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THE LIFE HISTORY STRATEGY OF A MINNOW, *BARBUS ANOPLUS*, IN A MAN-MADE LAKE IN SOUTH AFRICA.

Dissertation

Submitted in Partial Fulfilment of the

Requirements for the Degree of

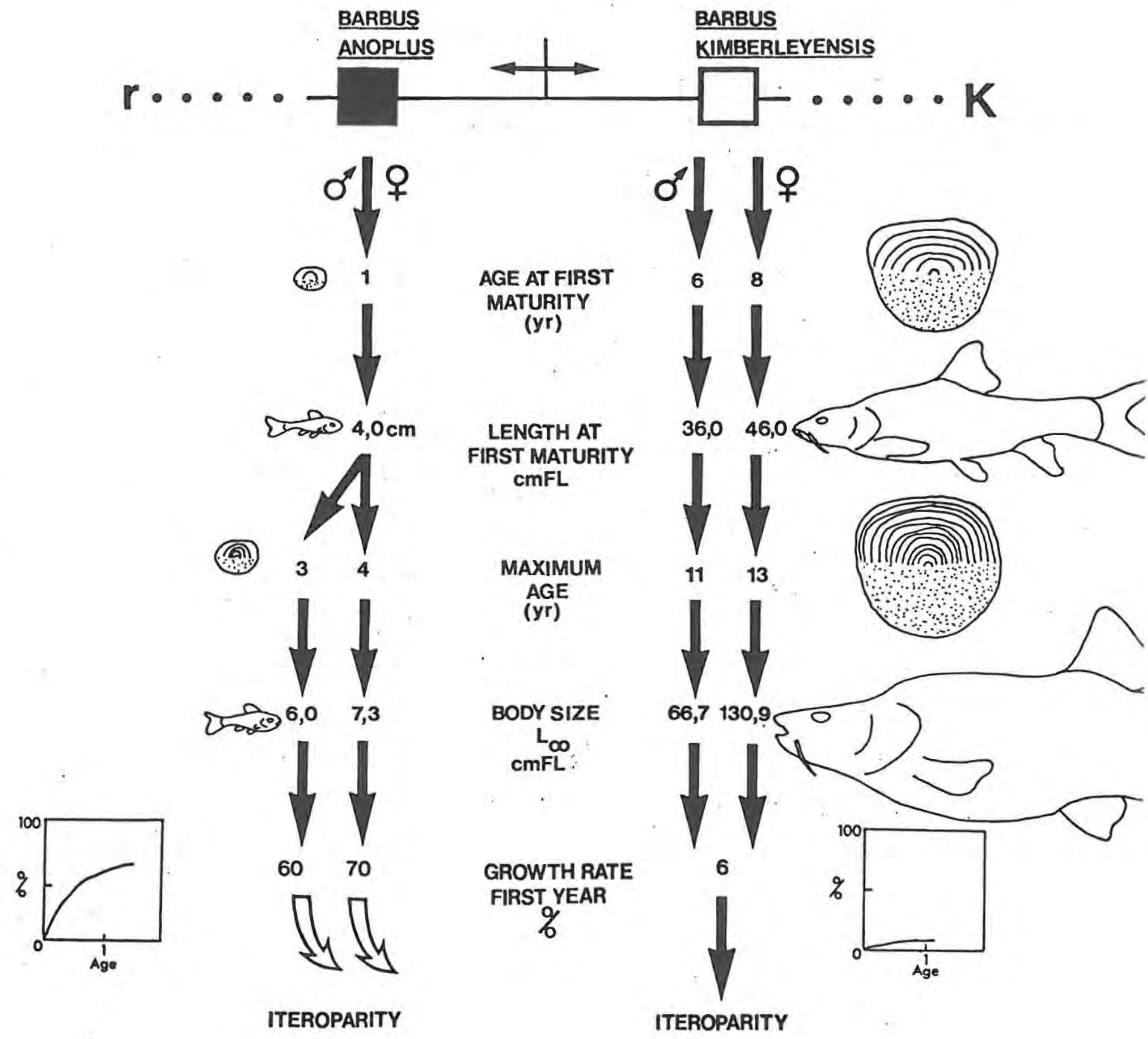
MASTER OF SCIENCE

of Rhodes University

by

JAMES ALFRED CAMBRAY

January 1982



FRONTISPIECE

r & K correlates in several life history parameters of <u>Barbus anoplus</u> and <u>Barbus kimberleyensis</u>*.

(In brief, the theory of r- and K-selection predicts that high reproductive effort and a short lifespan will be the favoured genotypic variations when a population is subject to a high and variable density independent mortality rate. Conversely, when mortality rates are more predictable then natural selection will favour reduced reproductive effort each year and greater longevity. The minnow, <u>B. anoplus</u> is on the r side of the r-K continuum, and the large <u>B. kimberleyensis</u> on the right side. Iteroparity is repeat spawning).

* Data for <u>B. kimberleyensis</u> from Mulder (1971).

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ACKNOWLEDGEMENTS

I would like to thank the following people for sharing their knowledge and for showing enthusiasm in the present work.

Firstly, I would like to express special thanks to M.N. Bruton for his excellent supervision and sound advice at all stages of this work. He encouraged me to develop my own thoughts on life history strategies which enabled me to understand and enjoy my fish study. I.G. Gaigher is thanked for useful discussions and his support at the commencement of this project.

The Director of the Cape Department of Nature and Environmental Conservation provided funding and equipment for this project, which is deeply appreciated.

The Director of the J.L.B. Smith Institute of Ichthyology is thanked for the use of their excellent facilities and for making the final three weeks of writing up comfortable and productive at the Institute. The acting head of the Department of Ichthyology and Fisheries Science is thanked for use of equipment and arranging for typing, copying and binding facilities.

Members of the Ichthyology staff at the J.L.B. Smith Institute are thanked, P.B.N. Jackson for use of trawl specimens, T. Tómasson for discussions on growth and help with juvenile collections, L. de Villiers for her drawing of B. anoplus. A special thanks to R. Stobbs for his continued excellent photographic support and to H. Tomlinson who even appeared to enjoy typing the final draft.

A. Bruton of the University of Fort Hare is thanked for his Scanning electron microscopy work on tubercles and pharyngeal teeth.

The curator of the freshwater fish collection at the Albany Museum, P.H. Skelton, is thanked for several enthusiastic discussions on the distribution pattern and taxonomy of B. anoplus. I also benefited from discussions with R.A. Jubb.

Members of the Institute for Freshwater Studies at Rhodes University, B.R. Allanson, R.C. Hart, D. Eccles and W. Selkirk are thanked for sharing their reports, which enabled me to more fully understand the environment in which I studied B. anoplus.

For assistance in the field I would like to thank Q. Hahndiek, A. Kalsen and A. Onteng. I am also grateful to S. Thorne for one of the Grassridge reservoir surveys carried out under extreme climatic conditions. D. Vogel provided laboratory assistance and typed the first draft.

I would also like to thank all those who responded to my requests for: identification of food items (see p.194); for aquarium breeding techniques of small barbs, B. Polling; for sectioning otoliths, T. Hecht; for predation on small barbs, F. Junor, A. Whitfield, H. Kok and C.J. Kleynhans.

My wife, Eve, provided assistance, proofread the first draft, and always gave enthusiastic support and listened to both my problems and ideas throughout the course of the study.. Also to my five year old son, Garth, who is under the impression that he is doing his M.Sc.

This thesis is dedicated to my wife Eve and my sons Garth and Conrad.

ABSTRACT

Aspects of the life history strategy of Barbus anoplus Weber were studied in a turbid man-made lake (P.K. le Roux impoundment, Orange River system, South Africa).

The minnow has successfully colonized the shoreline of the P.K. le Roux impoundment, where the preferred habitats of the chubbyhead barb are flooded stream beds, erosion gullies and flooded ruderal communities.

B. anoplus reaches sexual maturity in one year, at a length of about 40mm FL. They have a multiple spawning habit, with the first spawn in November or December and the second spawn in February or March. A part of the adult population undertakes a spawning migration up inflowing tributaries, while the other part breeds along the shoreline.

The eggs and young develop rapidly and a proportion of the protolarvae float near the water surface, where they are probably dispersed by water currents.

Most of the males die-off after their second summer, whereas many females live into a third summer. Females also attain a larger maximum size (73mm FL) than males (60mm FL). The importance of increasing the reproductive potential of B. anoplus by multiple spawning is discussed.

Feeding studies indicate that B. anoplus are opportunistic predators on invertebrates. The feeding habits of minnows collected from four different habitats varied. Minnows collected in the open water fed mainly on zooplankton, while shoreline populations fed on chironomid larvae and zooplankton. The most varied diet was found in fish living in a

well-vegetated tributary of the impoundment which was not subject to inundation.

B. anoplus is basically an r-strategist (i.e. it is small in size, short-lived, males have bright colouration, high seasonal reproductive potential). These characteristics enable the species to colonize and successfully inhabit unstable environments and probably accounts for the fact that it is the most widespread species south of the Limpopo River system.

It is recommended that *B. anoplus* be considered as a candidate in southern Africa for further studies on life history strategies.

CHAPTER 1

INTRODUCTION

Eighty-one percent of the fifty-two Barbus species in southern Africa (Bruton et al., 1981) are less than 150mm FL, yet almost no research has been carried out on these smaller species. One of these small species, B. anoplus (Fig.1) is the most widepsread fish species south of the Limpopo River system (Skelton, 1980). The distribution and taxonomy of B. anoplus have been studied by Jubb (1967), Gaigher (1976), Skelton (1980) and Skelton & Cambray (in press), but no detailed ecological studies had been done prior to the present study.

B. anoplus successfully colonized the marginal areas of the P.K. le Roux impoundment on the Orange River system (dam wall closed in September, 1976) which provided a good opportunity for detailed studies of the minnow.

The founder fish population in the P.K. le Roux impoundment was subject to several man-induced changes in recent times. Firstly, the Hendrik Verwoerd Dam wall was completed in 1970. The environment of the fish living in the river below the dam wall was changed from the natural flow regime to daily pulses of water flow, depending on power demand, as the turbines in the hydroelectric power station were switched on and off. The seasonal cycle was also upset because the river flowed strongly in winter (dry season) as well as in summer (the rainy season). The second disruption occurred in 1976 when the P.K. le Roux Dam wall was closed, and the fish population became the founder stock of a man-made lake.

Those species which were best able to adapt to the lacustrine environment survived and spread during the early productive phases of impoundment, whereas less adaptive species decreased in numbers and disappeared. These post-impoundment changes in fish populations have been followed

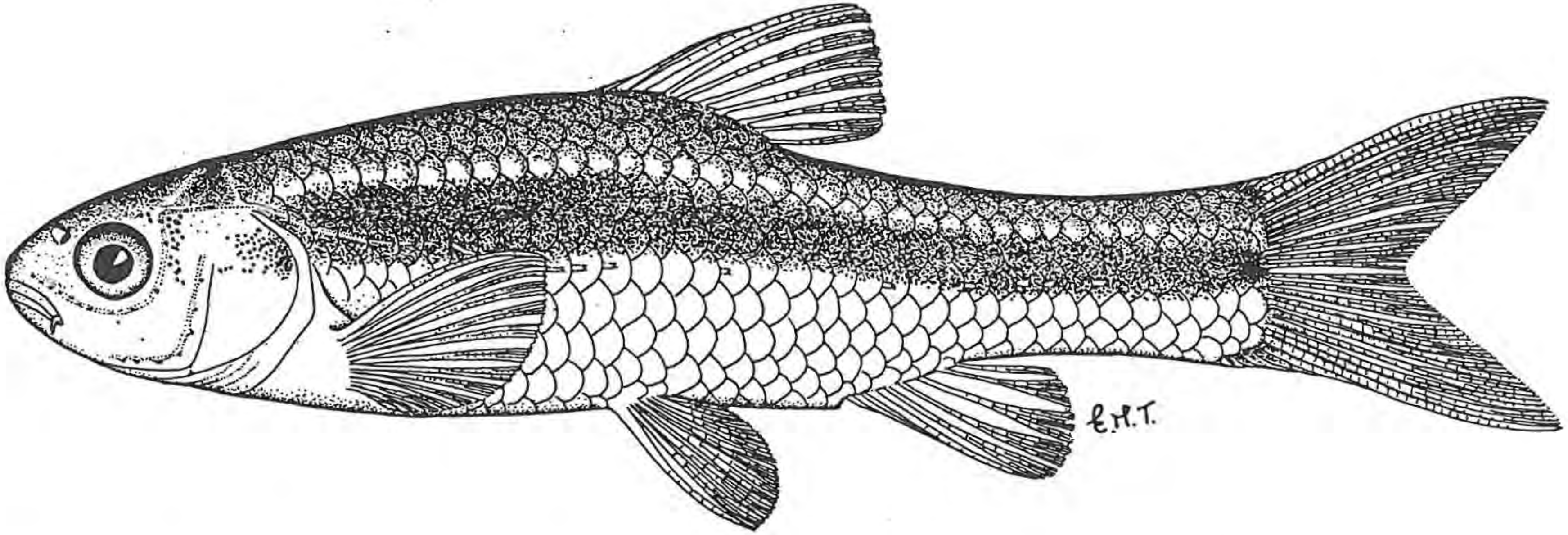


Fig. 1 The chubbyhead barb, Barbus anoplus Weber, 1897. (Drawn by E.M. Tarr).

in several African man-made lakes, for example Kariba (Harding, 1964), Volta (Petr, 1967), Kainji (Lelek, 1973) Hendrik Verwoerd (Hamman, 1980) and P.K. le Roux (Gaigher *et al.*, 1981).

The environmental changes caused by impoundment are complex, and each system behaves in a different manner. A prime factor determining the initial success or failure of a particular fish species in any newly formed lake is the degree to which it is able to utilise the newly available food resources (Blake, 1977). In addition to feeding, the breeding biology of the species plays an important role in determining the success of a species. Fish which can breed throughout the impoundment would be more successful than those species which have a more restricted breeding behaviour.

Collections of small fish in the marginal areas of all the basins of the P.K. le Roux impoundment revealed a high density of *B. anoplus*, especially in the lower basins near the dam wall. *B. anoplus* had successfully colonized the reservoir from a relatively small founder stock. The necessity for a study of the life history characteristics of this minnow species became obvious, and formed part of an integrated programme of the ecology of the P.K. le Roux impoundment. The programme includes studies on the physico-chemical limnology, zooplankton studies, the population dynamics of the larger fish species, and studies on the feeding habits of *B. holubi* and *C. gariepinus.*

This study was limited by the turbidity of the water in the impoundment. It was unfortunate that more behavioural work could not be done on the minnow. In several shallow inflowing streams the minnow could be observed, but following a few millimetres of rainfall the streams became turbid and no observations could be made.

The main theme of the thesis concerns the understanding of the colonizing ability of B. anoplus. Life history strategies were studied to obtain a more thorough understanding of the reasons for the success of this small species in the P.K. le Roux impoundment. In addition, it was thought that these strategies might reveal why B. anoplus has been so successful in southern Africa as a whole.

Reproduction, growth and feeding strategies were identified as the most important aspects to be studied in detail in order to obtain a thorough understanding of this short-lived colonizing species.

Since this is the first comprehensive study of a minnow species in South Africa, work on other small Barbus species in Africa is reviewed and when possible I have tried to evaluate the role of the small Barbus species in southern Africa.

It is hoped that this work will stimulate more ecological work on this important group of fishes, the small Barbus species. Their important role as insectivores, forage fish as well as being prime examples of r-strategists when compared to the larger Barbus species, deserves the further attention of researchers. The working hypothesis of this study has been: 'B. anoplus is a colonizing species. Some of the life history strategies which have enabled it to successfully colonize the shoreline of the P.K. le Roux impoundment, also explain its widespread success in southern Africa.

A twenty-five month study was designed to collect data to test this working hypothesis. Regular collections of B. anoplus throughout the study period provided material for analyzing age and growth, population structure, changes in gonadal condition, spawning frequency and food preferences. The majority of the minnows were collected from the lower basins where the species had been the most successful. More intensive surveys around the shoreline of the impoundment provided data on relative densities in various habitats and data on interspecific competition.

As the life history aspects of this small Barbus species emerged, the framework of the r and K continuum was used to help conceptualize and understand some of the life history strategies of the chubbyhead minnow. This continuum has its limitations, which are mentioned in the text.

FRONTISPIECE EXPLANATION

Throughout this thesis I will refer to the term as r-and K selection. These terms are defined briefly here, for there is a vast literature on the subject (Stearns, 1976).

The r and K continuum is a model (MacArthur & Wilson, 1967) and as such occurs only in an idealized sense. The idealized r-selected species exists in an ecological vacuum with no density effects and no competition. In contrast the idealized K-selected species occurs in a completely saturated ecosystem where densities are high compared to carrying capacities and competition for resources is intense (Adams, 1980). In the frontispiece I have separated these idealized 'species' r and K by a broken line; the 'real-life' continuum begins with the solid line.

The gene pool of any species will contain within it some range of variation of both r-and-K selected traits. This range is not fully shown in the simplistic diagram, however some indication is shown between the sexes of the same species and in the iteroparous reproductive strategy which does not fit into the r-strategist category.

The continuum of life history types between the extremes show a shift (left to right) to greater body size, greater age at maturation, greater longevity and a change in commitment of available energy resources to gonadal development.

In the frontispiece the minnow, B. anoplus, is located on the left of the continuum and the large B. kimberleyensis is on the far right. The life history parameters are based on the B. anoplus population in the P.K. le Roux impoundment (this study) and on B. kimberleyensis from the Vaal River (Mulder, 1971).

The contrasting characteristics of r and K selection (after Perrin, 1980);

r species	K species
Climate unpredictable	Climate predictable
Short generation time, high r_{max}, early reproduction	Long generation time, low r_{max}, late reproduction
Small body size	Large body size
Altricial development	Precocial development
Much density-independent mortality, often juvenile mortality	High survival rate, especially of reproductive stages
High fecundity	Low fecundity with high parental investment
Semelparity	Iteroparity, often with synchronous breeding
Panmictic	Territorial/colonial
Intraspecific competition, often of 'scramble' type	Intraspecific competition, often of 'contest' type
Low investment in 'defence' and interspecific competitive mechanisms	High investment in 'defence' and other interspecific competitive mechanisms
Time efficient	Food and space resource efficient
Populations often 'overshoot'	Populations seldom 'overshoot'
Population density very variable ('boom and bust')	Population density relatively constant from generation to generation

Ecological theory on r versus K selection has proven to be a useful tool in conceptualizing different extremes in life history strategies (Southwood, 1976). We must however also seek alternative explanations, which should be impartially considered in the light of the best available evidence (Perrin, 1980).

