning "may have been some preliminary activity before the offshore movement".

An unusual case of non-marine spawning is the successful reproduction of *Mugil saliens* in a brackish inland lake. This species was introduced into Lake Quarun in Egypt for fisheries purposes and reproduced successfully in this brackish (24 - 38^{o}/oo), shallow (up to 8 m), 21 450 ha water body (El-Zarka & Kamel 1965; Ishak *et al.* 1982). The two other mullet species introduced into Lake Quarun, *Mugil cephalus* and *Mugil capito* have, however, not reproduced there.

In nearly all well-authenticated reports of mullet spawning (Tables 52& 53), the spawning site is offshore over deep water. An exception appears to be *Crenimugil crenilabis*, which was observed by Helfrich & Allen (1975) to spawn over shallow water (4 - 6 m) within a tropical atoll lagoon.

The well-documented evidence of *Mugil cephalus* spawning in deep offshore waters of the south Atlantic coast of the USA and offshore in the

Table 52. The spawning season and locality of authenticated examples of Mugilidae (other than *Mugil cephalus*) spawning in various parts of the world.

Species	Spawning locality	Country	Evidence	Period	Authority
Mugil curema	outer continental shelf, depth 37 m	S. Florida	spawning shoal, eggs & larvae in plankton	March - Sept.	Anderson (1957)
Mugil curema	88 km offshore over 1 050 m	W. Gulf of Mexico	larvae in plankton	May	Caldwell & Anderson (1959)
Mugil saliens	8 km offshore in 500 - 700 m	Caspian Sea	eggs & larvae in plankton	May - Sept.	Avanesov (1972)
Mugil auratus	48 km offshore in depths of 300 - 600 m	Caspian Sea	eggs & larvae in plankton	July - Oct.	Avanesov (1972)
Crenimugil crenilabis	shallow (4 - 6 m) atoll lagoon	Marshall Islands	spawning shoal, eggs recovered	June	Helfrich & Allen (1975)

Table 53. The spawning season and spawning locality of *Mugil cephalus* in various parts of the world.

Period	Spawning locality	Country	Evidence	Authority
Feb.	tidal mangrove	Florida, USA	spawning behaviour	Breder (1940)
March - July	near mouths of estuaries	Eastern Australia	gonad stages, fishermen	Kesteven (1942)
Oct. - March	8 - 32 km offshore	Florida, USA	gonad stages, fishermen	Broadhead (1953)
Oct. - Feb.	offshore - 37 m	S. Atlantic, USA	larvae sampled at site	Anderson (1958)*
Dec.	64 - 80 km offshore, 1 372 m	Gulf of Mexico	spawning behaviour, eggs and larvae sampled	Arnold & Thomson (1958)*
Dec.	89 - 98 km offshore	Texas, USA	fertilized eggs	Finucane *et al.* (1978)*

* authenticated reports

Gulf of Mexico (Table 53), correlates with the size of fry recruited into adjacent inshore areas and estuaries. Along the south-eastern and southern coast of the USA *Mugil cephalus* larvae less than 16 mm have not been found in estuaries (Broadhead 1953; Anderson 1958; Arnold & Thompson 1958). The absence of mullet fry <10 mm FL in inshore or estuarine areas, as well as the active recruitment of fry above this size into estuaries (commonly above 15 mm), is found in many countries (Table 54). Available data on mullet recruitment into estuaries around the world, therefore, do not support the idea of inshore spawning near river mouths.

Apart from the danger of fish eggs or larvae from inshore spawning being transported by wave action or tidal currents into areas detrimental for survival, water depth itself may be important for incubation and larval development (Nash & Koningsberger 1981). *Mugil cephalus* eggs tend to sink during incubation in standing water (Tang 1964; Yashouv 1969) and a standard procedure during artificial propagation of this species is to keep the incubating eggs in suspension by maintaining a slow circulation of water (Nash *et al.* 1974). Fertilized *Myxus capensis* eggs were also found to sink in still water in this study. Sylvester & Nash (1975) speculate that the high tolerance to temperature changes during incubation and hatching shown by *Mugil cephalus* eggs enable them to "accommodate temperature changes as they sink through the water". The larvae of *Mugil cephalus* undergo two periods of sinking, between the second and third day and between the sixth and seventh day (Kuo *et al.* 1973). Both *Mugil cephalus* eggs and larvae have been sampled in deep water (150 - 200 m) near Japan (Hotta 1955, in Sylvester & Nash 1975).

In summary, the evidence from the literature therefore favours an offshore spawning of *Mugil cephalus* and most other Mugilidae, with active recruitment into estuaries after at least two to three weeks of larval development at sea. This is in agreement with the proposed spawning area of *Myxus capensis* and *Mugil cephalus* in the eastern Cape.

SPAWNING SEASON

The spawning season of *Mugil cephalus* in this study is similar to that found in Natal and Australia (Table 55). Over a large part of its

Table 54. The smallest size at first recruitment of mullet into estuaries and inshore areas in various parts of the world. Size given as FL unless specified.

Locality	Species	Size at first recruitment (mm)	Authority
Hong Kong	*Mugil cephalus*	23	Bromhall (1954)
Japan	"	20	Suzuki (1965)
Israel	"	15	Bograd (1961)
Egypt	"	15 - 19	El-Zarka & Kamel (1965)
South Africa (Natal)	"	11	Wallace (1975a)
South Africa (E. Cape)	"	16	This study
Hawaii	"	17	Major (1978)
Sri Lanka	"	10	De Silva & Silva (1979)
Australia	"	15,5	Grant & Spain (1975a)
USA	"	16 SL	Anderson (1975)
Israel	*Mugil ramada*	10,4	Bograd (1961)
"	*Mugil auratus*	19 TL	"
"	*Mugil labrosus*	17	"
"	*Mugil saliens*	12	"
Egypt	*Mugil capito*	12	El-Zarka & Kamel (1965)
India	*Mugil tade*	20 (mode)	Pillay (1954)
Ireland	*Crenimugil labrosus*	15	Kennedy & Fitzmaurice (1969)
England	*Crenimugil labrosus*	18	Cunningham (1896, in Hickling 1970).
Malaysia	*Liza malinoptera*	13	Ching (1977)
South Africa (Natal)	*Liza macrolepis*	14	Wallace (1975a)
" "	*Liza dumerili*	10 - 20	Wallace (1975a)
" "	*Valamugil buchanini*	20 - 30	Wallace (1975a)
" "	*Valamugil cunnesius*	20	Wallace (1975a)
South Africa (E. Cape)	*Myxus capensis*	11	This study
Australia	*Valamugil seheli*	13,5	Grant & Spain (1975b)
"	*Liza vagiensis*	21,5	Grant & Spain (1975c)

range, *Mugil cephalus* spawns in autumn or winter during periods of decreasing or low temperatures (Thomson 1963).

This species is widely distributed and it is not surprising that different populations have adapted their spawning behaviour to suit local conditions. In the Black Sea *Mugil cephalus* spawns in summer from June to August (Apekin & Vilenskaya 1978) when temperatures are increasing. This summer spawning appears to be an adaptation to the very low minimum winter temperatures (3 - 6° C) in the Black Sea. Nearly all (97%) of *Mugil cephalus* eggs found off the Cape of Good Hope were collected in January and February (summer) when mean sea temperatures were 18,9 and 18,3° C respectively (Brownell 1979). This apparent summer spawning, in contrast to a winter spawning off the eastern Cape coast, is probably an adaptation to the low mean sea temperatures from May - August (13,0 - 14,8° C) in this area (Brownell 1979).

In some regions *Mugil cephalus* has a very extended spawning season. In the Mex canal in Egypt, connecting Lake Mariut to the Mediterranean Sea, fry <35 mm TL were found all year, although numbers dropped in summer (El-Zarka & Kamel 1965). *Mugil cephalus* fry (<35 mm TL) were also reported in all months of the year from a Sri Lankan coastal lagoon (De Silva & Silva 1979).

Table 55. The spawning season of *Mugil cephalus* from various localities in the Southern-Hemisphere.

Locality	Spawning Season		Authority
	Months	Main Season	
E. Cape, SA	IV - X (peak VI - VIII)	winter	This study
Natal, SA	V - IX	winter	Wallace (1975b)
E. Australia	III - VIII	winter	Kesteven (1942)
W. Australia	III - IX	winter	Thomson (1951)
NW. Australia	V - VIII	winter	Grant & Spain (1975)

Mugil cephalus egg and larvae have a high tolerance of temperature variations (Sylvester & Nash 1975) and these authors consider that this species is preadapted in this regard to a wide variety of climatic conditions. The effective temperature range for incubation of *Mugil cephalus* eggs is 11 - 24° C, with an optimum of 22° C (Nash & Koningsberger 1981). This is within the annual range of monthly mean sea temperatures (16 - 22° C) found off the eastern Cape coast (Christensen 1980).

From the above it can be inferred that there are probably no innate behavioural or climatic barriers preventing *Mugil cephalus* from spawning all year round in the eastern Cape. The well-defined winter spawning along the eastern Cape coast may therefore be timed to best suit the optimum ecophysiological needs of the larvae and fry.

A prolonged spawning and hence recruitment period in estuarine fish is considered by Wallace (1975b, p. 19),

> "to have a 'buffering' action against failure of recruitment as a result of adverse climatic conditions".

However, many southern African marine fish also have extended spawning seasons (Brownell 1979). This indicates that an extended spawning season can also be important to ensure breeding success in spite of short-term unfavourable conditions at sea for the incubation of the eggs and survival of larvae.

The all-year round spawning of *Myxus capensis* appears to have additional advantages related to its catadromous behaviour in an unstable riverine environment. As mentioned by Bok (1979), it would enable the infrequent and irregular periods of high river flow to be used at any time of the year by adult fish to migrate downstream to a saline environment for spawning. In addition, the numerous rapids impeding the upstream migration of *Myxus capensis* fry may only be negotiable at certain levels of river flow (see Chapter 7). An extended recruitment period will therefore counteract detrimental effects due to short-term adverse river conditions.

An understanding of the selection pressures associated with the evolution of all-year round spawning, as opposed to a relatively short, well-defined spawning period, may indicate the significance of these tactics in

Myxus capensis and *Mugil cephalus*. A short, well-defined spawning period is obviously associated with high survival of progeny during the particular spawning period. The development of all-year round spawning, on the other hand, is probably in response to a lack of advantage associated with spawning at any particular time, i.e. survival of eggs and fry is dependent on unpredictable environmental factors. As it is very likely that the eggs and young fry of *Mugil cephalus* and *Myxus capensis* have similar requirements (peak spawning times do overlap to some extent), differences in the length of the spawning periods may be due to different selection pressures on the older fry. It is postulated, therefore, that the extended recruitment period of *Myxus capensis* is associated with the obligatory need of this species to recruit into an unpredictable freshwater habitat. The relatively restricted spawning period of *Mugil cephalus*, on the other hand, indicates that its breeding strategy is not adapted to optimally exploit the freshwater reaches of eastern Cape rivers.

MAINTENANCE OF BROODSTOCK FISH IN SEA WATER

The finding that adult *Myxus capensis*, captured in freshwater habitats and acclimated to sea water, did not show significant gonadal development, indicates that factors other than (or in addition to) salinity initiate gonadal development in this species.

Water temperatures and photoperiod are two important factors which initiate gonadal development in temperate and sub-temperate species (Hoar 1959). Kuo *et al.* (1974) have demonstrated the regulatory influence these two factors have on gonadal maturation of *Mugil cephalus*. As *Myxus capensis* spawns throughout the year however, these factors would probably not play a limiting role.

The lack of gonadal development of the broodstock fish in the present study may be related to sub-optimal feeding conditions as indicated by their low relative condition. Under these conditions, the cost of maintenance probably did not allow the fish to allocate energy to reproduction (Purdom 1979). *Mugil cephalus* only undergoes gonadal development in freshwater under favourable conditions such as low density and a plentiful supply of natural food (Abraham 1966; Yashouv 1969). The influence of food supply on the regulation of gonadal development has been found in many fish species (Scott 1962; Nikolskii 1969; Wootton 1979).

Other, less easily defined factors may also have inhibited gonadal maturation of the captive broodstock *Myxus capensis*. Scott (1979) found that the European minnow, *Phoxinus phoxinus*, will not spawn in still-water aquaria and ripe specimens undergo massive atresia of vittelogenic oocytes within a few days of being transferred from their natural habitat to aquarium tanks. This author suggests that captivity may induce "a generalized stress response a symptom of which is gonad degeneration".

The minimal degree of gonadal development of *Myxus capensis* in natural freshwater areas, as well as the lack of gonadal development of the broodstock fish maintained in the various sea water systems, indicate that this species may have more particular requirements for gonadal development than *Mugil cephalus*. Further research, using broodstock in outdoor ponds containing diluted and pure sea water, is needed to establish these requirements. In Taiwan, where *Mugil cephalus* has been artificially propagated for many years (Tang 1964; Liao *et al.* 1971; Liao *et al.* 1972; Liao 1975; Chen 1976), virtually all broodstock fish are netted at sea during their natural spawning migration. The series of hormone injections to induce spawning is usually initiated a few hours after the fish are caught and placed in holding tanks. The presence of ripe (stage IV) *Myxus capensis* in estuaries and ripe as well as ripe-running (stage V) fish in inshore areas in the eastern Cape, indicates that methods similar to those used in Taiwan could be used for induced spawning of *Myxus capensis* in this country.

SIZE AT SEXUAL MATURITY AND SEX RATIO

Female *Myxus capensis* mature at a larger size and usually greater age than males. Data for *Mugil cephalus* from this study are scarce, but from studies elsewhere (Table 51) there appears to be a similar tendency in most populations of this species. The relatively larger size of females is probably a strategy to maximize egg production as the total population fecundity is approximately proportional to the total weight of mature females present (Weatherley 1972). The sex ratio in favour of females (in *Myxus capensis*) will therefore also increase population fecundity. The size of the male fish does not appear to greatly influence spawning success as there is normally more than enough sperm in fish that engage in external fertilization, especially group spawners. (Beverton & Holt 1957; Nikolskii 1969). Mullet appear to fit into this spawning category. Several males were found to attend to each female *Mugil cephalus* (Arnold & Thompson 1958), while in *Crenimugil crenilabis*, the release of milt and eggs occurs when the whole school erupts "in a frenzy of jumping, thrashing fish" (Helfrich & Allen 1975).

The wide range of size (and age) at sexual maturity of *Myxus capensis* appears to be a very important adaptation in response to this species unstable riverine habitat. As discussed above, both male and female fish migrate out of freshwater areas to undergo sexual maturation in salt water and very few (if any) spent fish return to freshwater zones. Therefore, if all fish matured (i.e. migrated downstream) at 2+ or 3+ years of age, there would only be three year classes in freshwater. Such a population structure would be very vulnerable to the effects of prolonged adverse environmental conditions, particularly those associated with droughts.

During droughts, when rivers in the eastern Cape can cease to flow for up to two years, recruitment stocks would be unable to migrate into freshwater areas and may suffer heavy mortalities. In addition, breeding migrations would, of course, also be prevented and the cycle of spawning and recruitment would be interrupted. If, for example, the river started to flow after a hypothetical period of about two years, most of the fish in freshwater would potentially be old enough to spawn. If all potential spawners did participate in a spawning migration at the first opportunity after a drought, the river would be virtually depopulated until recruitment from this post-drought spawning run took place. In the absence of a range of size at sexual maturity, these "post-drought" fish would reach maturity at the same time and the cycle would be perpetuated. Such a situation of population peaks and troughs would result in: (i) inefficient utilization of the riverine resources available and (ii) of greater importance, it may make such a population highly vulnerable to untimely droughts or spawning/recruitment failure in the future. By having a wide range of ages at sexual maturity, the reproductive effort of the population is spread over a number of years. Not only will such a population be able to absorb and recover from a series of spawning and recruitment failures occurring consecutively for a number of years, but it will have the potential to level our resultant population fluctuations as well.

This strategy of a range of ages at sexual maturity has been found in Far East salmon (Nikolskii 1969). *Oncorhynchus keta* breeds at 2+ to 7+ years of age, while *O. gorbuscha* breeding populations consist of 1+ to 2+ year old fish. The above author associates these differences in range of age at sexual maturity with the degree of stability of the spawning conditions of the two salmon species, with *O. gorbuscha* having comparatively more stable spawning conditions than *O. keta*.

The predominance of male *Mugil cephalus* in populations in freshwater was in direct contrast to that found for *Myxus capensis*. This scarcity of female *Mugil cephalus* in freshwater reaches of eastern Cape rivers therefore indicates that those areas are not effectively utilized by this species as additional feeding areas to increase population fecundity.

As estuarine populations of *Mugil cephalus* have equal numbers of males and females, the scarcity of females in the freshwater zones of eastern Cape rivers may be due to a variety of factors, such as: (i) a weaker upriver migratory urge in the females; (ii) a tendency for females to migrate downriver at an earlier age and (iii) increased female mortality in fresh water. Evidence that sexual differences in migratory behaviour results in fewer female *Mugil cephalus* in the freshwater zones of rivers, was indicated by the sex ratio of an artificial population. A random sample (n = 1 091) of 2+ to 5+ year old *Mugil cephalus*, previously stocked as fry into an isolated farm dam (dam 1, Chapter 6), consisted of 51% females, i.e. similar to that found in estuaries. A random sample (n = 277) of similar aged *Myxus capensis* from this dam, on the other hand, consisted of 78% females. This could indicate that the sex ratio is genetically as well as environmentally determined in *Myxus capensis*. However, it is possible that factors causing increased mortality of male *Myxus capensis* may have been present in both the natural and artificial environments studied.

FECUNDITY AND GONOSOMATIC INDEX

The fecundity and GSI values of *Myxus capensis* are similar to those of other mullet species, except for *Mugil cephalus* which has higher GSI and fecundity values (Table 56). The mean size of the fertilized or fully ripe transluscent eggs of *Myxus capensis* (0,88 mm) is very similar to that of other mullet species (Table 57).

Constraints on egg size are set by the optimal size of the larvae, which is related to factors such as size of available food items, size and abundance of predators and abundance of competitors (Wootton 1979). The marine spawning of *Myxus capensis* and other Mugilidae is apparent as their egg sizes fall within the modal size group (0,75 - 1,25 mm) of the frequency distribution of egg diameters of over 100 marine species (Wootton 1979). Freshwater species tend to have larger eggs than marine species.

REPRODUCTIVE EFFORT

The energy required for reproduction can be separated into that required for spawning migrations and spawning behaviour and that required for gonadal development. Due to its greater upstream penetration, *Myxus capensis* would be expected to spend more energy on its spawning migration than *Mugil cephalus*. In some migratory fish species, the energy costs of migration can be very high. Sockeye salmon in the Fraser River, for example, utilize approximately 90% of their body fat and about 15% of their body protein during the upriver stage of their spawning migration (Idler & Clemens 1959, in Northcote 1978). The distance *Myxus capensis* has to cover from freshwater to the marine spawning areas would usually be less than 75 km and seldom more than 150 km. In addition, this downriver migration is thought to take place mainly during periods of high river flow, when strong water currents would greatly assist the fish swimming downstream. The energy cost of the spawning migration of *Myxus capensis* may therefore be considerably less than that for salmon.

Evidence presented elsewhere (Chapter 7) indicates that estuaries, particularly marine-dominated systems, may be trophically less suitable for *Myxus capensis* than freshwater areas. As the bulk of gonadal development

Table 56. The GSI and absolute fecundity of various species of Mugilidae.

Species	Max. GSI value		Absolute Fecundity range (x 10^3)	Length range of females (mm)	Locality	Authors
	males	females				
Mugil cephalus			861 - 2 632	320 - 540 SL	St Lucia, RSA	Whitfield & Blaber (1978)
"	>6,8	20	1 275 - 2 781	350 - 590 TL	Australia	Kesteven (1942)
"		40	2 900 -16 800	>380	Black Sea	Apekin & Vilenskaya (1978)
"	13,5	13,4			Florida (fresh-water)	Shireman (1975)
"		>24,0	1 572 - 4 774	*ca* 340 - 600 FL	Queensland (Aust.)	Grant & Spain (1975)
Mugil capito		14,0	46 - 317	170 - 340 TL	Lake Borollus, Egypt	El-Maghraby *et al.* (1974)
Liza subviridis		15,0	40 - 145	103 - 139	Malaysia	Chan & Chuz (1980)
Liza malinoptera			16 - 27	67 - 88	Malaysia	Ching (1977)
Mugil tade			90 - 322	230 - 322	Bengal	Pillay (1954)
Aldrichetta forsteria			125 - 630	245 - 391	Australia	Thomson (1957)
Mugil auratus			158 - 926		Black Sea	Nikolskii (1963)
Crenimugil labrosus	8,0	16,6	372 - 646	470 - 560	Britain	Hickling (1970)
Liza ramada			581 - 1 243	440 - 530	Britain	Hickling (1970)
Myxus capensis	1,34	15,9	150 - 509	280 - 430	eastern Cape, RSA	This study

Table 57. Size of fertilized egg and oil globule in various species of mullet.

Species	Egg diam (mm) mean (range)	Oil glubule diam (mm)	Locality	Authority
Mugil cephalus	0,93	0,38	Taiwan	Tang (1964)
"	0,93 (0,88 - 0,98)	0,33	Hawaii	Kuo *et al.* (1973)
"	0,93 - 0,95	0,38	Taiwan	Chen (1976)
"	0,95 (0,91 - 0,99)	0,33	Gulf of Mexico	Finucane (1978
Mugil curema	0,82 (0,77 - 0,86)	0,30	Florida coast	Anderson (1957)
Mugil saliens	0,73 (0,62 - 0,80)		Caspian Sea	Avanesov (1972)
Mugil auratus	0,84 (0,80 - 0,90)		Caspian Sea	Avanesov (1972)
Crenimugil crenilabis	1,0	0,30	Marshall Is.	Helfrich & Allen (1975)
Myxus capensis	0,88 (0,84 - 0,92)	0,30	South Africa	This study

occurs in estuarine (and possibly marine) areas, their inability to adequately replace the energy required for this purpose through feeding, places additional stress upon the female fish. This is reflected in the positive correlation between loss of condition, calculated both with and without ovaries, with increasing GSI value (Fig. 69).

This loss in condition (calculated with gonads) prior to spawning is unusual and in contrast to the 'normal' rise in relative condition to a pre-spawning maximum as found, for example, in perch, *Perca fluviatilis*, (Le Cren 1951); pike *Esox lucius* (Bregazzi & Kennedy 1980) and roach, *Rutilus rutilus*, (Mann 1973). In mullet, an increase in condition (K) (from formula $K = \frac{W}{L^3} \times 100$, where W = total fish mass, L = fish length) of female fish has been found to coincide with the beginning of the breeding season in *Mugil tade* (Pillay 1954), *Mugil cephalus* (Broadhead 1953) and *Aldrichetta forsteri* (Thomson 1957). When there is abundant food available prior to spawning, the growth of the gonads does not necessarily occur at the expense of the somatic energy reserves. In some fish, e.g. *Barbus anoplus* in Lake le Roux (Cambray 1982) and the gudgeon, *Gobio gobio*, in southern England (Mann 1980), the relative condition (excluding gonad mass) also increases to a pre-spawning maximum.

The spatial separation of the marine spawning areas and the preferred freshwater feeding areas therefore ensures that the total reproductive effort, in terms of energy cost and loss of condition, is particularly high in *Myxus capensis*. This probably accounts for the very low post-spawning survival.

SPAWNING BEHAVIOUR

No direct observations of mullet spawning were made during this study. The discussion of the spawning behaviour of *Myxus capensis* is therefore partly speculative.

The maximum length of time *Myxus capensis* spends in marine-dominated estuaries such as the Kowie, before moving out to marine areas for spawning purposes, is not accurately known. The minimum duration of the estuarine phase (necessary for the development of ripe gonads after migrating from fresh water) could theoretically be only a few weeks.

For example, gonads of *Mugil capito* in Lake Borrolus in Egypt develop from the maturing stages (stage III) to the ripe condition (stage IV) in less than 15 days (El-Maghraby *et al.* 1974).

The evidence given above shows that *Myxus capensis* spawns all year round. Individual female fish appear to release all the eggs over a short time period (ie. are single spawners), but with different fish spawning at different times. As populations of *Myxus capensis* are relatively small, this year-round spawning means that limited numbers of fish would spawn at any one time. An important consideration would therefore be that sufficient numbers of pre-spawning fish congregate and synchronize final gonadal maturation to ensure that successful spawning can take place.

The importance of pre-spawning behaviour in ensuring breeding success has been postulated by a number of authors. When describing direct observations of the year-round spawning of the Atlantic parrotfish *Sparisoma rubripinne*, Randall & Randall (1963) proposed that:

> " the reproductive potential of a fish is greatly increased when large groups assemble at specific sites for spawning".

Again, when describing the spawning behaviour of the catadromous *Galaxias maculatus*, Benzie (1968) suggested that:

> "the aggregation of fish in the spawning area facilitates completion of their maturation".

In the St Lucia system, the leaping behaviour of *Mugil cephalus* during pre-spawning aggregation and migration is considered to be a means of attracting ripe individuals into large shoals, postulated to be essential for the spawning success of this species (Whitfield & Blaber 1978).

Similar aggregations of prespawning mullet in eastern Cape estuaries were not found in this study and have not been reported by other workers. However, beach seine fishermen have reported the occasional catch of large numbers of "mullet in roe" in the surf zone off the beach adjacent to the Great Fish River mouth. It is postulated that the ripe-running *Myxus capensis* captured in the surf zone off the Great Fish River beach in this study, were prespawning fish undergoing final maturation of their gonads and aggregating into sufficiently large shoals of ripe-running fish, before moving to offshore spawning sites.

The predominance of males in the ripe-running shoals of *Myxus capensis* captured in the surf zone, may indicate (as is the case of *Mugil cephalus*) that several males fertilize the eggs of a single female. Males may also remain in the marine zone for a longer period and partake in a number of "spawning runs" to offshore areas. The better relative condition of ripe male fish compared to ripe females, as well as the comparatively small size of the ripe testes, indicate that males are physiologically preadapted to be multiple spawners.

In Australia pre-spawning shoals of *Mugil cephalus* gather in the lower reaches of estuaries before the seaward spawning migration is triggered by strong offshore winds (Thomson 1955). Similar winds may also stimulate *Myxus capensis* spawning. The only large shoal of ripe-running *Myxus capensis* encountered in this study was netted in the surf zone after a two day period of berg winds (northwest, offshore winds). More data are needed, however, before firm conclusions of the influence of weather conditions on mullet spawning in the study area can be made.

CHAPTER 6. FISHERIES POTENTIAL

INTRODUCTION

Intensive warm-water fish culture in South Africa is virtually non-existent at present. Apart from a small number of trout farms in the western Cape, there are no commercial farms in the Cape Province. The successful harvesting of fish from large man-made impoundments in the eastern Cape in recent years however, has shown the considerable potential of this form of "extensive aquaculture". A major drawback is that the exploitable fish populations in these impoundments at present consist of the indigenous cyprinid *Labeo umbratus* and the exotic common carp *Cyprinus carpio*. Both these species are not esteemed table fish in South Africa and hence demand low market prices. It was therefore felt that both *Myxus capensis* and *Mugil cephalus*, which are comparatively superior table fish, may be suitable for stocking into freshwater impoundments to improve their fisheries potential.

A further reason for research into the feasibility of such stockings was to investigate the angling potential of these euryhaline mullet in freshwater impoundments. Because of the scarcity of indigenous angling fish species in the Cape Province, conservation authorities have made available a number of exotic species such as black bass (*Micropterus spp.*) and trout (*Salmo spp.*) for angling purposes. Indigenous species in this area have evolved over a long period in the absence of major predators and have subsequently not developed strong anti-predator strategies. These exotic predators have consequently had a markedly detrimental impact on indigenous fish species, particularly the small minnow species (Skelton 1983). Predation by exotics is considered to be a factor threatening nine of the 12 Cape *Red Data* species (Skelton 1977). The replacement of exotic predators with a relatively harmless, non-breeding indigenous fish species with good angling properties, would therefore be of major conservation significance. In addition, *Myxus capensis* populations have declined drastically in recent years due to weir construction impeding upriver migrations

(Chapter 7). The stocking of dams and rivers within its geographical range could partly overcome this problem and improve its conservation status.

The culture of mullet in brackish and freshwater ponds has been practiced for many years in the Indo-Pacific region and Mediterranean countries (Bardach *et al.* 1972). The large-scale culture of mugilids could play an important part in relieving the increasing world-wide shortage of animal protein, particularly in the Third World (Oren 1981; Nash & Koningsberger 1981). Stimulated by programmes such as the International Biological/Marine Production (IBP/PM) "Mullet Project", research and development of mullet culture has increased dramatically over the last decade (Liao 1981; Oren 1981).

A number of countries have increased the fisheries potential of their inland waters through large-scale mullet stockings. Millions of mullet fry (including *Mugil cephalus*) have been stocked into Lake Mariut and Lake Quarun in Egypt (El-Zarka & Kamel 1965) and into Lake Kinneret (Sea of Galilee) in Israel (Bar-Ilan 1975). In the USSR, millions of *Liza aurata* and *L. saliens* fry were captured in the Caspian Sea and successfully transported to the Aral Sea between 1954 and 1956 (Ben-Yami 1981). Mullet catches today form an important component of the extensive fisheries in the waters mentioned above.

Attempts at artificial propagation of *Myxus capensis* (described in Chapter 5) were unsuccessful. Artificial spawning of *Mugil cephalus* has been carried out successfully in a number of countries (Yashouv 1969; Shehadeh & Ellis 1970; Liao *et al.* 1971; Shehadeh *et al.* 1973) and successful techniques for the rearing of larvae on a small scale have been developed (Kuo *et al.* 1973; Nash *et al.* 1974; Liao 1975). High larval mortality is still a major problem, however, and techniques for mass propagation of *Mugil cephalus* have not yet been perfected (Nash & Kuo 1975; Nash & Koningsberger 1981). Consequently, the culture of mugilids still relies almost entirely on the capture of wild fry (Bardach *et al.* 1972; Chen 1976; Ben-Yami 1981). Since fry are extremely sensitive to handling, special attention is needed to reduce mortalities during their capture, transportation and stocking. High fry mortality can be a serious problem as it aggravates the increasing difficulty in obtaining sufficient fry for aquaculture purposes (Tang 1975; Ben-Yami 1981).

The success of any large-scale capture and stocking programme depends, in part, on a knowledge of the peak recruitment periods of the fry. Marked temporal differences occur in the recruitment of fry of various mugilid species into estuaries along the South African east coast (Wallace & van der Elst 1975) and elsewhere (Bograd 1961; El-Maghraby, Hashem & El-Sedfy 1974; Kurian 1975). The periods of recruitment of *Mugil cephalus* and *Myxus capensis* fry into eastern Cape rivers was established during this research programme and is described in detail in Chapter 5 .

The main objectives of this study were therefore to: (i) develop efficient techniques for the capture, transportation and stocking of large numbers of fry without incurring high mortalities; (ii) determine the growth rates of these two mullet species in various water bodies and (iii) estimate the potential of the two species for extensive aquaculture as well as for angling.

During an eight year period (1975 - 1982) over 130 000 *Mugil cephalus* and 50 000 *Myxus capensis* fry were captured, transported and stocked into a variety of water bodies in the eastern Cape Province, South Africa. The results of this work are described below.

STUDY AREA

Netting for mullet fry took place in a number of rivers along the eastern Cape coast (Fig. 9). The Kowie, Swartkops and Great Fish rivers were more intensively netted, with the majority of mullet fry used for stocking purposes coming from the latter two rivers. Netting operations were restricted to the heads of the estuaries in either completely fresh or slightly brackish ($5^{o}/oo$ salinity) water. The capture of fry in these areas has a number of advantages: (i) there is no need to acclimatize the fry to fresh water when stocking into dams - this is a distinct advantage as abrupt salinity changes are often a major source of mortality (Mires *et al.* 1975); (ii) large numbers of fry (15-40 mm FL) often accumulate in these usually shallow areas where partial barriers to fish movement such as rapids, causeways or weirs are commonly found and (iii) fry of only *Mugil cephalus* and *Myxus capensis* are usually present in these areas.

MATERIALS AND METHODS

CAPTURE

A variety of 2-5 mm (stretched mesh) seine and dip-nets were used to capture mullet fry. A sample of at least 10, usually more than 30, was preserved in 5% formalin for later identification and measurement. With experience it was found that even small fry of *Mugil cephalus* and *Myxus capensis* could be distinguished with the naked eye in the field. In this study, only mullet smaller than 50 mm FL were classified as fry.

As mullet fry are very sensitive to handling, special techniques were developed for their capture. The most successful net, causing least injury to the fry, proved to be a short seine net (2-4 mm mesh) approximately 4 m long by 1,5 m deep with a shallow bag incorporating a cod-end consisting of a canvas bag of *ca* 20 l volume. Each end of the net was attached to a 2 m pole and could be operated by two people. Seining was usually carried out in shallow water (<1 m). After each haul, the fry were concentrated in the water of the canvas bag and then poured into a suitable container. By keeping the fry immersed in water virtually all the time, this capture method minimized skin abrasion and scale loss, which is a major cause of subsequent mortalities (Ben-Yami 1981; personal observations).

TRANSPORTATION OF FRY

The fry were transported in plastic drums (100 and 200 l capacity) in water from the capture site and the salinity increased to $5^{o}/oo$ by adding coarse 'rock' salt (NaCl). Transporting freshwater fish in a weak salt solution has been shown to alleviate osmotic breakdown caused by stress and scale damage (Hattingh *et al.* 1975) and to reduce the chances of subsequent fungal (*Saprolegnia*) infections (Yashouv & Ben-Shachar 1967). The transportation water was continuously oxygenated. Densities of 120 fry l^{-1} during transportation were not exceeded in this study, but far greater densities are theoretically possible (Ben-Yami 1981; Hamman 1981). Mullet fry were held for over 18 hours and successfully transported over 1 000 km using the above techniques.

STOCKING OF FRY AND MONITORING OF GROWTH

Before the fry were released, water from their new environment was mixed with the transportation water to facilitate acclimatization of the fry. Mullet fry were stocked into a variety of freshwater impoundments in the eastern Cape (Table 58). Fry were captured and stocked in winter and spring and sampled for growth in late autumn or winter. In this way growth over the summer season could be determined. Both seine and gill nets covering a wide range of mesh sizes were used to obtain unbiased samples for growth determinations.

RESULTS AND DISCUSSION

RECRUITMENT OF FRY

Details of the recruitment periods of both mullet species are given in Chapter 5 . Predominantly monospecific shoals of *Mugil cephalus* were caught during the initial phase of this species recruitment period (June, July and August), with increasing numbers of *Myxus capensis* appearing in the catches later in the recruitment period. By October or November, pure *Myxus capensis* shoals were often encountered. Therefore, although the recruitment periods of the two species overlap, the peak recruitment of *Myxus capensis* appears to be one to three months later than *Mugil cephalus*. Capturing monospecific shoals is important for stocking purposes; it is difficult to separate a mixed bag of mullet fry as mortalities are increased by handling.

MORTALITIES

Mortalities observed during transportation were usually less than 2% and appeared to result mainly from mechanical damage incurred during netting. Additional mortalities did occur within a week or so after stocking, but were usually difficult to estimate. 'Stocking mortality' was estimated from fry stocked into glass aquaria and cement tanks and was found to be less than 10% within the first 10 days after capture and transportation. These mortalities were mainly due to secondary infection or damaged areas of the skin and fins by *Saprolegnia sp.*

The above mortalities compare favourably with those reported for mullet fry in the literature. Liao (1981) reports the handling mortality

Table 58. Details of dams into which mullet fry were stocked to determine growth rates.

Dam No	Locality of dam	Name of farm or dam	Approx. area (ha)	Approx. Stocking density (fish/ha)		Water Quality		
				Mugil cephalus	*Myxus capensis*	pH	Secchi Disc (cm)	Alkalinity (ppm Ca CO_3)
1	33° 43' S, 25° 30' E	Amanzi	5,0	a 500 b 700	300	8,3 - 8,6	60 - 100	111 - 115
2	33° 27' S, 25° 07' E	Morgenpracht	1,0	a 200 b 1 500	1 000	8,2 - 8,4	*ca* 50	115 - 179
3	33° 18' S, 26° 28' E	Strowan	0,5	200	800	7,6 - 9,0	25 - 60	55 - 92
4	33° 08' S, 26° 43' E	Grasslands	0,5	a 1 000 b 1 500	200	8,2 - 8,5	12	300 - 436
5	33° 28' S, 26° 30' E	Avondale	0,3		500			
6	33° 19' S, 26° 31' E	Hamilton Dam	0,5		5 000	7,9	70	95
7	32° 59' S, 27° 51' E	Amalinda	8 x 0,2	10 000	1 000 - 10 000	8,1 - 8,4	25 - 45	120 - 145
8	33° 26' S, 27° 04' E	Crossroads	3,0	1 000		8,6	*ca* 20	310
9	33° 29' S, 26° 20' E	Mountain View	0,4	400		8,1	7	135
10	33° 19' S, 26° 32' E	Douglas Reserv.	0,5	1 200	1 000	7,0	150	42
11	33° 28' S, 26° 31' E	Avondale	0,04	2 000				

of *Mugil cephalus* fry collected from the sea in Taiwan as 70%. Handling and transportation mortality of *L. aurata* and *L. saliens* fry (30-40 mm) transported from the Caspian to the Aral Sea (Ben-Yami 1981) was 14%, which did not include stocking mortality. The mortality of *Mugil cephalus* fry during acclimatization (7-10 days) in nursery ponds in Taiwan (i.e. stocking mortality) ranges between 5-15% and is thought to be mainly due to the delayed effects of "mechanical injury during catching and handling" (Tang 1975).

As shown in Table 59 , the total mortalities (i.e. stocking mortality plus 'natural'long-term mortality) of *Mugil cephalus* fry (< 30 mm FL) stocked directly into 0.02 ha earth ponds, which were drained over 200 days later, were substantial (mean = 44%). However, larger fry which were nursed for three months prior to stocking showed a comparable mortality (54%). *Myxus capensis* fry stocked into the above ponds showed similar mortalities (mean 47%) while larger yearling fish generally showed lower mortalities (Table 60). The high total mortalities of mullet fry found in this study are similar to mortalities in fish ponds reported in the literature (Table 61).

Long-term mortality of mullet fry stocked directly into large dams was difficult to gauge and would be expected to vary greatly depending upon factors such as predation pressure, availability of suitable food, water quality etc. When stocking into large impoundments there seems to be little benefit in applying nursery procedures as practiced when stocking fry into smaller fish ponds. In Taiwan (Tang 1975), newly caught fry are held in acclimatization ponds and artificially fed for 7-10 days before being stocked into larger growing ponds. In Israel, mullet fry are initially stocked into nursery ponds at high densities (30 000 per ha) for 60-100 days before being moved to production ponds (Pruginin *et al.* 1975). Unless there is a danger that the fry would be subject to heavy predation if stocked into an impoundment at a small size, the increased risk of mortality due to the additional handling and transportation during a nursery period would minimize any such advantage.

Table 59. The stocking details and mortality of *Mugil cephalus* fry grown in 0.02 ha earth ponds at Amalinda Fish Station, East London.

Date stocked	Growth period (days)	Stocking density no/ha	Mean length at stocking (mm)	% Mortality
16-8-76	202	1 500	29	63
16-8-76	202	4 000	29	54
16-8-76	202	800	29	38
16-8-76	202	300	29	50
16-8-76	202	400	29	25
16-8-76	202	200	29	0
22-8-80	248	10 000	20 - 30	*49
22-8-80	248	5 000	20 - 30	*55
22-8-80	248	10 000	20 - 30	*65
4-12-79	154	10 000	63	**54

* mean of three ponds

** mean of two ponds

Table 60. The stocking details and mortality of *Myxus capensis* fry and yearlings grown in 0.02 ha earth ponds at Amalinda Fish Station.

Date stocked	Growth period (days)	Stocking density no/ha	Mean length at stocking (mm)	% Mortality
16-9-76	134	1 000	31	55
16-9-76	134	2 000	31	35
22-8-80	248	10 000	20 - 25	*50
16-9-76	134	1 000	145	10
16-9-76	134	2 000	136	15
16-9-76	134	300	106	17
16-9-76	134	400	124	50

* mean of three ponds

Table 61. The total mortality of mullet fry stocked into fish ponds in various countries.

Species	Mortality (%)	Country	Authors
Mugil cephalus	66	Egypt	El-Zarka & Kamel 1965
Mullet fry	95	India	Thomson 1966 in Ben-Yami 1981
Mugil cephalus	50	Israel	Mires 1970
Liza ramada	50	Israel	Mires 1970
Mugil cephalus	88	Egypt	Eisawy *et al.* 1974
Mugil capito	75	Egypt	Eisawy *et al.* 1974
Liza aurata	68	Israel	Chervinski 1976
Mugil cephalus	50	Taiwan	Liao 1981

Table 62. Growth of *Myxus capensis* stocked as small fry (initial mean fork length between 23 - 28 mm) into various dams in spring (October and November). For details of dams see Table 58.

Dam	Mean fork length (mm) after number of growing seasons		
	1	2	3
1	[+]106	238	331
2	139	193	277
3a	100		
3b	111		
4			267
5		202	
7	[++]105 (101 - 108)		
10	116		
Mean length	113	211	292
[+++]Calc. mass (g)	16	119	338

[+] first season's growth occurred in a small dam adjacent to No 1 (supplied by the same water source) at a stocking density of 10 000/ha.

[++] value is mean of eight ponds with range given in brackets.

[+++] calculated from the Kowie River length : mass ratio (mass = 0,000004 $FL^{3,2153}$)

Table 63. Growth of *Mugil cephalus* stocked as fry (initial mean fork length range 22 - 28 mm) into various earth dams in spring. For details of dams see Table 58 .

Dam Number	Mean fork length (mm) after number of growing seasons					
	1	2	3		4	
			male	female	male	female
1a	218	372	435	480	475	545
1b	225					
2a		331				
2b	236					
3	165					
4a	201	332				
4b	238					
7	[+]180 (164 - 191)					
8	185	366				
9		342				
10	191					
11	185					
Mean FL	202	349	435	480	475	545
Calc. mass	[++]114	[++]688	[+++]1 501	2 018	[+++]1 955	2 956

a and b values indicate that these dams were stocked on two separate occasions (see Table 58).

[+] value given is mean (range in brackets) of nine experimental ponds

[++] calculated using length : mass relationship for Swartkops River *Mugil cephalus* (mass = $0{,}000018\ FL^{3{,}0059}$)

[+++] calculated using length : mass relationship determined from *Mugil cephalus* of 400 - 564 mm fork length from Amanzi Dam (Dam 1) (mass = $0{,}000003\ FL^{3{,}2879}$)

GROWTH RATES OF STOCKED FRY

Growth rates of *Myxus capensis* and *Mugil cephalus* fry stocked into a variety of dams in spring and subsequently sampled in autumn or winter are presented in Tables 62 and 63 . Research on ageing natural populations of both mullet species in this area (Chapter 4), has shown that scale annuli are deposited in spring and for practical purposes early spring can be taken as the "birthdate" of both species. The growth data of mullet stocked into artificial impoundments can therefore be compared to corresponding length at age data of mullet from natural systems.

The mean growth of *Myxus capensis* stocked into the various dams was found to be very similar to that found under natural conditions in the Kowie, Swartkops and Great Fish river systems (Chapter 4). For example, three-year-old *Myxus capensis* grown in dams did not differ on average by more than 8 mm FL or 34 g from similar aged mullet from the natural riverine populations. The largest sizes reached by *Myxus capensis* after one, two and three years' growth in the various dams (Table 62) were 31 g (139 mm FL), 175 g (238 mm FL) and 506 g (331 mm FL), respectively. At least three years is therefore needed before a marketable size is reached.

Female *Myxus capensis* were found to grow markedly faster than male fish after the third year. In dam 6, stocked at 5 000/ha, the modal lengths of female and male fish were 345 - 360 and 315 - 320 mm FL respectively, after four growing seasons (Fig.73).

Unlike *Myxus capensis*, the growth rate of *Mugil cephalus* stocked into the various dams was found to be markedly higher than in natural riverine populations (Chapter 4). For example, *Mugil cephalus* in the dams were 200 - 500 g heavier than the riverine mullet after two years' growth. The largest sizes reached by *Mugil cephalus* after the first and second years' growth in the various dams were 244 g (236 mm FL) and 960 g (372 mm FL) respectively (Table 63). When the mean mass of the two mullet species in all the dams is compared after two years' growth, the mean mass of *Mugil cephalus* (688 g) is almost six times that of *Myxus capensis* (119 g).

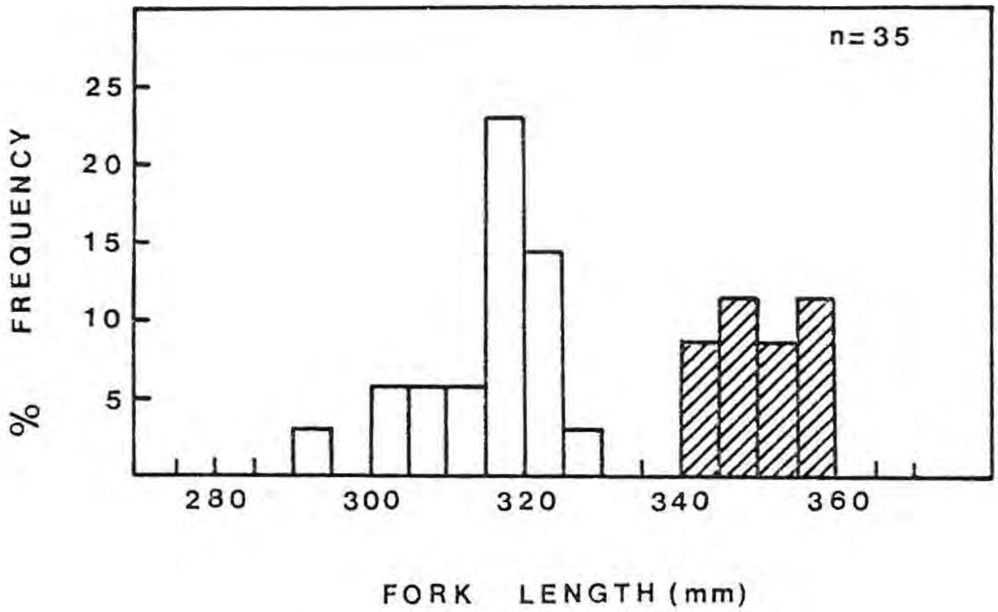


Figure 73. The length attained by male (open histograms) and female (cross hatched histograms) *Myxus capensis* after five growing seasons in dam 6 (see Table 58).

The markedly faster growth of female compared to male *Mugil cephalus* after the second year is clearly shown in the growth data of fish stocked into dam 1 (Table 63). The larger size of the females becomes apparent during the third growth season and is very pronounced at the end of the fourth growth season, when females were on average 70 mm longer and 1 000 g heavier than the males. The largest fish caught in this dam after four growing seasons was a female of 564 mm FL weighing 3 600 g.

Mugil cephalus trapped in fresh water impoundments in the eastern Cape are known to live to an age of at least eight years and show rapid growth, reaching lengths of well over 600 mm. A major flood of the Great Fish River in early March 1974 allowed *Mugil cephalus* to enter a natural freshwater vlei (*ca* five ha) adjacent to the estuary. When sampled in May 1980 (i.e. over six years later), five fish (all females) of over 600 mm FL were captured, the largest 675 mm FL and weighing 5 585 g. The ages of these fish were estimated (using scale analysis) to be seven to eight years.

FISH FARMING AND ANGLING POTENTIAL

Both mullet species flourish when stocked as fry into freshwater impoundments. The considerably faster growth rate of *Mugil cephalus*, however, makes it the obvious choice for extensive fish farming. The high growth rates of this species were recorded in 'average' farm dams without the benefit of additional food or fertilization. The stocking densities per unit surface area in these dams were, however, relatively low. A major consideration when stocking this species is that mature fish (after about two years of age) tend to move down-river out of an impoundment if given the opportunity. The overflow will therefore have to be screened to prevent the escape of the larger fish. Irrigation storage dams which seldom overflow are therefore well suited for extensive mullet culture.

The considerable production potential of these two species under extensive culture conditions was clearly demonstrated from the results obtained from dam 1 on Amanzi Estates. A total of approximately 8 700 *Mugil cephalus* and 5 800 *Myxus capensis* were stocked into this *ca* 8 ha dam during the period November 1978 to October 1981. The dam was harvested sporadically from April 1980 to April 1982 and during low water level conditions in March 1983 when approximately 95% of the remaining mullet were netted. Details of the mullet harvested are given in Table 64 . The finding that over 400 g of wet fish were produced from every *Mugil cephalus* fry stocked, illustrates the potential harvest if far greater numbers are stocked into larger impoundments. Even over a four-year period, the production of over 500 kg per ha clearly shows the potential of these extensive culture techniques. The survival rates of 29 and 18% for *Mugil cephalus* and *Myxus capensis* respectively, were achieved in spite of the presence of predatory large-mouth black bass (*Micropterus salmoides*) in the dam.

The results obtained at Amanzi Estates compare favourably with those reported elsewhere. Ben-Yami (1981) estimated, using the total numbers of mullet caught, that survival of mullet fry stocked into Lake Kinneret in Israel was about 10%. The total catch of mullet from this lake up to 1973 was 1 800 tons, with an average fish mass of about 1 kg. Each fingerling stocked had produced approximately 100 g of fish. The nearly 20 million mullet fry (mainly *Mugil cephalus* and *L. ramada*) stocked into Lake Kinneret from 1958 to 1973 initiated the development of a lucrative mullet fishery, resulting in revenue of well over three million US dollars (Bar-Ilan 1975).

While the slower growth rates and smaller maximum size of *Myxus capensis* make it comparatively less suitable for extensive fish culture, this species has potential for stocking into dams for angling purposes. In most coastal rivers in the eastern Cape *Myxus capensis* is the largest indigenous angling fish present (apart from eels) and good catches of this sought-after table fish are often made by mullet fishermen. The popular bait consists of small, soft-bodied insects such as termites or flying ants (order Isoptera) fished 0,5 - 2 m below the surface using a float. A trout fly rubbed with the above insects and drawn slowly through the water is also used. Besides being a high quality eating fish, this mullet is also a powerful swimmer and has excellent angling properties. A dam on the outskirts of Grahamstown (No 6, Table 58) stocked with *Myxus capensis* fry in 1977 has provided good angling and

Table 64. Details of mullet harvested from dam 1 on Amanzi Estates (see text).

	Mullet Species	
	Mugil cephalus	*Myxus capensis*
Number stocked	8 700	5 800
Number harvested	2 554	1 014
Survival (%)	29,4	18,0
Total mass harvested (kg)	3 520	582
Mean individual mass harvested (g)	1 378	559
Maximum individual mass harvested (g)	3 992	948
Production obtained per indiv. fish stocked (g)	405	100

has proved so popular among mullet fishermen that a notice enforcing a daily bag limit of four fish per person per day has now been erected. There are no records of *Mugil cephalus* being caught with a baited hook and line in freshwater areas in the eastern Cape. Local anglers, however, report catching this species in estuaries using fish liver or diced fish flesh as bait. Evanoff (1953, in Thomson 1966) reports that *Mugil cephalus* seldom takes bait, though a small hook baited with dough is sometimes successful in both Australia and America. If angling techniques for catching this species can be developed, the considerable jumping powers and large maximum size (>5 kg locally), would make it a prized angling fish.

CONCLUSION

This research has shown the feasibility and potential benefits derived from stocking these euryhaline mullet species into freshwater impoundments. Both species were found to tolerate low winter temperatures of 6 - 8° C and would therefore be suitable for stocking into large inland impoundments in the Cape Province (and elsewhere in southern Africa) where a lack of high-quality indigenous fish species often exists. These mullet feed largely on algae, diatoms and detritus and are unable to reproduce in fresh water. Therefore little ecological damage from such stockings is possible.

In the long term, the supply of adequate numbers of mullet fry for stocking purposes still remains a constraint to the development of mullet farming in this country. In addition, large-scale netting of natural populations of mullet fry could be detrimental to mullet stocks. The large research effort directed towards perfecting techniques for the artificial propagation of mullet in various countries should ensure that the technology will soon be available for the large-scale propagation of fry. Only when these techniques are implemented will the full angling and aquaculture potential of both mullet species be realized.

CHAPTER 7. DISTRIBUTION, ABUNDANCE AND CONSERVATION STATUS

GEOGRAPHICAL DISTRIBUTION

Mugil cephalus is found in estuaries and inshore coastal waters of all seas between 42° N and 42° S (Thomson 1963). In South Africa it is found along the entire seaboard from Kosi Bay on the east coast to the Orange River on the west coast (Day 1981), (Fig. 1). *Mugil cephalus* penetrates into the freshwater zones of rivers in Australia, USA, India and Israel (Thomson 1963, 1966), and in South Africa, *Mugil cephalus* has also been caught high up in the freshwater zones of rivers. In both the Breede River on the south Cape coast (Gaigher *et al.* 1978) and Berg River on the west Cape coast (Louw 1968), this species has been found over 50 km upstream of the tidal influence. On the east coast of southern Africa, *Mugil cephalus* has been found in Inyamiti Pan in Ndumu Game Reserve 100 km up the Maputo River (Pooley 1975), and in Lake Teza situated on the Umzumduzi River about 40 km by river from its connection with St Lucia estuary (Bruton *et al.* 1978).

Myxus capensis, in contrast to *Mugil cephalus*, is endemic to South Africa and extends from Kosi Bay (Blaber 1976) to the Breede River (Gaigher *et al.* 1978), (Fig. 1). The factors limiting the distribution of this species are unknown, but may be related to marine spawning requirements and/or suitable conditions in the upper estuaries and freshwater zones of riverine habitats. The main study area in the eastern Cape is near the centre of this species' geographical range.

In Natal, Crass (1964) describes *Myxus capensis* as the one mullet species that "grows to maturity in fresh water", but states that "Specimens have been obtained in Natal only within a few miles of the sea". Blaber (1977) reports that *Myxus capensis* is common in Natal and Pondoland estuaries, although more abundant in the south, and has a preference for freshwater areas. In the brackish (10 - 25°/oo salinity) St Lucia Lake system, however, this species was found to be rare by Blaber (1976) and he proposed that it is perhaps excluded from this system by interspecific competition. Bruton and Appleton (1975) found that *Myxus capensis* is common in freshwater Mgobezeleni Lake as well as in the saline waters of the Mgobezeleni (Sodwana) estuary. The reported absence of *Myxus capensis* from the freshwater and brackish lakes of the Kosi System is therefore puzzling, particularly as they were found in the Kosi estuary (Blaber 1978). This lake system is, however, the northernmost limit of this species distribution range.

Very little information is available on the abundance and distribution of *Myxus capensis* in Transkei. Branch and Grindley (1979) caught limited numbers in the Mngazana estuary and Plumstead (pers. comm. 1982) found that they constitute 5 - 15% of gill net catches in the Great Kei estuary. Apart from the capture of *Myxus capensis* 177 km upriver from the estuary in the Great Kei River (this study), there are no authenticated records of this species from the freshwater zones of Transkeian rivers. In the Cape Province the distribution of *Myxus capensis* extends from the Great Kei to the Breede River, and Smith and Smith (1966) state:

> "This is an unusual species in that in the southern Cape it appears to prefer fresh or brackish water, seldom being caught in the sea".

DISTRIBUTION AND ABUNDANCE IN ESTUARIES

In addition to *Mugil cephalus* and *Myxus capensis*, the southern mullet, *Liza richardsoni*, was found in both estuarine and freshwater areas of some eastern Cape rivers. Comparative data on this species is therefore included in the analysis of relative distribution of the two other euryhaline mullet.

As identical netting gear and effort was used in the Great Fish and Kowie estuaries, (Chapter 3), standardized C P U E data (mean overnight catch in a standard fleet of gill nets) enabled useful comparisons between the two estuaries to be made. The C P U E for both *Myxus capensis* and *L. richardsoni* from the Great Fish is 5x that from the Kowie estuary (Table 65), while the C P U E for *Mugil cephalus* is even larger (15 x) in the Great Fish estuary.