Pianka (1970) suggests that, whereas insects tend to be r-selected and terrestrial vertebrates K-selected, fish (and other aquatic organisms) span the range of the r-K continuum.

In a semelparous (i.e. monocarpic, 'big-bang' or single reproducer) organism with fluctuations in pre-reproductive mortality, it is predicted that only a fraction of the population would reproduce annually (Schaffer, 1974). This alternative set of predicted responses to environmental conditions has been termed bet-hedging (Stearns, 1976).

In unpredictable environments, for instance the shores of a large river or a man-made lake, fish are generally relatively unspecialized and many have the ability to modify their reproductive tactics in accordance with environmental fluctuations (Mann & Mills, 1979). Cottus gobio can produce one or more batches of eggs during one season, depending on the water temperature and food availability (Fox, 1978).

With such variations, is the concept of r and K selection valid for fish life history studies? Mann & Mills (1979) note that the choice by a fish species of a particular set of life history tactics cannot usually be predicted from the theories of r-and K-selection. They suggest that when pre-reproductive survival is uncertain, and the fluctuations in that survival rate are greater than those in adult fish, then the reverse of r-and K-predictions occurs. Selection will not be towards semelparity but towards iteroparity (i.e. polycarpy or repeat spawning) and increased longevity, as has been shown in Clupea harengus in the Northern Atlantic (Cushing, 1967). Theoretical studies indicate that the increased fluctuations in mortality of immature fish can favour reproduction over several years (iteroparity; Murphy, 1968), and also reduce reproductive effort in all individuals (Schaffer, 1974). Where mortality rate fluctuations are largely in the sexually mature stages, then increased reproductive effort and a shorter lifespan will be selected (Schaffer, 1974) as would be predicted by the r and K theory (Mann & Mills, 1979).

Adams (1980) and Gunderson (1980) have both found that the r-K selection theory provides a useful basis for comparing life history strategies within marine fishes.

I found the r and K selection theory a useful tool in this study of the early stages of our understanding of the life history tactics of B. anoplus,but I agree that it is a simplistic explanation and there are internal inconsistencies within the theory (Perrin, 1980).

The assemblages of traits predicted by r and K selection or by bet-hedging are not 'iron clad entities' permitting no exceptions. In nature, organisms may respond with some traits which maximize r, and with others which are bet-hedging (Stearns, 1976). B. anoplus is one of these organisms.

Species are not simply subjected to a single selective pressure, or even to a single set of selective pressures, therefore the r- and K concepts should only be applied in a comparative sense between groups of species that have some degree of functional similarity (Adams, 1980).

I suggest that in time 'natural selection' will act on the variability of our individual theories.

CHAPTER 2

TAXONOMY, ZOOGEOGRAPHY AND DISTRIBUTION

Taxonomy

B. anoplus Weber, 1897, was originally described from the Buffels River, Gouritz system, South Africa. The species name, *anoplus*, means unarmed and refers to the flexible non-serrated dorsal spine. The common names are chubbyhead barb and vetkopghieliemientjie (Jackson, 1975). The snout is bluntly rounded like that of the European chub, hence the name chubbyhead (Barnard, 1943).

Specimens collected from the Eastern Cape and Natal were originally named *B. karkensis* Gilchrist & Thompson, 1913. Boulenger (1916) suggested that *B. karkensis* was a synonym of *B. anoplus*, which occurred in the Orange, Olifants and Gouritz River systems. Jubb (1968) synonymised *B. karkensis* with *B. anoplus*. Barnard (1943) further subdivided *B. anoplus* into three geographically isolated forms: *B. anoplus typica* (Gouritz system); *B. anoplus cernuus* (Olifants River system) and *B. anoplus oraniensis* (Orange River system).

B. motebensis Steindachner 1894, is also very similar to *B. anoplus* and is distinguished by the following two characters:

(i) breeding males of *B. motebensis* have numerous conical nuptial tubercles on the snout, forehead and under the jaw, which are always absent from *B. anoplus*;

(ii) *B. motebensis* has a lower mean caudal scale count (14, range: 12-16) than *B. anoplus* (16; Jubb, 1968)

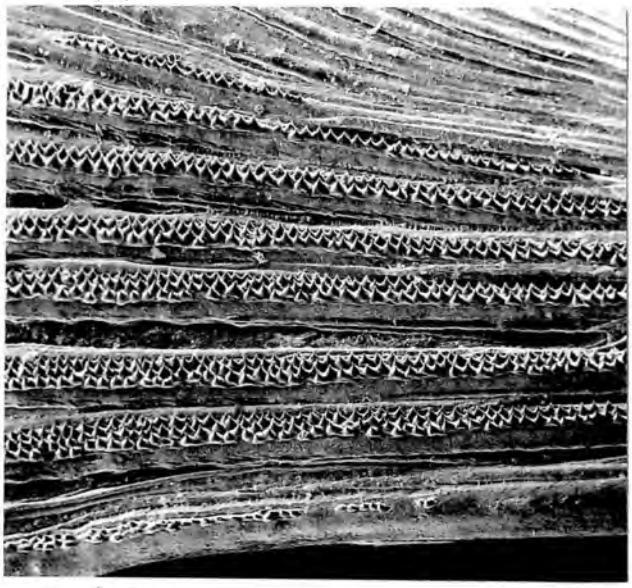
In the Transvaal Groenewald (1958) classified all his specimens as *B. anoplus* and suggested that *B. motebensis* and *B. anoplus* might be synonymous.

Gaigher (1976) experienced extreme difficulty in separating *B. anoplus* and *B. motebensis* when doing a fish distribution survey in the Transvaal. Caudal peduncle scale counts did not prove reliable, as some tubercled males gave a mean count of 16, while other populations, with males without tubercles, had a mean caudal peduncle scale count typical of *B. motebensis* (14 range: 12-16). Gaigher (1976) also suggested that the two species be synonymised.

Gaigher (1976) found that certain populations of *B. anoplus* do develop head tubercles. Skelton (1980) indicated that development of pectoral fin tubercles is consistent in the species. In the *B. anoplus* taken from the P.K. le Roux impoundment, bands of conical tubercles in 2-3 deep rows are present on the pectoral fins (Plate 1a) and small conical tubercles occur on the head of mature males (Plate 1b) during the breeding season.

Dr P.H. Skelton (curator) Dept. of Freshwater Ichthyology, Albany Museum, Grahamstown, considers *B. anoplus* and *B. motebensis* to be valid taxonomic taxa for the following reasons: no detailed taxonomic study embracing a full range of pertinent characters has yet been made; the characters which have been considered include barbels and lateral line development which are not necessarily good cyprinid characters. Tubercle development in males, which is the one known substantial difference between the species has been rejected as valid, but could be of major significance in breeding for the species (Skelton, pers.comm.).

(a)



(b)

Plate 1 Tubercles on a male B. anoplus, 49,3mm FL, 43,4mm SL, collected at site 8, P.K. le Roux impoundment on 3.1.1980. (a) Tubercles on pectoral fin, scale bar 0,5mm (b) Tubercles on the forehead, scale bar 0,1mm

Zoogeography and distribution

The cyprinids are well represented in Africa (Lowe-McConnell, 1975) (Fig.2). The dominance of the freshwater fish fauna by cyprinids increases progressively at higher latitudes in southern Africa (Bowmaker *et al*., 1978). In the Zaire River 13% (52 species) of the fish fauna are cyprinids compared to 76% (16 species) in the south coastal system (Bowmaker *et al*., 1978).

The cyprinids in southern Africa (the region from the Cunene and Zambezi Rivers southwards excluding the Shire River and Lake Malawi) fall mainly into two genera, *Barbus* and *Labeo*, which are widespread throughout Africa and beyond to Europe (*Barbus*) and Asia (*Barbus* and *Labeo*) (Skelton, 1980). In Africa the dominance of the fish fauna by *Barbus* species is most evident in southern Africa (Fig. 2). In southern Africa, 72% of the cyprinids belong to the genus *Barbus* and in the Cape Province 83% of the cyprinids are *Barbus* species. The *Barbus* species can be further subdivided into the large *Barbus* (yellowfish) and the minnows. Eighty-one percent of the fifty-two *Barbus* species in southern Africa (Bruton *et al*., 1981) are less than 150mm FL in length.

The minnow, *B. anoplus* is the single most widespread species south of the Limpopo River system (Fig.3) (Skelton, 1980).

B. anoplus is found in the Orange-Vaal River system but does not occur below the Augrabies Falls (Jubb, 1967). In a recent survey, Skelton & Cambray (in press) collected only two specimens in the Middle Orange, at Prieska (29°39'38"S; 22°44'41"E) and no records of the species are known from the system below this point. The Orange River distribution is discussed in more detail below.

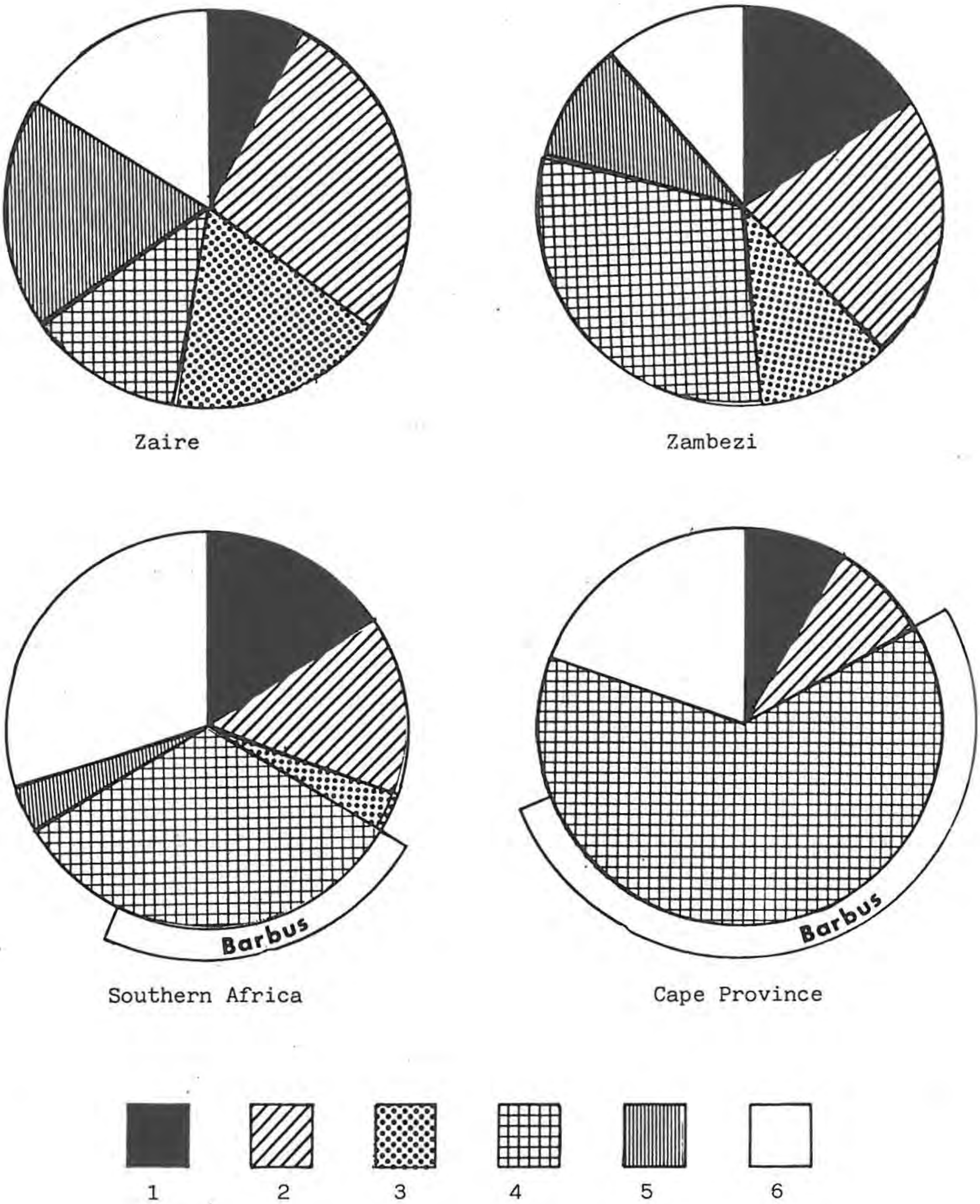


Fig. 2 Proportional composition of the freshwater fish faunas of the Zaire and Zambezi Rivers (after Lowe-McConnell, 1975), Southern Africa and the Cape Province.

(1. Cichlids; 2. Catfishes; 3. Characoids; 4. Cyprinids; 5. Mormyroids; 6. Others).

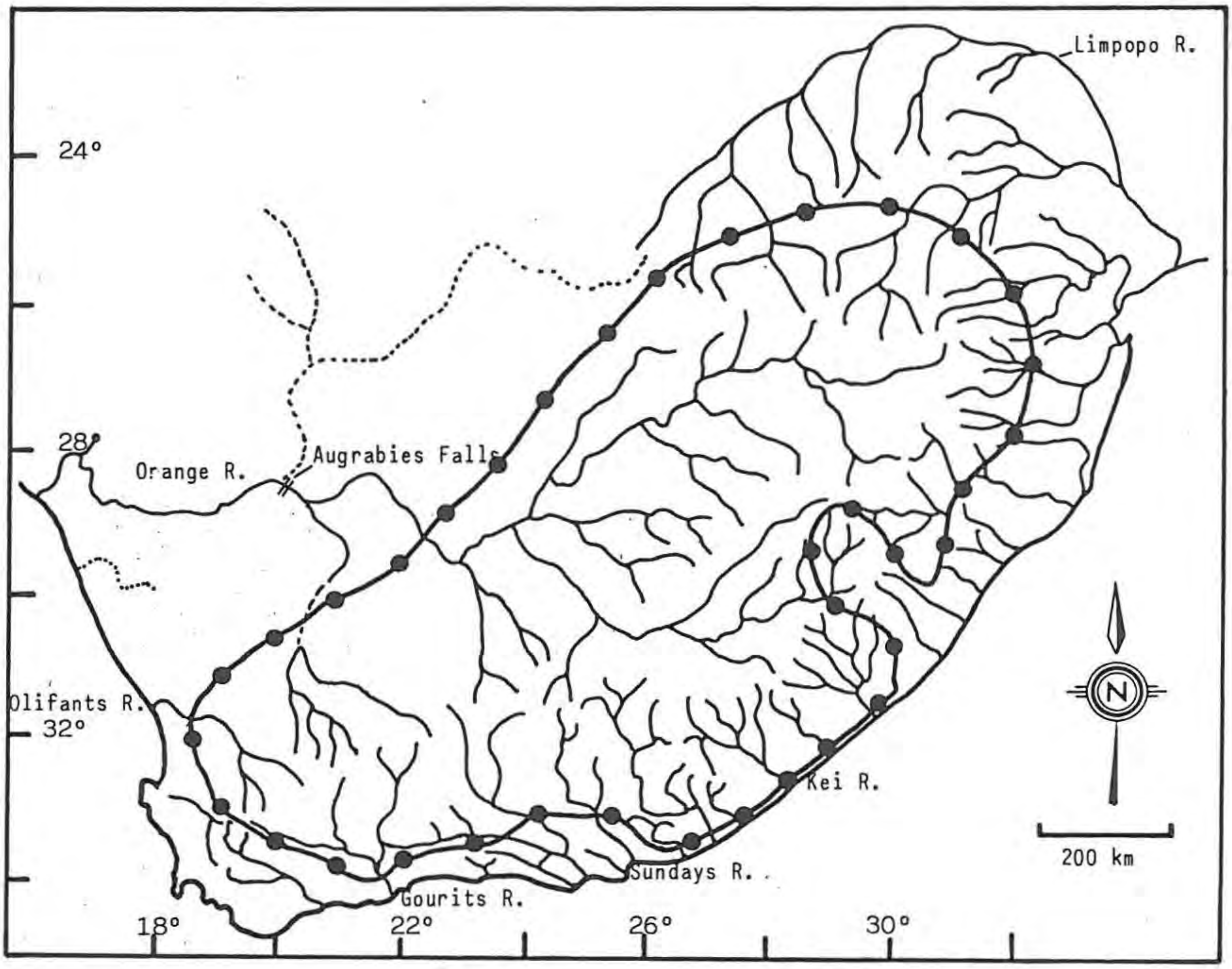


Fig. 3 The range of distribution of B. anoplus and B. motebensis (bounded by chained line) (after Skelton, 1980).

B. anoplus does not occur in the high altitude tributaries of Lesotho (Jubb, 1967). This species is present in several south and south eastern coastal rivers: the Clanwilliam-Olifants, the Gouritz River system, the Gamtoos system, the Sundays River system and coastal rivers to the east, as far north as the Umtamvuma River in Natal (Skelton, 1980). B. anoplus has also been recorded from the Illovo, Umgeni, northern tributaries of the Tugela, the Umfolozi and Pongolo Rivers in Natal (Crass, 1964, 1966). B. anoplus also occurs in the Inkomati River system (Gaigher, 1969, 1976, Gaigher & Pott, 1972). In Natal and Transvaal the species only occurs above 915m, unlike the Cape, where it occurs at lower altitudes (below 500m; Gaigher, 1973, 1976; Crass, 1964).

An isolated population has been found in the upper reaches of the Kuiseb River and its tributary, the Gaub River in South West Africa (Dixon & Blom, 1974). Dixon & Blom (1974) suggested that the Kuiseb River population were probably introduced from the Orange or Olifants by local farmers. A natural colonisation between the Kuiseb River which is in close proximity to the upper reaches of the Molopo River (a tributary of the Orange River) could have taken place in the past, during wetter climatic conditions (Gaigher, 1976).

No obvious physical reasons are known why B. anoplus cannot exist below Prieska in the Orange River System. Skelton & Cambray (in press) speculated that a possible factor may be that the temperature regimes are unsuitable for B. anoplus in the lower Orange River. They derived this suggestion from the correlation of the distribution of the species with the effective temperature (ET) distribution provided by Stuckenberg (1969). B. anoplus is confined more or less within the 16°ET isoline whereas the lower Orange region rises above this line. This distribution pattern could have been reinforced by changes in the present temperature regime (Skelton & Cambray, in press) towards slightly warmer temperatures as has occurred on past occasions (see Werger, 1978).