Although the Great Fish estuary supports far larger numbers of all three euryhaline mullet species than the Kowie, their relative abundance in the various parts of each system is similar (Fig.74). *L. richardsoni* constitutes 80 - 90% of the mullet catches in the lower and middle reaches of both estuaries, while *Mugil cephalus* comprises 79 and 86% of mullet catches in the upper reaches of the Kowie and Great Fish estuaries, respectively. *Myxus capensis* was only found in the upper, more brackish

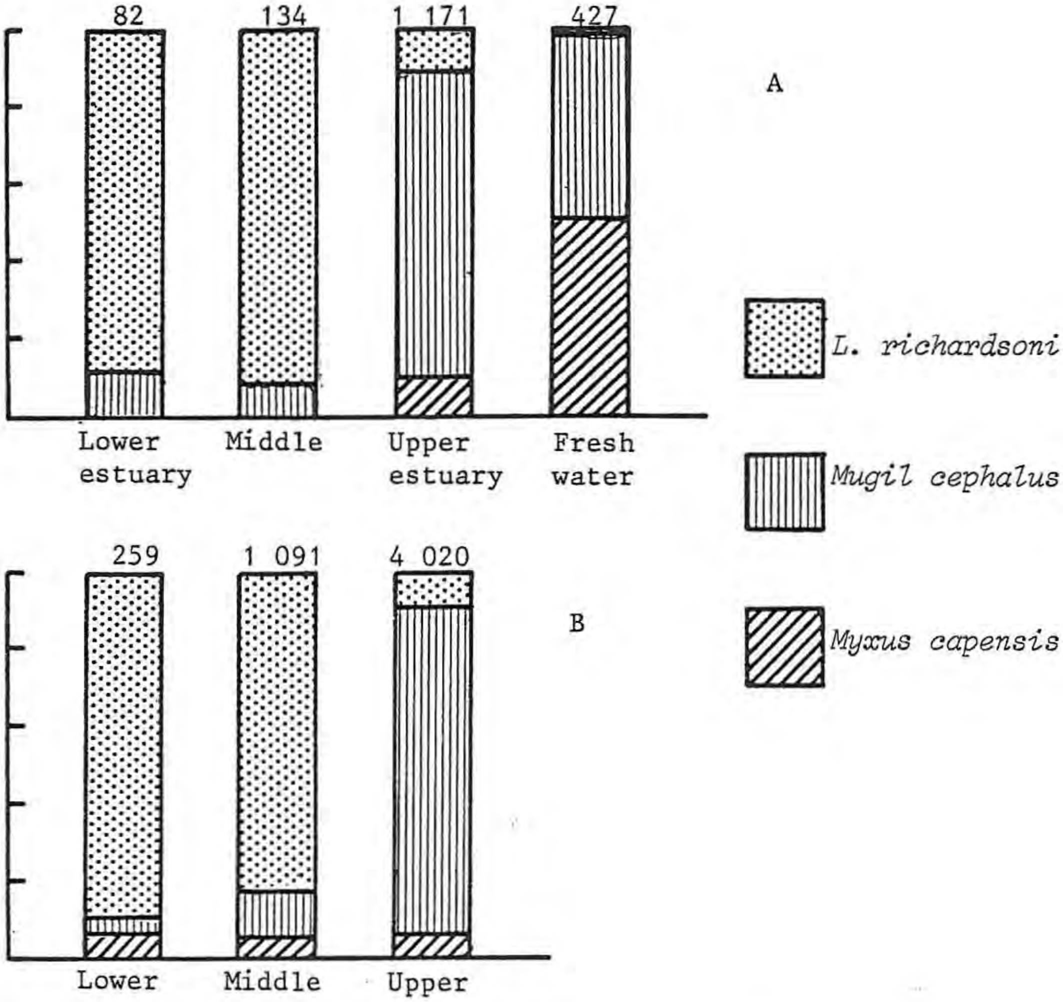


Figure 74 . The relative frequency of occurrence of the three euryhaline mullet species caught in gill nets in various parts of the Kowie (A) and Great Fish (B) estuaries, as well as in freshwater immediately above the head of the Kowie estuary. Numerals indicate sample size.

reaches of the Kowie estuary. In the Great Fish estuary, this species was captured in increasing numbers in the lower (19), middle (69) and upper (256) reaches, representing overall C P U E values of 0,83, 3,0 and 11,1 for the three areas, respectively. These three mullet species together constituted 97,7 and 94,7% of the total mullet gill net catch from the Great Fish and Kowie estuaries, respectively (Table 66).

Table 65. The C P U E for *Myxus capensis*, *Mugil cephalus* and *Liza richardsoni* from the Great Fish and Kowie estuaries (this study) as well as from comparative studies on four other eastern Cape estuaries. C P U E calculated as number of fish caught in a standard fleet of gill nets set overnight (see text).

Estuary	MAR ($m^3 \times 10^6$)	Catch per unit effort			Source
		Myxus capensis	*Mugil cephalus*	*Liza richardsoni*	
Great Fish	479	5,0	51,5	21,4	This study
Kowie	23	1,0	3,5	4,4	This study
Swartkops	84	none	2,7	3,9	Marais & Baird (1980)
Sundays	29	0,1	3,8	2,8	Marais (1981)
Kromme	105	none	0,4	1,7	Marais (1983a)
Gamtoos	458	5,6	3,6	1,8	Marais (1983b)

The preference of *Myxus capensis* for the upper, freshwater-dominated areas of the Great Fish and Kowie estuaries has also been reported for other estuaries. In the Gamtoos estuary Marais (1983b) caught most *Myxus capensis* in the middle and upper reaches where surface salinities were usually $< 5^{\circ}/oo$. In Natal and Pondoland estuaries, this species "shows a preference for freshwater areas" (Blaber 1977). Whitfield (1980) found that *Myxus capensis* show a preference for the upper and middle reaches of the Mhlanga estuary where salinities did not exceed $14^{\circ}/oo$ and were usually $<5^{\circ}/oo$.

The monthly C P U E for *Myxus capensis* and *Mugil cephalus* in the upper reaches of the Kowie and Great Fish estuaries are shown in Figs. 75 & 76 .

Table 66. The percentage occurrence of mullet species as determined from long-term (monthly sampling for at least one year) gill net surveys in some eastern Cape estuaries.

Estuary	Total mullet catch (n)	% of Total mullet catch						Source
		Myxus capensis	*Mugil cephalus*	*Liza rich.*	*Liza dum.*	*Liza tric.*	Other mullet	
Kowie	1 465	8,5	64,2	22,0	3,3	1,6	0,3	This study
Great Fish	5 497	6,3	64,6	26,8	0,6	1,7	0,02	This study
Swartkops	534	0	32,2	36,9	6,4	24,2	0,4	Marais & Baird (1980)
Sundays	475	0,6	40,2	39,0	3,8	15,6	0,8	Marais (1981)
Kromme	143	0	14,0	53,2	4,2	28,0	0,7	Marais (1983a)
Gamtoos	699	46,6	30,2	15,0	1,6	5,9	0,7	Marais (1983b)

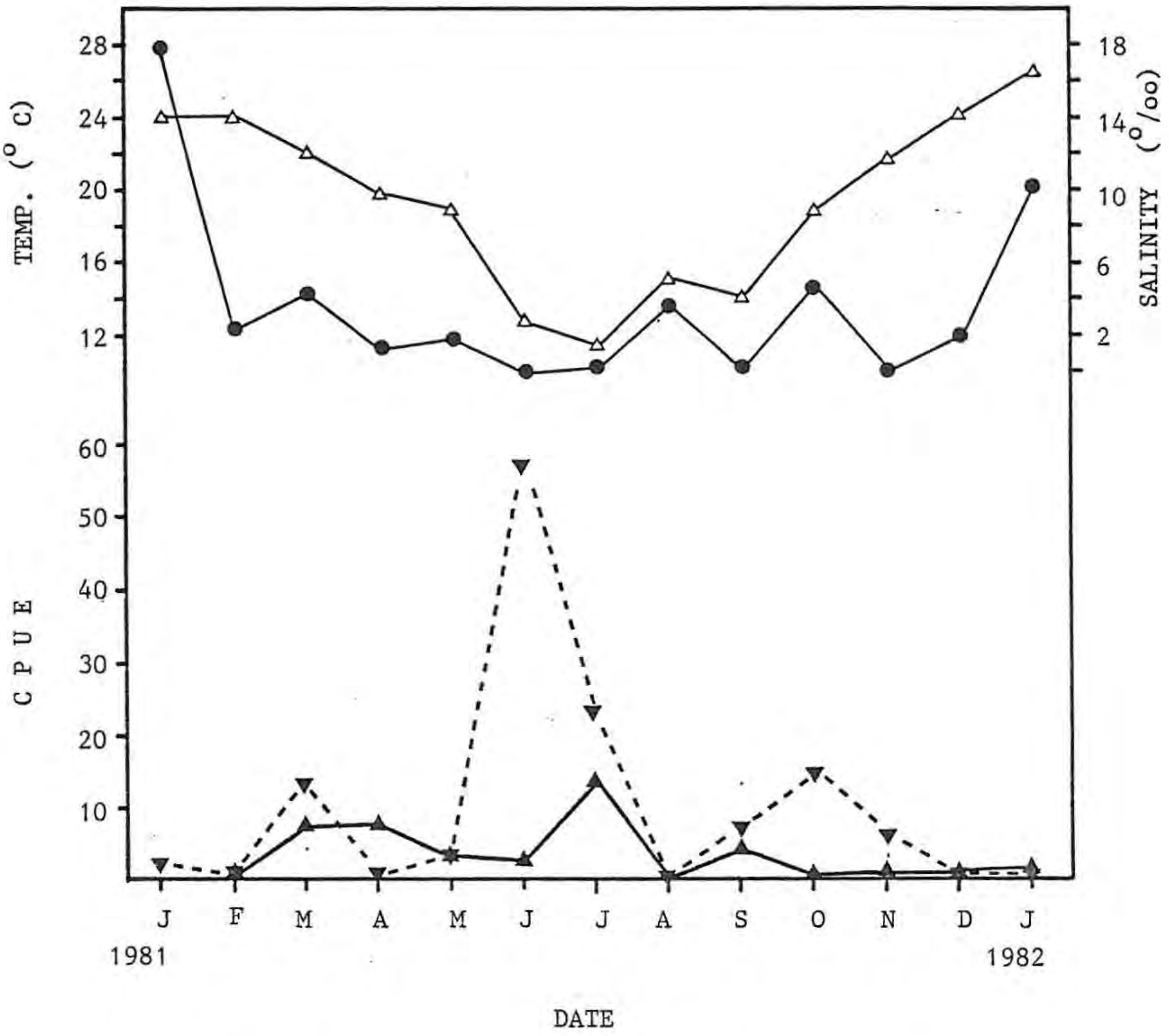


Figure 75. The monthly surface salinity (closed circles), mean water temperature (open triangles) and C P U E (see text) of *Mugil cephalus* (inverted closed triangles and dotted line) and *Myxus capensis* (closed triangles) at station 3 in the Kowie estuary.

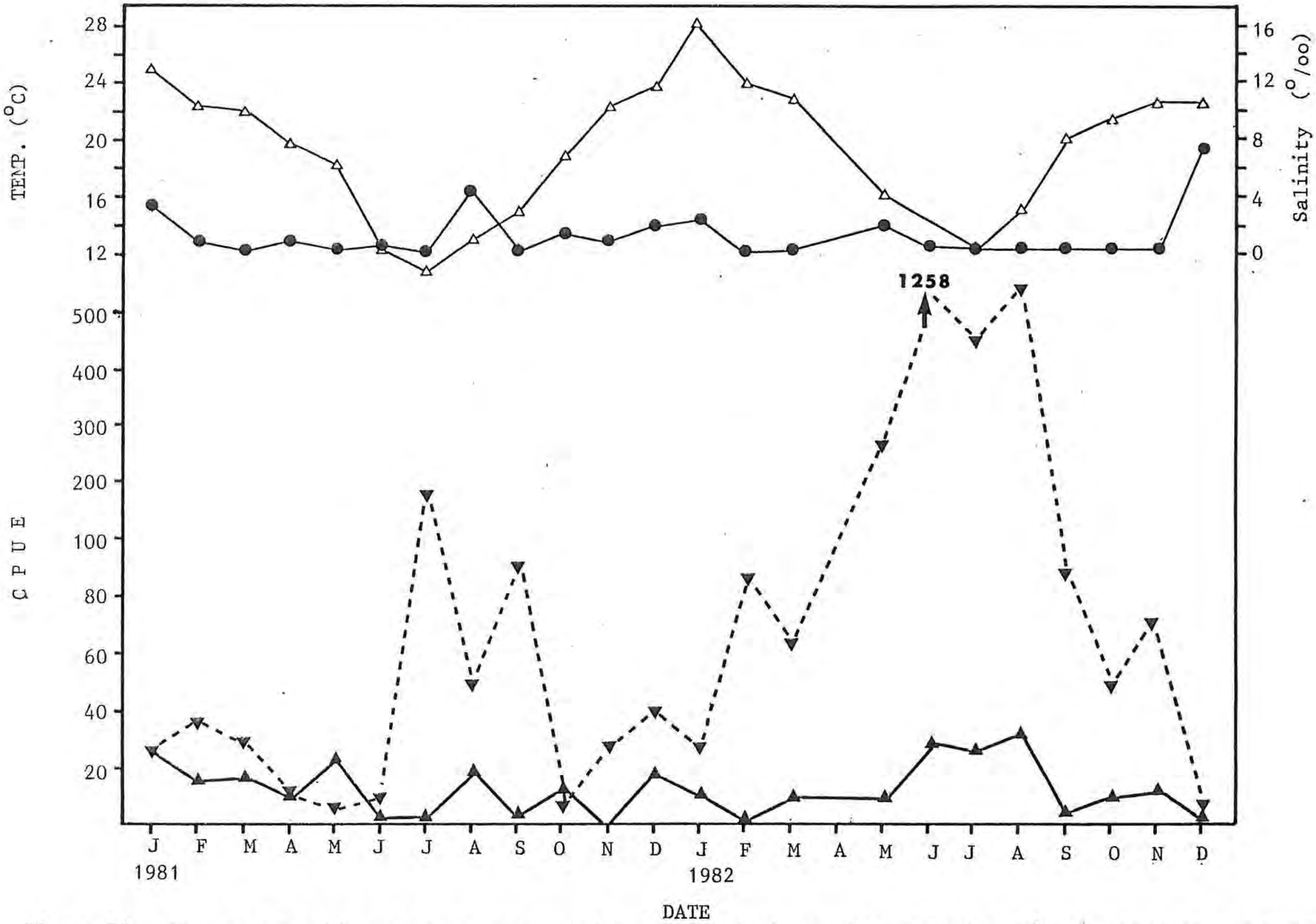


Figure 76. The mean monthly water temperature (open triangles), surface salinity (closed circles) and C P U E (see text) of *Mugil cephalus* (inverted closed triangles and dotted line) and *Myxus capensis* (closed triangles) at Station 3 in the Great Fish estuary.

There is no clear trend in the seasonal abundance of *Myxus capensis*, but *Mugil cephalus* became markedly more abundant during winter in the upper reaches of both estuaries. This was particularly apparent in the 1982 winter catches in the Great Fish estuary when the C P U E peaked at 1 258 fish in June (Fig. 76). This increase in *Mugil cephalus* abundance was not apparent in the lower reaches of the estuary at this time (Fig. 77), and therefore probably resulted from large-scale downriver movements.

A combination of low salinities (*ca* 1°/oo) and low water temperatures (12°C) was thought to have caused mortalities of *Mugil cephalus* in St Lucia estuary (Blaber & Whitfield 1976). It is tempting, therefore, to suggest that the mass movement of this species from freshwater reaches to brackish estuarine areas in winter is a strategy to avoid this potentially lethal combination. However, *Mugil cephalus* from the Great Fish estuary stocked into inland farm dams are known to survive water temperatures as low as 6° C (Bok, unpubl. data).

The catch data (Figs. 76&77) clearly show that *Mugil cephalus* prefers the low salinity or completely freshwater areas of the upper Great Fish estuary. Large numbers of *Mugil cephalus* were only found in the lower Great Fish estuary during floods. For example, the only time the C P U E for this species exceeded 4 at station 2 in the Great Fish estuary was when increased river flow reduced the salinity (surface and bottom) at this site to 0°/oo in July 1981. A C P U E of 93 was recorded at station 2 at this time (Fig. 77).

Further evidence for this species' preference for low salinity water was indicated when the C P U E at station 3 in the Great Fish estuary dropped markedly in December 1982 when relatively high salinities were recorded at this site (Fig. 76). Further gill netting a few days later at station 3 and at sites further upriver, revealed the presence of large concentrations of *Mugil cephalus* in low salinity water (Table 67). In addition, there was a clear trend for the younger fish (age 1+ years) to penetrate further upstream into the completely freshwater areas (Table 67). All the areas mentioned above are well within the tidal influence of the estuary which extends some 16 km from the mouth.

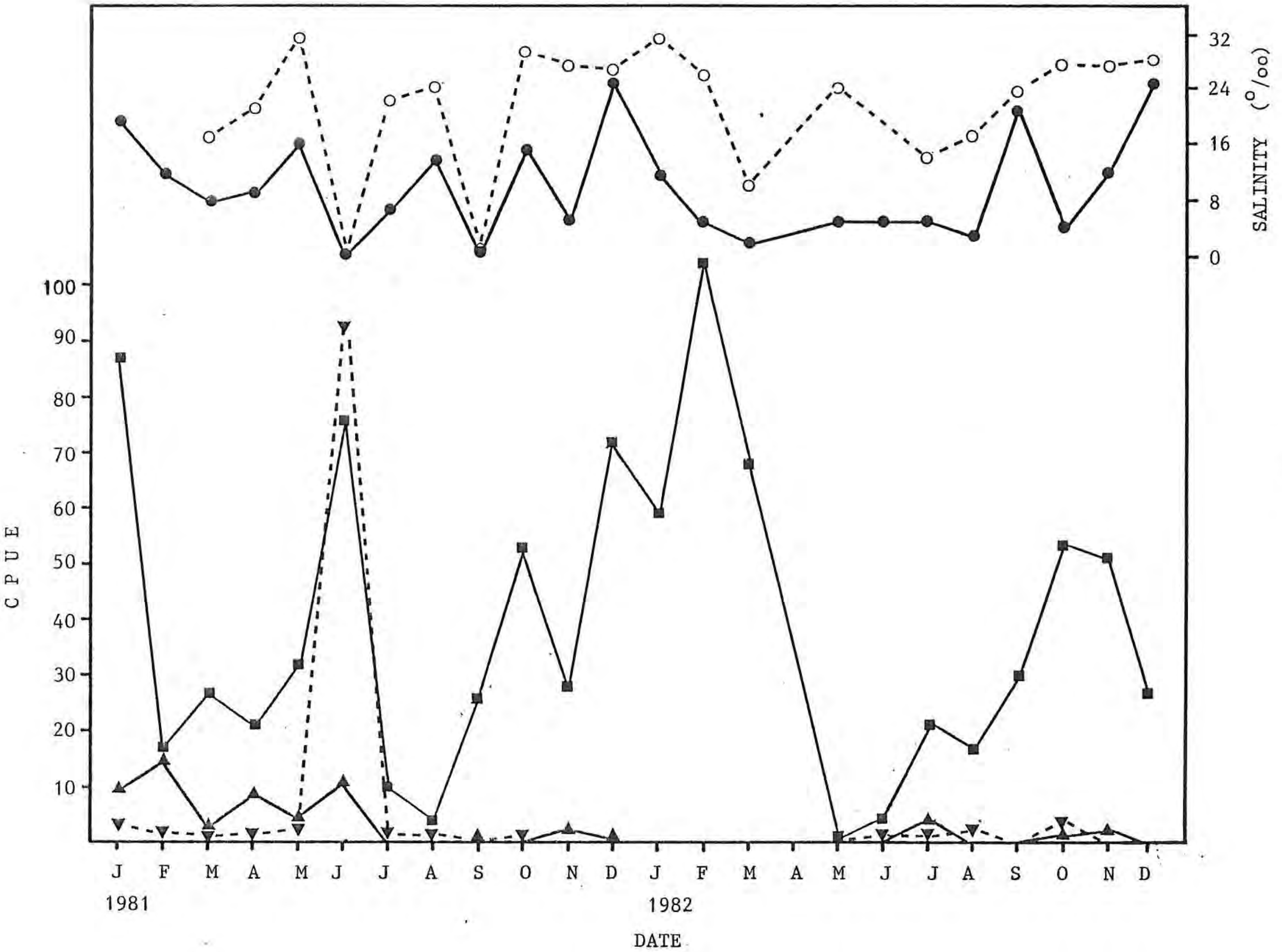


Figure 77. The surface (open circles) and bottom (closed circles) salinities and C P U E (see text) of *L. richardsoni* (squares), *Mugil cephalus* (inverted triangles and dotted line) and *Myxus capensis* (triangles) at Stn. 2 in th Great Fish estuary.

Table 67. The C P U E and estimated % age composition of *Mugil cephalus* caught in the upper reaches of the Great Fish estuary in December 1982.

Distance from mouth (km)	Salinity (^{o}/oo) over tidal cycle Surf	Bottom	C P U E	Estimated age composition (%) 1+	2+	3+
6 (Stn. 3)	4 - 8	4 - 11	41	48,8	43,9	7,3
7,5	1 - 2	2 - 4	158	62,0	34,8	3,2
10	0	0	638	99,1	0,9	0

The preference of *Mugil cephalus* for the upper, freshwater-dominated areas of estuaries has also been found in the Sundays (Marais 1981) and Gamtoos (Marais 1983 b) estuaries. In the Swan-Avon estuary in Western Australia, Chubb *et al.* (1981) found that the majority of *Mugil cephalus* were caught in the upper parts of this system. In addition, as found in the Great Fish estuary, maximum numbers in the Swan-Avon estuary were caught in winter months (June, July and August) during the period of greatest freshwater inflow. Both Marais (1981) and Chubb *et al.* (1981) consider that the distribution of mullet in these systems may be related to the large amounts of detritus in the upper reaches.

The distribution of *Mugil cephalus* in estuaries on the east coast of southern Africa, however, does not appear to show this pattern. In the Kosi System, for example, *Mugil cephalus* >200 mm SL were more abundant in the more saline parts of the estuary (Blaber 1977), where the substrate was rich in preferred food items such as Foraminifera. The occurrence of relatively large amounts of smaller (5 - 200 mm SL) *Mugil cephalus* in the upper reaches of the Kosi System was suggested by Blaber (1977) to be a strategy to avoid predation rather than for the utilization of preferred food resources. Also, Whitfield (1980) found that *Mugil cephalus* was most abundant in the lower reaches of the Mhlanga estuary and attributed the relatively low mullet biomass in the upper regions to the high silt content of the substrate. The above findings are in direct contrast to the situation in the Great Fish estuary where large numbers of *Mugil cephalus* occur in the freshwater, silted-up regions of the upper estuary. This apparent anomaly, while outside the scope of the present study, merits further research.

The lengths, mesh sizes and setting periods of gill nets used in this study were very similar to those employed in work on the Swartkops (Marais & Baird 1980), Sundays (Marais 1981), Kromme (Marais 1983a) and Gamtoos (1983b) estuaries. C P U E and relative frequencies of mullet from the various estuaries can therefore be compared (Tables 65 and 66).

The C P U E values of *Myxus capensis* caught in the Great Fish and Gamtoos estuaries (5,0 and 5,6 respectively) are similar but higher than C P U E values found in any of the other estuaries (Table 65). The fact that *Myxus capensis* forms only 8,5% of total mullet catch in the Great Fish compared to 46% in the Gamtoos (Table 65), reflects the very high densities of *L. richardsoni* and particularly *Mugil cephalus* in the former estuary. In both the Swartkops and the Kromme estuary, no *Myxus capensis* were caught in spite of extensive gill netting surveys conducted monthly for at least one year (Marais & Baird 1980; Marais 1983). In less extensive gill netting surveys of other eastern Cape estuaries (Table 67), *Myxus capensis* were often absent and only prominent in catches from the Keiskamma and Kwelera estuaries.

The abundance of *Myxus capensis* in estuaries appears closely related to the amount of freshwater inflow. The mean annual runoff of both the Gamtoos (458×10^6 m^3) and the Great Fish (479×10^6 m^3) are far greater than the Kromme (105×10^6 m^3), Swartkops (84×10^6 m^3), Sundays (29×10^6 m^3) and Kowie (23×10^6 m^3) rivers. Both the Gamtoos (Marais 1983b) and the Great Fish estuaries (see Chapter 2) have marked salinity gradients and low salinities are normally found throughout both systems. In both estuaries more than half of the area effected by the tides usually have surface salinities $<5^{o}/oo$. The Gamtoos and the Great Fish estuaries can therefore be termed freshwater-dominated systems. In the other estuaries listed in Tables 65&67 with smaller mean annual runoffs, marine influence usually penetrates to the head of the estuary. High salinities are commonly found in the upper reaches and only during or for limited periods after floods do low salinities occur throughout these systems. The data from this study as well as the findings of Marais (1983b) show a positive correlation between abundance of *Myxus capensis* and the amount

Table 67. The percentage occurrence of mullet species in gill net catches from various eastern Cape estuaries. The mean annual runoff (MAR) of the rivers is also given.

Estuary	MAR ($m^3 \times 10^6$)	Total mullet catch (n)	Percentage of total mullet catch					
			Myxus capensis	*Mugil cephalus*	*Liza rich.*	*Liza dum.*	*Liza tric.*	other
Kariega	15	18	0	22	50	17	11	0
Old Woman's		18	6	56	28	11	0	0
Mpekweni	2	11	0	82	0	0	18	0
Mtati	3,5	56	2	61	23	7	7	0
Keiskamma	133	221	20	74	4	0	1	0
Chulumnae	25	87	7	24	2	40	1	25
Gqunube	35	26	0	0	85	4	0	11
Kwelera	32	55	16	33	27	15	5	4
Quko	41	14	0	0	71	21	7	0

of freshwater inflow in eastern Cape estuaries.

The small number of adult *Myxus capensis* found in the marine-dominated estuaries suggest that a large proportion may be migrants from freshwater areas undergoing gonadal maturation prior to spawning at sea. In the Kowie estuary, for example, few adult females were normally caught. However, in April 1976, gill nets placed just below the head of the estuary during a flood, caught 14 adult female *Myxus capensis* of which over 70% showed signs of initial sexual activity (Fig. 78). This indicated that a spawning run had been intercepted. The next month three sexually "active" adult females were caught at this site, two with ovaries in advanced stage III and unusually high GSI values of 1,27 and 1,43. This indicated that progressive ripening of the ovaries had occurred.

DISTRIBUTION AND ABUNDANCE IN FRESHWATER ZONES

L. richardsoni were caught in freshwater reaches above the Kowie and Great Fish estuaries, but did not penetrate further than one and 10 km up the former and latter rivers, respectively. The frequency distribution of *L. richardsoni* captured in the freshwater and estuarine areas of the Kowie and Great Fish rivers are given in Fig. 79 . As this species only reaches first sexual maturity when >240 mm FL (Bok, unpubl. data), only sub-adults were present in freshwater areas. These findings, together with the absence of this species from freshwater zones of other eastern Cape rivers sampled, indicate that freshwater areas of rivers in the eastern Cape are not an important habitat for *L. richardsoni*.

Although both *Mugil cephalus* and *Myxus capensis* penetrate considerable distances up eastern Cape rivers, *Myxus capensis* usually penetrated further upriver (Table 68. In many rivers only *Myxus capensis* were caught. In the three rivers most extensively sampled, the numbers of *Myxus capensis* relative to *Mugil cephalus* increased as the distance upstream of the estuary increased. In the Kowie, relatively large numbers of *Mugil cephalus* (48% of mullet catch - Fig.74) were present in a freshwater pool immediately above the head of the estuary. However, in spite of intensive sampling over a three-year period, *Mugil cephalus* did not penetrate above this pool, i.e. more than one kilometer upstream of the

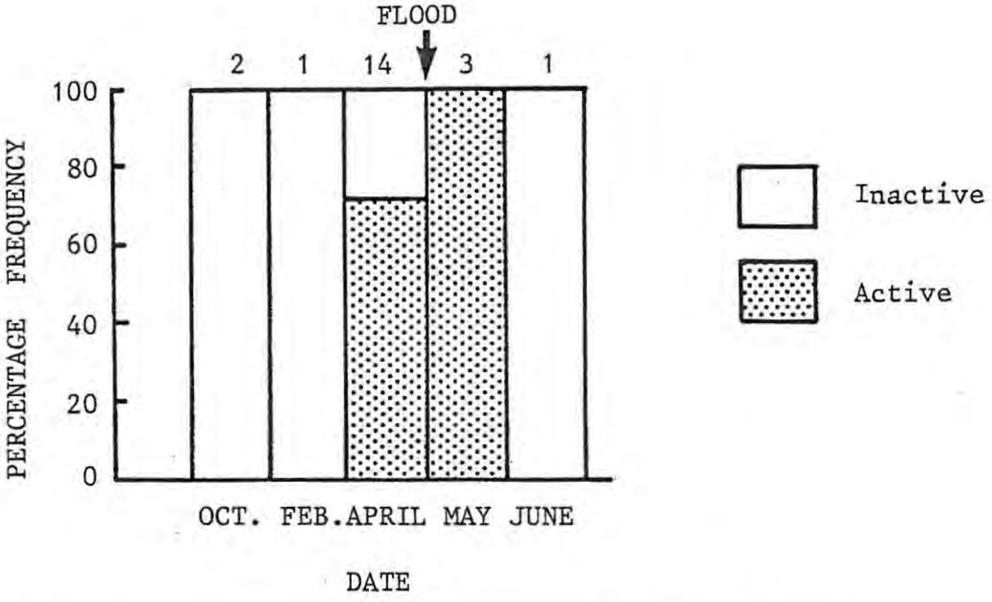


Figure 78. The percentage frequency of adult *Myxus capensis* with "active" gonads caught just below the Kowie River ebb and flow before and after flood conditions (see text).

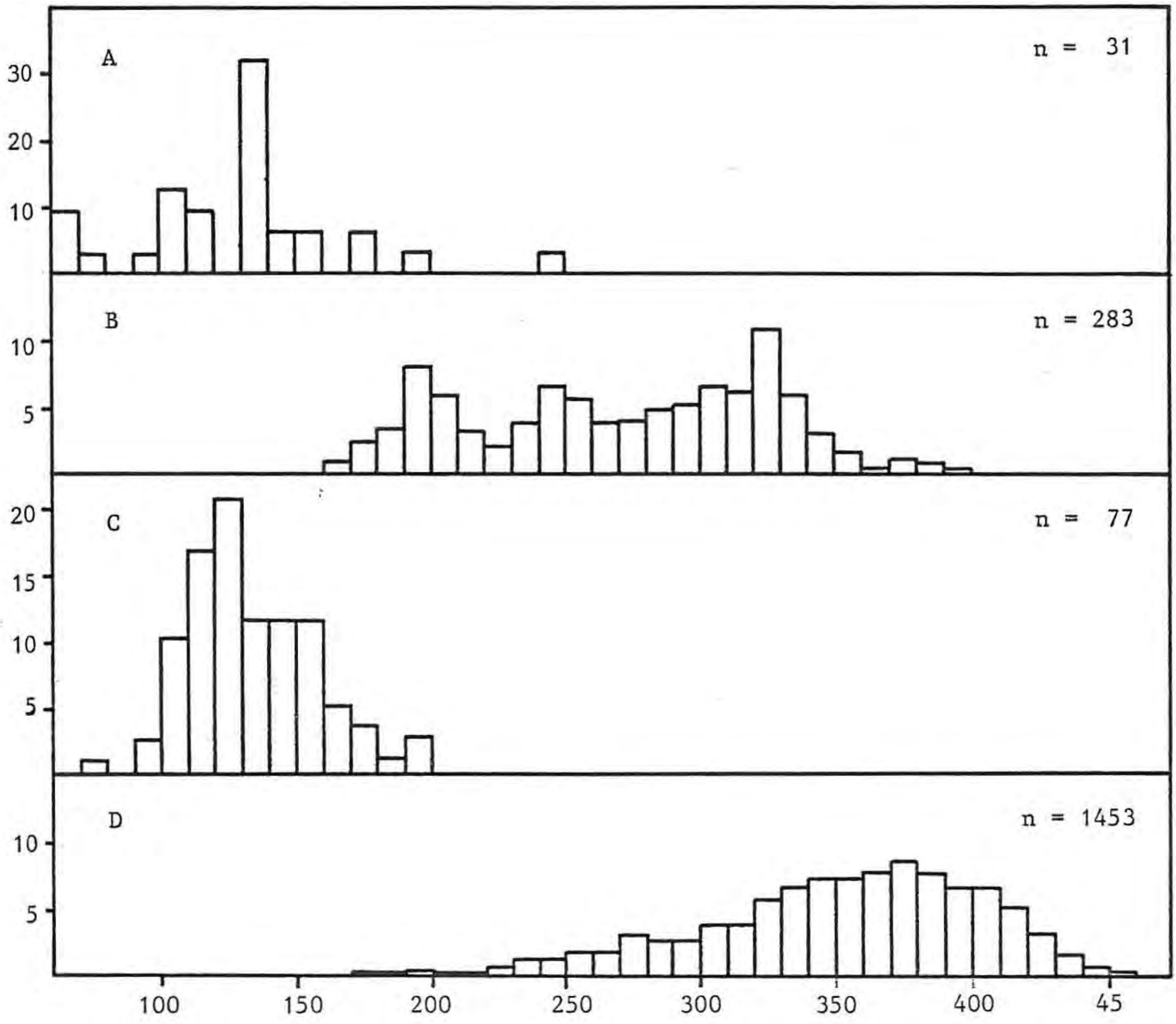


Figure 79. The length frequency of *L. richardsoni* sampled from the Kowie River (fresh water) (A), Kowie estuary (B), Great Fish River (fresh water) (C) and Great Fish estuary (D).

Table 68. The maximum recorded penetration of *Myxus capensis* and *Mugil cephalus* into freshwater areas of eastern Cape rivers. The mean annual runoff (MAR) of the rivers is also given (Noble & Hemens 1978).

River System (tributary)	Km from head of estuary		MAR ($m^3 \times 10^6$)
	Myxus capensis	*Mugil cephalus*	
Kromme	8		105
Gamtoos (Groot)	120	120	485
Gamtoos (Kouga)	105	75	
Maitland	8	0,5	
Swartkops (Elands)	26	19	84
Sundays	51	51	29
Bushmans	15	15	38
Kariega	44		15
Kowie	37	1	23
Kleinemonde West	2		
Great Fish	110	78	479
Keiskamma	17		133
Buffalo	5		82
Nahoon	20		
Gqunube	18		35
Kwelera	42		32
Great Kei	173		1 001

head of the Kowie estuary.

Although *Mugil cephalus* penetrates further upriver in the Great Fish and Swartkops compared to the Kowie River, the numbers relative to *Myxus capensis* decreased markedly as the distance from the estuary increased (Figs.80 & 81). In summary, the data show that *Myxus capensis* penetrates further upriver and is more abundant in freshwater reaches than *Mugil cephalus*.

The sex ratios of *Myxus capensis* from various areas of the Swartkops, Kowie and Great Fish rivers (Table 69) show a tendency for females to be relatively more abundant in the upper reaches. However, this tendency is not marked, and is probably related to the faster growth and greater longevity of females (Chapter 4), rather than their having a stronger upriver migratory drive than the males.

The relatively larger numbers of *Myxus capensis* in the freshwater compared to the estuarine zones of eastern Cape rivers, as well as the considerable upriver penetration of this species, indicates that the freshwater zones are the preferred habitat of this species in the eastern Cape. Large adult *Myxus capensis* (n = 2, FL 352 and 342 mm) have been captured in seawater lagoons (salinity 30 - 40^{o}/oo) near the mouth of the Kowie River. As entry to these lagoons (via the stone-packed berm separating it from the main river channel) can only occur as small fry, these fish had not entered fresh water at any stage. This may indicate that there is no purely physiological need for *Myxus capensis* to spend part of its life in fresh water.

A possible explanation for this species preference for freshwater areas may be related to trophic competition with other mullet species in eastern Cape estuaries. Possible competitors include the two other euryhaline species, *Mugil cephalus* and *L. richardsoni*. Blaber (1976, 1977) studied the feeding ecology of 11 mullet species (including *Mugil cephalus* and *Myxus capensis*) in estuaries on the east coast of South Africa. He found that interspecific competition for food was reduced by different species selecting particles of different sizes and possibly also by differences in feeding periodicity. In addition Blaber (1977) found that:

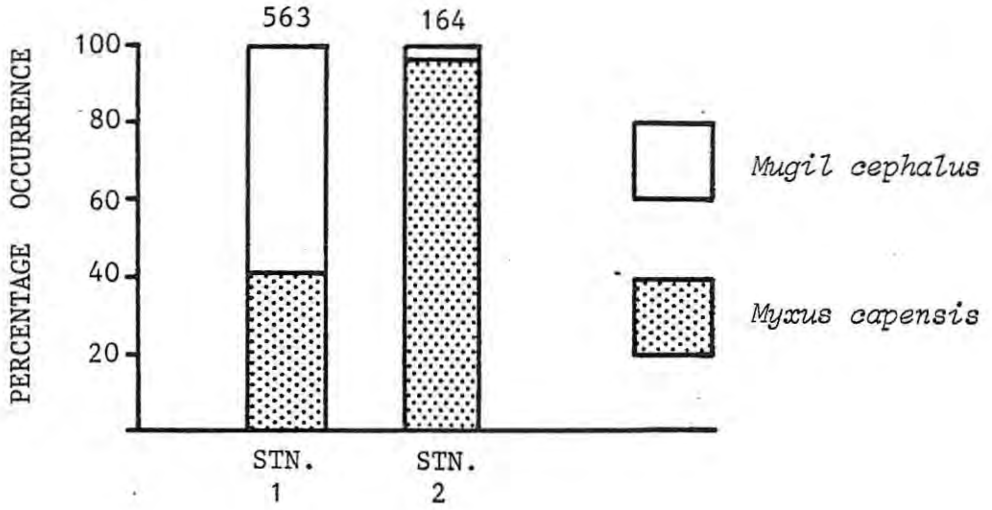


Figure 80. The percentage occurrence of *Mugil cephalus* and *Myxus capensis* in gill net catches at Stations 1 & 2 in the Swartkops River. Numerals indicate sample size. Stn. 1 = 2 km upriver of ebb and flow; Stn. 2 = >17 upriver of ebb and flow.

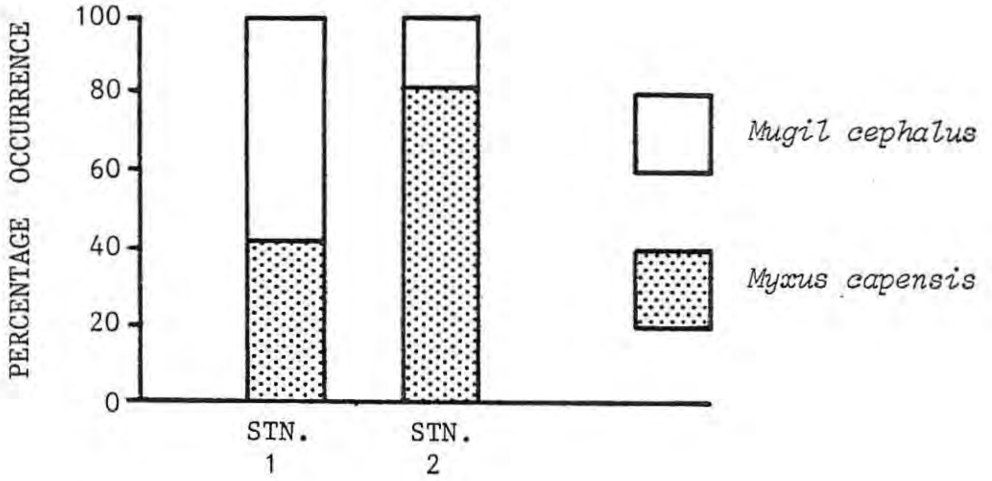


Figure 81. The percentage occurrence of *Mugil cephalus* and *Myxus capensis* in gill net and seine net catches in the lower (Stn. 1) and upper (Stn. 2) sections of the freshwater reaches of the Great Fish River. Stn. 1 <27 km from the ebb and flow; Stn. 2 >27 km from the ebb and flow.

Table 69. The sex ratio of *Myxus capensis* captured at various distances upriver from the estuaries in the Swartkops, Kowie and Great Fish rivers.

River	Stn.	Dist. from estuary (km)	No. of fish caught		% females	ratio of males : females
			males	females		
Swartkops	1	1 - 2	93	111	54	1 : 1,2
	2	22 - 35	54	102	65	1 : 1,9
Kowie	1	0,5	80	107	57	1 : 1,3
	3	26 - 29	53	93	64	1 : 1,8
	4	34 - 37	203	357	64	1 : 1,8
Great Fish	1	0 - 27	23	49	68	1 : 2,1
	2	>27	21	56	73	1 : 2,7

> "Most species are sufficiently flexible in their feeding ecology to cope with a variety of estuarine substrates and still avoid serious interspecific competition by partitioning the resources according to substrate particle size".

However, competitive interactions may still occur and Blaber (1976) suggested that the virtual absence of *Myxus capensis* in brackish lake St Lucia may be due to interspecific competition. The importance of trophic competition as a means to explain the relative abundance of *Myxus capensis* in eastern Cape estuaries is, however, questionable and deserves further study.

In comparison to the estuaries of the eastern Cape, most of the freshwater zones of the rivers support low species numbers as well as low biomass of indigenous fish species (Jubb 1967; Skelton 1980). The most prolific species in this area, the relatively large cyprinid, *Labeo umbratus*, is detritivorous (Groenewald 1957). However, this species occurs naturally in only the large rivers such as the Gamtoos, Sundays, Great Fish and Keiskamma rivers (Jubb 1967). The only other relatively large detritivore in eastern Cape rivers is the Mozambique tilapia, *Oreochromis mossambicus* which is, however, largely confined to areas not far from the heads of the estuaries (personal observation). In addition, apart from four species of anguillid eels, there are no large piscivorous fish present in these rivers. *Myxus capensis* may have been "pre-adapted" to exploit freshwater habitats because of a preference for the upper, freshwater reaches of estuaries. This species may therefore have evolved its catadromous life history in response to both the relatively lower predation pressure and the abundant trophic resources of the freshwater zones.

FACTORS EFFECTING UPRIVER MIGRATION

The distribution and extent of the upriver penetration of mullet within a particular river system is influenced by natural as well as man-made constraints. Some of the natural constraining factors include:

(i) *water quality* - natural variations due to the influence of different geological features in the catchment areas;

(ii) *river flow* - suitable river flow for fish movement will depend on the physical characteristics of the river bed and swimming ability of the fish;

(iii) *physical barriers* - natural features such as waterfalls and rapids;

(iv) *presence of suitable habitats* - for example, pools of suitable size and depth to provide adequate food resources and shelter from predation.

Each of the above four natural factors has been altered to some extent by man in nearly all of the rivers in the eastern Cape. However, before the effects of man-induced changes can be fully appreciated, an understanding of the influence of natural factors on mullet distribution within a system is required.

(i) *Water quality.*

As mentioned in Chapter 2 , rivers of the southern Cape draining Table Mountain Sandstones (TMS) of the Cape Fold Belt mountains are typically acidic, mineral-deficient and have a low productivity (Noble & Hemens 1978). Surveys undertaken during this study as well as in previous years by Smith & Smith (1966) failed to reveal the presence of adult *Myxus capensis* in these acidic rivers. An intensive survey of the mildly acidic (pH 6,2 - 6,6) Kromme River in May 1982 captured only one *Myxus capensis* (240 mm FL) eight kilometers from the head of the estuary. The only records of *Myxus capensis* between the Kromme and Knysna systems are those of juvenile fish from the lower reaches of the Van Stadens, Groot and Tsitsikamma rivers (Skelton, pers. comm 1983). Smith & Smith (1966), when describing the freshwater fish of this area stated:

> "In that about 300 mile comparatively well watered stretch, the freshwater fish fauna is among the poorest of comparable areas with rivers in the Republic".

Although more comprehensive surveys are necessary, it appears that the oligotrophic, acidic nature of the southern Cape Fold Belt rivers make them unsuitable for mullet, especially adults.

A possible example of natural differences in water quality within a river system influencing the distribution of mullet, is indicated in the Swartkops River system. The changes in water quality from minerally deficient, acidic water in the upper Elands tributary and upper Swartkops to minerally enriched, alkaline waters in the lower reaches, are described in detail in Chapter 2. This study showed *Myxus capensis* (and *Mugil cephalus*) to be present in large numbers in the lower Elands River and lower Swartkops River only. Although there are no apparent physical barriers preventing further upriver migration of mullet into areas with large deep pools (preferred mullet habitat), no mullet were captured during intensive gill netting surveys in these upper reaches. It is possible therefore that further upriver penetration in this system is inhibited by unsuitable water quality.

(ii) *River flow and barriers to fish movement.*

A very important natural constraint affecting fish movement in river systems is suitable river flow. This is particularly important in eastern Cape rivers where river flow is usually highly variable. The flow patterns of this three rivers studied, particularly the Kowie River, are described in some detail in Chapter 2 under "Climate and Hydrology".

From field observations at different levels of river flow in the Kowie River, it was estimated that fish movement over natural rapids could probably take place at river flows of as low as 0,5 m^3/ S. At lower flows, shallow water depth probably impedes the movement of fish larger than about 200 mm FL. *Myxus capensis* <100 mm FL have been observed negotiating rapids under low flow conditions in water depths of less than 50 mm. Their small size enables these fish to gain maximum advantage from the numerous eddies and counter-currents present in the rapids and to rest in relatively still water behind rocks and near the stream bed. By darting from rock to rock, full advantage is taken of the considerable "burst speed" potential of these small fish (Katopodis 1977; Brett & Glass 1973), which may be much greater in terms of body length per second than large fish (Wardle, in Miller 1979).

However, small size could be a major disadvantage in open water conditions. Swimming speed is positively related to length, with maximum speed attained by a fish approximately equal to 10 times its own length per second (Harden-Jones 1968). An important consideration is that under "normal" conditions, rivers in the eastern Cape consist of large, still pools separated by shallow stony runs or rapids. Under these conditions it is conceivable that, in the absence of high natural or man-made barriers, small (< about 120 mm FL) mullet may be able to negotiate these rapids more easily than large adult fish. The migratory urge and swimming ability of small *Myxus capensis* was demonstrated by the presence of juvenile fish (mean FL = 65 mm; range = 56 - 79; n = 35) over 80 km upriver from the head of the Great Fish estuary in February 1977. From knowledge of growth rates and size at first recruitment into freshwater (Chapters 4 and 5), it was estimated that this distance was covered in 2 - 3 months. The journey entailed a climb of approximately 75 m and the negotiation of numerous rapids (this stretch of river has been surveyed by the author using a canoe). It is significant that there were no weirs in this stretch of river, and no floods occurred during the migratory period.

A series of photographs of a low gauging weir 11 kilometers from the head of the Kowie estuary (Wolfcrag P401) at varying river flows, (Figs 82 & 83), illustrates that high flow conditions are essential to enable fish (especially small fish) to negotiate this barrier. Even low weirs can therefore restrict fish movement to periods of peak flow.

The frequency and duration of flood peaks in a river such as the Kowie with its numerous weirs (Fig. 16 , Chapter 2) will therefore largely determine the periods of potential fish movement in the system. The maximum daily flow rates in the Kowie River from 1974 to 1977 (Fig. 84) illustrate that these periods of high river flow occur infrequently and normally exist for only a few days. The inhibiting effect of low weirs is therefore considerable. Any factors reducing the frequency and duration of these flow peaks, such as dam construction, excessive water extraction, changing the run-off characteristics of the catchment, etc., could negatively effect fish movement.

Seine and dip-netting immediately below Wolfcrag weir on the Kowie River showed that large numbers of sub-adult mullet (< 180 mm FL, usually < 140 mm FL) accumulated at this site (Fig. 85). This length range may be the critical size range for negotiating this particular weir. It may be significant that in spite of extensive sampling for small fish above this weir (using traps, rotenone, seine netting and hook and line), the smallest *Myxus capensis* caught measured 151 mm FL.

Figure 82. Wolfcrag gauging weir on the Kowie River during "normal" low flow conditions.

Figure 83. Wolfcrag gauging weir on the Kowie River during high flood conditions. The gauging notch against rock-face is completely submerged.

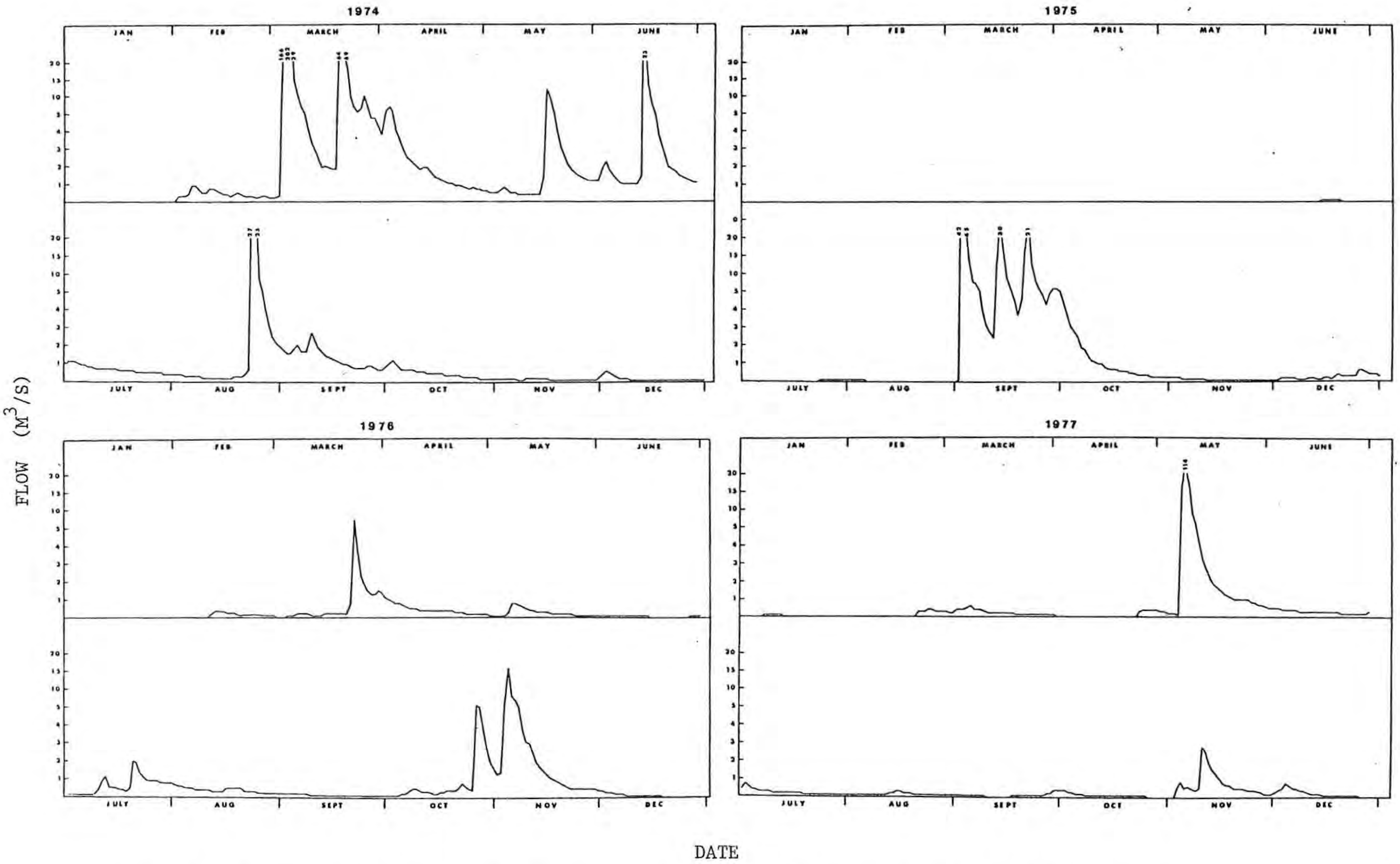


Figure 84 . The maximum daily flow rates at Wolfcrag gauging weir from Jan. 1974 to Dec. 1977. Flow scale expanded above 5 m^3/S for clarity.

The length distribution of *Myxus capensis* captured in the lower and upper reaches of the Kowie (Fig. 86) and Swartkops (Fig. 87) rivers shows a tendency for the larger fish to be found further upriver. In the Great Fish River (Fig. 87) however, this trend is not apparent. This may be due to comparatively better conditions for fish migration in the latter river resulting from the absence of man-made and "difficult" natural barriers. In addition, the Great Fish River has a comparatively large MAR (Table 68) and its flow was augmented in 1975 by water from the Orange River via the Orange-Fish tunnel. This apparent suitability for migration is reflected in the far greater distances which both *Myxus capensis* and *Mugil cephalus* penetrate up the Great Fish compared to most other rivers (Table 68). In most rivers there is a positive correlation between MAR and the extent of upriver penetration of mullet (Table 68), again emphasising the important influence of river flow on fish movement.

CONSERVATION STATUS OF *MYXUS CAPENSIS* IN THE EASTERN CAPE

Surveys conducted during this study showed the presence of *Myxus capensis* in most of the larger coastal rivers from the Great Kei to the Kromme (Table 68). All areas downstream of the point of highest upriver penetration can be considered potential *Myxus capensis* habitat. This means that there are over 700 km of potentially suitable freshwater riverine habitat in the eastern Cape for this species.

However, in virtually all these rivers *Myxus capensis* populations appear to have been negatively effected by man-induced habitat changes (Table 69). A major threat to these populations is the wide-scale construction of weirs and dams on the coastal rivers. As mentioned by Skelton (1983):

> "the construction of relatively small-scale weirs by individual riparian landowners has effectively changed (not necessarily detrimentally) the character of practically all rivers and streams in South Africa".

In nearly all rivers surveyed, except the Gamtoos, Great Fish and Great Kei, there exists some form of man-made barrier impeding fish movement at or within a few kilometers of the head of the estuary (Table 69).

The effect of such weirs can be disastrous. For example, the recent (*ca* 1974) erection of a three m high weir within one kilometer of the head of the Kariega estuary, appears largely responsible for the recent

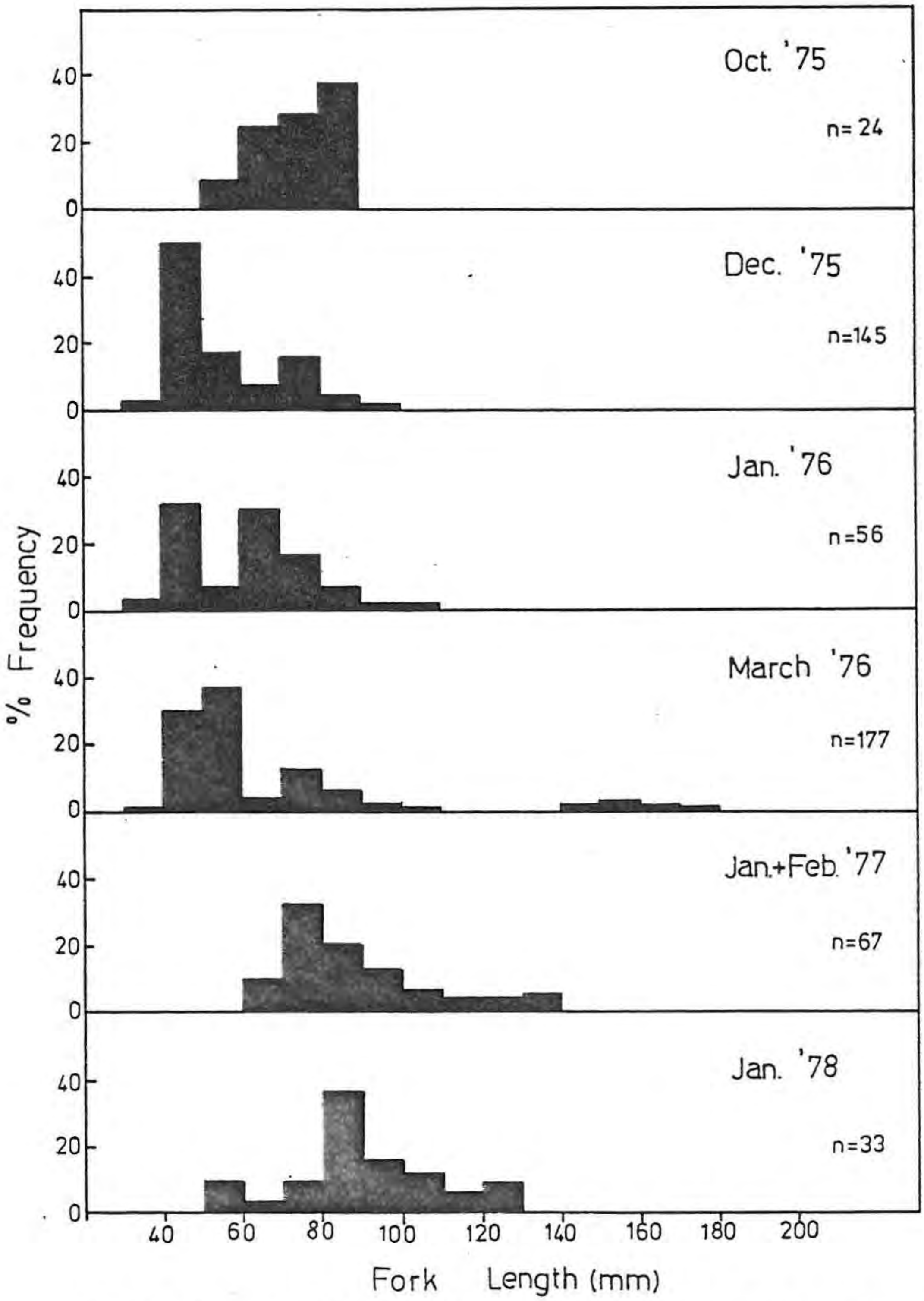


Figure 85. The length frequency distribution of *Myxus capensis* caught below Wolfcrags gauging weir on the Kowie River.