The distribution of B. anoplus and other Orange River species may be the result of an historical factor (Skelton, 1980). Skelton (1980) has suggested that the Orange River was formerly two independant systems: (a) the upper Orange, draining south west to reach the sea via the Olifants River, and (b) the lower Orange with an enlarged northern drainage, which is now remnant in the Molopo River, and its tributaries. The wide distribution of Pseudocrenilabrus philander, Barbus paludinosus and B. trimaculatus (widespread African species) and the absence of B. anoplus to the west of Prieska may all have been a consequence of the early drainage lines. Temperature regimes have possibly reinforced this distribution, operating at upper tolerance levels for the more temperate B. anoplus and at lower tolerance levels for the tropical B. paludinosus, B. trimaculatus and P. philander (Skelton & Cambray, in press).

B. anoplus is confined to the main body of the Karroo geological system in southern Africa. Skelton and Cambray (in press) noted that this correlation is very accurate, for example it is at Prieska that the Dwyka series Karroo system (east) meets the Transvaal system (west). In addition, B. anoplus is the only primary freshwater fish in the rivers of the Transkei from the Great Kei River in the south to the Umtamvuma River in the north (a region known as the Transkei gap, Bowmaker et al., 1978; Cambray, 1978). The Karroo systems reaches the coast across this region. Thirdly, in the Clanwilliam Olifants River system of the western Cape, B. anoplus is not found where Cape system geology prevails. In a tributary of the Clanwilliam Olifants system, the Brandkraal River, a population of B. anoplus has been found from the zone of interface between the Cape and the Karroo systems. Water quality may possibly be a limiting factor in the distribution of *B. anoplus*, (Skelton & Cambray, in press) as Karroo system rocks impart distinctive characteristics to the groundwater (Bond, 1946).

CHAPTER 3

STUDY AREA

Orange river:

The Orange River is the largest river (2200km) in Africa south of the Zambezi River, and has a catchment area of 650 000km^2 (Edwards, 1974). The headwaters are in the Drakensberg highlands (3500m) in Lesotho and high plateau regions on the eastern side of the subcontinent and drain into two major tributaries, the Vaal in the north and the Orange. These tributaries join and flow westwards with an average gradient of 1,5m per km. (Edwards, 1974) to reach the Atlantic Ocean at Alexander Bay (Fig.4).

The Orange River crosses the central plateau of South Africa and ranges through a variety of ecological conditions, from the temperate, cool, moist alpine highlands of Lesotho through increasingly more arid country to the Namib Desert near the estuary.

The river is characterized by marked fluctuations of annual temperature and flow, a very high summer silt load, a lack of vegetation and a homogeneity of habitat. The poor fish fauna (15 species) can probably be attributed to these harsh conditions (Bowmaker et al., 1978).

The Orange River is divided into three regions: the upper Orange, from its source in Lesotho to its confluence with the Vaal; the middle Orange, from the confluence to the Augrabies Falls; and the lower Orange from the Augrabies Falls to the Atlantic Ocean.

The middle and lower reaches flow through progressively drier terrain so there is relatively little inflow from these regions (Skelton, 1980). Kriel (1972) noted that, apart from the Vaal River, the catchment of the Orange River below the Hendrik Verwoerd Dam wall yields very little water, less than 5% of the mean annual runoff.

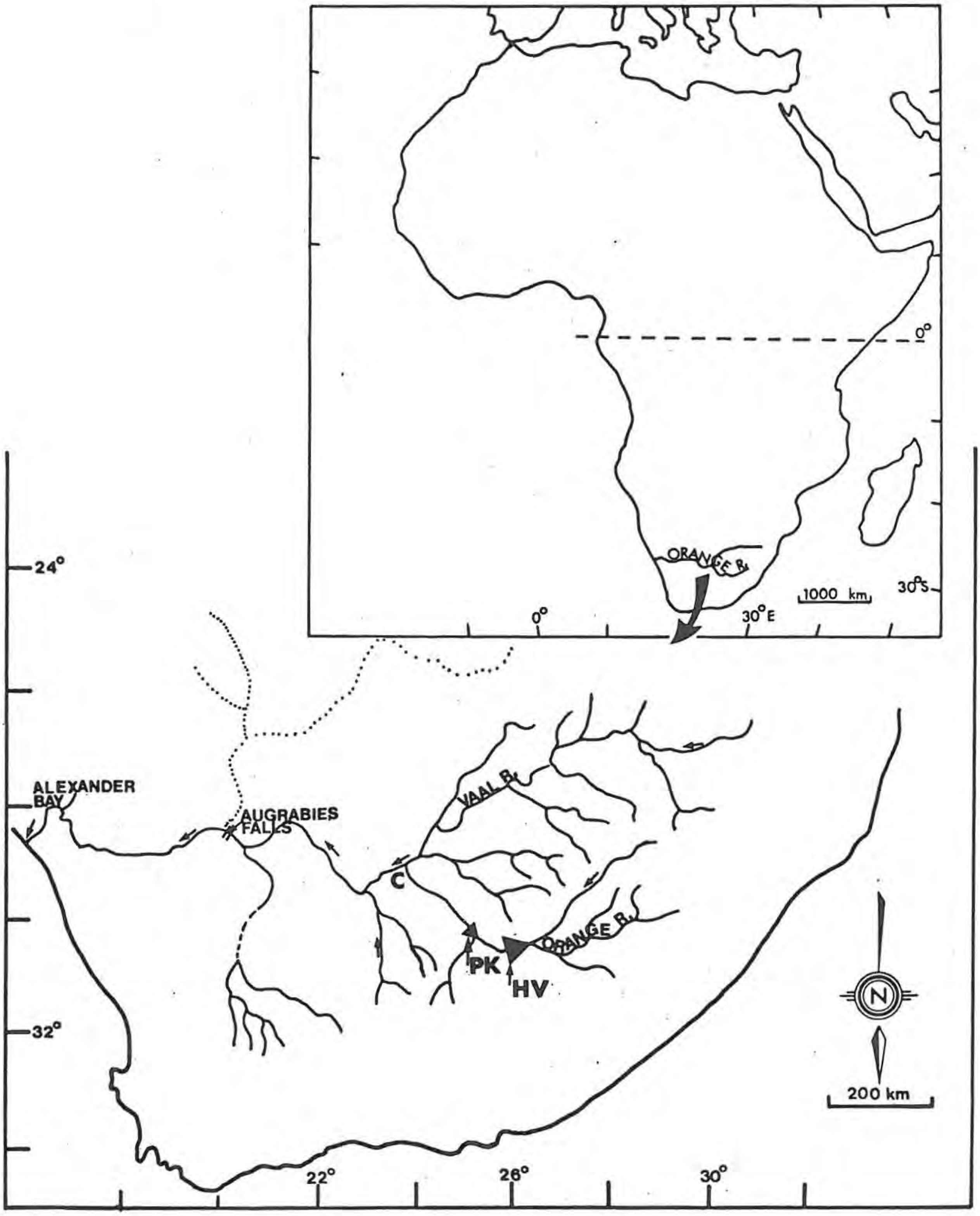


Fig. 4. The Orange River system. C: confluence of Orange and Vaal Rivers. P.K.: P.K. le Roux impoundment. HV: Hendrik Verwoerd impoundment.

The unregulated seasonal variation in flow is substantial. About 25% of the runoff occurs during the six months May to October, whereas 75% occurs during the six summer months, November to April (Kriel, 1972). By contrast, the regulated Orange River, which lies below the P.K. le Roux Dam wall, now receives 54% flow in summer and 46% in winter (Cambray, 1981).

Annual runoff in the Orange River also varies from year to year. Flow records from 1913 show that the maximum runoff for a hydrographic year amounted to 267% of the mean, to the minimum of 17,5% of the mean (Kriel, 1972). The Orange River has also stopped flowing on several occasions.

In summary, van Zinderen Bakker (1974, p. VII) described the Orange River as follows: "The Orange River is born in the green alpine pastures of the high mountains of Lesotho and the northeastern Cape province. Its crystal clear cold water cascades down the mountain slopes through swamps decorated with millions of red-hot pokers and gradually reaches the civilised world where mud and silt and material strange to a youthful river destroy its character and appearance. The river can come down in tremendous floods which rush down the eerie gorge of the Augrabies Falls and speed on as an alien river through endless desert lands to the coast".

B. anoplus, as part of the fauna of this river system, has developed life history strategies to cope with the severe floods and droughts which characterize the Orange river system.

The Orange River Project:

An historical review of the vast Orange River Project was given by Alexander (1974). Sir William Willcocks in 1903 first suggested bold projects along the Orange River, including a diversion weir at Van der Kloof. But it was not until 1962 that government approval was given and within a year a start was made on one of the largest water supply schemes on the continent of Africa.

The first large impoundment, the Hendrik Verwoerd Dam started to fill in September 1970. This impoundment was designed to provide adequate storage ($5952 \times 10^6 m^3$) for the seasonal runoff (mean annual runoff $7180 \times 10^6 m^3$) from the Orange River catchment and from the Caledon, Telle and Kraai rivers, and to control the flow in the river which is subject to periodic floods (Kriel, 1972). The water is used for generating electricity and for agriculture and domestic uses in the middle and lower Orange. The intake for a 83km long diversion tunnel is located within the Hendrik Verwoerd Dam. Water is transferred out of the Orange River system into the Fish and Sundays Rivers valleys for agricultural, domestic and industrial uses.

The P.K. le Roux Dam, located immediately downstream of the Verwoerd reservoir, lies at an altitude of 1090 m.a.s.l. (river bed level). The reservoir has a capacity of 54% ($3185 \times 10^6 m^3$) of its sister impoundment. The former impoundment started to fill in September 1976, and overflowed for the first time in April 1978. The main purpose of the dam is power generation (two 110 megawatt turbines) and diversion of water for irrigation into canals on both banks of the river. The P.K. le Roux dam is fjord-like, with very few gradually sloping littoral areas. The Orange River bed is deep and steeply carved into dolorite capped deposits. Consequently the man made lake is characterized by steeply sloping banks which are strewn with dolorite boulders (Plates 2 & 3). The morphometric parameters of the P.K. le Roux impoundment are given in the following Table.

TABLE 1

Morphometric parameters of the P.K. le Roux reservoir(adapted from Allanson, 1981

Length	73,44km
Mean breadth	1,74km
Surface Area	128,1km^2
Volume	3,19km^3
Maximum Depth	73m
Mean Depth	23m
Length of Shoreline	404,5km
Altitude (river bed level)	1090 m.a.s.l.
Dam wall first closed	September 1976
First overflowed	April 1978
Uses	storage, irrigation, hydroelectric power, flood buffer

Plate 2. Aerial photograph of the steep-sloping P.K. le Roux shoreline (photo T. Tómasson)

Plate 3. Typical P.K. le Roux impoundment shoreline strewn with dolerite boulders.

Sediment in the Orange River:

The source tributaries of the Orange River are derived from seepage bogs in the Drakensberg where the water is clear and acidic (Grobbelaar & Stegmann, 1976a). When these waters pass through lower altitudes they cross Beaufort Sediments which contribute large quantitites of dissolved and suspended matter (Keulder, 1979) making the system extremely turbid. Sixty-three percent of the sediment emanates from South Africa where the Orange River passes over extremely erodable soils (Kriel, 1972).

The average percentage sediment load in the Orange River is 0,56 by volume, so that the average annual inflow of sediment into the Verwoerd reservoir is about 32 x $10^6 m^3$ per annum, of which 90% is deposited in the reservoir (Kriel, 1972). The silt load increases in summer with the increase in rainfall and decreases in winter and early summer.

The high silt load in many South African waters not only affects the physico-chemical characteristics of the water but also the biotic communities in it. the long time spent by phytoplankton in the dark aphotic zone has an adverse effect on primary production (Grobbelaar & Stegmann, 1976b). In the 1977/78 summer, following heavy floods in the catchment area, the Hendrik Verwoerd Dam overflowed into the P.K. le Roux impoundment for the first time. This considerably reduced the water clarity of the lower impoundment, where secchi disc readings near the dam wall dropped from over 200cm to 20cm (Allanson & Hart, 1979). As water clarity improved slightly after this period there were corresponding increases in the annual maxima of chlorophyllα concentrations and zooplankton biomass (Hart, 1981).

Gaigher et al., (1981) and Tómasson (1981) have suggested that the April 1978 heavy floods which caused the turbidity to rise sharply resulted in a heavy mortality of B. holubi. The increased turbidity forced yellowfish populations out of the pelagic zone, where they visually select zooplankton (Eccles, 1980), into the littoral zone (Tómasson, 1981). Due to fluctuating water levels the benthos was probably impoverished, and this may have resulted in a heavy mortality of the fish species (Tómasson, 1981).

Rainfall in the P.K. le Roux impoundment area:

The P.K. le Roux impoundment is situated in an area where seventy-two percent of the total rainfall occurs during summer and autumn, with a definite peak in March (Fig. 5), calculated from rainfall data at Fauresmith for the period 1929 - 1973 (Table 2). Fauresmith (29°46'S, 25°19'E) is the nearest recording station and is 60km north-east of the P.K. le Roux Dam wall.

South Africa has been divided into 27 rainfall districts (Weather Bureau 1960 in Jooste, 1980). The P.K. le Roux impoundment is situated in District 15. The mean monthly rainfall is expressed as a percentage of the total annual rainfall for this district in Table 3.

Rainfall is not reliable, especially during winter (the period of minimal rainfall) when the chances of receiving the normal rainfall are only 32%. Jooste (1980) noted that the frequency of recorded droughts for District 15 also shows the unreliability of rainfall (Table 4).

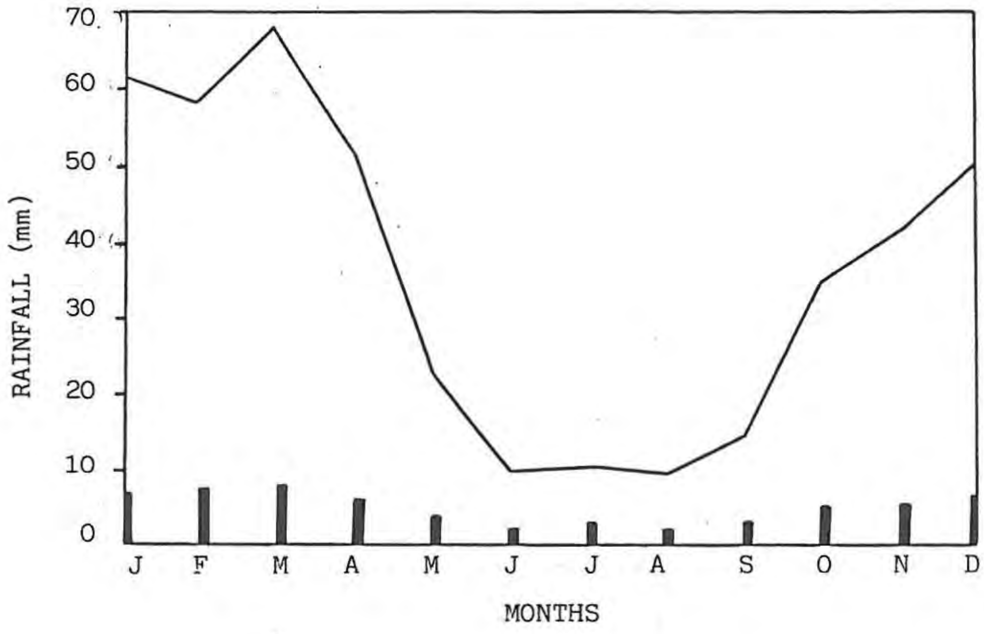


Fig. 5 Rainfall distribution and number of days with rain at Fauresmith (after Jooste, 1980).

TABLE 2

Average monthly rainfall for Fauresmith

(Weather Bureau, 1964 in Jooste, 1980)

MONTH	AVERAGE RAINFALL (mm) 1929 - 1973	NO. OF RAIN DAYS
January	61,5	7
February	58,5	8
March	68,7	8
April	51,7	6
May	22,5	4
June	9,8	2
July	10,1	3
August	9,6	2
September	14,5	3
October	34,5	5
November	40,3	5
December	49,4	6
YEAR	431,1	59

TABLE 3

Mean monthly and seasonal rainfall as percentage of the total annual rainfall for rainfall district 15 (after Jooste, 1980).

MONTH	% OF ANNUAL RAINFALL
January	13,5
February	15,7
March	18,3
April	9,4
May	5,7
June	2,4
July	2,2
August	2,7
September	4,3
October	6,6
November	8,8
December	10,4

Summer (December, January, February) = 39,6%

Autumn (March, April, May) = 33,4%

Winter (June, July, August) = 7,3%

Spring (September, October, November) = 19,7%

TABLE 4

Frequency of droughts (less than 75% of mean) of different duration for District 15 (Weather Bureau, 1960 in Jooste, 1980).

Duration (months)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Frequency	13	2	3	1	1	-	1	-	1	2	2	1	1	1	-	-	-	1

Droughts of up to 11 months are not uncommon in the area and may last up to 18 months. Moolman (1946, in Jooste, 1980) pointed out that these periodic droughts could also be seen in the flow of the Orange River. In the spring of 1933, no water passed over the gauges for 38 days during October to November.

Jooste's (1980) analysis of the rainfall in District 15 from 1880 to 1970 agreed with the finding of Tyson (1978) that rainfall oscillates on a quasi 20 year wave.

Rainfall in the P.K. le Roux area normally occurs in the form of thunderstorms i.e. high intensity rain of short duration. The highest 24 hour rainfall measured at Fauresmith is 103,6mm. Thunder occurs on 50-60 days per annum in the region (Jooste, 1980).

The P.K. le Roux impoundment falls into climatic region 6a (Jackson, 1951). It is described as a semi-arid plateau interior (Southern sub-region), with the rainfall more evenly distributed with March the wettest and July the driest month.

The variation in the mean monthly temperature range and mean annual precipitation for the area is given on a climate diagram for Fauresmith (Fig. 6) (after Jooste, 1980).