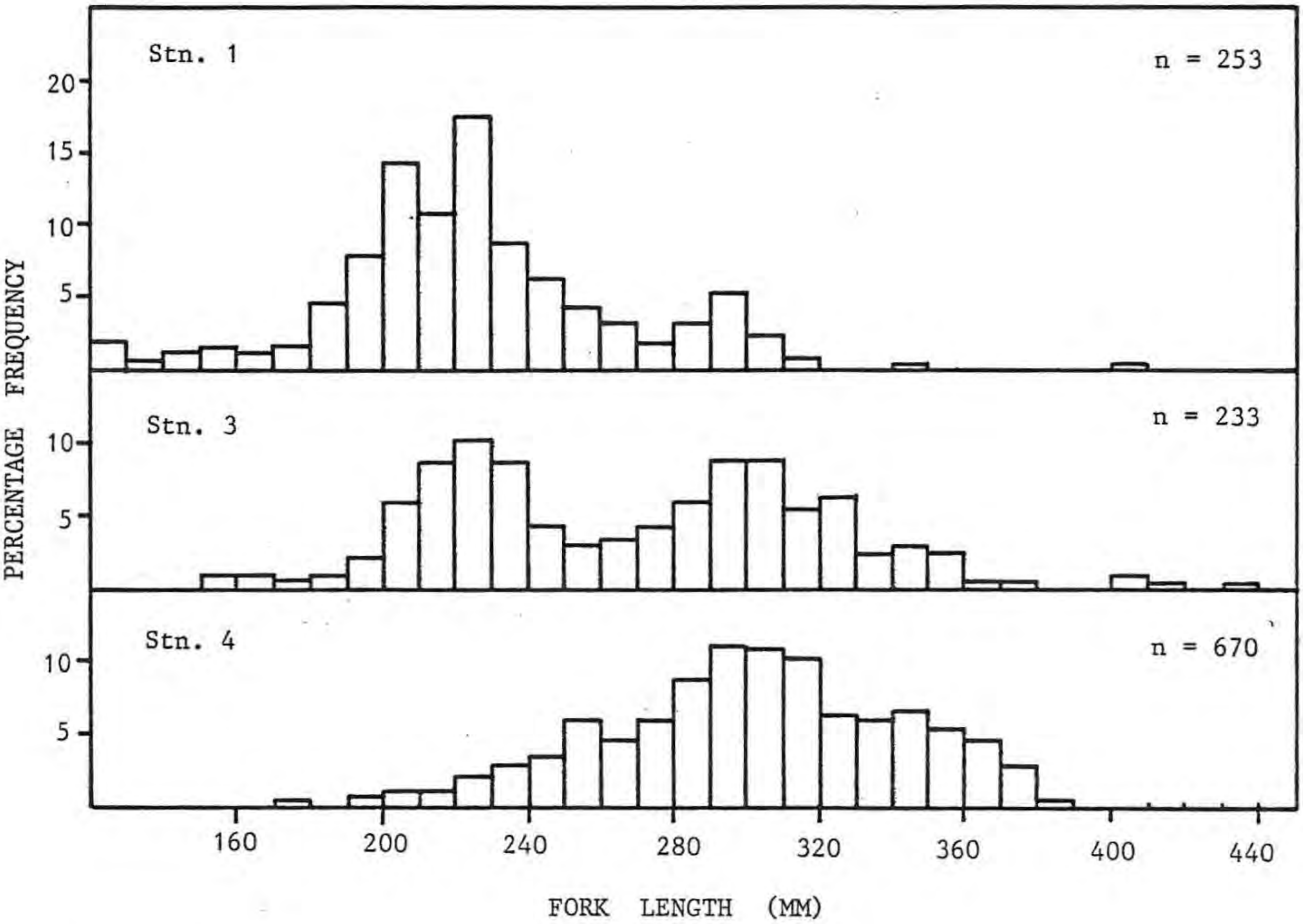


Figure 86. The length frequency distribution of *Myxus capensis* caught using gill nets, traps and angling at various stations in the Kowie River.

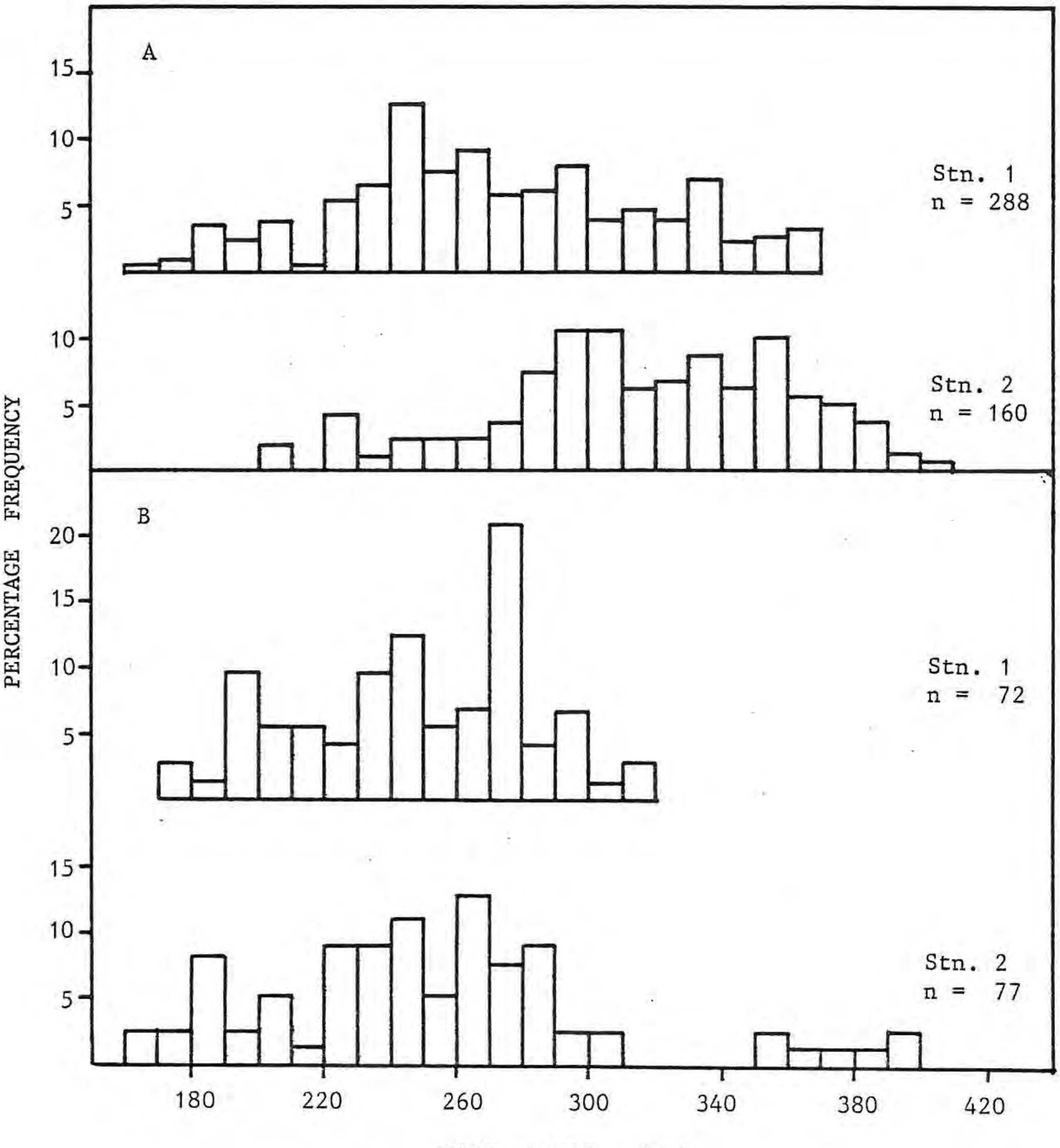


Figure 87. The length frequency distribution of *Myxus capensis* in gill net catches at Stations 1 & 2 (see text) in the Swartkops (A) and Great Fish (B) rivers.

Table 69. Conservation status of *Myxus capensis* in eastern Cape rivers. The categories, endangered, vulnerable and rare are used according to definitions given by Skelton (1977).

River System	Furthest Upriver penetration		Relative Abundance		Man-induced factors effecting survival in system	Conservation status in system
	Distance (km)	Limiting factor	Fresh water	Estuary		
Great Kei	173	unknown	wide range, low numbers	common	excessive siltation reducing fish holding capacity, possible unfavourable interaction with introduced *Barbus holubi*.	unknown, possibly vulnerable
Quko			absent	absent	no fish captured in pools immediately above head of estuary, reason unknown.	
Kwelera	42	unsuitable habitat	common	common	low weir at head of estuary, silting up of deep pools in upper reaches, excessive water extraction.	vulnerable
Gonubie	18	waterfall *ca* 25 km upriver	common in lower reaches	absent	1,2 m weir at head of estuary, plus other small weirs, farmer (Mr. T.B. Luck) reports presence upriver (25 km) to waterfall.	vulnerable
Nahoon	20	large dam	rare	unknown	barrier (road culvert) at head of estuary, large fish kills due to dumping pineapple wastes, impassable barrier 24 km from head of estuary.	endangered
Buffalo	5	weir	rare	absent	pollution from harbour at mouth, only 10 km of potential riverine habitat due to impassable weir.	endangered
Chuluminae			absent	rare	1 m high weir at head of estuary, limited suitable habitat possibly degraded by siltation.	rare
Keiskamma	17	unknown	rare	common	0,5 m weir at ebb & flow where accumulating fish seen to suffer heavy mortalities due to predation; a number of low weirs inhibiting movement; dam construction in upper catchment reducing river flow.	vulnerable
Great Fish	110	natural rapids	common	common	recent (1977) erection of weir 27 km from head of estuary negotiable only during floods; excessive soil erosion reducing depth in pools, introduction of non-endemic species from Orange River via Orange-Fish tunnel.	vulnerable

Table 69. Continued.

River System	Furthest Upriver penetration		Relative Abundance		Man-induced factors effecting survival in system	Conservation status in system
	Distance (km)	Limiting factor	Fresh water	Estuary		
Kleinemonde	2	unsuitable habitat	rare	unknown	weir at head of estuary only passable during floods.	rare
Kowie	37	weir	previously common	present	recent erection (1979) of 3 m high weir at head of estuary, threatens entire population; several smaller weirs upstream inhibiting movement.	endangered
Kariga	44	weir *ca* 50 km from estuary	previously common	absent	erection in of 2,5 m high weir *ca* 1 km from head of estuary has apparently blocked all up-river migration, no fish caught in recent surveys.	endangered
Bushmans	15	suspect natural rapids	common	unknown	relatively large numbers of black bass (*Micropterus salmoides*) in system possibly predating on mullet fry.	possibly vulnerable
Sundays	51	4 m weir	common	rare	possible negative effects of introduced non-endemic Orange River fish species, via tunnel, *Clarias gariepinus*, an efficient predator, is now established in this system.	possibly vulnerable
Swartkops	26	possibly natural water quality	common	absent	siltation in lower Elands tributary, excessive water extraction, pollution from industries in lower Swartkops, recent (1983) erection of partial barrier 1 km from head of estuary.	vulnerable
Maitland	8	unknown	rare	unknown	unknown, but limited natural habitat due to small size of system.	rare
Gamtoos	120 (Groot) 105 (Kouga)	unknown, possibly natural large dam	common	common	no major barriers on Gamtoos River or Groot tributary, large areas of suitable habitat, impassable barrier on Kouga 6 km upriver of junction with Groot/Gamtoos limits habitat in Kouga tributary.	good
Kromme	8	unknown	rare	absent	thought to be naturally rare in system, recent construction of impassable dam wall *ca* 5 km from head of estuary will further limit populations.	endangered

disappearance of *Myxus capensis* from above this weir where they had previously been abundant (Bok, unpubl. data). Also, in the Kowie River, the erection of a weir about 40 km from the head of the estuary, (Fig. 88) has prevented further upriver migration of *Myxus capensis* and effectively reduced its range in this river system by about 40 km (Bok, 1979, 1980). A high weir was erected in 1979 50 m upstream of the Kowie ebb and flow (Fig. 4) and, if impassable, may result in the complete disappearance of this species from this system.

Large numbers of migrating fish tend to accumulate immediately below man-made barriers, often in shallow water, and have been seen to suffer heavy mortalities from predators, especially piscivirous birds (Jackson 1979; Bok 1980). These barriers can therefore not only permanently cut off many km of suitable habitat, but, even if passable during floods, could drastically increase the mortality rate of migrating fish.

Other forms of man-induced habitat changes also threaten the viability of *Myxus capensis* populations in many areas. Factors affecting the survival of freshwater fishes in southern Africa have been discussed in detail by Crass (1969), Chutter (1973), Skelton (1977), Gaigher (1979), Jackson (1979), Gaigher *et al.* (1980) and Skelton (1983). All these authors emphasise that habitat degradation caused by various farming practices and malpractices have probably been one of the major factors responsible for the decline in freshwater fishes in southern Africa.

Crass (1969) states that:

> "It is doubtful if a single one of the major rivers of South Africa reaches the sea in a condition that has not been severely affected by land use in the catchment".

This author describes is some detail the severe silting caused by man-induced soil erosion in the catchments, as well as the excess water extraction for irrigation that has seriously degraded most Natal rivers. Soil erosion is a major problem throughout South Africa where between 100 and 150 million tons of sediment are transported annually by South African rivers (Noble & Hemens 1978). Siltation is evident in many Cape rivers and according to Skelton (1977) is probably causing the decline of at least five threatenend Cape freshwater fish species.

Figure 88. Weir on Kowie River *ca* 40 km from the head of the estuary, which prevents the upriver penetration of *Myxus capensis*. Note the water falls onto a shallow rock shelf below the wall.

Siltation, by increasing turbidity can reduce photosynthesis and hence algal and macrophyte production. Food resources, including stream invertebrates (Chutter 1969), may therefore be negatively effected. A possible more important factor for mullet is the reduction of the fish-holding capacity of rivers by the filling of previously deep pools with sediment. These deep (often >4 m) permanent pools at present constitute a viable and safe habitat for large mullet, especially during periods of low or no river flow. The filling up of these pools would therefore greatly reduce the viability of this riverine habitat, especially during times of drought.

Any form of land use resulting in the removal of or a change in the natural vegetation of the catchment, may have important consequences to fish life. Allochthonous detritus has been documented as the primary energy source for many stream ecosystems (Hynes *et al.* 1974). In most Cape rivers, fishes are thought to exist largely on a detritus food chain (Gaigher *et al.* 1980). From data on the feeding ecology of *Myxus capensis* and *Mugil cephalus* in estuarine environments (Marais 1975; Blaber 1976, 1977; Whitfield 1980), organic detritus or benthic floc probably forms the major portion of the diet of both mullet species in freshwater. Large-scale bush-clearing, which is at present occurring at an increasing rate in the eastern Cape (pers. obs.) may therefore seriously disrupt these detritus food chains.

Other factors affecting the survival of fish species in South African rivers have been discussed by Crass (1969), Skelton (1977, 1983), Jackson (1979), Brooks & Gardner (1980), Gaigher *et al.* (1980) and include:

(i) mineralization and eutrophication; (ii) pesticides and herbicides; (iii) introduction of exotic aquatic animals and plants, (iv) alteration of flow patterns as a result of dam construction.

The presence of the exotic predatory black-bass (*Micropterus salmoides*) in many eastern Cape rivers was postulated by some workers to be partly responsible for the decline in the status of *Myxus capensis* (PBN Jackson, pers. comm. 1975). However, the number of *Micropterus salmoides* in most eastern Cape rivers is usually low. In addition, mullet fry stocked into dams with established *Micropterus salmoides* populations have shown survival rates of 20 - 30% after four years (Chapter 6). The effect of predation by *Micropterus salmoides* on the survival of mullet in most rivers in the eastern Cape may therefore not be significant compared to the man-induced factors discussed above.

The factors effecting survival, distribution and abundance of *Myxus capensis* in eastern Cape rivers are illustrated diagrammatically in Fig. 89. The detrimental effects which these man-induced habitat changes have had on *Myxus capensis* populations in freshwater areas in the eastern Cape are severe. As shown in Table 69, the only river system in which the status of *Myxus capensis* appears not to be threatened at present, is the Gamtoos. Largely due to the findings emerging from the present study, *Myxus capensis* has recently been included in the *Red Data* list of endangered fish species in South Africa (Skelton 1983).

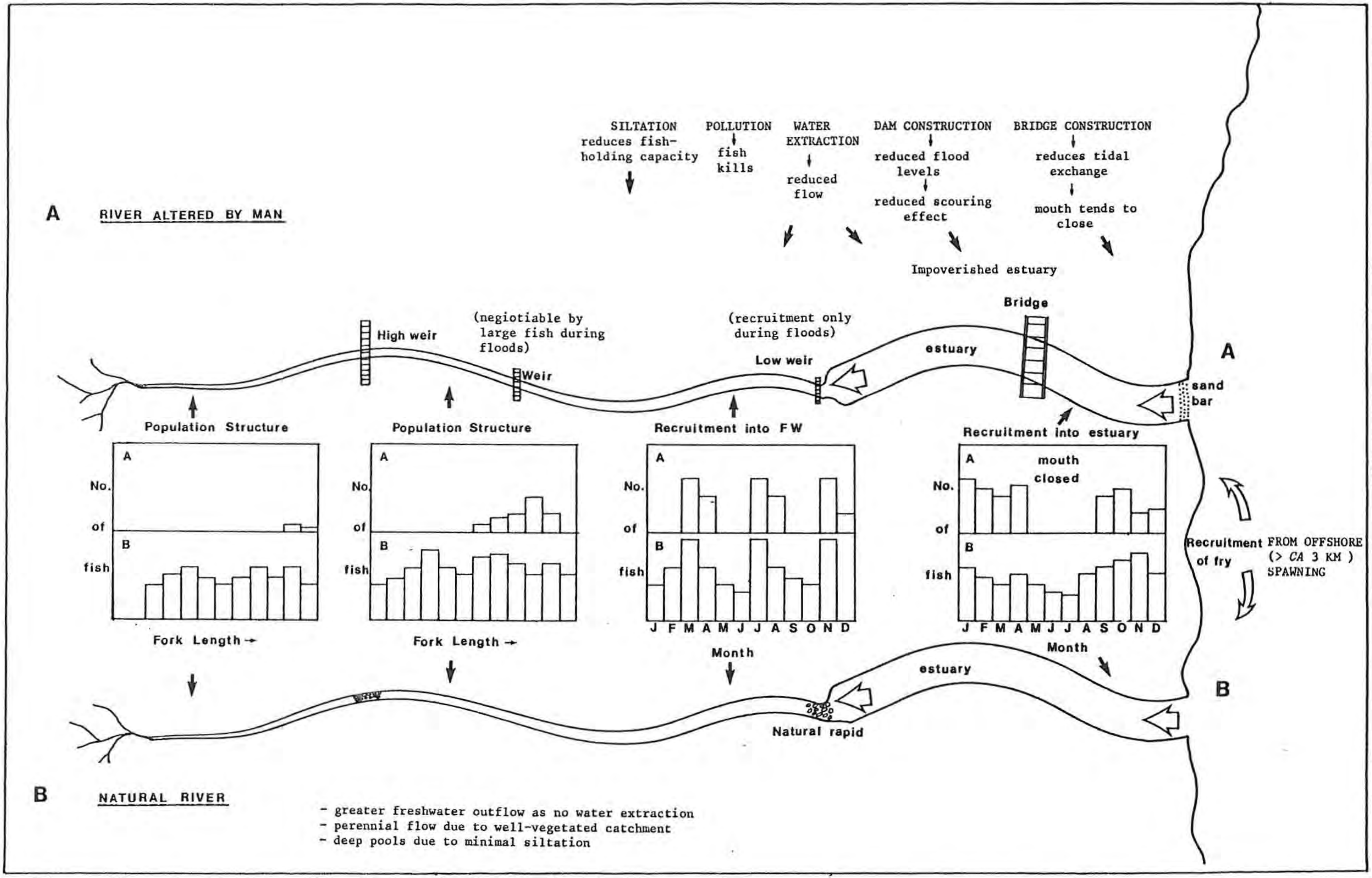


Figure 89. Factors affecting the survival, distribution and abundance of *Myxus capensis* in rivers in the eastern Cape.

CHAPTER 8. FINAL DISCUSSION

LIFE HISTORY STRATEGY

Myxus capensis fry migrate into fresh water at a small size (15 - 40 mm FL) and usually return to an estuarine or marine environment only when the maximum size is attained and large energy reserves necessary for spawning purposes have been accumulated. Virtually all growth and production therefore takes place in the freshwater feeding areas. Movement into fresh water appears to be a typical feeding migration designed to increase abundance via changes in growth, fecundity or survival (Northcote 1978).

Life history tactics of *Myxus capensis*, such as a sex ratio in favour of females and a marked predominance of females in the larger size classes due to their faster growth, larger ultimate size and longer time spent in fresh water (Table 70), are typical of migratory fish species. The migratory part of the population of anadromous species such as salmon (*Salvelinus sp.*) and *Barbus brachycephalus* is often dominated by female fish (Nikolskii 1969). Northcote (1978), in a review on migratory strategies of fish, cites many examples of anadromous fish species, particularly migratory salmonids, in which the females migrate to a greater degree, spend more time in the rich feeding habitats and are larger than the males. In the catadromous freshwater eels, both in southern Africa (Jubb 1964) and in Europe (Tesch 1977), females have a stronger migratory urge, grow faster, reach a larger ultimate size and remain in fresh water longer than males. As postulated for *Myxus capensis*, Northcote (1978) considers that these tactics in migratory species increase the population fecundity by maximizing egg production.

Before man-induced changes to the environment, *Myxus capensis* flourished in spite of the constraints associated with the spatial separation of the freshwater feeding and marine spawning areas in a region in which highly variable river flow is the norm. This species appears to have adapted its life history style in a number of ways to overcome these constraints and successfully exploit the freshwater environment. These tactics, which were discussed in earlier chapters, are summarized in Table 70. Their adaptive significance is emphasized when comparisons are made with *Mugil cephalus*, which is not specialized to exploit freshwater habitats and is therefore not

Table 10. Life history tactics of *Myxus capensis* which may enhance size, fecundity and abundance in freshwater reaches of eastern Cape rivers.

	Tactic of *Myxus capensis*	Possible adaptive significance for *Myxus capensis*	Tactic of *Mugil cephalus*
1)	Reduced gonadal development in freshwater, advanced development only once in estuary.	- improved migratory ability; reduces risk of energy wastage if ripe fish are isolated in freshwater reaches.	- advanced gonadal development in fresh water, fully ripe specimens reported in fresh water elsewhere.
2)	Downriver spawning migration at large size and when sufficient energy reserves have been accumulated.	- enables full exploitation of food reserves available in fresh water to increase growth and hence fecundity.	- in most rivers migrate downriver as sub-adults.
3)	Year-round spawning & recruitment.	- buffering effect against short-term adverse conditions for egg/larval survival, recruitment into estuary and, particularly, recruitment into fresh water; enables infrequent floods to be used at any time for downriver spawning migration.	- seven-month spawning season, with pronounced 2 - 3 month peak.
4)	Sex ratio in favour of females, predominance of females in large size classes.	- maximizes egg production and ensures high population fecundity.	- sex ratio in fresh water in favour of males.
5)	Relatively wide range in size and age (2+ to 5+ years) at first sexual maturity.	- insurance against consecutive poor years due to isolation in fresh water during droughts preventing breeding and recruitment.	- few fish older than 2+ in freshwater; nearly all spawning fish 2+ and 3+ years old.
6)	Relatively constant first year growth, possibly "fixed" upper growth limit.	- optimize superior upriver migratory ability of small mullet under low flow (normal) conditions.	- can drastically increase growth in in first year under favourable conditions.

subject to the same selection pressures.

The mechanisms involved in the selection of life history tactics in response to particular environmental conditions have stimulated a great deal of theoretical discussion, much of it condensed in the theories of r- and K-selection and bet-hedging (Stearns 1976). Briefly, r- selection is considered to operate in unstable and unpredictable environments when the population is subject to variable density-independent mortality rates. Typical components of an r- strategy include early maturity, small body size, high fecundity and high reproductive effort, semelparity (single reproduction in an organism's lifetime) and a short lifespan. K- selection, in contrast, is thought to operate in stable environments where mortality rates are more predictable and subject to density-dependent factors. Tactics such as late maturity, reproduction over several years (iteroparity), large body size, reduced reproductive effort, and long life span are considered to be characteristic of a K- strategist.

The theories of r- and K- selection, while useful in conceptualizing extremes in life history strategies, often have limited predictive value, particularly when applied to aquatic organisms (Pianka 1970). Many fish species do not show the life history tactics predicted by the theory, but often the reverse (Mann & Mills 1979). For example, where there is a large fluctuation in juvenile mortality and relatively stable adult mortality, Murphy (1968) proposed that selection will be for long life and iteroparity, i.e. K- rather than r- characteristics will be selected for. The important factor determining the adaptive response is the age-specificity of the mortality, whether density-dependent or density-independent (Schaffer 1974). For a semelparous organism with a widely fluctuating juvenile mortality, it may be advantageous for only a fraction of the adults to breed every year. *Myxus capensis* probably fits into this category and the wide range of age at first (and final) maturity and prolonged spawning season, is probably an adaptation to retain the advantages of iteroparity without sacrificing high individual fecundity. Similar advantages of bet-hedging traits have been postulated for Atlantic salmon (Murphy 1968; Mann & Mills 1979).

In nature, the numerous interacting life history tactics that are found in a species arise from the evolutionary trade-offs of costs versus benefits in the process of adaptation to its particular environment (Southwood 1977). The generalizations of the r- and K- selection theories in many instances do not possess the detail necessary to enable predictions, such as those listed in Table 70, to be made or to increase one's understanding of evolutionary adaptations. In a review of the evolution of life history traits, Stearns (1977) found that the predictions of available theories are not consistent with much of the evidence and states:

> "We do not yet have a general and reliable theory of life history evolution".

It may therefore be more profitable to seek alternative explanations based on a thorough understanding of the range of selective pressures operating on a species and the variety of possible adaptive responses available to the organism.

Myxus capensis is fairly common in most Natal estuaries (Blaber 1977), but is apparently scarce in the freshwater reaches of rivers (Crass 1964; Pike pers. comm. 1983). This indicates that conditions in fresh water in Natal may be relatively unfavourable for this species. Possible adaptive responses of *Myxus capensis* to the particular environmental conditions in Natal may be reflected in differences in life history styles between populations from Natal and the eastern Province. Further comparative work in this area would be valuable. By studying one species which exhibits variations in life history tactics in different environments we may gain a deeper understanding of the selection pressures causing an evolutionary trend (Mann & Mills 1979).

Variations in life history styles among adjacent populations of Atlantic salmon in North America are well documented and are considered to have adaptive significance (Schaffer & Elson 1975; Schaffer 1979). However, these local populations of Atlantic salmon usually spawn in their river of origin and are at least partly isolated genetically, a prerequisite for the evolution of different characteristics by natural selection.

The marine spawning of *Myxus capensis* argues against genetic isolation of populations from adjacent rivers. Evidence in support of a common gene pool incorporating populations from adjacent rivers was obtained during the recent (1982/1983) drought in the eastern Cape. In June 1983, *Myxus capensis* fry < 30 mm FL were captured at the heads of the Kromme, Baakens, Swartkops, Bushmans, Kowie and Chulumae estuaries, at least a year after the flow in these rivers had either stopped or been reduced to a mere trickle, which precluded downriver spawning migration. These fry were therefore probably the spawn of *Myxus capensis* from the Gamtoos and Great Fish rivers, neither of which stopped flowing during this period and in which adults are common in the upper estuarine areas (Marais 1983b; This study).

The substantial distance between eastern Cape and Natal estuaries (*ca* 250 km) may allow some degree of genetic isolation. Research on *Mugil cephalus* in Hawaii indicates that efficient isolating mechanisms may exist between adjacent populations. Peterson & Shehadeh (1971) analysed the variations in nuclear eye-lens proteins of *Mugil cephalus* from adjacent Hawaiian islands and found nearly complete genetic isolation in three sub-populations. Genetic isolation of the eastern Cape and Natal populations would allow them to become differentiated by means of natural selection. Further studies comparing life history data, and using the electrophoretic techniques of Peterson & Shehadeh (1971), are required to answer the important question of whether real differences exist between eastern Cape and Natal populations of *Myxus capensis*.

MANAGEMENT AND CONSERVATION CONSIDERATIONS

The specialized catadromous life history of *Myxus capensis* in the eastern Cape has made this species particularly vulnerable to man-induced changes in the freshwater environment. Of the different harmful changes discussed in Chapter 7, the construction of barriers to migration has had the most severe impact, and has been largely responsible for the inclusion of this species on the *Red Data* list of threatened fish species (Skelton 1983). The building of weirs or other barriers within this species natural range should therefore be viewed in a very serious light and should only be considered once the full biological consequences have been assessed.

Various proposals for the conservation of indigenous fish in southern Africa have been discussed by other authors (e.g. Crass 1969; Gaigher *et al.* 1980; Skelton 1983) and are applicable to *Myxus capensis* as well. The proposals outlined below are specifically aimed at the conservation and wise utilization of both *Mugil cephalus* and *Myxus capensis* in freshwater areas of the eastern Cape.

(i) *Translocation.*

A short-term solution, which is being carried out by conservation bodies at present, is the netting and translocation of mullet to points above barriers to migration. To avoid any possible genetic contamination (unlikely because of probable free flow of genes among local populations), fish from the same or adjacent river systems should be used for this purpose. An extension of this procedure is the stocking of farm dams in the catchment areas within its geographical range. The replacement of exotic predatory fish species (presently available to the public for angling purposes) with mullet, will have considerable conservation benefits.

(ii) *Fish ladders.*

The construction of fish ladders on man-made barriers to migration will be essential if *Myxus capensis* is to be restored to its previous status As the majority of existing barriers are relatively low (< 2 m) the construction of such fish-ladders should be both practically feasible and relatively inexpensive.

Fish ladders elsewhere have been designed mainly for use by large fish with better swimming ability and possibly different migratory behaviour compared to *Myxus capensis*. Knowledge of swimming performance of 0+ and 1+ year old *Myxus capensis* under a variety of conditions (e.g. water quality, temperature, light intensity etc.) will be needed in order to design a successful fish ladder for this species. The location of the barrier in relation to the estuary will also influence fish ladder design. For example, under natural condition, only small (15 - 40 mm FL) fish usually recruit from the estuary into freshwater, while the mean size of the migratory fish increases in relation to the distance upriver.

(iii) *Artificial propagation.*

The full potential of both mullet species for pond culture or fisheries purposes will only be realized when large-scale artificial propagation is carried out (Chapter 6). When the economic importance of both these mullet species are fully realized, the need for their conservation will be more widely appreciated. Artificial propagation will also benefit conservation programmes as large-scale restocking of rivers will be possible without the potential detrimental effects of netting wild populations.

The successful colonization of the freshwater reaches of eastern Cape rivers by *Myxus capensis* has depended upon its ability to adapt its life history in response to this unpredictable environment. Comparisons with closely related but more estuarine-dependent *Mugil cephalus* have given valuable insights into the possible adaptive significance of these life history tactics. This comparative approach has facilitated a better understanding of the selection pressures responsible for the development of such tactics. The knowledge gained of the life history of *Myxus capensis* has enabled proposals to be put forward for the utilization as well as for the conservation of this threatened species. The advantages associated with the life history strategy evolved by *Myxus capensis* should ensure that once the factors causing their decline in eastern Cape rivers have been removed, this species will have the ability to re-establish itself in its improved habitat.

REFERENCES

Abraham, B. (1963). A study of the oogenesis and egg resorption in mullets *Mugil cephalus* and *Mugil capito* in Israel. *Prog. tech. Pap. gen. Fish. Coun. Mediterr. 7* : 435 - 453.

Abraham, M., N. Blanc & A. Yashouv (1966). Oogenesis in five species of grey mullets (Teleostei : Mugilidae) from natural and landlocked habitats. *Israel J. Zool. 15* : 155 - 172.

Albertini-Berhaut, J. (1975). Biologie des stades juvéniles de Téléostéens Mugilidae *Mugil auratus* Risso 1810, *Mugil capito* Cuvier 1829 et *Mugil saliens* Risso 1810. III. Croissance linéaire et pondérali de *Mugil capito* dans le Golfe de Marseille. *Aquaculture 5* : 179 - 197.

Allanson, B.R. & J.D. van Wyk (1969). An introduction to the physics and chemistry of some lakes in northern Zululand. *Trans. R. Soc. S. Afr. 38* : 217 - 240.

Alm, G. (1959). Connection between maturity, size and age in fishes. *Institute of Freshwater Research, Drottningholm. 40* : 5 - 145.

Anderson, W.W. (1957). Early development, spawning, growth and occurrence of the silver mullet (*Mugil curema*) along the south Atlantic coast of the United States. *Fish. Bull. US Fish. Wildl. Serv. 57 (119)* : 397 - 414.

Anderson, W.W. (1958). Larval development, growth and spawning of striped mullet (*Mugil cephalus*) along the south Atlantic coast of the United States. *Fish. Bull. US Wildl. Serv. 58* : 501 - 519.

Apekin, V.S. & N.I. Vilenskaya (1978). A description of the sexual cycle and state of the gonads during the spawning migration of the striped mullet, *Mugil cephalus*. *J. Ichthyol. 18(3)* : 446 - 456.

Arnold, E.L. & J.R. Thompson (1958). Offshore spawning of the striped mullet, *Mugil cephalus* in the Gulf of Mexico. *Copeia (2)* 130 - 132.

Avanesov, E.M. (1972). Present spawning conditions of mullets (Genus *Mugil*) in the Caspian Sea. *J. Ichthyol. 12 (3)* : 419 - 425.

Bagenal, T.B. (1978). Aspects of fish fecundity. In *Ecology of freshwater fish production* (ed. S.D. Gerking). Blackwell, Oxford. pp. 75 - 101.

Bagenal, T.B. & F.W. Tesch (1978). Age and growth. In *Methods for assessment of fish production in fresh waters.* (ed. T.B. Bagenal). Blackwell, Oxford. pp. 101 - 136.

Bardach, J.E., J.H. Ryther & W.O. McLarney (1972). *Aquaculture: The Farming and husbandry of Freshwater and Marine Organisms.* Wiley Inter-Science, J. Wiley & Sons, London.

Bar-Ilan, M. (1975). Stocking of *Mugil capito* and *Mugil cephalus* and their commercial catch in Lake Kinneret. *Aquaculture 5* : 85 - 89.

Ben-Yami, M. (1981). Handling, transportation and stocking of fry. In *Aquaculture of grey mullet.* International Biological Programme 26. (ed. O.H. Oren). Cambridge University Press, Cambridge.

Benzie, V. (1968). Some ecological aspects of the spawning behaviour and early development of the common whitebait, *Galaxias maculatus attenuatus* (Jenys). *Proc. N.Z. ecol. Soc. 15* : 31 - 39.

von Bertalanffy, L. (1957). Quantitative laws in metabolism and growth. *Q. Rev. Biol. 32* : 217 - 231.

Beverton, R.J. H. & S.J. Holt (1957). On the dynamics of exploited fish populations. *Fishery Invest., Lond. (2), 19,* pp. 533.

Blaber, S.J.M. (1976). The food and feeding ecology of Mugilidae in the St Lucia Lake system. *Biol. J. Linn. Soc. 8* : 267 - 277.

Blaber, S.J.M. (1977). The feeding ecology and relative abundance of mullet (Mugilidae) in Natal and Pondoland estuaries. *Biol. J. Linn. Soc. 9* : 259 - 275.

Blaber, S.J.M. (1978). Fishes of the Kosi System. *Lammergeyer 24* : 28 - 41.

Blaber, S.J.M. (1980). The estuarine fishes of Maputaland. pp.198 - 203. In *Studies on the ecology of Maputaland.* (eds. M.N. Bruton & K.H. Cooper). Rhodes University, Grahamstown.

Blaber, S.J.M. & A.K. Whitfield (1976). Large-scale mortality of fish at St Lucia. *S. Afr. J. Sci. 72* : 218.

Blaber, S.J.M. & A.K. Whitfield (1977). The feeding ecology of juvenile mullet (Mugilidae) in south-east African estuaries. *Biol. J. Linn. Soc. 9 (3)* : 277 - 284.

Bograd, L. (1961). Occurrence of *Mugil* in the rivers of Israel. *Bull. Res. Counc. Isr. 93 (7)* : 169 - 190.

Bok, A.H. (1979). The distribution and ecology of two mullet species in some freshwater rivers in the Eastern Cape, South Africa. *J. Limnol. Soc. sth. Afr. 5 (2)* : 97 - 102.

Bok, A.H. (1980). Freshwater mullet in the Eastern Cape. *Eastern Cape Naturalist 69* : 12 - 14.

Bond, G.W. (1946). A geochemical survey of the underground water supplies of the Union of South Africa. *Mem. geol. Surv. Un. S. Afr. 41* : pp. 208.

Branch, G.M. & J.R. Grindley (1979). Ecology of southern African estuaries. Part XI. Mngazana: a mangrove estuary in Transkei. *S. Afr. J. Zool. 14* : 149 - 170.

Breder, C.M. (1940). The spawning of *Mugil cephalus* on the Florida West Coast. *Copeia 2* : 138 - 139.

Breder, C.M. & D.E. Rosen (1966). *Modes of reproduction in fishes.* T.F.H. Publications, Jersey City. pp. 941.

Bregazzi, P.R. & C.R. Kennedy (1980). The biology of pike, *Esox lucius* L., in a southern eutrophic lake. *J. Fish. Biol. 17* : 19 - 112.

Brett, J.R. & N.R. Glass (1973). Metabolic rates and critical swimming speeds of sockeye salmon, *Oncorhynchus nerka*, in relation to size and temperature. *J. Fish. Res. Bd. Can. 30* : 379 - 387.

Broadhead, G.C. (1953). Investigations of the black mullet, *Mugil cephalus* L., in northwest Florida. *Florida Bd. Conserv. Tech. Ser., 7* : 1 - 33.

Broadhead, G.C. (1958). Growth of the black mullet (*Mugil cephalus* L) in west and northwest Florida. *Florida Bd. Conserv. Tech. Ser. 25* : 1 - 29.

Bromhall, J.D. (1954). A note on the reproduction of the grey mullet, *Mugil cephalus* Linnaeus. *Hong Kong Univ. Fish. Jour. (1)* : 19 - 34.

Brooks, P.M. & B.D. Gardner (1980). Effect of cattle dip containing toxaphene on the fauna of a South African river. *J. Limnol. Soc. sth. Afr. 6 (2)* : 113 - 118.

Brownell, C.L. (1979). Stages in the early development of 40 marine fish species with pelagic eggs from the Cape of Good Hope. *Ichthyol. Bull. Rhodes Univ. 40* : 1 - 84.

Brulhet, J. (1975). Observations on the biology of *Mugil cephalus ashentensis* and the possibility of its aquaculture on the Mauritanian coast. *Aquaculture 5* : 271 - 281.

Brusle, J. (1981). Sexuality and biology of reproduction in grey mullets. In *Aquaculture of grey mullets.* International Biological Programme 26. (ed. O.H. Oren). Cambridge University Press, Cambridge.

Bruton, M.N. (1979). The food and feeding behaviour of *Clarias gariepinus* (Pisces : Clariidae) in Lake Sibaya, South Africa, with emphasis on its role as a predator of cichlids. *Trans. zool. Soc. Lond. 35* : 47 - 114.

Bruton, M.N. & C.C. Appleton (1975). Survey of Mgobezeleni lake-system in Zululand, with a note on the effect of a bridge on the mangrove swamp. *Trans. R. Soc. S. Afr. 41 (3)* : 283 - 294.

Bruton, M.N., G. Wilson & C. Musil (1978). Environmental impact assessment: Proposed Umfolozi dams on Lake Teza. Unpublished report to Natal Parks Board. pp. 10.

Caldwell, D.K. & W.W. Anderson (1959). Offshore occurrence of larval silver mullet, *Mugil curema*, in the western Gulf of Mexico. *Copeia (3)* : 252 - 253.

Cambray, J.A. (1982). The life history strategy of a minnow, *Barbus anoplus* in a man-made lake. Unpublished M.Sc. Thesis. Rhodes University, Grahamstown. pp. 235.

Cech, J.J. & D.E. Wohlschlag (1975). Summer growth depression in the striped mullet, *Mugil cephalus* L. *Contrib. Mar. Sci. 19* : 91 - 100.

Chan, E.H. & T.E. Chua (1980). Reproduction in the greenback grey mullet, *Liza subviridis* (Valenciennes, 1836). *J. Fish. Biol. 16* : 505 - 519.

Chen, T.P. (1976). Aquacultural practices in Taiwan. Fishing News Books Limited, England.

Chervinski, J. (1976). Growth of the golden grey mullet (*Liza aurata* (Risso) in saltwater ponds during 1974. *Aquaculture 7* : 51 - 57.

Ching, C.V. (1977). Studies on the small grey mullet *Liza malinoptera* (Valenciennes). *J. Fish. Biol. 11* : 293 - 308.

Christensen, M.S. (1980). Sea-surface temperature charts for Southern Africa. *S. Afr. J. Sci. 76* : 541 - 546.

Chubb, C.F., I.C. Potter, C.J. Grant, R.C.J. Lenanton & J. Wallace (1981). Age structure, growth rates and movements of sea mullet, *Mugil cephalus* L., and yellow-eye mullet, *Aldrichetta forsteri* (Valenciennes), in the Swan-Avon River System, Western Australia. *Aust. J. Mar. Freshwater Res. 32* : 605 - 628.

Chutter, F.M. (1969). The effects of silt and sand on the invertebrate fauna of streams and rivers. *Hydrobiologia 34* : 57 - 76.

Chutter, F.M. (1973). An ecological account of the past and future of South African rivers. *News Lett. Limnol. Soc. sth. Afr. 21* : 22 - 24.

Cloern, J.E. & F.H. Nichols (1978). A von Bertalanffy growth model with a seasonally varying coefficient. *J. Fish. Res. Bd. Can. 35* : 1 479 - 1 482.

Crass, R.S. (1964). *Freshwater fishes of Natal.* Shuter & Shooter, Pietermaritzburg. pp. 167.

Crass, R.S. (1969). The effects of land use on freshwater fish in South Africa, with particular reference to Natal. *Hydrobiologia 34* : 38 - 56.

Day, J.H. (1981). *Estuarine ecology with particular reference to southern Africa.* Cape Town. A.A. Balkema. pp. 411.

De Silva, S.S. & E.I.L. Silva (1979). Biology of young grey mullet, *Mugil cephalus* L., populations in a coastal lagoon in Sri Lanka. *J. Fish. Biol. 15* : 9 - 20.

De Villiers, G. (1976). Exploitation of Harders along Southern African Shores. The South African Shipping News and Fishing Industry Review : May 1976.

Dyer, R.A. (1937). The vegetation of the divisions of Albany and Bathurst. *Botanical Survey Memoir No. 17.* Government Printer, Pretoria. pp. 139.

Eckstein, B. (1975). Possible reasons for the infertility of grey mullets confined to fresh water. *Aquaculture 5* : 9 - 17.

Eisawy, A.M., M.M. Ishak & A. Hamza (1974). Experimental rearing of of two mullet species *Mugil cephalus* and *Mugil capito* in Egyptian fish farms. *Bull. Inst. Ocean Fish. A.R.E. 4* : 57 - 96.

El-Maghraby, A.M., M.T. Hashem & H.M. El- Sedfy (1974). Species composition and distribution of the mullet fry in Lake Borollus. *Bull. Inst. Ocean Fish. A.R.E. 4* : 3 - 31.

El-Zarka, S. & F. Kamel (1965). Mullet fry transportation and its contribution to the fisheries of inland brackish lakes in the United Arab Republic. *Proc. gen. Fish. Coun. Medit.*, *8* : 209 - 226.

Erman, F. (1959). Observations on the biology of the common grey mullet (*Mugil cephalus*). *Proc. gen. Fish. Coun. Medit. 5* : 157 - 169.

Everhart, W.H., A.W. Eipper & W.D. Youngs (1975). *Principles of fishery science.* Cornell University Press. Ithaca. pp. 288.

FAO (1981). Methods of collecting and analysing size and age data for fish stock assessment. FAO Fisheries Circular 736 : 1 - 100.

Finucane, J.H., L.A. Collins & L.E. Barger (1978). Spawning of the striped mullet *Mugil cephalus* in the northwestern Gulf of Mexico. *Northeast Gulf Sci. 2* : 148 - 150.

Gaigher, I.G. (1979). Overgrazing endangers fish species. *Afr. Wildlife 33* : 41.

Gaigher, I.G., H.H. Braak & C.T. Stewart (1978). The results of a survey of fishes of the Breede River, Bontebok National Park from 20 to 21 Jan. 1978. Internal Report. Cape Dept. of Nature and Environmental Conservation.

Gaigher, I.G., K.C.D. Hamman & S.C. Thorne (1980a) Possible adaptive significance of sex ratio and sexual differences in size at maturity in the Orange River Labeo, *Labeo capensis*. *J. Limnol. Soc. sth.Afr. 6 (1)* : 35 - 38.

Gaigher, I.G., K.C.D. Hamman & S.C. Thorne (1980b). The distribution, conservation status and factors affecting the survival of indigenous fishes in the Cape Province. *Koedoe 23* : 57 - 88.

Grant, C.J. & A.V. Spain (1975a). Reproduction, growth and size allometry of *Mugil cephalus* Linnaeus (Pisces : Mugilidae) from north Queensland inshore waters. *Aust. J. Zool. 23* : 181 - 201.

Grant, C.J. & A.V. Spain (1975b). Reproduction, growth and size allometry of *Valamugil scheli* (Forskal) (Pisces : Mugilidae) from north Queensland inshore waters. *Aust. J. Zool. 23* : 463 - 74.

Grant, C.J. & A.V. Spain (1975c). Reproduction, growth and size allometry of *Liza vaigiensis* (Quoy & Gaimard) (Pisces : Mugilidae) from north Queensland inshore waters. *Aust. J. Zool. 23* : 475 - 86.

Groenewald, A.A. van J. (1957). The results of a survey of the fish population of the Vaal River during the period April to December, 1956. Internal Report. Dept. of Nature Conservation, T.P.A Pretoria. pp. 120.

Hamman, R.L. (1981). Transporting endangered fish species in plastic bags. *Prog. Fish-Cult. 43 (4)* : 212 - 213.

Harden Jones, F.R. (1968). *Fish Migration.* Edward Arnold, London.

Harris, J.A. (1968). The yellow-eye mullet. Age structure, growth rate and spawning cycle of a population of yellow-eye mullet *Aldrichetta forsteri* (Cuv. & Val.) from Coorong Lagoon, South Australia. *Trans. R. Soc. South Austr. 92* : 37 - 50.

Harrison, A.D. & J.D. Agnew (1962). The distribution of invertebrates endemic to acid streams in the western and southern Cape Province. *Ann. Cape. Prov. (nat. Hist.) 2* : 273 - 291.

Hattingh, J., F. Le Roux Fourie & J.H.J. Van Vuren (1975). The transport of freshwater fish. *J. Fish. Biol. 7* : 447 - 449.

Helfrich, P. & P.M. Allen (1975). Observations on the spawning of mullet, *Crenimugil crenilabis* (Forskål), at Enewetak, Marshall Islands. *Micronesia 11 (2)* : 219 - 225.

Hendricks, L.J. (1961). The striped mullet *Mugil cephalus* L. *Fish. Bull, Calif. 113* : 95 - 103.

Heydorn, A.E.F. & K.L. Tinley (1980). Estuaries of the Cape. Part I. Synopsis of the Cape Coast. Natural features, dynamics and utilization. *CSIR Research Report 380*. pp. 97.

Heydorn, A.E.F. & J.R. Grindley (1982). Estuaries of the Cape. Part II. Synopsis of available information on individual systems. Report No. 10. Kowie (CSE 10). *CSIR Research Report 409*. pp. 58.

Hickling, C.F. (1970). A contribution to the natural history of the English grey mullets (Pisces : Mugilidae). *J. mar. biol. Ass. U.K. 50* : 609 - 633.

Hile, R. (1970). Body-scale relation and calculation of growth in fishes. *Trans. Am. Fish. Soc. 99* : 468 - 474.

Hoar, W.S. (1959). Endocrine factors on the ecological adaptation of fishes. In *Comparative Endocrinology* (ed. A. Gorbman). Wiley, New York. pp. 123.

Hynes, H.B.N., N.K. Kaushik, M.A. Lock, D.L. Lush, Z.S.J. Stocker, R.R. Wallace & D.D. Williams (1974). Benthos and allochthonous organic matter in streams. *J. Fish. Res. Bd. Can. 31* : 545 - 553.

Ishak, M.M., S.A. Abdel-Malek & M.M. Shafik (1982). Development of mullet fisheries (Mugilidae) in Lake Quarun, Egypt. *Aquaculture 27* : 251 - 260.

Jackson, P.B.N. (1979). Heritage of history : our freshwater fishes. *Afr. Wildlife 33* : 36 - 39.

Jacot Guillarmod, A. (1974). Vegetation. *Report on the Swartkops River basin, 2* : 1 - 82.

Johnson D.W. & E.L. McClendon (1970). Differential distribution of the striped mullet, *Mugil cephalus* Linnaeus. *Calif. Fish and Game 56 (2)* : 138 - 139.

Jubb, R.A. (1964). The eels of South African rivers and observations on their ecology. *Monographia Biol. 14* : 186 - 205.

Jubb, R.A. (1967). *Freshwater Fishes of Southern Africa.* A.A. Balkema, Cape Town.

Katopodis, C. (1977). Design of culverts for fish passage. Proc. 3rd National Hydrotechnical Conference, Quebec. pp. 949 - 971.

Kennedy, M. & P. Fitzmaurice (1969). Age and growth of Thick-lipped Grey Mullet *Crenimugil labrosus* (Risso) in Irish waters. *J. mar. biol. Ass. U.K. 49* : 683 - 699.

Kesteven, G.L. (1942). Studies in the biology of the Australian mullet. 1. Account of the fishery and preliminary statement of the biology of *Mugil dobula* Gunther. *Bull. Coun. scient. ind. Res., Melb. 157* : 1 - 147.

King, L.C. (1963). *South African Scenery*, third edition. Oliver and Boyd, London. pp. 308.

Kingsley, M.C.S. (1980). von Bertalanffy growth parameters. *Trans. Am. Fish. Soc. 109* : 252 - 253.

Kuo, C.M., Z.H. Shehadeh & K.K. Milisen (1973). A preliminary report on the development, growth and survival of laboratory reared larvae of the grey mullet, *Mugil cephalus* L. *J. Fish. Biol. 5* : 459 - 470.

Kuo, C., C.E. Nash & Z.H. Shehadeh (1974). A procedural guide to induce spawning in grey mullet (*Mugil cephalus* L). *Aquaculture 3* : 1 - 14.

Kurian, C.V. (1975). Mullets and mullet fisheries of India. *Aquaculture 5* : 114.

Lasiak, T.A. (1983). Aspects of the reproductive biology of the southern mullet, *Liza richardsoni*, from Algoa Bay, South Africa. *S. Afr. J. Zool. 18* : 89 - 95.

Lenanton, R.C.J. (1977). Aspects of the ecology of fish and commercial crustaceans of the Blackwood River estuary, Western Australia. *Fish. Res. Bull. West. Aust. No. 19.*

Lenanton, R.C.J. (1982). Alternative non-estuarine nursery habitats for some commercially and recreationally important fish species of south-western Australia. *Aust. J. Mar. Freshw. Res., 33* : 881 - 900.

Le Cren (1951). The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). *J. Anim. Ecol. 20* : 201 - 209.

Liao, I-C. (1975). Experiments on induced breeding of the grey mullet in Taiwan from 1963 to 1973. *Aquaculture 6* : 31 - 58.

Liao, I-C. (1981). Cultivation methods. In *Aquaculture of grey mullets.* International Biological Programme 26. (ed. O.H. Oren). Cambridge University Press, Cambridge.

Liao, I-C, Y-J Lu, T-C Huang & M-C Lin (1971). Experiments on the induced breeding of grey mullet, *Mugil cephalus* Linnaeus. *J C R R Fish. Ser. (11)* : 1 - 29.

Liao, I-C, C.S. Cheng, L.C. Tseng, M.Y. Lim, L.S. Hsieh & H.P. Chen (1972). Preliminary report on the mass propagation of grey mullets, *Mugil cephalus. J C R R Fish. Ser. (12)* : 1 - 14.

Linder D.R., K. Strawn & R.W. Luebke (1975). The culture of striped mullet (*Mugil cephalus* Linnaeus) in ponds receiving heated effluent from a power plant. *Aquaculture 5 (2)* : 151 - 161.

Louw, R.J. (1968). Internal report. Cape Dept. of Nature and Environmental Conservation.

Major, P.F. (1978). Aspects of estuarine intertidal ecology of juvenile striped mullet, *Mugil cephalus*, in Hawaii. *Fish. Bull., US. 76 (2)* : 299 - 314.

Mann, R.H.K. (1973). Observations on the age, growth, reproduction and food of the roach *Rutilus rutilus* (L.) in two rivers in southern England. *J. Fish. Biol. 5* : 707 - 736.

Mann, R.H.K. (1980). The growth and reproductive strategy of the gudgeon *Gobio gobio* (L.) in two hard-water rivers in southern England. *J. Fish. Biol. 17* : 163 - 176.

Mann, R.H.K. & C.A. Mills (1979). Demographic aspects of fish fecundity. In *Fish Phenology : anabolic adaptiveness in teleosts.* (ed. P.J. Miller). *Symp. zool. Soc. Lond. 44* : 161 - 177.

Marais, J.F.K. (1976). Comparative studies on the nutritional ecology of mullet in the Swartkops estuary. pp. 136. Thesis. University of Port Elizabeth, Port Elizabeth, S. Africa.

Marais, J.F.K. (1980). Aspects of food intake, food selection, and alimentary canal morphology of *Mugil cephalus* (Linnaeus, 1758), *Liza tricuspidens* (Smith, 1935), *L. richardsoni* (Smith 1846), and *L. dumerili* (Steindachner, 1869). *J. Exp. Mar. Biol. Ecol., 44 (2 - 3)* : 193 - 209.

Marais, J.F.K. (1981). Seasonal abundance, distribution and catch per unit effort by gill nets of fishes in the Sundays estuary. *S. Afr. J. Zool. 16* : 144 - 150.

Marais, J.F.K. (1982). The effects of river flooding on the fish populations of two Eastern Cape estuaries. *S. Afr. J. Zool 17* : 96 - 104.

Marais, J.F.K. (1983a). Seasonal abundance, distribution and catch per unit effort of fishes in the Krom estuary, South Africa. *S. Afr. J. Zool. 18 (2)* 96 - 102.

Marais, J.F.K. (1983b). Fish abundance and distribution in the Gamtoos estuary with notes on the effect of floods. *S. Afr. J. Zool. 18 (2)* : 103 - 109.

Marais, J.F.K. & T. Erasmus (1977). Chemical composition of alimentary canal contents of mullet (Teleostei : Mugilidae) caught in the Swartkops estuary near Port Elizabeth, S.A. *Aquaculture 10 (3)* : 263 - 273.

Marais, J.F.K. & D. Baird (1980). Seasonal abundance, distribution and catch per unit effort of fishes in the Swartkops estuary. *S. Afr. J. Zool. 15* : 66 - 71.

Masson, H. & J.F.K. Marais (1975). Stomach content analysis of mullet from the Swartkops Estuary. *Zoologica Africana 10 (2)* : 193 - 207.

McDowall, R.M. (1978). *New Zealand Freshwater Fishes.* Heinemann, Auckland. pp. 230.

Melville-Smith, R. (1981). The ichthyoplankton of the Kromme River estuary. *S. Afr. J. Zool. 16* : 71 - 72.

Melville-Smith, R. & D. Baird (1979). Abundance, distribution and species composition of fish larvae in the Swartkops Estuary, Port Elizabeth. *S. Afr. J. Sci. 75 (12)* : 564.

Miller, P.J. (1979). Adaptiveness and implications of small size in teleosts. In *Fish Phenology : anabolic adaptations in teleosts.* (ed. P.J. Miller). *Symp. zool. Soc. Lond. 44* : 263 - 306.

Mires, D. (1970). Preliminary observations on the effects of salinity and temperature changes in *Mugil capito* fry. *Bamidgeh 22* : 19 - 24.

Mires, D., S. Shilo & Y. Shak (1975). Further observations on the effects of salinity and temperature changes on *Mugil cephalus* fry. *Aquaculture 5* : 110.

Murphy, G.I. (1968). Pattern in life history and the environment. *Am. Nat. 102* : 390 - 404.

Nash, C.E., C.M. Kuo & S.C. McConnel (1974). Operational procedures for rearing larvae of the grey mullet (*Mugil cephalus* L.). *Aquaculture 3* : 15 - 24.