Aquatic and riverine plant communities:

Edwards & Nel (1972) investigated the distribution and occurrence of aquatic macrophytes in the Verwoerd Dam catchment area outside Lesotho. Aquatic plants occurred at only 201 (11%) of the sites. No aquatic macrophytes were found in the courses of the Caledon and Orange Rivers, probably owing to their physically unstable flood character and siltiness (Edwards, 1969). In 95% of the sites where aquatic macrophytes occurred,

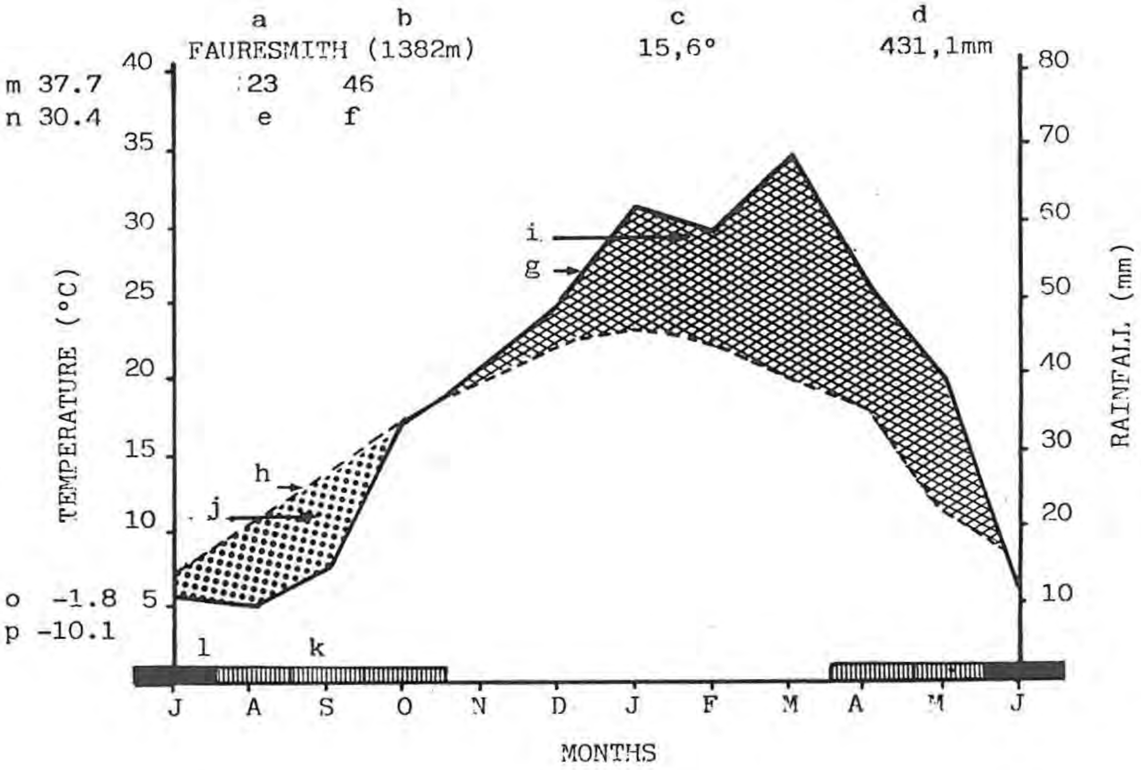


Fig. 6 Climate diagram for Fauresmith (after Jooste , 1980).
a = station, b= height above sea level, c = mean annual temperature,
d = mean annual precipitation, e = number of years for years for
temperature data, f = number of years for precipitation data,
g = curve of mean monthly precipitation, h = curve of mean monthly
temperature, i = relatively humid season, j = relatively dry season,
k = months with absolute minimum temperature below 0°C,
l = months with mean daily minimum temperature below 0°C,
m = absolute maximum temperature; n = mean daily maximum of
warmest month, o = mean daily minimum of coldest month;
p = absolute minimum teperature.

only one or two species were present. Fifteen true aquatic species were found, the most common being the rooted aquatics; Potamogeton pusillus, Lagarosiphon major, P. thunbergii and P. pectinatus.

The aquatic fern, Azolla filiculoides was the most frequent and only significant floating aquatic species. The aquatic macrophyte communities are best developed in the quiet waters of small dams and slow-moving streams (Edwards, 1974).

The extensive sandbanks of the river are an alternating dry and wet habitat, subject to flooding. In low water periods the sand banks were covered in various ruderal communities of herbs and grass species (Edwards, 1974). Several of these species are important in colonizing the exposed fluctuating shoreline of the two large Orange River impoundments, especially Polygonum lapathifolium sub sp. maculatum and Argemone subfusiformis (Mexican poppy), Cirsium volgare (Scotch thistle) and Salsola kali (tumble weed). Jooste (1980) also noted that several of these weed species fulfil an important role as pioneers on degraded and disturbed ground. They play a valuable role on the temporary inundated area along the shores of the P.K. le Roux impoundment where they can cover vast areas after the water has receded (Plate 4).

Flooded terrestrial vegetation:

Above the Vaal confluence, the Upper Orange River Valley is composed mainly of two major vegetation types, dwarf shrub Karroo and grassland (Edwards, 1974).

Werger (1973), in a survey of phytogeographical literature concluded that the Upper Orange River Valley fell into three chorological regions:

Plate 4 Ruderal community which had colonized the shoreline when the reservoir waters had receded. The water has now flooded this community and provides an ideal habitat for B. anoplus.

(a) The Afro-montane Region, east of Aliwal North;

(b) The Sundano-Zambesian Region of the Zambesian Domain, between Aliwal North and the Petrusville area (Hendrik Verwoerd and P.K. le Roux impoundments fall into this region);

(c) The Karroo-Namib Region of the Karroo Domain, west of the Petrusville area.

Plant species typical for these three regions are listed by Werger (1973).

Acocks (1975) classified the vegetation of the area as mainly False Upper Karroo, with the original plant communities being replaced through selective overgrazing by Merino sheep. In a phytosociological study of the Rolfontein Nature Reserve (situated on the Cape shore of the P.K. le Roux impoundment) (see p.44). Jooste (1980) classified the original plant communities along the medium-to-steep slopes as, primarily, the Rhus undulata-Stachys rugosa community, with the Rhus undulata-Stachys rugosa-Setaria lindenbergiana community on the steep slopes. These are now the main inundated communities along the shore-line of the impoundment.

Some physical and biotic characteristics of the P.K. le Roux reservoir: The formation and breakdown of the thermocline in the P.K. le Roux impoundment follows a pattern typical of a number of monomictic reservoirs in Southern Africa (Allanson, 1981). The thermocline is established in November/December and is seasonally depressed until May/June, when overturn leads to homothermy (Allanson & Hart, 1979).

Hart (1981) found a pronounced cyclical seasonal behaviour of the system. The temporal variations in zooplankton standing stocks in relation to changes in water temperature, secchi disc transparency and chlorophyll content of surface waters are evident (Fig. 7 ; Hart, 1981). As water clarity

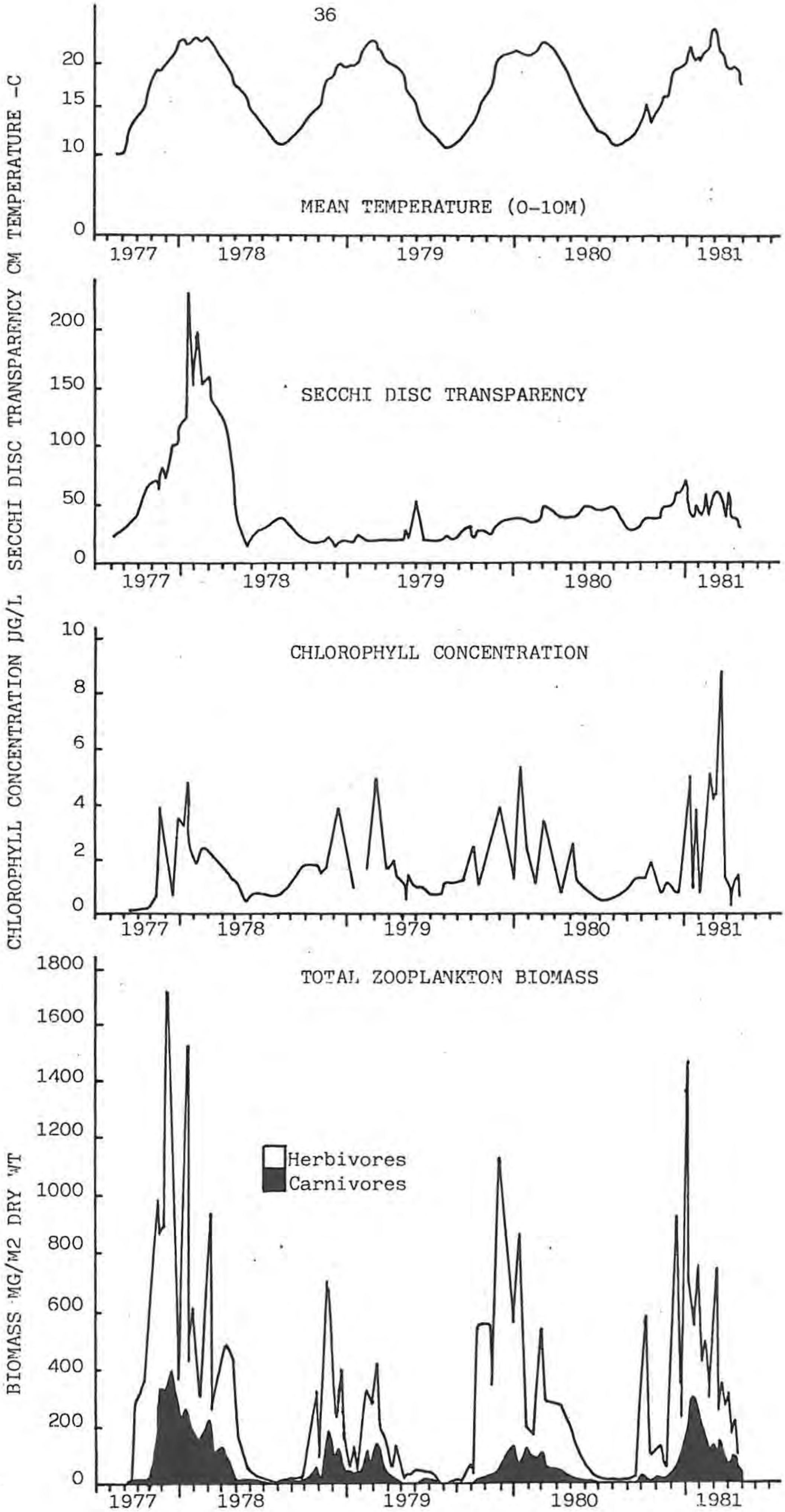


Fig. 7 Seasonal variations in total zooplankton biomass in relation to mean water temperature (0-10m stratum), water clarity and chlorophyll concentration at Station 1

improves, there is a corresponding increase in the annual maxima of chlorophyll concentrations and zooplankton biomass.

The seasonal abundance patterns of copepod zooplankters were fairly consistent between years. The microphagous herbivore Metadiaptomus meridianus consistently exhibited the highest annual mean standing stock of any zooplankter. The abundance of the predatory calanoid, Lovenula excellens, which feeds upon M. meridianus, followed the typical predatory-prey cycle. The cyclopoid copepods had a protracted seasonal occurrence (Hart, 1981).

In contrast, Hart (1981) found that the daphnid Cladocera exhibited variable and unpredictable seasonal abundance patterns, most evident in 1980/81 when a previously unrecorded species Daphnia longispina became dominant. Hart (1981) suggested that this trend was due to size-selective structuring of a plankton community by visually foraging planktivorous fish (e.g. B. holubi, B. anoplus).

The zooplankton species composition will probably continue to fluctuate, because of the continually varying transparency regimes which are linked to the hydrological management of the reservoir (Hart, 1981). The appearance and dominance of the large daphnid D. gibba during the 1979/80 summer when turbidity was high can probably be explained by the "visual refuge" provided by the turbid waters in reducing effective "reactive distances" and the predatory efficiency of visual planktivores (Hart, 1981).

The successional phenomena of zooplankton in the P.K. le Roux reservoir, are initiated with a spring pulse of M. meridianus and D. barbata which occurs around 13 - 14°C and successive species (D. longispina, L. excellens,

D. barbata, Cyclopoida and Moinia brachiata) progressively attain lower maximum standing stocks (Hart, 1981).

Hart (1981) has found a great deal of spatial variability in the abundance of zooplankton throughout the reservoir, attributed to the complex hydrological behaviour of this impoundment. Monthly sampling from stations along the major axis revealed a consistent zooplankton abundance upstream of the dam wall.

Fish community of the P.K. le Roux impoundment:

The fish fauna of the P.K. le Roux reservoir consists of only 10 species: six cyprinids - Barbus anoplus, B. holubi, B. kimberleyensis, Labeo capensis, L. umbratus, Cyprinus carpio, one clariid - Clarias gariepinus, one cichlid - Tilapia sparrmanii, one bagrid species - Gephyroglanis sclateri and the occasional trout, Salmo trutta.

A gill-net survey has monitored the trends of the sub-adult and adult fish of the larger species from pre-impoundment September 1976 (Gaigher et al., 1977a, Gaigher et al., 1977b and Gaigher et al., 1981) until present. A juvenile fish survey of the marginal habitats has located breeding and nursery sites for some of the fish species (Cambray & Hahndiek, 1980).

Before inundation in September, 1976, B. holubi and L. capensis were the dominant species each making up 46% of the total catch. Immediately after impoundment the relative density of B. holubi increased to 75% while that of L. capensis decreased to 18%. These relative densities were generally static until April 1978 when the turbidity of the impoundment increased, secchi disc readings decreased from 200cm to 20cm (Allanson & Hart, 1979). The relative density of B. holubi rapidly declines after April 1978 while that of *L. capensis* increased due to post-impoundment recruitment (Fig. 8). The catches of the other species remained low throughout this period (Gaigher *et al.*, 1981). The catch per unit effort data (Gaigher *et al.*, 1981) led them to suggest that *L. capensis* appeared to be the only species with a good potential for commercial utilization.

The most productive areas in the impoundment are the flooded valley areas of the tributary rivers, where the greatest concentrations of fish occur (Cambray & Hahndiek 1980).

Cambray & Hahndiek (1980) found that tributaries of various sizes were important breeding and nursery sites within the impoundment. The main breeding grounds for *B. holubi* are in the upper reaches of the impoundment. From the upper reaches the juvenile *B. holubi* spread to the rest of the impoundment. *L. capensis* spawn in the main tributaries and the upper riverine area.

Inundated rocky gorges, dolerite outcrops and mountainous slopes, which commonly occur around the impoundment, are relatively less populated.

The offshore fish population is mainly *B. holubi* of medium size, with the next most abundant species being *L. capensis*, *B. anoplus* and *L. umbratus* (Jackson, 1981).

Tómasson (1981) has shown that the hydrological management of the upstream Hendrik Verwoerd impoundment plays an important role in the spawning success and year class strength of *B. holubi*. When the water is taken from the warm epilimnion, the fish can breed earlier, and year class strength will be higher, than in years when cold hypolimnetic water is released during the breeding season.

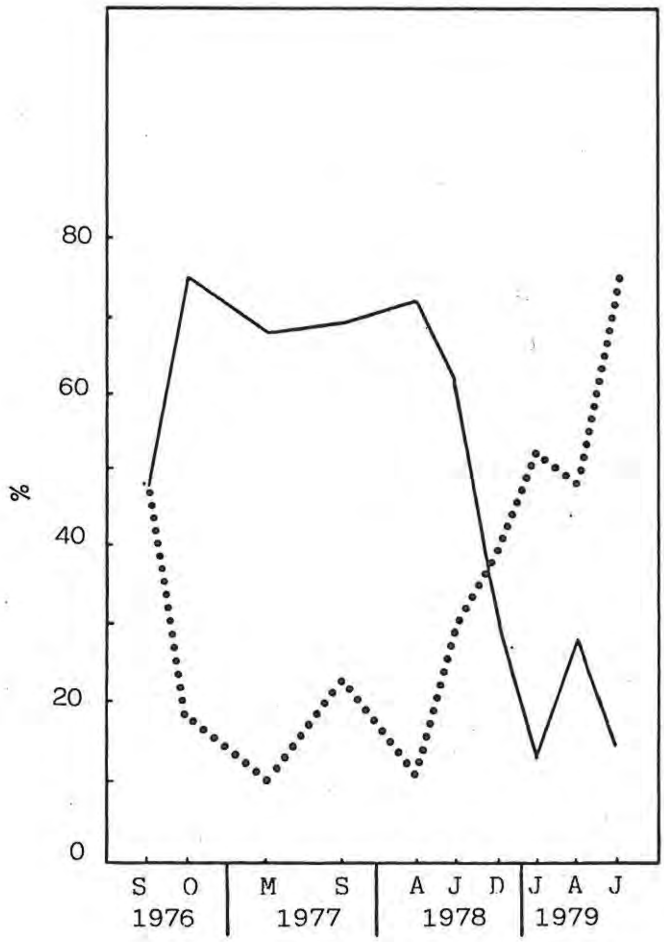


Fig. 8 The relative densities of B. holubi (solid line) and L. capensis (dotted line) collected with gill nets from the Orange River in September 1976 and from the P.K. le Roux impoundment from October 1976 to July 1979 (after Gaigher et al., 1981).

B. anoplus, C. carpio and T. sparrmanii were found to breed throughout the impoundment (Cambray & Hahndiek, 1980). The juvenile fish surveys in the Hendrik Verwoerd Dam (Cambray et al., 1978) revealed that B. anoplus was not as abundant in the Hendrik Verwoerd Dam (April 1976 - 12,3%, April 1977 - 43,1% of total catch) compared to the P.K. le Roux results (March 1978 - 95,6%, March 1979 - 80,1% and April 1980 = 63,4%). The boulders as well as the submerged trees would provide some protection for small fish in the P.K. le Roux impoundment. In contrast, in the Verwoerd impoundment the shoreline is very open and affords little, if any, protection from predators. Occasionally in the Hendrik Verwoerd reservoir, flooded terrestrial vegetation provides cover, but as the water recedes, these shelters are lost.

CHAPTER 4

HABITAT PREFERENCES

Introduction

The Orange River population of B. anoplus had to locate new habitats after their original habitats were flooded by the rising waters in the P.K. le Roux impoundment.

The fluctuating shoreline of the impoundment offered a highly variable situation to the founder stock of the chubbyhead minnow. The minnow's life history strategies had evolved in the Orange River, now B. anoplus had to adapt to a turbid, man-made lake. The boulder-strewn, steep sloping shoreline, and the flooded riverine vallies provided new opportunities for a colonizing species.

Minnow seine net surveys around the 400km shoreline, located preferred habitats, spawning and nursery areas for B. anoplus. A trawl net, and a purse seine provided information on the open water habitat.

Information on species associates, predators and parasitic infestations are also included in this chapter.