Nash, C.E. & C.M. Kuo (1975). Hypotheses for problems impeding the mass propagation of grey mullet and other finfish. *Aquaculture 5 (2)* : 119 - 134.

Nash, C.E. & R.S. Koningsberger (1981). Artificial propagation. In *Aquaculture of grey mullets.* International Biological Programme 26. (ed. O.H. Oren). Cambridge University Press, Cambridge.

Nikolskii, G.V. (1961). *Special Ichthyology.* Translated from Russian. Israel Programme for Scientific Translations. pp. 538.

Nikolskii, G.V. (1963). *The Ecology of fishes.* Academic Press. London. pp. 352.

Nikolskii, G.V. (1969). *Theory of fish population dynamics as the biological background for rational exploitation and management of fishery resources.* (ed. R. Jones). Oliver and Boyd, Edinburgh. pp. 323.

Noble, R.G. & J. Hemens (1978). Inland water ecosystems in South Africa - a review of research needs. *S. Afr. Natl. Sci. Programmes Rep. 34 :* pp. 150.

Northcote, T.G. (1978). Migratory strategies and production in freshwater fishes. In *Ecology of freshwater fish production.* (ed. S.D. Gerking) pp. 326 - 359. Blackwell, Oxford.

Odum, W.E. (1970). Utilization of the direct grazing and plant detritus food chains by the striped mullet *Mugil cephalus.* In *Marine Food Chains.* (ed. J.H. Steele) pp. 220 - 240. Edinburgh : Univ. Calif. Press.

Oren, O.H. (1971). International Biological Programme : Co-ordinated studies on grey mullet. *Mar. Biol. 10* : 30 - 33.

Oren, O.H. (1975). Opening address IBP/PM international symposium on the grey mullets and their culture. *Aquaculture 5* : 3 - 8.

Oren, O.H. (1981). (Ed.) *Aquaculture of grey mullets.* International Biological Programme 26. Cambridge University Press, Cambridge.

Peterson, G.L. & Z.H. Shehadeh (1971). Subpopulations of the Hawaiian grey mullet *Mugil cephalus* : analysis of variations of nuclear eye-lens protein electropherograms and nuclear eye-lens weights. *Mar. Biol. 11* : 52 - 60.

Pianka, E.R. (1970). On "r" and "K" selection. *Am. Nat. 104* : 592 - 597.

Pike, T. (1979). Fish survey of pans on the Mfolozi River floodplain. Internal report. Natal Parks, Game and Fish Preservation Board, Pietermaritzburg, Natal, South Africa.

Pillay, T.V.R. (1954). The biology of the grey mullet, *Mugil tade* (Forskål), with notes on its fishery in Bengal. *Proc. Natl. Inst. Sci. India 20 (2)* : 187 - 217.

Pillay, S.R. (1972). A bibliography of the grey mullets, family Mugilidae. FAO *Fisheries Technical paper no. 109, Rome.*

Pooley, A.C. (1975). New fish records for Ndumu Game Reserve. *Lammergeyer 22* : 50 - 51.

Pruginin, Y., S. Shilo & D. Mires (1975). Grey mullet : a component in polyculture in Israel. *Aquaculture 5* : 291 - 298.

Purdom, C.E. (1979). Genetics of growth and reproduction in teleosts. In *Fish phenology : anabolic adaptiveness in teleosts.* (ed. P.J. Miller). *Symp. zool. Soc. Lond. 44* : 207 - 217.

Quignard, J.P. & H. Farrugio (1981). Age and growth of grey mullet. In *Aquaculture of grey mullets.* International Biological Programme 26. (ed. O.H. Oren). Cambridge University Press, Cambridge.

Randall, J.E. & H.A. Randall (1963). The spawning and early development of the Atlantic parrot fish, *Sparisoma rubripinne*, with notes on other scarid and labrid fishes. *Zoologica N:Y: 48* : 49 - 59.

Ratte, T.W. (1977). Age and growth of the mullet *Mugil richardsoni* (Smith) in the Berg River Estuary. Internal Report. Cape Dept. of Nature and Environmental Conservation.

Richards, C.E. & M. Castagna (1976). Distribution, growth and predation of juvenile white mullet (*Mugil curema*) in ocean-side waters of Virginia's eastern shore. *Chesapeake Sci. 18 (4)* : 308 - 309.

Ricker, W.E. (1975). *Computation and Interpretation of Biological Statistics of Fish Populations. Fish. Res. Bd. Can. Bull. 191.*

Schaffer, W.M. (1974). Optimal reproductive effort in fluctuating environments. *Am. Nat. 108* : 783 - 790.

Schaffer, W.M. (1979). The theory of life-history evolution and its application to Atlantic salmon. In *Fish Phenology : anabolic adaptations in teleosts.* (ed. P.J. Miller). *Symp. zool. Soc. London 44* : 307 - 326.

Schaffer, W.M. & P.F. Elson (1975). The adaptive significance of variations in life history among local populations in North America. *Ecology 56* : 577 - 590.

Scott, D.P. (1962). Effect of food quantity on fecundity of rainbow trout, *Salmo gairdneri. J. Fish. Res. Bd. Can. 19* : 715 - 731.

Scott, D.B.C. (1979). Environmental timing and the control of reproduction in teleost fish. In *Fish Phenology : anabolic adaptations in teleosts.* (ed. P.J. Miller). *Symp. zool. Soc. London 44* : 105 - 132.

Shehadeh, Z.H. & J.N. Ellis (1970). Induced spawning of striped mullet, *Mugil cephalus* L. *J. Fish. Biol. 2 (4)* : 355 - 360.

Shehadeh, Z.H., C.M. Kuo & K.K. Milisen (1973). Induced spawning of grey mullet *Mugil cephalus* L. with fractionated salmon pituitary extract. *J. Fish. Biol. 5* : 471 - 478.

Shireman, J.V. (1975). Gonadal development of striped mullet (*Mugil cephalus*) in fresh water. *Prog. Fish. Cult. 37* : 205 - 208.

Skelton, P.H. (1977). *South African Red Data Book - Fishes.* S.A. National Scientific Programmes Report No. 14.

Skelton, P.H. (1980). Aspects of freshwater fish biogeography in the eastern Cape. *The Eastern Cape Naturalist 24* : 17 - 22.

Skelton, P.H. (1983). Perspectives on the conservation of threatened fishes in southern Africa. *The Naturalist 27* : 3 - 12.

Smith, J.L.B. (1937). Fresh water fishes of the Eastern Cape Province. A guide to the Vertebrate Fauna of the Eastern Cape Province of South Africa. Part II Albany Museum, Grahamstown.

Smith, J.L.B. (1949). The sea fishes of Southern Africa; 1st ed. South Africa, Central News Agency. pp. 1 - 550.

Smith, J.L.B & M.M. Smith (1966). *Fishes of the Tsitsikama Coastal National Park.* Natn. Parks Bd. South Africa. pp. 161.

Southwood, T.R.E. (1977). Habitat, the templet for ecological strategies? *J. Anim. Ecol. 46* : 337 - 365.

Stearns, S.C. (1976). Life-history tactics : a review of the ideas. *Quart. Rev. Biol. 51* : 3 - 47.

Stearns, S.C. (1977). The evolution of life history traits : a critique of the theory and a review of the data. *A. Rev. Ecol. Syst. 8* : 145 - 171.

Suzuki, K. (1965). Biology of the striped mullet, *Mugil cephalus* Linn. 1. Food content of young. *Rep. Fact. Prefect. Univ. Mie. 5* : 295 - 305.

Sylvester, J.R. & C.E. Nash (1975). Thermal tolerance of eggs and larvae of Hawaiian striped mullet, *Mugil cephalus* L. *Trans. Am. Fish. Soc. 104* : 104 - 147.

Sylvester, J.R., C.E. Nash & C.R. Emberson (1975). Salinity and oxygen tolerances of eggs and larvae of Hawaiian striped mullet, *Mugil cephalus* L. *J. Fish. Biol. 7* : 621 - 629.

Tang, Y.A. (1964). Induced spawning of striped mullet by hormone injection. *Jap. J. Ichthyol. 12* : 23 - 28.

Tang, Y.A. (1975). Collection, handling and distribution of grey mullet fingerlings in Taiwan. *Aquaculture 5* : 81 - 84.

Tesch, F.W. (1971). Age and Growth. In *Methods of Assessment of Fish Production in Fresh Waters.* (ed. W.E. Ricker). IBP Handbook No. 3. Blackwell, London.

Tesch, F.W. (1977). *The Eel. Biology and management of anguillid eels.* Chapman & Hall, London. pp. 434.

Thakur, N.K. (1967). Studies on the age and growth of *Mugil cephalus* Linnaeus from the Mahanadi estuarine system. *Proc. Natl. Inst. Sci. India, Sect. B. (Biol. sci.) 33* : 128 - 143.

Thomson, J.M. (1951). Growth and habits of the sea mullet, *Mugil dobula*, Gunther, in Western Australia. *Aust. J. Mar. Freshw. Res. 2* : 193 - 225.

Thomson, J.M. (1955). The movement and migration of Mullet (*Mugil cephalus*). *Aust. J. Mar. Freshwater Res. 6* : 328 - 47.

Thomson, J.M. (1957). Interpretation of the scales of the yellow-eye mullet, *Aldrichetta forsteri* (Cuvier & Valenciennes) (Mugilidae) *Aust. J. Mar. Freshw. Res. 8* : 14 - 28.

Thomson, J.M. (1963). Synopsis of biological data on the grey mullet *Mugil cephalus* Linnaeus 1758. *C.S.I.R.O. Aust. Fish. Oceanogr. Fish. Synopsis No. 1.* pp. 66.

Thomson, J.M. (1966). The Grey Mullets. *Oceanogr. Mar. Biol. Ann. Rev. 4* : 301 - 335.

Tomasson, T. (1983). The biology and management considerations of abundant large cyprinids in Lake Le Roux, Orange River, South Africa. Ph.D. thesis. Rhodes University, Grahamstown. pp. 218.

Van der Elst, R.P. & J.H. Wallace (1976). Identification of the juvenile mullet of the east coast of South Africa. *J. Fish. Biol. 9* : 371 - 374.

Van der Horst, G. (1976). Aspects of the reproductive biology of *Liza dumerili* (Steindachner, 1869) (Teleostei : Mugilidae) with special reference to sperm. Ph.D. thesis, University of Port Elizabeth, South Africa. pp. 377.

Van der Horst, G. & T. Erasmus (1978). The breeding cycle of male *Liza dumerili* (Teleostei : Mugilidae) in the mouth of the Swartkops estuary. *Zoologica Africana 13 (2)* : 259 - 273.

Van der Horst, G & T. Erasmus (1981). Spawning time and spawning grounds of mullet with special reference to *Liza dumerili* (Steindachner, 1869). *S. Afr. J. Sci. 77* : 73 - 78.

Walford, L.A. (1946). A new graphic method of describing growth of animals. *Biol. Bull. mar. biol. Lab., Woods Hole 90* : 141 - 147.

Wallace, J.N. (1975a). The estuarine fishes of the East Coast of South Africa. I. Species composition and length distribution in the estuarine and marine environments. II. Seasonal abundance and migrations. *Invest. Rep. Oceangr. Res. Inst. 40* : 1 - 72.

Wallace, J.N. (1975b). The estuarine fishes of the East Coast of South Africa. Part III Reproduction. *Invest. Rep. oceanogr. Res. Inst. 41* : 1 - 48.

Wallace, J.N. & R.P. van der Elst (1975). The estuarine fishes of the East Coast of South Africa. Part IV. Occurrence of juveniles in estuaries. Part V. Biology, estuarine dependence and status. *Invest. Rep. Oceanogr. Res. Inst. 42* : 1 - 63.

Weather Bureau (1954). Climate of South Africa. Part 1. Climate Statistics (WB 19). The Government Printer, Pretoria.

Weather Bureau (1957). Climate of South Africa. Part 4. Rainfall Maps (WB 22). The Government Printer, Pretoria.

Weatherley, A.H. (1972). *Growth and ecology of fish populations.* Academic Press, London. pp. 293.

Webb, B.F. (1973). Fish populations of the Avon-Heathcote estuary. II. Breeding and gonad maturity. *New Zeal. J. Mar. Fresh. Res. 7* : 45 - 66.

Whitfield, A.K. (1980a). A quantitative study of the trophic relationships within the fish community of the Mhlanga estuary. *Est. coast. mar. Sci. 10* : 417 - 435.

Whitfield, A.K. (1980b). Distribution of fishes in the Mhlanga estuary in relation to food resources. *S. Afr. J. Zool. 15* : 159 - 165.

Whitfield, A.K. (1980c). Food chains in Lake St Lucia. In *Studies on the ecology of Maputaland.* (eds. M.N. Bruton & K.H. Cooper). Rhodes University, Grahamstown.

Whitfield, A.K. & S.J.M. Blaber (1978a). Distribution, movements and fecundity of Mugilidae at Lake St. Lucia. *Lammergeyer 26* : 53 - 63.

Whitfield, A.K. & S.J.M. Blaber (1978b). Resource segregation among iliophagous fish in Lake St Lucia, Zululand. *Env. Biol. Fish. 3 (3)* : 293 - 296.

Whitfield, A.K. & S.J.M. Blaber (1979). Predation on striped mullet (*Mugil cephalus*)by *Crocodylus niloticus* at St Lucia, South Africa. *Copeia 2* : 266 - 269.

Wooton, R.J. (1979). Energy costs of egg production and environmental determinants of fecundity in teleost fishes. In *Fish Phenology: anabolic adaptations in teleosts.* (ed. P.J. Miller). *Symp. zool. Soc. Lond. 44* : 133 - 159.

Yashouv, A. (1969). Preliminary report on induced spawning of *Mugil cephalus* reared in captivity in freshwater ponds. *Bamidgeh 21* : 19 - 24.

Yashouv, A. & A. Ben Shachar (1967). Breeding and growth of Mugilidae II. Feeding experiments under laboratory conditions with *Mugil cephalus* and *Mugil capito* Cuvier. *Bamidgeh 19* : 50 - 66.

APPENDIX 1.

BOK, A.H. (1979). The distribution and ecology of two mullet species in some freshwater rivers in the Eastern Cape, South Africa. *J. Limnol. Soc. sth. Afr. 5 (2)* : 97 - 102.

J. Limnol. Soc. sth. Afr.,
5(2), 97 - 102. 1979.

THE DISTRIBUTION AND ECOLOGY OF TWO MULLET SPECIES IN SOME FRESH WATER RIVERS IN THE EASTERN CAPE, SOUTH AFRICA

A.H. Bok

Department of Nature and Environmental Conservation,
Private Bag X1006, Grahamstown, 6140, South Africa

SUMMARY

Data on the relative abundance, penetration and breeding biology of the freshwater mullet *Myxus capensis* and the flathead mullet *Mugil cephalus* in the freshwater reaches of some Eastern Cape coastal rivers are described. The differences found between the two species indicate that *Myxus capensis* is more specialized for a catadromous life history in an unstable riverine environment. Evidence showing the importance of the freshwater phase for the latter species is given and the disastrous effects of the erection of barriers to fish movement are stressed.

INTRODUCTION

The freshwater mullet *Myxus capensis* (Valenciennes in C. and V., 1936) which is endemic to the east and south coast of South Africa from the Kosi Lake system (Blaber, 1978) to the Breede River (Gaigher *et al.*, 1978) is known to occur in the freshwater zone of Eastern Cape rivers (Smith, 1937). Reports have been received from fishermen and riparian landowners that this popular angling mullet was becoming scarcer in the Eastern Cape and had completely disappeared from a number of areas in local rivers (such as the upper reaches of the Kowie and Assegaai) where they had previously been plentiful. It was also reported that *Myxus capensis* may breed in fresh water. This finding, if substantiated, would have been important as all other members of the Mugilidae appear to spawn only in the marine environment (Ekstein, 1975; Wallace, 1975).

No previous biological study has been carried out on *Myxus capensis* and very little is known about its status, distribution and ecology. Therefore, an investigation on the occurrence and biology of this species was initiated in order to reveal possible reasons for the reported decline in numbers and range, as well as possible adaptations to a freshwater environment.

Initial fish sampling revealed the presence of the flathead mullet, *Mugil cephalus* (L., 1758) high up in the freshwater zone of the rivers studied. The study was broadened to include this fish, not only because no ecological study of this species in fresh water in South Africa has been reported in the literature, but because this cosmopolitan mullet is commonly found in seas and estuaries as well as in fresh water in most areas between latitudes 42^0 S and 42^0 N (Thomson, 1963) and has been widely studied. Ecological data on *Mugil cephalus* in local freshwater, riverine habitats was therefore also considered to have useful comparative value.

SURVEY METHODS

Adult fish

Monthly gill netting was carried out in the Kowie River over a three year period from March 1975 at a variety of sites from just seaward of the head of the estuary to the furthest point of penetration of the mullet. Normally one or two fleets of gill nets, each consisting of seven 10 m sections with stretched mesh sizes of 44, 50, 65, 75, 89, 100 and 115 mm joined in series, were set overnight across large pools. At irregular intervals the lower estuary was sampled using gill nets.

Irregular sampling with seine nets, fyke nets, rotenone and hook and line was also carried out. Data collected from the fresh, unpreserved fish included: fork length, individual fish mass (to the nearest gram), gonad mass (to nearest 0,1g) and the gonad maturity stage as modified from Kesteven by Bagenal and Braum (1968).

At approximately 3-4 months intervals, the Fish and Swartkops Rivers were sampled from just above the ebb and flow to the furthest known point of mullet penetration. Seine and gill nets were used in the Fish River, and only gill nets in the Swartkops River. The other rivers were sampled using gill nets.

Juvenile fish

Regular monthly netting using 2 mm and 5 mm (stretched mesh) minnow seine and dip nets was carried out at the Kowie ebb and flow. Normally netting took place in shallow water below a series of small rapids at the head of the estuary. The fish were placed into a 5-10% formalin solution and the fork lengths recorded at a later date. The smaller fish were identified with a microscope using the characteristic tooth structure of each species, as recommended by Van der Elst and Wallace (1976).

STUDY AREA

The work was restricted to a number of rivers situated in the Eastern Cape Coastal Area (Figure 1).

The most intensively studied river, the Kowie, arises in the hills around Grahamstown and its 22 km long estuary enters the sea at Port Alfred via a permanently open mouth. This is a "reservoir type" river consisting of large deep (>6 m) pools connected by shallow stony rapids. The banks of the Kowie are usually steep and thickly wooded which precluded the use of seine nets.

The Swartkops is also a "reservoir type" river and although larger, is physically similar to the Kowie. It enters the sea near Port Elizabeth via a 16 km long, permanently open estuary.

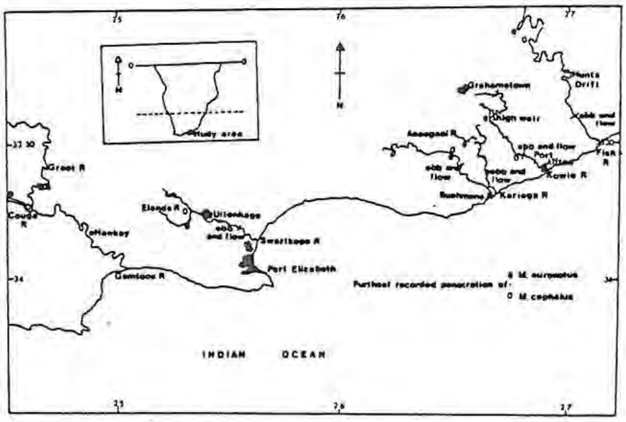


Figure 1. Map of the main study area on the south-east coast of South Africa showing the upstream penetration of *Mugil cephalus* and *Myxus capensis*.

0377-9688/79/020097-06$02.50

The Fish River, by far the largest river of the three arises in the Karroo and is typically a "sandbank" type river with large, usually shallow (<2 m), silt-laden pools.

RESULTS

Gonadal development of *Myxus capensis*.

In spite of year round regular sampling at various sites in the Kowie River over almost a 3 year period, no ripe *Myxus capensis* have been found in the freshwater reaches. Only a minimal degree of gonadal development was found in fishes from this area: the gonads change from a clear yellow to an opaque-orange state when small white ova are sometimes visible and the gonosomatic index (GSI = (mass of gonads/body mass)100) rises to over 0,5, with a recorded maximum of 0,73. Ovaries in the latter state correspond to the Stage III of the maturity scale of Kesteven modified by Bagenal and Braum (1968). As shown in Figure 2, the greatest number of female *Myxus capensis* in fresh water in the Kowie River with Stage III or "active" gonads were found in the autumn and winter months.

Very few adult female *Myxus capensis* were normally caught in the upper reaches of the Kowie estuary. However in April 1976, gill nets placed just below the head of the estuary during a flood, caught 14 adult female *Myxus capensis* of which over 70% were in Stage III (Figure 3). This indicated that a spawning run had been intercepted. The next month three adult female *Myxus capensis* were caught at this site; one with gonads in Stage III and the other two with well developed gonads in Stage IV and with GSI values of 1,27 and 1,43, which were by far the highest values recorded.

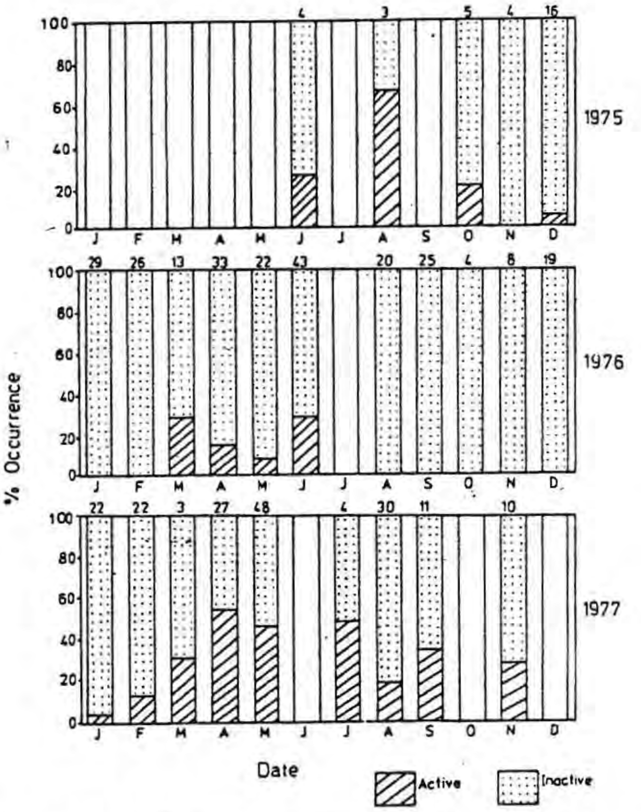


Figure 2. The percentage occurrence of adult female *Myxus capensis* in gill net catches in the Kowie River (upstream of ebb and flow) with "active" gonads. The number of adult female fish in each catch is given at the top of each column.

Recruitment of juveniles

The regular monthly netting for juvenile fish at the ebb and flow of the Kowie estuary, which is 22 km from the sea, (see Figure 1) showed that large numbers of juvenile *Myxus capensis* (10 to 40 mm fork length) are present almost all year round (Figure 4). A more intensive recruitment of the smaller fry appears to take place in the late winter and early summer months.

Mugil cephalus, in contrast to the extended recruitment period of *Myxus capensis*; was found to have a well-defined and relatively short recruitment period into the upper reaches of the Kowie River. The main

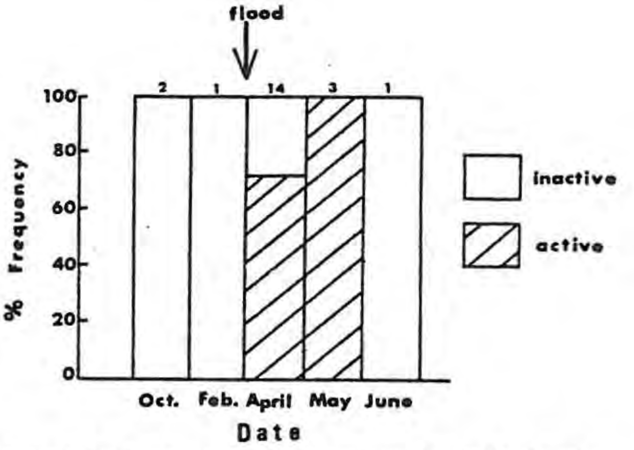


Figure 3. The percentage frequency of adult female *Myxus capensis* with "active" gonads caught just below the Kowie River ebb and flow before and after flood conditions (see text) from October 1975 to June 1976.

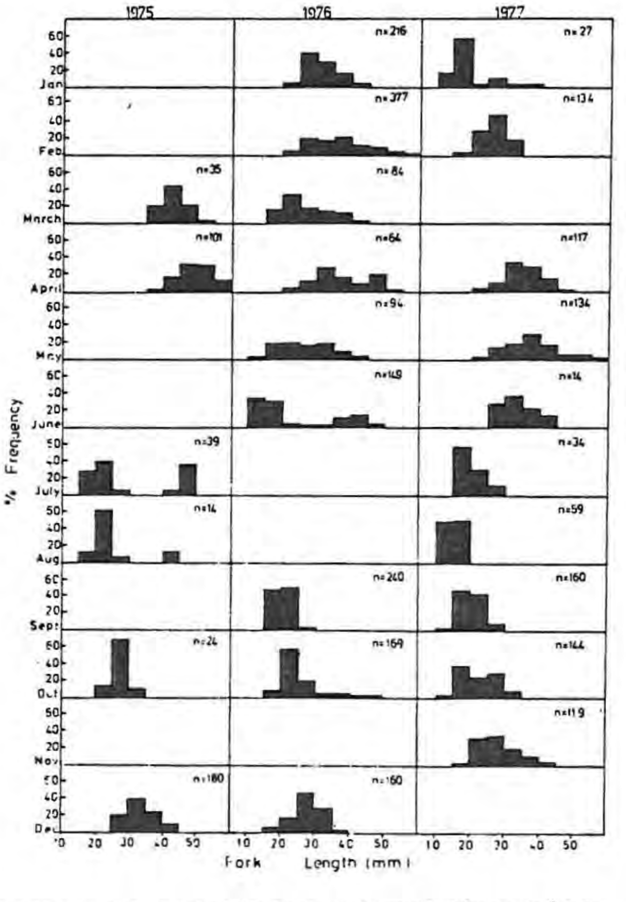


Figure 4. The length frequency distribution of juvenile *Myxus capensis* caught at the ebb and flow of the Kowie Estuary.

recruitment of fry (15 - 40 mm fork length) took place from July to October with smaller numbers in May, June and November (Figure 5).

Penetration into fresh water

The results of gill net catches in the saline and fresh waters of the Kowie River can be seen in Figure 6. *Myxus capensis* was not caught in the more saline parts of the lower estuary, but made up 9% of the mullet catches in the brackish water immediately below the tidal limit of the estuary, and was the most common (51%) in fresh water just above the tidal limit of the estuary.

Mugil cephalus showed the opposite trend and although by far the most abundant mullet (82% of mullet catch) in the upper reaches of the estuary, were not found in comparatively large numbers (48% of mullet catch) above the tidal limit. These mullet did not penetrate far into the freshwater reaches of the Kowie and in spite of extensive sampling over a three year period, no *Mugil cephalus* have been caught more than one km upstream of the head of the estuary.

A third mullet species, the southern mullet, *Liza richardsoni* (Smith) was found to penetrate in very limited numbers into completely fresh water immediately above the ebb and flow of the Kowie River. This mullet was the most abundant in catches in the lower estuary, making up 89% of the mullet catch; the numbers dropped markedly to 9% just below the ebb and flow and only 5 fish (or 1%) were caught in gill nets above the estuary. Due to the limited numbers caught in fresh water, little useful biological information was obtained. This species was not found in the freshwater reaches of any of the other rivers sampled.

The trend apparent in the Kowie River, namely that relatively more *Myxus capensis* than *Mugil cephalus* are found as the distance upstream of the estuary increases, is apparent in the catch records of both the Fish and Swartkops Rivers. Although *Mugil cephalus* penetrates further upstream in these two rivers than in the Kowie River, the numbers relative to *Myxus capensis* decreased markedly as the distance from the estuary increased (Figure 7 and 8). In the Fish River, *Mugil cephalus* makes up 58% of the mullet catch from the ebb and flow to Hunt's Drift (a distance of 27 km), but only 19% of the mullet catch above Hunt's Drift. In the Swartkops River, the proportion of *Mugil cephalus* dropped from 60% 2 km upstream of the ebb flow, to only 4% of the mullet catch in the Elands River tributary over 15 km upstream of the ebb and flow.