Methods

To study the habitat preference and distribution of the minnow in the P.K. le Roux impoundment, 26 - 35 sites around the entire impoundment shoreline (approx. 400km) were surveyed, at least every 4 months from December 1978 to April 1981. For ease of reference the shoreline to be surveyed was divided into 5km sections (Fig. 9). For example, site 14 would indicate one section of the Hondeblaf River, so 14 would be written on the data sheet followed by a brief habitat description. At each locality the following was recorded: date, time, water temperature (°C at 30cm), wind direction and velocity, wave height, stream flow, cloud cover, gear, effort (e.g. seine haul distance) and habitat description, which was coded as follows:

Habitat	Substrate
O - open shore	S - silt
S - stream or erosion gully	G - gravel or rocks
R - river	F - flooded vegetation (aquatic or terrestrial)

For example, a combination of OS was recorded on the field data sheets for an open shore with a silty substrate. Plates 5,6 & 7 show representative habitat types which were used as stations during this study.

As is characteristic of most man-made lakes primarily managed for hydro-electric power generation and irrigation, the P.K. le Roux impoundment undergoes marked water level fluctuations (Plate 8). This presents a major problem in a sampling programme which is concerned with the littoral zone. In one survey period a site would be flooded macrophytes (e.g. Berg River, site 72) and in another survey period the previous collection site would be far from the macrophytes and only a silty, rocky habitat could be sampled (Plate 9).

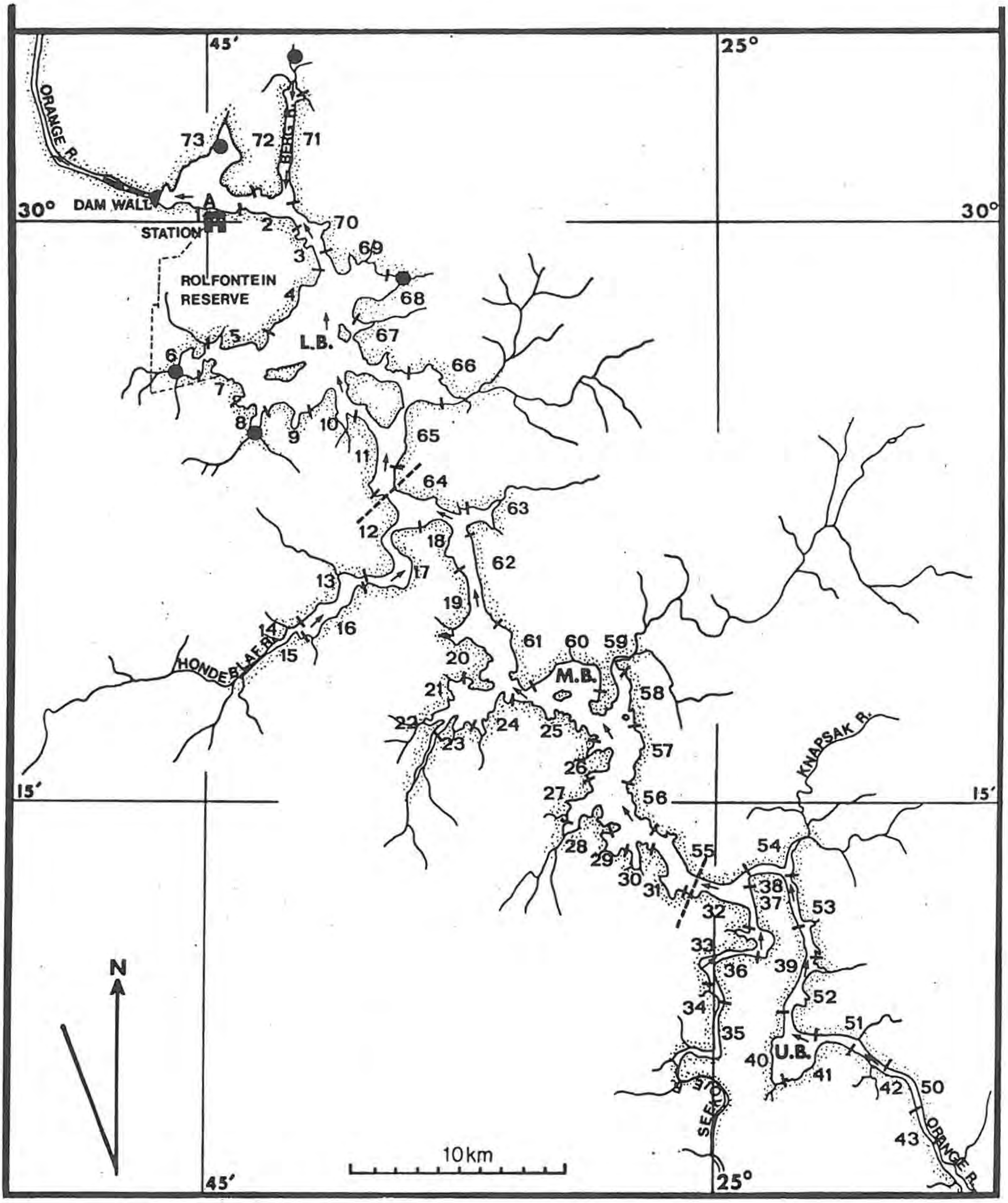


Fig. 9 P.K. le Roux impoundment, Orange River System, South Africa. Numbers 1 to 73 refer to 5km shoreline sections. L.B - lower basins marked by dashed line. M.B. - middle basins. U.B. - upper basins. Station - Douglas Hey Limnological Research Station. Closed circles represent the regular monthly stations, 6,8,68,72 & 73.

(a)

Site 6 - Habitat type SF

(b)

Site 6 - Habitat type OF

Plate 5 Two sampling sites in the P.K. le Roux impoundment, a - site 6 - Rolfontein stream, rotenone is being applied, note enclosure (e), b - open shoreline at site 6.

(a)

Site 68 Habitat type SS

(b)

Site 73 Habitat type OG

Plate 6 Two sampling sites in the P.K. le Roux impoundment, (a) site 68, (b) site 73, note dam wall in background (arrow).

(a)

Site 24 - Habitat type OS

(b)

Site 8 - Habitat type SS

Plate 7 (a) Open shoreline habitat, (b) Erosion gully P.K. le Roux impoundment.

Plate 8 P.K. le Roux impoundment water level fluctuations, dotted line indicates high water level, circles represent various collection localities as the water level receded for site 6, Rolfontein stream (see Plate 5).

(a)

(b)

Plate 9 The effect of water level fluctuations on habitat type sampled at one locality over the 25 month sampling programme - (a) Berg River site 72 water level high, (b) water level low.

The main collecting gear throughout this study was a minnow seine net with three metre wings, which tapered from 170cm near the funnel mouth to 80cm at the end of the wing. The net was constructed of 60% monofilament shade cloth, with the largest opening being 2mm stretched mesh. This net was similar in design to the one used by Cambray et al., (1978) in the Hendrik Verwoerd impoundment. At some of the more open localities a 15m long, 2m deep anchovy mesh (10mm stretched) seine net was used.

Cambray et al., (1978) outlines the many problems (e.g. submerged rocks, trees, wire) of a small seine net survey in the large turbid Hendrik Verwoerd impoundment. These problems also apply to the present survey in the P.K. le Roux impoundment. To overcome some of these limitations, additional sites were surveyed with a piscicide. These areas were usually covered with large boulders (Plate 3).

The catch per unit effort (CPUE) for every species collected with the minnow seine net in each habitat type was calculated by multiplying the total number of fish collected per habitat by ten and dividing by the total distance seined (m). This gave the number of fish/habitat/10m seine haul. The preferred habitats for B. anoplus were determined in this way.

The rotenone collections were mainly in one habitat type (SR) so only the species composition of each catch is given.

To compare the general distribution of B. anoplus in the impoundment, the man-made lake was arbitrarily divided into three basins (Fig.9)

Lower Basin - sites 1 - 11 and 65 - 73

Middle Basin - sites 12 - 21 and 55 - 64

Upper Basin - sites 32-54.

The number of sites surveyed with the minnow seine net was recorded for each basin. The number of fish collected (sample size) at each site was then assigned to one of the following five categories:

(a) 0, no fish collected per 10m seine.

(b) 1 - 9, up to 9 fish collected per 10m seine.

(c) 10 - 49, up to 49 fish collected per 10m seine.

(d) 50-99, up to 99 fish collected per 10m seine.

(e) 100, over 100 fish collected per 10m seine.

For each basin, the percentage of sites with each category (sample size) was calculated. For example, if 10 sites were sampled in the lower basin, 5 of which had 10 - 49 fish, 2 had 50 - 99 fish and 3 had over 100 fish, the following percentage of sites per category would be calculated: (a) 0,0%; (b) 0,0%; (c) 50,0%; (d) 20,0% and (e) 30,0%. These categories could then be compared to the other two basins to assess the abundance and distribution pattern of B. anoplus throughout the impoundment.

Purse seine collections:

A 50m long 5m deep purse seine, with a upper netting strip (3m) of anchovy mesh (10mm stretched) and a lower panel (2m) of 38mm (knot to knot) netting, was used to sample the open water niche. Very few fish were collected per set of net, and this method of collecting fish was discontinued early in the programme.

Depth distribution:

Several minnow traps were constructed and tried in the impoundment. It was hoped that these could be placed at different levels in the impoundment to assess the depth distribution of B. anoplus. After a period of trial runs, with baited and unbaited traps, no fish were collected and the programme was discontinued. There is probably a relatively low density of minnows in the open water niche, as was indicated by the trawl net catches (Jackson, pers.comm.).

Predators and Parasites:

Piscivorous fish were collected with a fleet of seven gill nets, each 100m long and 3m deep with the following stretched meshes; 35,45,57,73,93,118 and 150mm. Stomachs were preserved in 10% formalin.

Piscivorous birds were collected with a shotgun. Stomachs were preserved in 10% formalin.

Parasitic nematodes were counted in all minnows which had been dissected for stomach contents. Early in the study it became apparent that the numerous parasitic nematodes located in the body cavity of both male and female *B. anoplus* might play a role in the population dynamics of this minnow in the P.K. le Roux impoundment. Several attempts were made to have the nematodes properly identified, but were without success. There are nematodes in the *B. anoplus* I have lodged at the Albany Museum (AMSA/P 8800) and the J.L.B. Smith Institute (RUSI 15690), which would be available for future reference.

Field observations:

Field observations were limited to the clear inflowing streams because of the turbidity of impoundment localities. Records were kept of areas frequented by *B. anoplus*, and notes made on their behaviour in these areas (Plate 10).

Plate 10 Berg River site, 1km away from the turbid P.K.le Roux impoundment waters. Arrows indicate localities where B. anoplus occur.

Results and Discussion

Seine net survey:

Eleven surveys were completed covering 26-35 sites around the shoreline of the reservoir. B. anoplus was the most dominant species (62,9%) throughout all these collections (Table 5). During the breeding season, other species, such as B. holubi and L. capensis juveniles used the shallow marginal areas. Very few small C. gariepinus or T. sparrmanii were collected.

The relative importance of the nine habitat types sampled is shown in Fig. 10. The stream habitat with flooded vegetation (either aquatic or terrestrial) was preferred by B. anoplus of all sizes. Riverine areas with vegetation were also preferred. When vegetation was not present, high densities of minnows could be found in the rivers and streams but these densities were not as high as when vegetation was present. Very few minnows were collected from the more open habitats.

Juvenile B. holubi and L. capensis were mainly collected from stream sites with a gravel or rock substrate. The juveniles occupy these sites on a seasonal pattern, and move out usually as the water cools in late autumn. The highest densities of L. umbratus were collected from open shorelines with a silty substrate.

As is shown in Table 5, very few collections recorded high numbers of C. carpio. Their preferred habitat was in flooded stream beds.

Rotenone surveys:

The rotenone surveys also collected a high percentage of B. anoplus from the marginal habitats (72,8%) compared to other species (Table 6).

TABLE 5

Percentage species composition of minnow and juvenile fish (≤ 100mm TL) collected in the P.K. le Roux impoundment, December 1978 to April 1981, during extensive impoundment surveys.

Date	Sites surveyed	Barbus holubi	Barbus anoplus	Labeo capensis	Labeo umbratus	Clarias gariepinus	Cyprinus carpio	Tilapia sparrmanii	Unidentified.	n
December 1978	27	22,0	34,5	22,2	11,1	0,1	6,2	0,8	3,1	6870
March 1979	33	7,5	80,1	5,9	4,7	0,0	0,0	0,5	1,2	8448
June 1979	24	1,1	94,1	1,5	2,9	0,0	0,2	0,2	0,0	475
October 1979	31	3,9	93,5	1,5	1,0	0,0	0,0	0,1	0,0	4168
December 1979	31	6,8	84,4	4,0	3,0	0,0	1,7	0,1	0,0	5005
April 1980	34	15,0	63,4	16,6	1,0	0,1	0,2	3,7	0,0	8543
July 1980	35	4,9	87,6	1,7	4,9	0,0	0,0	1,0	0,0	3338
November 1980	31	25,2	33,8	27,5	0,4	0,0	10,6	1,4	1,0	5703
January 1981	26	14,2	32,6	20,2	2,7	0,0	28,8	0,1	1,4	8044
February 1981	26	6,1	52,1	11,7	27,9	1,7	0,5	0,2	0,0	5679
April 1981	28	10,3	35,4	21,7	30,7	0,7	0,8	0,5	0,0	7526
Total	–	10,6	62,9	12,2	8,2	0,2	4,5	0,8	0,6	63799

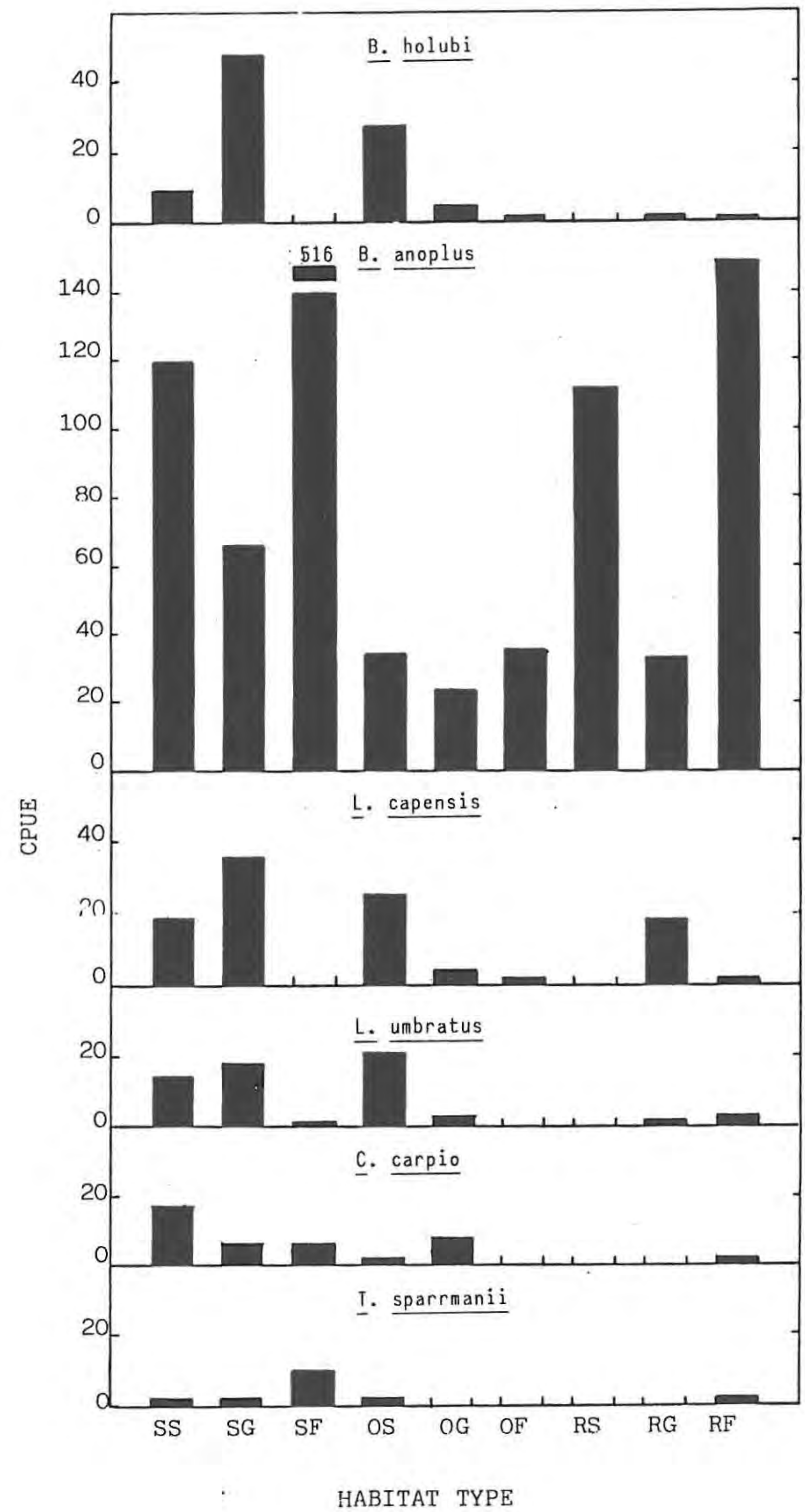


Fig.10 Catch per unit effort (10m seine haul) of six fish species correlated to habitat type (see text) in the P.K. le Roux impoundment (December 1978 to April 1981).

TABLE 6

Percentage species composition of fish collected in the P.K. le Roux impoundment using a piscicide.

All fish <100mm TL except *Clarias gariepinus* (<200mm TL).

Date	Site	Habitat type	Area (m^2)	*Barbus holubi*	*Barbus anoplus*	*Labeo capensis*	*Labeo umbratus*	*Cyprinus carpio*	*Clarias gariepinus*	*Tilapia sparrmanii*	*Gephyroglanis sclateri*	n
February 1980	8	SS	900	0,0	92,1	0,1	2,4	5,4	0,1	0,0	0,0	3319
April 1980	34	RG	15	3,8	63,8	30,0	0,0	0,0	1,3	1,3	0,0	80
April 1980	54	SG	50	21,8	4,6	69,9	1,5	0,0	1,8	0,4	0,0	455
April 1980	58	RG	15	0,0	85,7	8,6	1,0	0,0	3,4	1,4	0,0	209
April 1980	63	SS	20	0,0	98,4	1,0	0,1	0,0	0,1	0,3	0,0	692
April 1980	66	SG	80	0,0	98,7	0,2	0,0	0,0	0,0	1,1	0,0	447
April 1980	72	RG	20	0,0	83,3	0,0	0,0	0,0	16,7	0,0	0,0	12
July 1980	63	OG	50	0,0	100,0	0,0	0,0	0,0	0,0	0,0	0,0	199
July 1980	54	SG	40	0,0	84,6	8,8	0,0	0,0	0,0	6,6	0,0	91
July 1980	34	RG	30	0,0	96,1	1,3	2,6	0,0	0,0	0,0	0,0	76
November 1980	63	SG	20	8,4	62,6	4,4	0,0	1,4	0,0	22,6	0,7	297
November 1980	34	RG	300	17,3	42,2	39,1	0,0	0,0	0,0	0,8	0,6	803
January 1981	63	SG	100	0,0	99,0	0,0	0,5	0,5	0,0	0,0	0,0	197
January 1981	14	SG	25	0,0	44,7	0,0	0,0	53,2	0,0	0,0	2,1	47
January 1981	58	RS	80	0,0	1,2	1,6	0,8	96,3	0,0	0,0	0,0	245
January 1981	34	RS	400	0,3	33,9	11,4	1,9	51,6	0,6	0,3	0,0	316
January 1981	54	OG	100	0,0	4,6	81,8	9,1	4,6	0,0	0,0	0,0	22
February 1981	58	RG	20	0,0	100,0	0,0	0,0	0,0	0,0	0,0	0,0	4
February 1981	54	SG	30	0,0	35,3	51,5	13,2	0,0	0,0	0,0	0,0	68
March 1981	66	SG	200	0,0	76,4	0,6	21,9	0,8	0,0	0,3	0,0	1006
March 1981	72	RF	10	0,0	84,2	0,0	0,0	0,0	15,8	0,0	0,0	38
April 1981	6	SF	1230	0,0	65,8	0,1	1,4	32,6	0,4	0,4	0,0	2719
Total	-	-	3735	267	8258	807	371	1503	30	98	8	11342
Percentage of Total	-	-	-	2,4	72,8	7,1	3,3	13,3	0,3	0,9	0,1	-

These collections were mainly in rocky habitats where it was impossible to use the minnow seine net.

B. anoplus shoreline distribution pattern:

The highest CPUE of B. anoplus was obtained in the lower basins of the impoundment during the juvenile surveys (Table 7). Forty-seven percent of the sites in the lower basins had a CPUE of 100 or more fish as compared to 24,9% in the middle and 8,2% in the upper basins. Very few (8,7%) of the collections in the lower basins had a CPUE of 0 as compared to 13,1 and 20,9% for the middle and upper basins. When high densities of young-of-the-year L. capensis and B. holubi were present in the upper basins very few, if any, B. anoplus occurred at these sites (Table 8). This change in species composition was a seasonal phenomenon occurring after L. capensis and B. holubi had spawned in the upper reaches of the impoundment. It appears as if the high densities of the young of these species excludes B. anoplus from habitats in which they would normally be found. This is shown at the bottom of Table 8, where high densities of B. anoplus occur in habitats which were previously used as nursery areas for B. holubi and L. capensis young. When the juveniles of the larger species move out, B. anoplus re-colonises these sites.

Purse seine:

In the open water habitat the purse seine yielded a very low CPUE. Frequently the catch would be one or two minnows, and in many purse hauls no fish were collected (Plate 11).

Habitat preference discussion:

In the P.K. le Roux impoundment the preferred habitats of B. anoplus were found to be the more sheltered areas. Streams, rivers and erosion gullies with or without vegetation yielded the highest catches per unit

TABLE 7

Distribution pattern of Barbus anoplus, as shown by the percentage of sites at which different concentrations of fish were collected per 10 m seine haul, in three basins of the P.K. le Roux impoundment during ten survey periods. (December 1978 to April 1981).

	Lower Basins*						Middle Basins**						Upper Basins***					
		Sample size						Sample size						Sample size				
	No.of Sites	0	1-9	10-49	50-99	≥100	No.of Sites	0	1-9	10-49	50-99	≥100	No.of Sites	0	1-9	10-49	50-99	≥100
Dec. 1978	8	0,0	12,5	37,5	37,5	12,5	11	9,1	18,2	36,4	9,1	27,3	8	37,5	12,5	25,0	12,5	12,5
Mar. 1979	5	0,0	20,0	0,0	0,0	80,0	18	0,0	33,3	33,3	16,7	16,7	10	0,0	20,0	40,0	20,0	20,0
Jun. 1979	6	33,3	16,7	16,7	16,7	16,7	11	36,4	45,4	9,1	0,0	9,1	7	28,6	42,9	28,6	0,0	0,0
Dec. 1979	8	0,0	12,5	25,0	12,5	50,0	14	14,3	14,3	28,6	14,3	28,6	9	22,2	44,4	11,1	22,2	0,0
Apr. 1980	5	20,0	0,0	0,0	0,0	80,0	14	7,1	21,4	21,4	0,0	50,0	9	22,2	22,2	44,4	0,0	11,1
Jul. 1980	6	33,3	16,7	0,0	16,7	33,3	14	21,4	7,1	21,4	7,1	42,9	11	18,2	18,2	27,3	9,1	27,3
Nov. 1980	6	0,0	33,3	33,3	16,7	16,7	12	33,3	16,7	33,3	8,3	8,3	9	55,6	11,1	22,2	0,0	11,1
Jan. 1981	6	0,0	0,0	33,3	0,0	66,7	11	9,1	27,3	36,4	9,1	18,2	4	25,0	25,0	25,0	25,0	0,0
Feb. 1981	6	0,0	0,0	33,3	16,7	50,0	12	0,0	33,3	33,3	8,3	25,0	4	0,0	50,0	25,0	25,0	0,0
Apr. 1981	5	0,0	0,0	20,0	20,0	60,0	13	0,0	7,7	53,9	15,4	23,1	9	0,0	22,2	77,8	0,0	0,0
TOTAL	-	8,7	11,2	19,9	13,7	46,7	-	13,1	22,5	30,7	8,8	24,9	-	20,9	26,9	32,6	11,4	8,2

*Lower Basins - sites 1 to 11 and 65 to 73 **Middle Basins - sites 12 to 31 and 55 to 64 ***Upper Basins - sites 32 to 54

TABLE 8

Examples of possible exclusion of *Barbus anoplus* from areas in the P.K. le Roux impoundment by *Barbus holubi* and *Labeo capensis* juveniles.

Date	Site	Habitat type	*Barbus holubi*	*Barbus anoplus*	*Labeo capensis*	*Labeo umbratus*	*Cyprinus carpio*	*Clarias gariepinus*	*Tilapia sparrmanii*	n
December 1978	44	SG	49,7	0,0	41,9	8,0	0,0	0,0	0,4	2686
December 1978	50	SG	98,9	0,0	1,1	0,0	0,0	0,0	0,0	94
March 1979	44	SG	42,9	3,1	35,1	16,4	0,0	0,0	2,6	616
March 1979	49	SG	42,9	8,2	14,5	33,9	0,0	0,0	0,5	401
October 1979	43	SG	68,8	17,6	11,2	2,4	0,0	0,0	0,0	125
December 1979	50	SS	61,5	1,3	35,9	0,0	0,0	0,0	1.3	78
April 1980	40	SS	51,2	11,9	33,7	3,2	0,0	0,0	0,0	404
April 1980	43	SG	80,2	0,0	19,6	0,2	0,0	0,0	0,4	528
April 1980	44	SG	26,0	0,5	55,0	0,0	0,0	0,0	18,5	842
April 1980	48	SG	26,3	1,4	55,5	0,0	0,0	0,0	16,8	429
November 1980	49	SS	0,0	0,0	100,0	0,0	0,0	0,0	0,0	239
November 1980	43	RG	9,8	0,0	90,2	0,0	0,0	0,0	0,0	256
November 1980	49	SG	57,3	0,0	42,4	0,4	0,0	0,0	0,0	550
January 1981	40	SS	3,0	0,4	83,3	1,1	12,3	0,0	0,0	473
January 1981	41	SS	34,0	1,0	54,7	9,0	1,3	0,0	0,0	611
January 1981	49	SS	71,2	0,0	24,3	4,3	0,2	0,0	0,0	1284
April 1981	49	SS	82,6	2,0	11,1	4,0	0,3	0,0	0,0	350
April 1981	44	SG	40,5	2,0	41,2	15,3	1,3	0,0	0,0	306
n	-	-	4847	154	4291	646	74	0,0	260	10272
%	-	-	47,2	1,5	41,8	6,3	0,7	0,0	2,5	-
October 1979*	48	SG	5,4	88,8	2,6	2,9	0,0	0,0	0,0	349
October 1979*	49	SS	1,0	90,9	4,5	3,2	0,0	0,3	0,0	309
July 1980*	40	SS	2,1	80,8	3,1	13,6	0,0	0,0	0,4	287

* explained in text.

Plate 11 Purse seining in the P.K. le Roux impoundment.

effort. In a similar study in the Hendrik Verwoerd impoundment Cambray et al., (1978) came to similar conclusions.

The distribution throughout the P.K. le Roux impoundment indicates that the lower reaches near the dam wall are favoured by B. anoplus. The possibility exists that interspecific competition with the young of B. holubi and L. capensis plays an important role in the distribution of B. anoplus, especially in summer, in the upper riverine sections of the impoundment.

Crass (1960) studied the distribution of B. anoplus in more natural habitats and found that this species was the common minnow of streams in the upper midlands and Drakensberg foothills (1220 - 1554m altitude)in Natal. He also reported that B. anoplus inhabits marshy pools and the backwaters of rivers, and is unlikely to occur in swiftly flowing sections of rivers (Crass, 1964). Jubb (1965) recorded B. anoplus in the headwaters of the Caledon River, Orange River system, at 1981m above sea level.

In the Limpopo River B. anoplus (B. anoplus/motebensis of Gaigher, 1976) was only found above an altitude of 915m where it prefers slow rapids or pools in perennial streams (Gaigher, 1973). Surveys in the Eastern Cape Province below an altitude of 500m, show that B. anoplus is not dependant on perennial water in that area and it is abundant in the Maden Dam near King Williams Town (Gaigher, 1976). Gaigher (1976) records the species from a small earthen pond in the drainage area of the Tyume River, Keiskamma River system. Barnard (1943) reports a population from the relatively dry Hartz River near Taungs.

In a fish survey of the Middle and Lower Orange River, only 2 B. anoplus were collected, in a well vegetated pool, out of the main flow of water

(Skelton & Cambray, in press). This minnow appears to be limited to the Orange River above Prieska.

Using an electrofisher B. anoplus were collected immediately below the Hendrik Verwoerd Dam wall hydro-electric station. This is a highly manipulated area, where several hundred cumecs of water can be released into the river from the turbines, raising the water level by one to two metres. The presence of B. anoplus in this area indicates that they can tolerate rapid daily fluctuations in water flow.

Similarly, B. anoplus have been collected immediately below the P.K. le Roux dam wall where similar conditions prevail. These minnows have been taken from the P.K. le Roux turbine chambers when the turbines have been shut down for inspection. During the shutdown procedure, riverine fish move into the turbine chamber and are prevented from returning to the river when a large gate is lowered into position. The turbine chamber is then pumped dry and the accumulated fish can be surveyed. In one of the early shut down periods it was estimated that over 3 tonnes of fish were trapped in the chamber (Mr. J. Verwijs, ESCOM engineer, pers. comm.) Minnows are normally present in these fish "catches". B. anoplus are therefore in the river system waiting to migrate upstream past the dam wall barrier. The possibility exists that some of the fish come from the impoundment, but during several of the catches the turbine intake in the reservoir was below the thermocline, and it is unlikely that the fish were below the thermocline.

The minnows have successfully entered the irrigation canals below the P.K. le Roux Dam wall. In a survey of fishes in the canal system, it was found that B. anoplus were abundant and possibly breeding in the canals.

Jackson (1979) found that some B. anoplus were utilizing the open water niche of the P.K. le Roux. Trawl and purse seine results indicate that the minnows do not occur in large schools in the open water, the exception possibly being in the flooded river mouth areas where relatively large numbers have been taken with a purse seine net. We can only speculate as to why this species, which prefers shallow vegetated areas, is moving so far away from the shoreline habitats. It has been suggested that the minnows have become disorientated in the highly turbid waters of the impoundment (Jackson, pers.comm.). There is the possibility that the opportunistic nature of this species, enables it to "venture" out to colonize new areas within the system. Overcrowding in the preferred marginal habitats might cause certain individuals to migrate to a new area. One would imagine that, in this case, the shoreline would be followed. There is a possibility that B. anoplus might follow an abundant food resource such as zooplankton. The disadvantage of the open water niche, for a small species, would be lack of cover, which in this case is possibly overcome by the turbidity of the water which offers a "visual refuge". Hart (1981) has suggested that the large daphnid, D. gibba is sometimes more abundant when the P.K. le Roux waters are highly turbid, as the reduced water transparency offers them a "visual refuge".

Cambray et al., (1978), and Cambray (unpublished observations) working in the Hendrik Verwoerd impoundment, noted how B. anoplus utilized isolated patches of flooded shoreline terrestrial vegetation. This indicates the opportunistic nature of this species and how it could possibly be subject to periods of booms and busts, characteristic of an r-strategist (Perrin, 1980). The boom would be dependent on shelter, in this case flooded vegetation along the Verwoerd Dam shoreline. Breeding would take place and the newly hatched fish would use the vegetation as a nursery area. The bust would occur when the dam level drops, and the shoreline shelter and related food supplies of the minnow are exposed. This was possibly paralleled in the river situation by years of good flow in the river and its tributaries (boom) and subsequently by drought years (bust). Possibly the prolonged breeding season would enable this species to utilize periods when the vegetation was flooded, during any time of the breeding season.

In both the Hendrik Verwoerd and the P.K. le Roux impoundments B. anoplus penetrate into the shallow inflowing streams. At Suurbergspruit in the Hendrik Verwoerd Dam and at a site near the Seekoei River in the P.K. le Roux impoundment, minnows have been observed jumping over small rocky ledges ($\pm$ 20 - 30cm). Both these streams had very little flow and a water depth of only several centimetres. In other localities (e.g. Hondeblaf and Berg Rivers) they were observed in clear shallow flowing water on very exposed rock ledges (Plate 12).

In the Berg River the larger minnows frequented the pools and were usually observed hiding in the shade of overhanging vegetation or in small schools under rocks (Plate 10). The smaller fish (less than 30mm) could be seen in the open waters, especially in the shallow flowing sections. The Berg River is possibly a good example of their preferred habitat, a relatively small river flowing into the Orange River, with abundant macrophytes and filamentous algae growing in the water (Plate 13a). The river is shallow enough to limit the number of fish predators entering the system, with rocks, emergent and overhanging vegetation providing shelter from piscivorous birds. Invertebrate predators in these habitats might be one of the main risks to the minnows. Fluctuations in water level.

Plate 12 Arrows mark localities where schools of B. anoplus were living, in the Hondeblaf River, site 14.

(a)

(b)

Plate 13 The preferred habitats of B. anoplus, (a) Berg River, a natural habitat, (b) a sheltered, flooded stream course, site 21, in the P.K. le Roux impoundment.

could decimate certain populations which would be cut off from access to the Orange River.

Field observations of B. anoplus in Brakspruit, a shallow tributary of the Hendrik Verwoerd impoundment revealed that small schools of minnows (approx. 30 - 50 fish) sheltered under filamentous algae attached to overhanging vegetation. The minnows only occurred along one bank of the stream, and only where there were shelter "units". A walk along several kilometres of this river revealed that each one of these "units" was occupied by minnows.

The natural preferred habitat of B. anoplus is therefore shallow, well vegetated streams, or areas in streams with shelter such as rocks or fallen trees. In the impoundment the fish have had to adapt to utilizing available habitats such as erosion gullies, streams and flooded vegetation when it is available (Plate 13).

Predators and Parasites.

Piscivorous fish: Seventy B. kimberleyensis were collected in the gill nets and their 'stomach' contents were examined. Only 19 of the B. kimberleyensis 'stomachs' had identifiable scales, two of which contained the radiately straited scales of B. anoplus. Scales of the larger Barbus species and Labeo species occurred in 13 fish, C. carpio scales were found in 4 fish and the ctenoid scales of T. sparrmanii occurred in one 'stomach'. A separate study of the feeding habits of C. gariepinus has shown that B. anoplus is preyed on by Clarias in the impoundment (Bruton, pers.comm.).

Piscivorous birds: Four darters (Anhinga rufa) were mainly full of plant material and silt. One darter had eaten three L. capensis (± 10, ± 12, ± 14cm FL) while another darter contained one L. capensis (± 20cm FL).

One white breasted cormorant (Phalacrocorax carbo) had one B. holubi (±25cm FL) and three L. capensis (±16, ±18 & ±20cm FL). One grey heron (Adrea cinerea) was collected and contained three L. capensis (±5,0, ±16 & 17cm FL). The smaller fish (±5,0cm FL) was the only fish in the darters', cormorants' and herons' stomachs that was of minnow proportions. Two pied kingfishers (Ceryle rudis) were collected and contained B. anoplus otoliths, indicating that fish of between 3-5cm FL had been ingested. One kingfisher had eaten 8 B. anoplus, the second kingfisher contained two B. anoplus and one B. holubi (±5cm FL).

Parasitic nematodes: The greatest infestation (n = 24) occurred in a 54mm FL B. anoplus. Several heavily parasitized females had considerbly reduced gonads which would have lowered their reproductive potential. The progressively larger length groups, of both sexes, contained more parasites per fish (Table 9). The average number of parasites for the 1300 male and 1488 females examined were similar, 1,4 and 1,5 parasites per fish (Table 9). No seasonal trend in any length group was evident.

Only one cestode, Ligula species was found in a specimen. This large parasite occupied almost the entire body cavity.

Relative size within an ecosystem is especially important for consideration of trophic niche and predator prey relationships. By evolving down in size to suit a small prey resource brings the drawback of a greater chance of predation (Miller, 1979). Predators of small fish include other fish, piscivorous birds and a variety of invertebrates. B. kimberleyensis and C. gariepinus predate on B. anoplus in the P.K. le Roux impoundment. B. anoplus are probably an important part of the diet of the pied kingfisher, especially in winter, when B. anoplus are the only fish species in the clear shallow inflowing tributaries. In contrast the P.K. le Roux impoundment is highly turbid and would offer B. anoplus a 'visual refuge' from sight orientating predators such as B. kimberleyensis and piscivorous birds. The flooded terrestrial vegetation and boulder-strewn shoreline would also offer protection to a small fish species. In the clear inflowing streams B. anoplus are very secretive and are usually hiding in the shade of overhanging vegetation which would offer them some protection from kingfishers, but would make them more vulnerable to invertebrate predators.