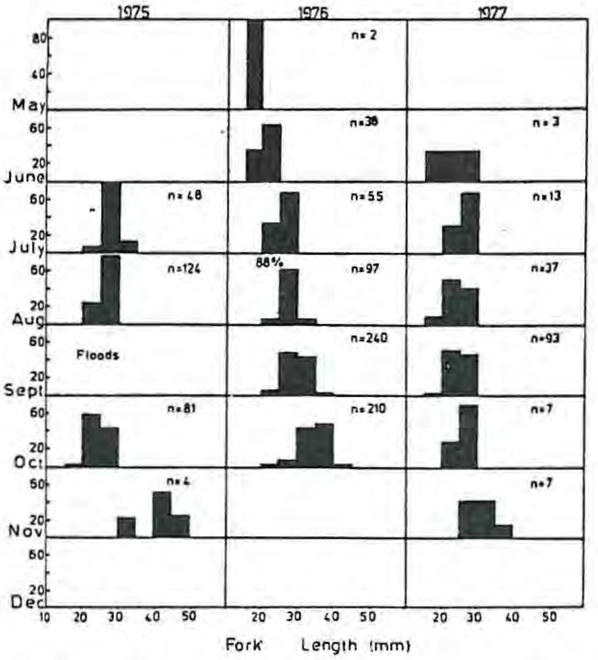


Figure 5. The length frequency distribution of juvenile *Mugil cephalus* caught at the ebb and flow of the Kowie estuary.

River System (tributary)	km from head of estuary *Myxus capensis*	 *Mugil cephalus*
Kowie	37	1
Swartkops (Elands)	26	19
Gamtoos (Groot)	135+	135+
Gamtoos (Couga)	120+	90+
Bushmans	15	15
Kariega (Assegaai)	44	-
Great Fish	110	77,5
Maitland	8	0,5
Keiskamma	17	-
Gqunube	18	-

Table 1. Upstream penetration of catadromous mullet species into freshwater in some Eastern Cape rivers. (+ distance from mouth)

The data collected to date on the penetration of these 2 mullet species into various Eastern Cape Rivers (Table 1), show that in most of the rivers sampled, *Myxus capensis* was found to penetrate further upstream. It can be seen that these mullet penetrate over 100 km upstream of the tidal influence of some rivers and further surveys may show this penetration to be even greater.

DISCUSSION

Recruitment of juveniles

The mullet fry captured at the ebb and flow of the Kowie estuary (particularly *Myxus capensis*) showed a strong upstream migratory urge and tended to accumulate immediately below any barrier inhibiting the upstream movement of fish. This indicates a point of origin downstream of the sampling area i.e. the lower estuary or sea. Further evidence that *Myxus capensis* do not breed in fresh water includes the finding that, in spite of regular sampling over a three year period in the freshwater reaches of the Kowie River, no sexually active fish have been found and also that small fry of this species have only been found in the estuary.

As *Mugil cephalus* larvae produced by artificial spawning techniques grew in the laboratory to a total lenght of 22,2 mm in 34 days (Liao *et al.*, 1971), the smaller fry of this species were probably caught at the Kowie ebb and flow about a month after hatching. As *Mugil cephalus* apparently migrates from estuaries to spawn in inshore waters at sea (Wallace (1975), it seems likely that spawning takes place close to the mouth of the Kowie and that effeicient use is made of tidal currents to supplement the limited swimming ability of the small fry in travelling upstream to the sampling site.

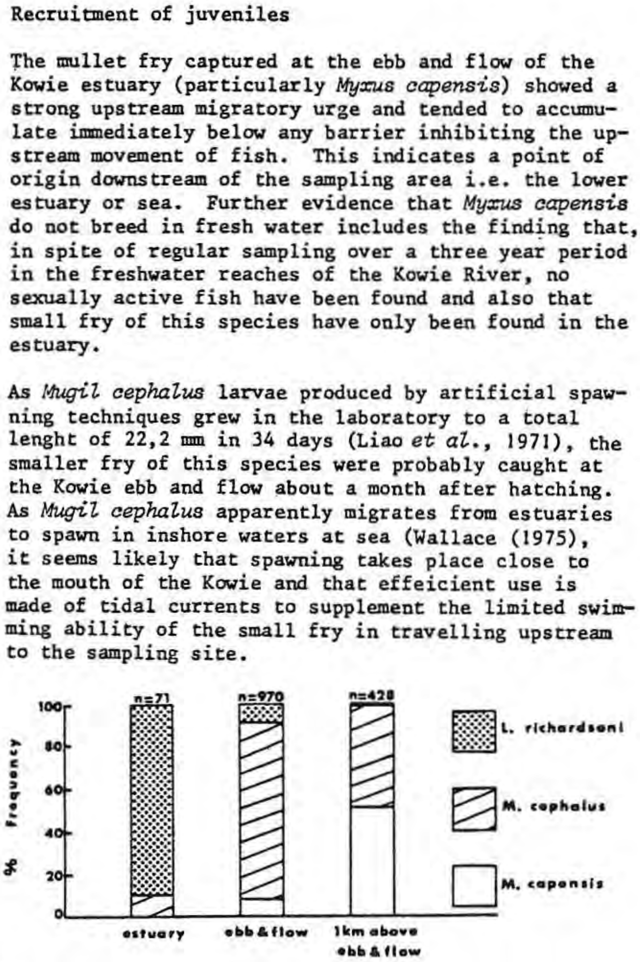


Figure 6. The relative frequency of the three euryhaline mullet species caught in gill nets in saline and fresh waters of the Kowie River.

The occurrence of large numbers of even smaller *Myxus capensis* (often below 15 mm fork length) at the Kowie ebb and flow, suggestes that they reach this area at a younger age than *Mugil cephalus*, or that the larval growth is slower. It seems likely that the spawning area of this species is also close to the river mouth, probably in the inshore marine environment beyond the breaker zone. As suggested by Wallace (1975), spawning in this area would allow advantage to be taken of the usually relatively stable environmental conditions that exist in this region, as well as ensuring early recruitment into the estuary. The only ripe-running *Myxus capensis* (a male, fork length of 276 mm) found to date, was netted in the surf zone 50 m from the mouth of the Fish River on 28.4.79 and supports the above proposal.

In Natal estuaries, recruitment of *Myxus capensis* of 2-5 cm total length is reported to occur from August to December (Wallace and Van der Elst, 1975) which corresponds to the intensive recruitment period into the upper reaches of the Kowie River. The recruitment period of *Mugil cephalus* into Natal estuaries, reported by the above authors to be mainly from June to October, is very similar to that found in the Kowie River. It therefore appears that this species spawns during the winter months which is slightly later than the spawning period from late summer to early winter, as reported by Thompson (1963) over most of its range.

The South-east coast region, the main habitat of *Myxus capensis*, has a fairly low rainfall (annual average 538 mm), with rain (and floods) liable to occur at nearly any time of the year (Weather Bureau, 1957). As the majority of the rivers in this area have small catchments, this results in short periods of high river flow (when fish movements are facilitated), which occur infrequently and at irregular times of the year. The extended juvenile recruitment and hence breeding period of *Myxus capensis* appears to be an adaptation to an unstable riverine environment. Not only can the infrequent periods of high river flow be used at most times of the year to migrate downstream into a saline environment for spawning, but the extended recruitment phase would reduce the chances of recruitment failure into fresh water due to short term adverse river conditions.

An extended period of juvenile recruitment of mullet such as *Liza macrolepis* (Smith, 1846), *Valamugil buchanani* (Bleeker, 1853) and *Valamugil cunnesius* (Valenciennes in C. and V., 1936) into Natal estuaries was found by Wallace and van der Elst (1975). These workers suggested that this would have a buffering action against recruitment failure due to floods or to the mouth being closed at certain times of the year. Suitable river flow at the time of recruitment is probably more critical for *Myxus capensis* as numerous obstacles, such as rapids, have to be negotiated during their upstream migration from the estuary into a suitable freshwater habitat. Often such barriers can only be negotiated by juveniles, with their limited swimming ability, at certain levels of river flow.

Gonadal development

Only a very limited number of adult *Mugil cephalus* (over 250 mm fork length) were caught in fresh water in the Kowie River and little data on sexual development was obtained. However, work elsewhere shows that this species reaches a fairly advanced stage of sexual development in fresh water. Shireman (1975) found female *Mugil cephalus* in fresh water in Louisiana, U.S.A. with GSI values of over 10 which appeared to be 'ripe and ready to spawn', while female fish with GSI values of up to 20 were reported in freshwater ponds in Israel (Yashouv, 1969). In spite of the energy loss involved, the resorption of ripe gonads in *Mugil cephalus* confined to fresh water appears to be a common occurrence (Shireman, 1975; Eckstein, 1975).

The limited sexual development of *Myxus capensis* in fresh water is in contrast to *Mugil cephalus* and appears to be a further adaptation to a catadromous life history. Due to the climatic conditions described above, there are extended periods when the rivers cease to flow or when the flow is so low that the fish are trapped in isolated pools for long periods. Under these conditions it is advantageous for gonad development to be inhibited so as to prevent the wasteful expenditure of energy in developing gonads which would possibly have to be resorbed at a later date. The results show that the gonads of female *Myxus capensis* develop further than Stage III only after the fish have migrated into an estuarine environment, when there should be a clear passage to the spawning area.

Penetration into fresh water

Mugil cephalus

The finding that *Mugil cephalus* is fairly common in fresh water in Eastern Cape rivers is in agreement with reports from other parts of Southern Africa. In the Western Cape, they have been found over 50 km upstream of the tidal influence in the Breede River (Gaigher *et al.*, 1978) and Berg River (Louw, 1968). On the east coast of southern Africa *Mugil cephalus* has been reported from Inyamiti Pan in the Ndumu Game Reserve some 100 km up the Maputo River (Pooley, 1975). and in Lake Teza situated on the Umzumduzi River about 40 km by river from its connection with the St Lucia Estuary (Bruton *et al*, 1978).

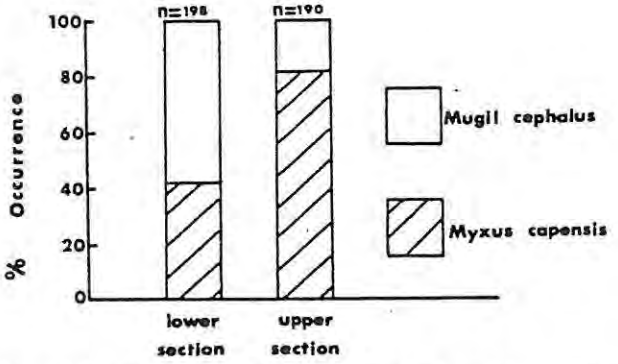


Figure 7. The percentage occurrence of *Mugil cephalus* and *Myxus capensis* in gill and seine net catches in two sections of the Fish River from June 1975 to February 1978. Lower section = from ebb and flow to Hunts Drift (27 km); Upper section = upstream of Hunts Drift.

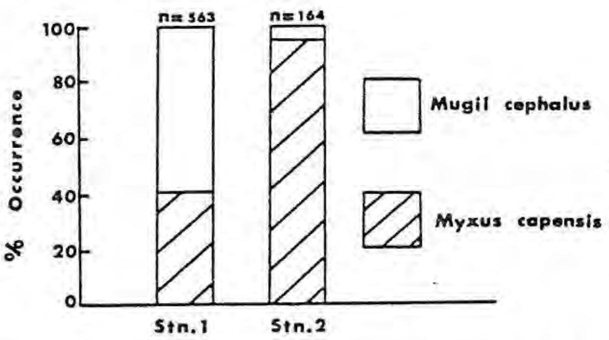


Figure 8. The percentage occurrence of *Mugil cephalus* and *Myxus capensis* in gill net catches in the Swartkops River (fresh water zone) from July 1975 to January 1978. Station 1 = 2 km upstream from ebb and flow; Station 2 = plus 17 km upstream of ebb and flow.

Myxus capensis

Although *Myxus capensis* has been reported to live in fresh water (e.g. Smith, 1937; Crass, 1964), data on the extent of its penetration up South African rivers in scanty. Bruton and Appleton (1975) found this mullet to be common in the Mgobezeleni stream and lake in Zululand some 2 km upstream from the head of the estuary. In the Western Cape, Gaigher *et al.* (1978) found *Myxus capensis* together with *Mugil cephalus* in gill nets in the Breede river below Swellendam over 50 km from the head of the estuary and it is notable that *Myxus capensis* comprised 79% of the total mullet catch from this area.

The finding that *Myxus capensis* appears to be restricted to the brackish areas and freshwater riverine zones in the Kowie river is supported by Marais (1976) for the Swartkops River who reported finding no *Myxus capensis* among about 7,000 mullet netted in the saline parts of the estuary. This is significant as the present study found this species to be common in fresh water above the Swartkops estuary.

Blaber (1977) found *Myxus capensis* to be common in Pondoland and Natal estuaries, but with a distinct preference for freshwater areas. This mullet is very rare in brackish lake St Lucia (Blaber, 1976) and he suggests that it is excluded by interspecific competition. It is probable that interspecific competition is an important reason for the virtual absence of *Myxus capensis* from the saline parts of Eastern Cape estuaries.

In summary, the ecological differences considered to have adaptive significance in relation to the catadromous behaviour of these two mullet species, as discussed above, are listed:

1. *Myxus capensis* has an extended juvenile recruitment period; *Mugil cephalus* has a short, well-defined juvenile recruitment period.
2. *Myxus capensis* shows very limited gonad development in fresh water; *Mugil cephalus* develops large ripe gonads in fresh water.
3. *Myxus capensis* is found to normally penetrate further upriver than *Mugil cephalus*.
4. The numbers of *Myxus capensis* relative to *Mugil cephalus* increase as the distance upstream from the estuary increases.
5. *Myxus capensis* occurs mainly in the freshwater zones of Eastern Cape rivers with small numbers in brackish water at the head of estuaries; *Mugil cephalus*, although found in fresh water, occurs in far greater numbers in all areas of estuaries and is common in the sea, occurring off riverless oceanic islands (Thomson, 1963).

The above differences indicates that, unlike *Mugil cephalus*, *Myxus capensis* has developed adaptations to a riverine environment and is specialized for a catadromous life history. The limited numbers found in the Eastern Cape estuaries indicate that a freshwater phase in its life-cycle is very important and may be obligatory under natural conditions.

However, the fact that adult fish must migrate downstream to breed in the estuary or sea and the juveniles need to migrate upstream into the riverine habitat once more, make these mullet particularly vulnerable to barriers preventing fish movement. The erection of weirs constitutes a real threat to this species. For example, there is evidence from landowners and Smith (1937) that *Myxus capensis* was common some 80 km upstream of the Kowie ebb and flow within living memory. This mullet's range reduction over the years can be traced to weirs built across the river bed and this study has found them to penetrate only half this distance up the Kowie to a weir some 40 km from the ebb and flow.

If, as the evidence suggests, the freshwater stage in the lifecycle of *Myxus capensis* is important and possibly obligatory, this raises important conservation implications. A barrier to fish movement will effectively and permanently cut off many miles of potential habitat for this catadromous fish. If the barrier is built at the ebb and flow of the estuary, it may even exterminate this species from the river system.

ACKNOWLEDGEMENTS

This work started when the author was attached to the J.L.B. Smith Institute of Ichthyology and I am indebted to the Director for research facilities and to staff members for their assistance, especially Mr P.B.N. Jackson for initiating the research and for useful advice throughout the study and Dr M.N. Bruton for critically reading the script. I would also like to thank the Director of the Cape Department of Nature and Environment Conservation of permission to publish this work. I am grateful to the numerous riparian farmers for their help and permission to fish on their property and to my wife, Jill, for help in the field.

REFERENCES

BAGENAL, T.B. & E. BRAUM (1968). Eggs and early life history. In: Methods of assessment of fish production in fresh waters. Ricker, W.E. (ed.). IBP Handbook 3, Blackwell, Oxford.

BLABER, S.J.M. & A.K. WHITFIELD (1976). Large scale mortality of fish at St Lucia. S. Afr. J. Sci. 72, 218.

BLABER, S.J.M. (1976). The food and feeding ecology of Mugilidae in the St Lucia Lake System. Biol. J. Linn. Soc. London 8, 267 - 277.

BLABER, S.J.M. (1977). The feeding ecology and relative abundance of mullet (Mugilidae) in Natal and Pondoland estuaries. Biol. J. Linn. Soc. London 9, 259 - 275.

BLABER, S.J.M. (1978). Fishes of the Kosi System. The Lammergeyer 24, 28 - 41.

BRUTON, M.N. & C.C. APPLETON (1975). Survey of Mgobezeleni Lake System in Zululand, with a note on the effect of a bridge on the Mangrove Swamp. Trans. R. Soc. S. Afr. 41, 283 - 294.

BRUTON, M.N., G. WILSON & C. MUSIL (1978). Environmental impact assessment: Proposed Umfolozi dams on Lake Teza. Unpublished Report to Natal Parks Board. 10 pp.

CRASS, R.S. (1964). Freshwater fishes of Natal. Shuter and Shooter, Pietermaritzburg.

ECKSTEIN, B. (1975). Possible reasons for the infertility of grey mullets confined to freshwater. Aquaculture 5, 9 - 17.

GAIGHER, I.G., H.H. BRAAK & C.T. STEWART (1978). Internal report, Cape Dept. of Nature and Environmental Conservation.

LIAO, I.C., Y.J. LU, T.L. HUANG & M.C. LIN (1971). Experiments on induced breeding of the grey mullet *Mugil cephalus* Linn. J.C.R.R. Fish Ser. 11, 1 - 23.

LOUW, R.J. (1968). Internal report, Cape Dept. of Nature and Environmental Conservation.

MARAIS, J.F.K. (1976). The nutritional ecology of mullets in the Swartkops Estuary. Ph.D. thesis, University of Port Elizabeth, Port Elizabeth.

MOORE, R.H. (1974). General ecology, distribution and relative abundance of *Mugil cephalus* and *Mugil curema* on the South Texas Coast. Contr. Mar. Sci. 18, 243 - 255.

SHIREMAN, J.V. (1975). Gonadal developement of striped mullet (*Mugil cephalus*) in freshwater. Prog. Fish Cult. 37, 205 - 208.

SMITH, J.L.B. (1937). Freshwater fishes of the Eastern Cape Province. A guide to the vertebrate fauna of the Eastern Cape Province of South Africa. Part II. Albany Museum, Grahamstown.

SMITH, J.L.B. (1949). The sea fishes of Southern

Africa. 1st ed. Central News Agency, Cape Town.

THOMSON, J.M. (1963). Synopsis of biological data on the grey mullet *Mugil cephalus* Linn., 1758. Commonw. Sci. Ind. Res. Org., Melbourne, Australia.

VAN DER ELST, R.P. & J.H. WALLACE (1976). Identification of the juvenile mullet of the east coast of South Africa. J. Fish Biol. 9, 371 - 374.

WALLACE, J.N. (1975). The estuarine fishes of the East Coast of South Africa. Part III. Reproduction. Invest. Rep. Oceanogr. Res. Inst. 41, 1 - 48.

WALLACE, J.N. & R.P. VAN DER ELST (1975). The estuarine fishes of the East Coast of South Africa. Part IV. Occurrence of juveniles in estuaries. Part V. Biology, estuarine dependence and status. Invest. Rep. Oceanogr. Res. Inst. 42, 1 - 63.

WEATHER BUREAU (1957). Climate of South Africa. Part 4. Rainfall Maps. The Government Printer, Pretoria.

YASHOUV, A. (1969). Preliminary report on induced spawning of *Mugil cephalus* (L) reared in captivity in freshwater ponds. Bamidgeh 21, 19 - 24.

KEY WORDS

Catadromous; *Mugil cephalus*; *Myxus capensis*; penetration into freshwater; Eastern Cape rivers; mullet.

APPENDIX 2.

BOK, A.H. (1980). Freshwater mullet in the Eastern Cape. *Eastern Cape Naturalist 69* : 12 - 14.

The Eastern Cape Naturalist No. 69. March 1980

Freshwater mullet in the Eastern Cape

A. Bok

Photograph by the author

Mullet in completely fresh water? In the Eastern Cape there are two species of mullet of marine origin (Family: Mugilidae) that are found high up in fresh water in coastal rivers. They are:

(i) The flathead mullet *(Mugil cephalus)*: these fish are more common in estuaries than in fresh water and are often seen leaping high out of the water when disturbed, especially by a strong light on a dark night. This species is very seldom caught on a hook and line in fresh water in the Eastern Cape which is a pity as they are known to reach over 7 kilograms. They are found all over the world in fresh and salt water and are very successfully used in freshwater fish farming in countries like Israel, Taiwan and India.

(ii) The freshwater mullet *(Myxus capensis* formerly *Mugil euronotus):* this species is mainly found in fresh water and in the very upper reaches of estuaries and has a very restricted range from Northern Zululand to about the Breede River. This mullet does not reach the the same size as the flathead mullet, with the usual adult size about 500–800 grams. The largest caught during the survey (in the Paul Sauer Dam on the Kouga River) weighed just over 2 kilograms and measured half a metre in length.

The two species can be easily distinguished as the freshwater mullet has a more pointed head and does not have the clear fatty tissue (adipose eyelids) that covers most of the eye of the flathead mullet. (As shown in figs. 1 and 2).

These mullet are not to be confused with the moggel *(Labeo umbratus)*, also called the mud-mullet or onderbek, which is a true freshwater fish found in large numbers in the bigger Eastern Cape rivers such as the Fish, Bushman's,

Weir on the Bloukrans River (tributary of the Kowie River), 40 kilometres upstream of the Ebb and Flow, found blocking upstream migration of mullet.

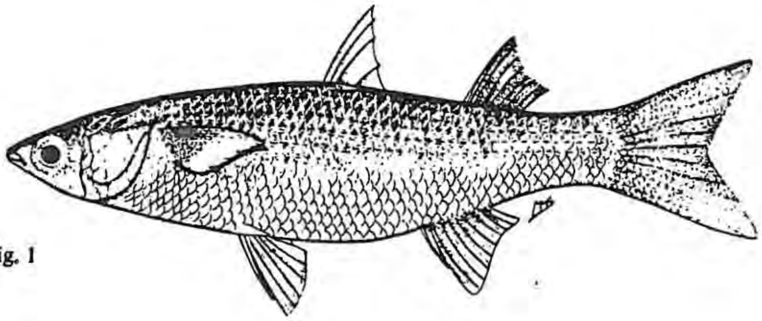


Fig. 1

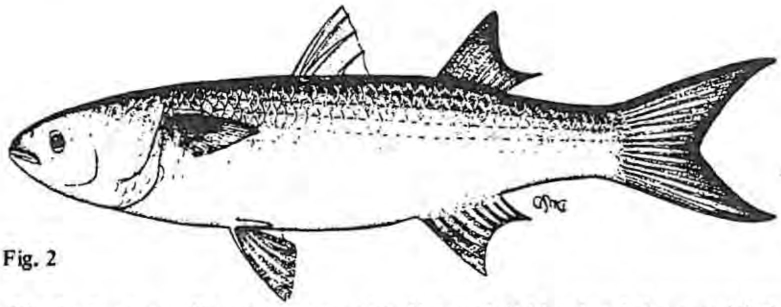


Fig. 2

Fig. 1 The freshwater mullet *(Myxus capensis)*. Note pointed head and absence of fatty tissue over the eyes

Fig. 2. The flathead mullet *(Mugil cephalus)*. Note blunt, flat head and fatty tissue over the eye (After Sea Fishes of Southern Africa by J.L.B. Smith)

Sundays and Gamtoos. This fish, which is seldom eaten by locals because its flesh is full of small Y-shaped bones, can easily be distinguished from the mullet described above as it has only one dorsal fin as opposed to the two of the mullet species.

Examination of stomach contents shows that the freshwater mullet feeds mainly on algae and detritus found on the river bottom, but (like most fish) is opportunistic and will also eat soft bodied insects, if available.

Research on the freshwater mullet was initiated in 1975 because:

(i) almost nothing was known of its biology and life history,

(ii) the numbers and range of these fish appear to have dwindled drastically over the last 10–20 years and

(iii) there were reports of these fish breeding in freshwater; an important finding if true, as all other members of the Mugilidae family spawn in a marine environment.

Investigations have shown that obstacles such as weirs and dams built across river beds have drastically interfered with the unusual migratory life history of these fish, cutting off many kilometres of suitable river areas. For example there is evidence that the freshwater mullet was common some 80 kilometres upstream of the Kowie ebb and flow within living memory. This mullet's range reduction over the years can be traced to weirs built across the river bed and this study has found them to penetrate only half this distance up the Kowie to a weir some 40 kilometres from the ebb and flow. (See photograph).

These mullet have a catadromous life-cycle (opposite to that of the anadromous salmon of North America) in that the adult fish do not become sexually active in freshwater, but after spending 3 to 6 years in rivers, migrate down into salt water via estuaries to become sexually mature. Spawning of mullet is thought to occur in the sea fairly close inshore, near the river mouths. The fact that full sexual maturity only takes place when the fish reach an estuarine environment is an important energy saving measure. Due to erratic rainfall along the Eastern Cape coast, the rivers often cease to flow for long periods and the fish are trapped in isolated pools in the rivers. Under these conditions it would be a waste of valuable energy for the fish to develop eggs (often forming up to 20–30 percent of body mass) which would have to be broken down and resorbed if downstream migration is impossible. There are obvious advantages for the sexual products to develop only on reaching a salt water environment when there should be a clear passage to the spawning site.

After hatching, the young fry move into estuaries and migrate upstream to colonize fresh water areas once more. Monthly sampling over a three year period at the Kowie ebb and flow has shown that shoals of small freshwater mullet fry between 15–40 mm in length migrate from the estuary into fresh water all year round with larger numbers usually in Spring. This implies an all year round spawning period as well. This is advantageous as it means that:

(i) the fish can take advantage of floods (that are liable to occur any time of the year) to migrate downstream to spawn at sea and

(ii) the extended period over which young fry make their way from the sea via the estuaries into fresh water would act as a buffer against short-term adverse river conditions such as the estuary mouth being closed, no river flow or heavy floods which could prevent upstream migration.

It is interesting to note that the fry of the flathead mullet on the other hand appear only for a relatively short period at the ebb and flow of the Kowie river, from May to November and also that this species, although also thought to breed at sea, reaches an advanced stage of sexual development in fresh water.

Further indications that the freshwater mullet has become more specialized than the flathead mullet in living in fresh water zones of the coastal rivers are:

(i) this species usually penetrates further upriver than the flathead mullet;

(ii) the numbers of the freshwater mullet relative to the flathead mullet increase as the distance upstream from the estuary increases;

(iii) while the freshwater mullet occurs mainly in the freshwater zones of Eastern Cape rivers with small numbers in brackish water at the head of the estuaries, the flathead mullet occurs in far greater numbers in the estuaries than in fresh water and is common in the sea, occurring off riverless oceanic islands. However, specialization has its drawbacks as it means that if the freshwater mullet is denied access to freshwater zones of rivers there could be disastrous consequences.

As the small fish migrating upriver have a limited swimming ability, a weir with a vertical drop of less than half a metre could prove impassable. The flathead mullet do not show the same persistance as the freshwater mullet when confronted by a weir at the ebb and flow of an estuary and return to the lower part of the estuary if access to fresh water is barred for more than a couple of months. The upstream migratory instinct of the freshwater mullet, on the other hand, appears to override all else. In rivers such as the Nahoon, Keiskamma and Kowie with weirs at or near the ebb and flow, one can see many thousands of these mullet 'trapped' by this instinct in confined and shallow stretches of river. Here thousands are eaten by predatory fish from the estuary (at high tide) and by the large numbers of herons, kingfishers, cormorants, hammerkops etc. that accumulate to take advantage of an easy meal.

In rivers with few large man-made barriers, for example the Gamtoos, both species have been caught 135 kilometres upriver from the mouth (in the Groot River tributary). In the Fish River, freshwater mullet have been caught at Double Drift and flathead mullet above Committees Drift, distances of 110 and 78 kilometres respectively from the head of the estuary.

Conservation measures being implemented at present include the netting of mullet below barriers and restocking into suitable areas above. This is a short-term and not very satisfactory solution. A far better long-term solution would be to construct fish-ladders on the offending weirs and to encourage the building of weirs designed to offer minimal resistance to upstream migrations. In the simplest form a fish-ladder consists of a series of steps or pools built from the top of the weir to the water below to enable the fish to jump from pool to pool and negotiate the barrier. These need not be too elaborate and if incorporated into the original design of a weir would add little to the total cost.

Future research will be aimed at finding the best design of such fish-ladders for use by the juvenile mullet in their upstream migrations. Riparian landowners, local authorities and Department of Water Affairs have reacted positively to these ideas. Hopefully in future years these mullet will once again become plentiful high up in our local rivers.

A. Bok,
Cape Department of Nature and Environmental Conservation
Private Bag 1006
Grahamstown. 6140