Parasitic nematode infestations were high in some B. anoplus, which consequently reduced their reproductive potential. In one heavily infested sexually mature female collected in October, 1980, no mature ova were present. The nematodes were found to be the main parasites on B. anoplus in the P.K. le Roux impoundment.

TABLE 9

Number of nemotodes in the body cavity of male and female B. anoplus of five different length groups collected in the P.K. le Roux impoundment, April 1979 to April 1981.

		Length group					
		15-24	25-34	35-44	45-54	≥55	TOTAL
	No. of fish	122	315	454	380	29	1300
Males	No. of parasites	28	117	593	979	96	1813
	No. of parasites/fish	0,2	0,4	1,3	2,6	3,3	1,4
	Max. No. of parasites/fish	3	7	9	24	15	-
Females	No. of fish	157	331	415	353	232	1488
	No. of parasites	41	145	428	807	860	2281
	No. of parasites/fish	0,3	0,4	1,0	2,3	3,7	1,5
	Max. No. of parasites/fish	3	5	8	9	20	-

CHAPTER 5

BREEDING BIOLOGY

Introduction

The reproductive cycle of *B. anoplus* in the P.K. le Roux impoundment was studied over a two year period, April 1979 to April 1981. The cycle and the reproductive strategies were related to certain environmental features of the study area. The study of reproductive strategies is crucial to the complete understanding of adaptations in organisms since all adaptation must in some manner relate to reproduction (Thompson,1975).

This is the first comprehensive study of a minnow species in South Africa. Therefore the reproductive strategies of small cyprinids from other parts of Africa and North America were reviewed and compared to those of *B. anoplus*. The following hypothesis was proposed and tested "*B. anoplus* is a colonizing species and has reproductive strategies that would be advantageous in a newly created habitat (i.e. an impoundment in this study)".

Methods

Collection:

B. anoplus were caught for the monthly routine gonad analyses using minnow and purse seine nets (see page 50).

Reproductive development was determined by measuring changes in the gonadal condition of the minnows at five sampling localities in the P.K. le Roux impoundment over a period of 25 months (April 1979 to April 1981). The following data were recorded: gonosomatic indices (GSI); subjective gonadal maturation stages; gonad widths; monthly development of ova diameter frequencies; largest ova diameters; nuptial tubercle development and the the appearance of newly hatched fry.

All data was recorded from specimens which had been preserved for two to five days in 10% formalin and all lengths are fork lengths unless otherwise stated.

Gonosomatic index:

The fish was surface dried on a paper towel then weighed to 10^{-3} grams. The gonads were dissected out, surface dried on a paper towel and weighed immediately to 10^{-4} grams. Gonosomatic indices were calculated for each specimen using the equation:

$$GSI = \frac{\text{Gonad weight x 100}}{\text{Total weight of fish}}$$

From these data mean gonosomatic indices, ranges and standard deviations were calculated for each monthly collection date for both sexes. When possible, at least 20 sexually mature (greater than 40mm) fish per sex were measured. The use of the gonosomatic index as an indicator of gonad development conceals the fact that several physiologically discrete processes are taking place within the gonad (Scott, 1979). More exact information can be obtained by the histological study of the gonad, which is an important area for future research on this species.

<u>B. anoplus</u> has a short intestinal tract (<0,8 gut length: SL, Skelton 1980). Because of this intestinal morphology it was not thought necessary to remove the food from the intestine before weighing the fish. It is unlikely that food content would alter the GSI to any significant degree.

Subjective maturation stages:

Stages of maturation were assigned to specimens after viewing the gonads at 20X with a dissecting microscope. The subjective gonadal maturation stages followed Nikolsky (1963) except that an additional stage was added for females after stage 5, which was called partially spent (stage 6) followed by spent (stage 7) (Table 10). When possible at least 100 fish of each sex were examined per month for gonadal maturation.

Gonad width:

Each month the gonadal width of a representative sample (usually 50 per sex) was measured to the nearest 0,1mm using an ocular micrometer in a dissecting miscroscope. The testes and ovaries were carefully dissected out and the widest part of the moist gonad (lateral)was recorded. All measurements were taken on the right ovary or right testis.

Ova diameter frequency:

A monthly sample of maturing or mature ovaries was collected for ova diameter frequency determination. A method of sub-sampling eggs was used to obtain the monthly frequency changes in ova sizes. The preserved ovaries (5% formalin) were shaken vigorously in a vial for several minutes, or until all the eggs were loose. While the eggs were still in suspension the entire contents were poured into a petri-dish. A perspex plate, with parallel lines engraved every 5mm, was placed on top of the microscope stage. The petri-dish was put on top of this plate. Only the eggs which touched the lines were measured. Each month, 100 eggs from five large females (i.e. 500 eggs per collection date) were measured to the nearest 0,05mm using a micrometer eyepiece. Small oocytes (less than 0,25mm) were not measured.

To overcome the tendency to select the widest or narrowest diameter of non-sperical ova, the measurements of each ovum were taken parallel to the horizontal axis of the ocular micrometer. The micrometer was always kept parallel to the selection lines on the perspex plate.

TABLE 10

Gonadal maturation stages for *B. anoplus* (modified from Nikolsky, 1963).

Stage 1. Immature:

Ovaries small, thin and translucent. Some with small translucent ova (<0,2mm in diameter). Testes small, thinner than the ovaries, and whitish.

Stage 2. Resting:

Ovaries small to moderate in size and translucent, with small ova (<0,25mm in diameter). Testes small and white.

Stage 3. Maturing:

Ovaries noticeably enlarged, filling most of the body cavity. Three sizes of ova present: >0,7mm in diameter and yellowish in colour; 0,25 - 0,7mm, with the nucleus obscured by yolk deposition; <0,25mm and still translucent. Testes greatly enlarged and whiter.

Stage 4. Late maturing:

Ovaries fill almost the entire body cavity. There are noticeably more mature ova scattered throughout the ovary than at stage 3. The same size eggs are present as in stage 3, but there are more mature ova (≥0,7mm). Ovaries now a distinctly yellow colour. Testes white and enlarged. Sexual products are not extruded when light pressure is applied.

Stage 5. Ripe-running:

Very similar in appearance to stage 4 in preserved specimens. Usually fish in this stage yield a few eggs when handled in the field. Egg sizes and ovary width similar to stage 4 in preserved specimens. Notes made while collecting fish in the field were useful for placement of males in this category. Testes width similar to stage 4, and colour is brilliant white in freshly dissected specimens.

(table continues)

(Table 10 continued)

Stage 6(a). Females - partially spent:

Ovary noticeably smaller than mature ovary with a smaller number of mature ova present. Mature ova still scattered throughout the ovary. The recruitment ova appear more dominant than in stage 5. Recruitment ova are defined here as the yolked ova, between 0,4 - 0,7mm which become mature ova (≥0,7mm) before the second spawning. Multiple clutches are difficult to interpret as the fish could be partially spent or late-maturing for the second spawning.

Stage 6(b). Spent:

In males the partially spent condition could not be distinguished from stage 5. In freshly collected specimens, the testes were slightly pink in colour and reduced in size. In preserved specimens only the reduced size was noticeable.

Stage 7. Fully spent:

An additional stage was added for females since ovaries could be classified as partially or fully spent. When fully spent the ovaries were small, translucent and retained only a few mature ova which were usually granular in structure and pale yellow (resorbing).

Largest ova diameters:

The size changes in the largest ova were followed to establish: when the first mature ova appear; their size range, and if mature ova are present throughout the breeding season. For each month, a subsample of 20 ova from the most mature group from each of five mature females was chosen and their diameters measured for calculation of the mean monthly diameter of large ova. Due to compression within the ovary and possibly preservation, many of the ova were not spherical, especially when the ovaries contained a high percentage of mature ova. Therefore the diameters were estimated by averaging measurements of the largest and smallest dimensions of each egg.

Tubercles:

Part of the analysis of reproductive state in males was based upon tuberculation. Breeding tubercles are epidermal structures which may function primarily in facilitating contact between individual fishes during spawning (Collette, 1977). In *Barbus* species tubercles are usually found only on males in ripe breeding condition. In *B. anoplus* they are usually small structures and microscopic examination is often necessary to identify them (Skelton, 1980). When possible, 20 mature *B. anoplus* males (>40 mm FL) were examined per month, and their stage of tubercle development on pectoral fin rays was recorded as follows:

Stage 0 - no tubercles observable at 40X

Stage 1 - little tuberculation, only a few scattered tubercles.

Stage 2 - moderate tuberculation, the tubercles are clearly more numerous than stage 1, but not as numerous or distinct as in stage 3.

Stage 3 - maximum tuberculation on fin rays, tubercles very crowded and pointed.

Fecundity:

The range of reproductive habits of fish is very large (Breder & Rosen, 1966). Definitions of fecundity that are acceptable in all circumstances have not yet been devised (Bagenal, 1978). Absolute fecundity (Bagenal, 1973) is defined as the number of mature yolked ova in the ovary just prior to spawning. In this study it was found that there was a possibility of an individual female spawning at least twice in one season.

Gale & Gale (1977) note that fractional spawning poses a substantial problem for the biologist attempting to determine fecundity by counting eggs in the ovary. They suggested that fish should be collected immediately before spawning commences, providing that the eggs destined for late spawning are mature enough to be counted. Bagenal (1978) indicated that the main problem in studies on the fecundity of multiple spawners is to distinguish between the reserve and developing oocytes. A common criterion has been the presence or absence of yolk. A count of the yolky eggs gives the fecundity for the season.

Wooton (1979) points out that in species that spawn several times within a breeding season, fecundity is the product of the number of spawnings and the mean number of eggs per spawning. Fecundity should be measured as the number of eggs spawned. For practical reasons it is usually measured as the number of eggs present in the ovary immediately before spawning, on the assumption that few mature eggs are retained. This method will obviously underestimate the fecundity of species that have multiple spawnings and over estimate the fecundity when a significant number of eggs are not shed.

In this study, absolute fecundity is defined as the number of all yolked ova (mature and immature) in the ovary just prior to spawning.

The number of mature yolked ova (≥0,7mm) was also counted before the first spawning (first mature ova 'fecundity') and this was followed by a count of the mature yolked ova before the second spawning. A separate count was made of any resorbing eggs after the first spawning.

Fish fecundity has traditionally been estimated in three ways (Carlander, 1950): (1) by a direct count of eggs in ovaries; (2) by counts or estimates made when females are stripped of their eggs and (3) by counting the eggs in a given weight or volume of the ovary, determining the total weight or volume of the ovary and then estimating the total number of eggs present by proportion.

In most studies on North American minnows direct counts of eggs rather than estimates have been made, and minute and yolkless ova were usually not counted.

Phillips (1969) compared the accuracy of the volumetric and gravimetric methods to the direct counts of eggs for a minnow species. He concluded the best approach for small fish was to decide which ova are mature and determine their numbers by actual counts.

Considering the relatively low number of yolked ova per fish in this study and the ability to separate and count only mature ova (micrometer used with accuracy of 0,05mm), the direct count approach was used to determine the absolute fecundity of B. anoplus, and the number of mature ova before the first and second spawnings.

Usually, only specimens whose abdomens are fully distended, as a result of the ovaries filling the body cavity, are examined (e.g. Heins et al.,1980). This criterion for selecting females for fecundity studies might prove to be misleading as only the most fecund fish in the population are studied.

Fish were therefore chosen at random in this study. In addition some females had well distended abdomens, but this was mainly caused by a high nematode infestation (see p.69).

All the fish required for each fecundity study were collected on the same date as recommended by Bagenal (1968). Ripe females over a wide size range were chosen in October, 1979 and 1980 and in February, 1980 and 1981. All ovaries were kept in formalin, until the eggs had hardened, then the vial was shaken until the eggs separated. The contents were then transferred to a grooved perspex counting tray. All counting of ova was done at 20X, and in this way mature ova (≥0,7mm) could be selected by using an ocular micrometer.

Pool breeding experiments:

The aim of the pool breeding experiment was to establish whether or not a spawning migration is necessary for the successful spawning of B. anoplus.

Two 3m diameter, 0,5m deep, and one 2,5m by 0,5m deep plastic pools were erected at the Douglas Hey Limnological Laboratory. In each pool, one half of the floor was covered with coarse gravel and the other half with river sand. In the 2,5m pool several potted aquatic macrophytes were placed in one corner. The pools were filled and topped periodically with tap water (Plate 14).

Adult fish were collected in early October 1980 from site 6. All fish could be sexed as females had distended abdomens and males were golden in colour. The fish were transported back to the pond site and introduced in the following ratios:

Pond 1 - 15 males and 7 females; Pond 2 - 6 males and 10 females and Pond 3 - 2 males and 5 females. The fish were fed on a prepared fish food (Tetramin) and the terrestrial insects which fell into the pools.

Plate 14 Pool breeding experiment set up at the Douglas Hey Limnological Research Station, P.K. le Roux impoundment.

Ponds 1 and 2 were aerated with a 15cm air-stone. It was noted that when this air-stone was accidently left near the side of the pool, some of the minnows would jump out. The agitation of the water by the air-stone probably simulated a waterfall, which the fish attempted to jump. Field observations of minnows both in the Verwoerd and P.K. le Roux impoundments have shown that these fish can jump over 30 cm barriers after rains have occurred.

Five males and 10 females were introduced into a small asbestos pool (1,5m x 0,6m x 0,3m). This pool had abundant macrophyte growth. Several indoor aquaria were also stocked with minnows. In these aquaria the water was gradually lowered, and then rainwater was added in an attempt to induce spawning.

Environmental records:

Air and water temperature data were collected on a weekly basis on a self recording thermohydrograph located in the marginal waters of the impoundment at site A (Fig 9).

The rainfall data were kindly supplied by the Department of Water Affairs, Rolfontein Nature Reserve and the Institute for Freshwater Studies.

Results

Gonosomatic Index (GSI):

All GSI values show that the spawning season extended from October to February or March in 1979/80 and 1980/81. Mean monthly maximum water temperatures ranged from 17°C to 26°C in marginal areas and there was a photoperiod of between 12 and 14 hours during this period (Fig.11).

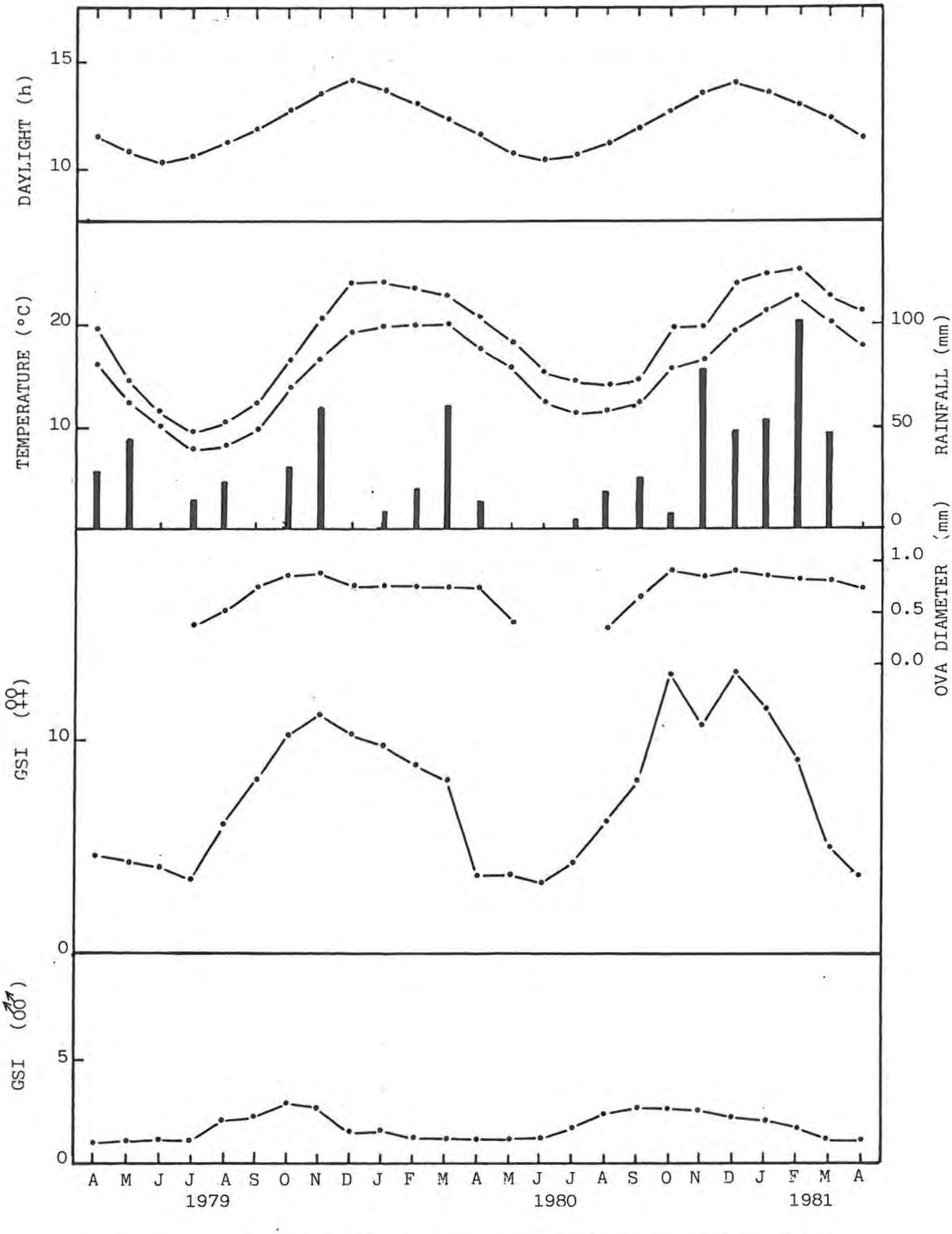


Fig. 11 Mean number of daylight hours, mean maximum and minimum water temperatures, monthly rainfall, mean diameter of largest ova, mean gonosomatic values for female and male fish, are shown for B. anoplus from the P.K. le Roux impoundment, Orange River system.

The highest mean GSI values in females occurred during November 1979 and October 1980 just prior to the first spawning (Fig.12). After the peak GSI periods, October to November 1979 and October to December 1980, there was a gradual decline in GSI values. The reduced GSI values would indicate a high proportion of partially spent females in the population.

The decrease in GSI values after March 1980 and February 1981 could be the result of subsequent spawning and/or resorption of ova. In the first season the majority of the ovaries were less than five percent of the body weight and at their winter low after March 1980. In 1981 the winter low was one month earlier, indicating a different spawning pattern between the two years.

The female GSI trend for fish in the length group 35-39mm also showed a seasonal pattern similar to the older females (Fig.12b), with an August to September increase peaking in October 1979, but there is a more abrupt decline after the October sampling date. A slight increase is seen in February prior to the second spawning. In the second year there are some notable differences. The peak is reached one month later (November) for the 35-39mm fish and the decrease for the smaller fish occurs one month earlier (January).

A seasonal pattern is discernible in female minnows as small as 30-34mm in the second year of the study (Fig.12c). These fish showed a peak in GSI values from September to December. In some of the fish the gonad weight was as much as 12% of the total body weight (a 33mm female in December 1980 - 12,2%).

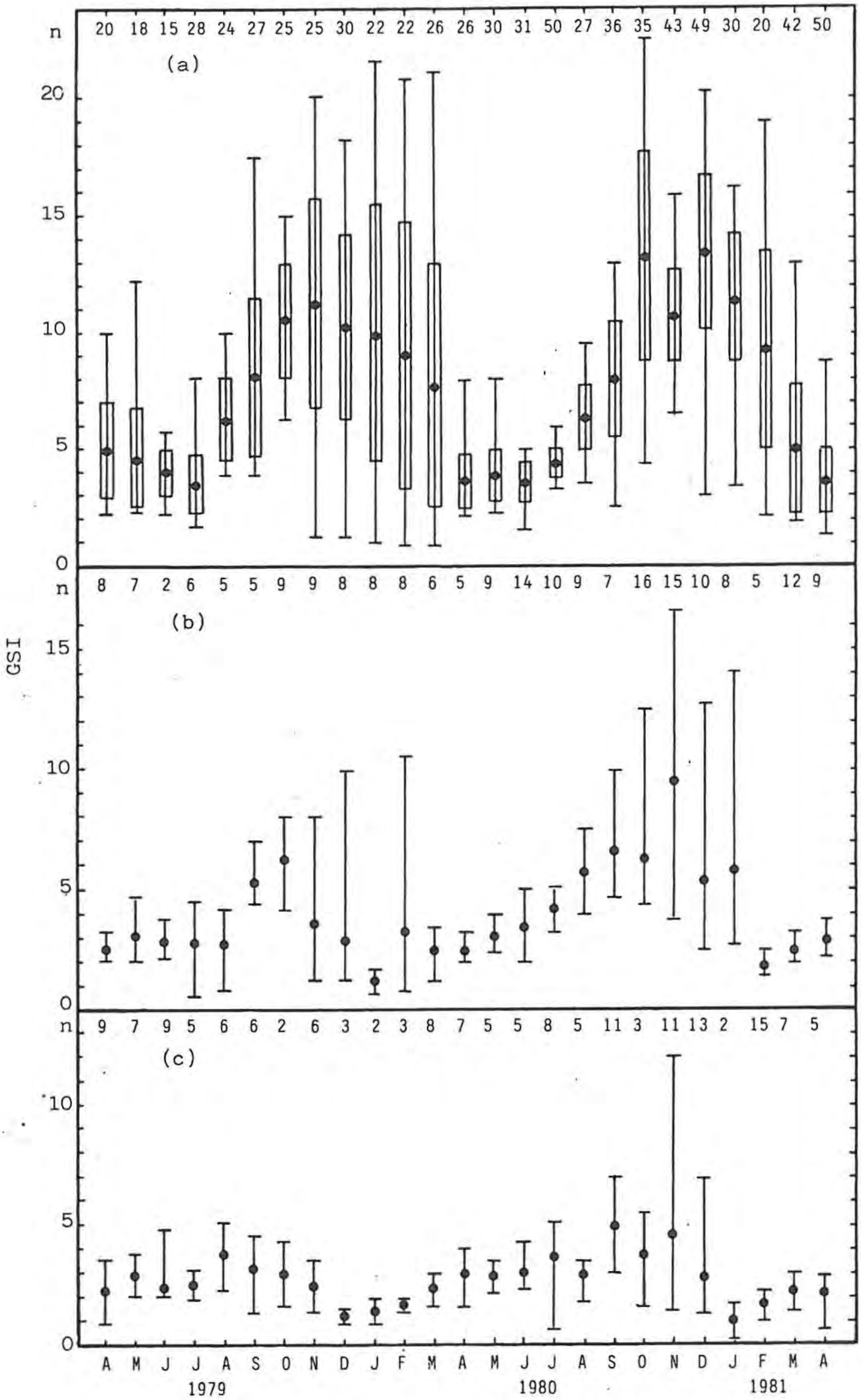


Fig.12 Monthly mean gonosomatic indices (GSI) for female *B. anoplus* of three length groups: (a) over 40mm FL; (b) 35-39mm FL and (c) 30-34mm FL, during a 25 month period in the P.K. le Roux impoundment (vertical bars are ranges, boxes ± 1s.d.)

The GSI values for mature females ranged from less than one percent in spent or undeveloped individuals to over 20% in ripe fish. The larger, generally older fish invest a relatively greater proportion of their resources in reproduction whereas the smaller age group 1^+ fish invest less.

As is common in most teleosts, GSI values were substantially lower in males (max. 4,5) than females (max. 22,6) (Fig.13).

GSI values for males followed a similar early developmental pattern, but the prolonged spawning period was not as obvious in the males, especially in the first year (Fig.13) The male pattern does not exhibit as rapid an increase or decrease as does the female pattern, and never exceeded 5% of the total body weight, compared with 20% in females.
The smaller males (35-39mm) also showed seasonal patterns (Fig.13b). Peaks occur in October of both years and the prolonged breeding season is evident in the second year, from October to January.

Due to the small size of the testes, very little can be seen in the 30-34mm males (Fig.13c). There is a slight peaking in both October periods. The numbers of fish in these samples were too low for significant comparisons.

In September and October there is erratic rainfall in the P.K. le Roux reservoir area. The rainfall pattern for both years (Fig.11) shows that the first part of the rainy season occurs in November, with some

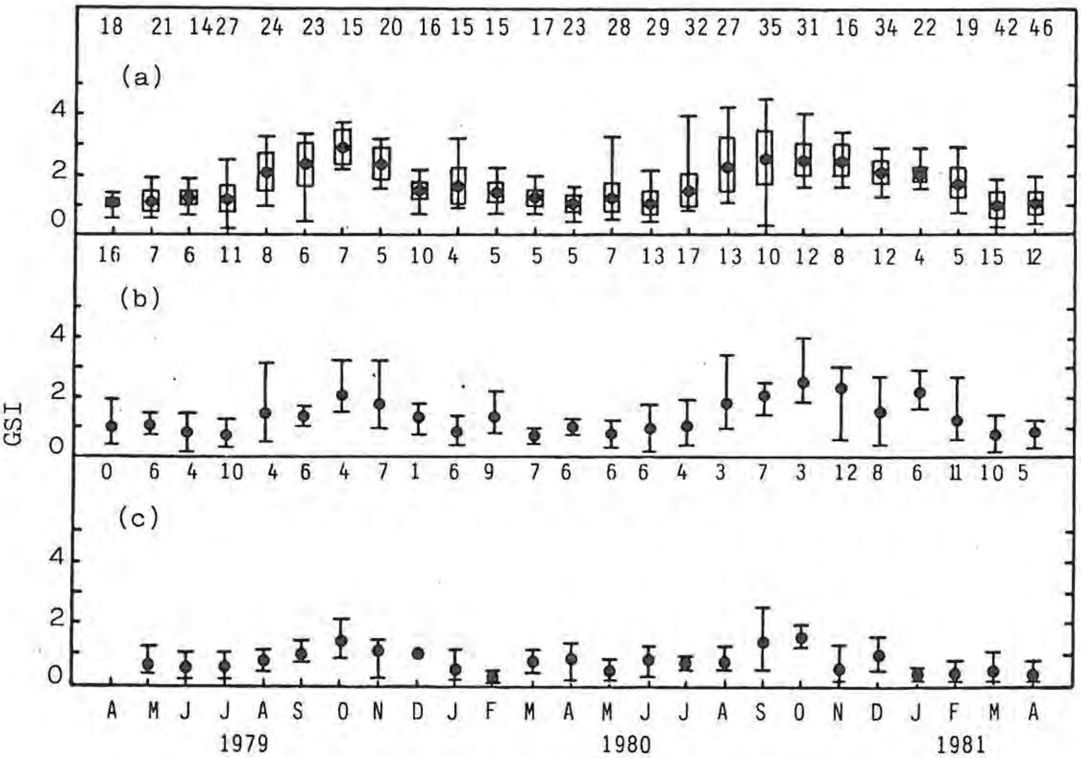


Fig. 13 Monthly mean gonosomatic indices for male *B. anoplus* of three length groups: (a) over 40mm FL; (b) 35-39mm FL and (c) 30-34mm FL, during a 25 month period in the P.K. le Roux impoundment (vertical bars are ranges, boxes are ± 1s.d.).

rain throughout the month. The rainfall pattern becomes erratic again between December and February. In 1980 the second and most marked decrease in GSI occurred in March, again corresponding to a period of steady rainfall. In 1981, the steady rainfall period was earlier, February, and once again the female GSI values fell off sharply after this period indicating that spawning had taken place.

The breeding season pattern would indicate that the peak spawnings occur during periods of fairly steady rainfall. In an impoundment environment we must also consider water level fluctuations (Fig. 14) which might play an important role, providing a breeding stimulus alone and/or when coupled with local rains. A drop in water level could probably result in an unfavourable spawning habitat, whereas an increase would result in flooded terrestrial vegetation, which could provide suitable cover for the fry and a substrate for the adhesive eggs. In the 1979/80 breeding season the water level was rising when the fish spawned. In the 1980/81 season the water level was dropping in November and December, which possibly caused the delay of the first spawning.

The daylight hours start to increase in July and by August in both years there is a marked increase in the gonad weight per female fish. Initiation of spawning does not occur until November when there are at least 13 hours of daylight and the second spawn occurs when there is still approximately 12 hours of daylight (Fig. 11).

The first spawning occurs when the water temperature is approximately 20°C and the second spawning when the water temperature is slightly warmer (22°C) (Fig. 11).

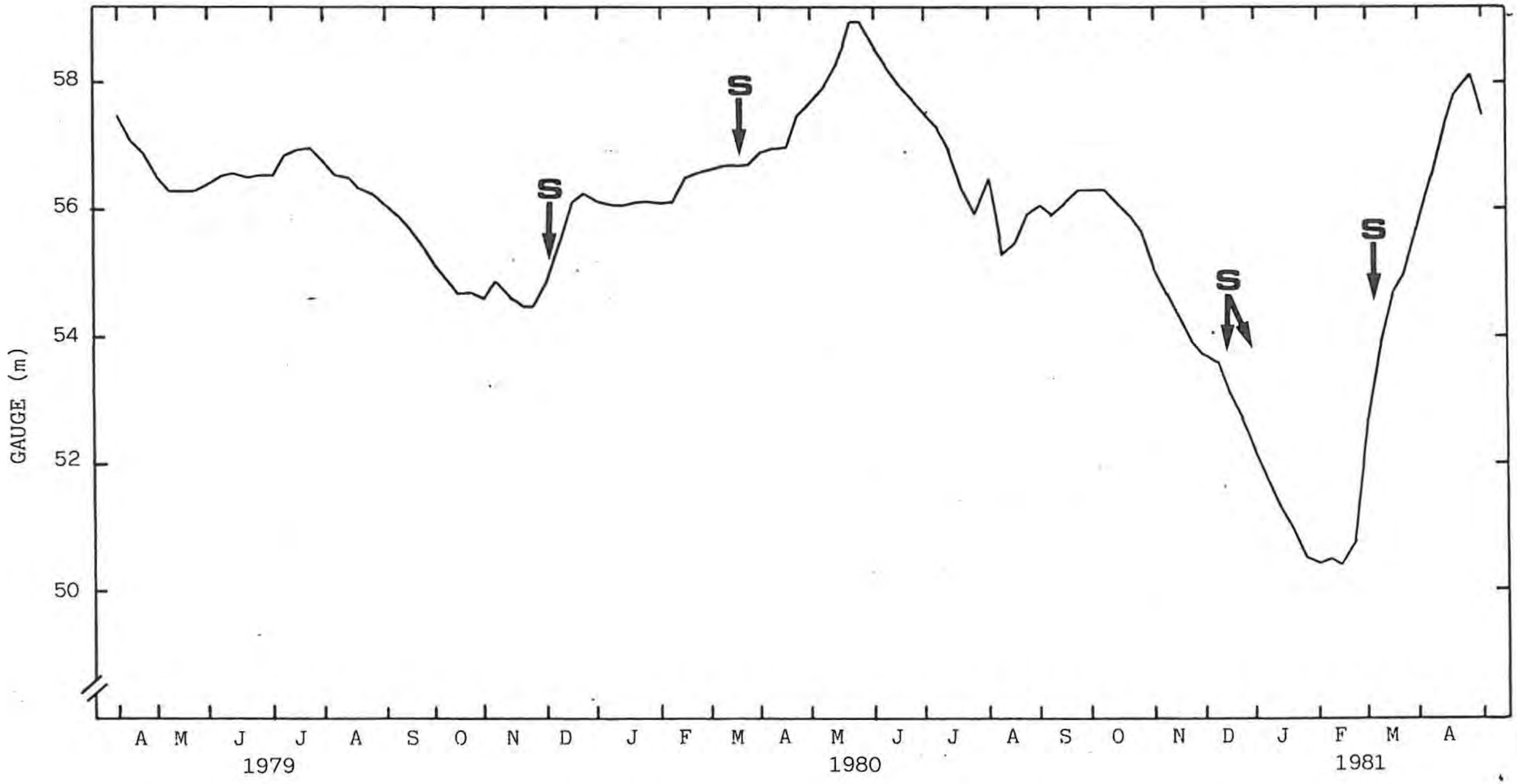


Fig. 14 Water-level fluctuations of the P.K. le Roux impoundment during the study period. (Data supplied by Department of Water Affairs), (S-indicates approximate spawning times for B. anoplus).

Relationship of gonad weight to length:

Table 11 and Fig. 15 show the monthly relationship of gonad weight to length for female minnows over 40mm. Gonads increase in weight from July and by August the larger fish are maturing rapidly. This is evident from the regression line for October 1980 (Fig. 15). In April 1981 the smaller fish are in a resting state, while the regression line indicates that the mature females still have some ova. This was confirmed by observations of ovaries. In a later section, dealing with ova diameter, residual ova are also evident.

TABLE 11

Details of regression equations from logarithmic transformations of monthly gonad weight to body length data in *B. anoplus*. Where a = y intercept, b = slope of regression line, r^2 = regression coefficient and n = number of fish in the sample.

1980	Ovary	$Log_{10}a$	b	r^2	n
1980	June	-6,9157	3,3646	0,70	31
	July	-6,1237	2,9611	0,86	50
	August	-7,7760	4,0519	0,87	27
	September	-6,2606	3,2141	0,68	35
	October	-10,5144	5,8642	0,85	35
	November	-5,8802	3,0644	0,82	43
	December	-8,8323	4,8490	0,62	49
1981	January	-5,3374	2,7397	0,45	30
	February	-7,9876	4,2216	0,45	20
	March	-9,5861	5,0104	0,67	42
	April	-8,7877	4,4490	0,82	50

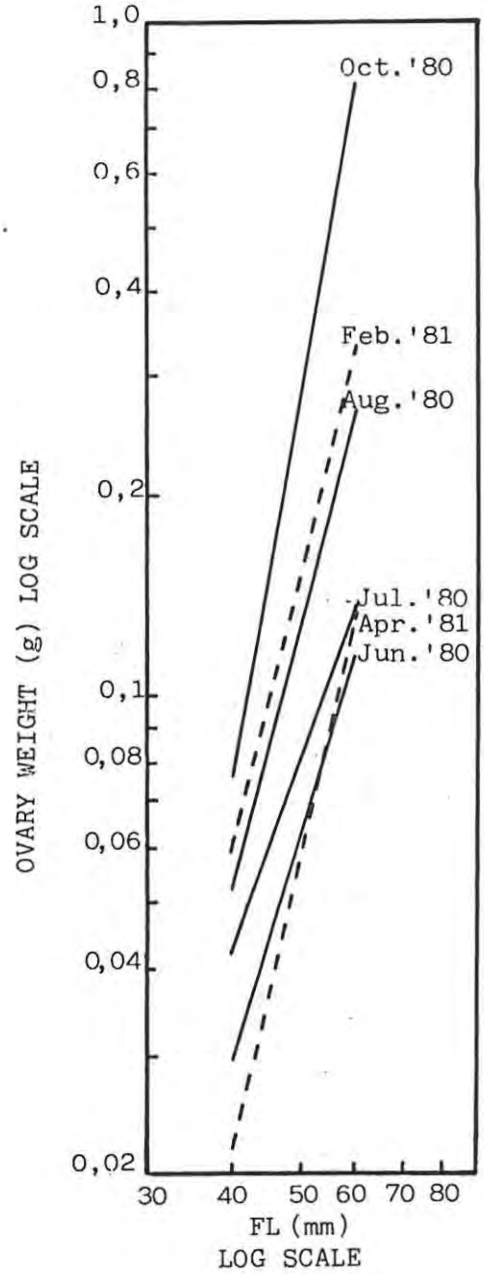


Fig. 15 Regressions of log ovary weight on log body length of B. anoplus for several months in the P.K. le Roux impoundment.

Subjective maturation stages:

The female maturation stages were more clearly defined and more emphasis could be put on female stages as indicators of the breeding cycle than for males (Fig. 16).

Stage 3 females first appear in August and by the end of October 61% are stage 3 and 30% in stage 4, 4% in stage 5, with several classified as partially spent. At the end of November 1% were fully spent, with most of the fish in stages 4,5, and 6. In March, 60% of the fish were in a resting condition and 20% were spent.

The majority of the males (Fig.16b) are in the resting stage (2) from May to July. In August over 50% of the males were classified as stage 3 which increased to over 70% by the end of September. In October the first ripe-running (stage 5) males were collected and over 40% of the males were at stage 4 of development. In December 50% of the males were ripe-running. At the end of April; the fish were again in a resting condition. In the second year a very similar trend is followed. This pattern follows the GSI values closely and confirms the long breeding season.

In the second year a similar pattern can be followed with a prolonged breeding season from October to March, and the spent fish of the second spawn occurring earlier (February) than the previous season. As was demonstrated with the more quantitive gonosomatic index, there is a distinct recurring seasonal pattern shown by the maturation stages which closely follows the temperature and photoperiod graphs (Fig.11).

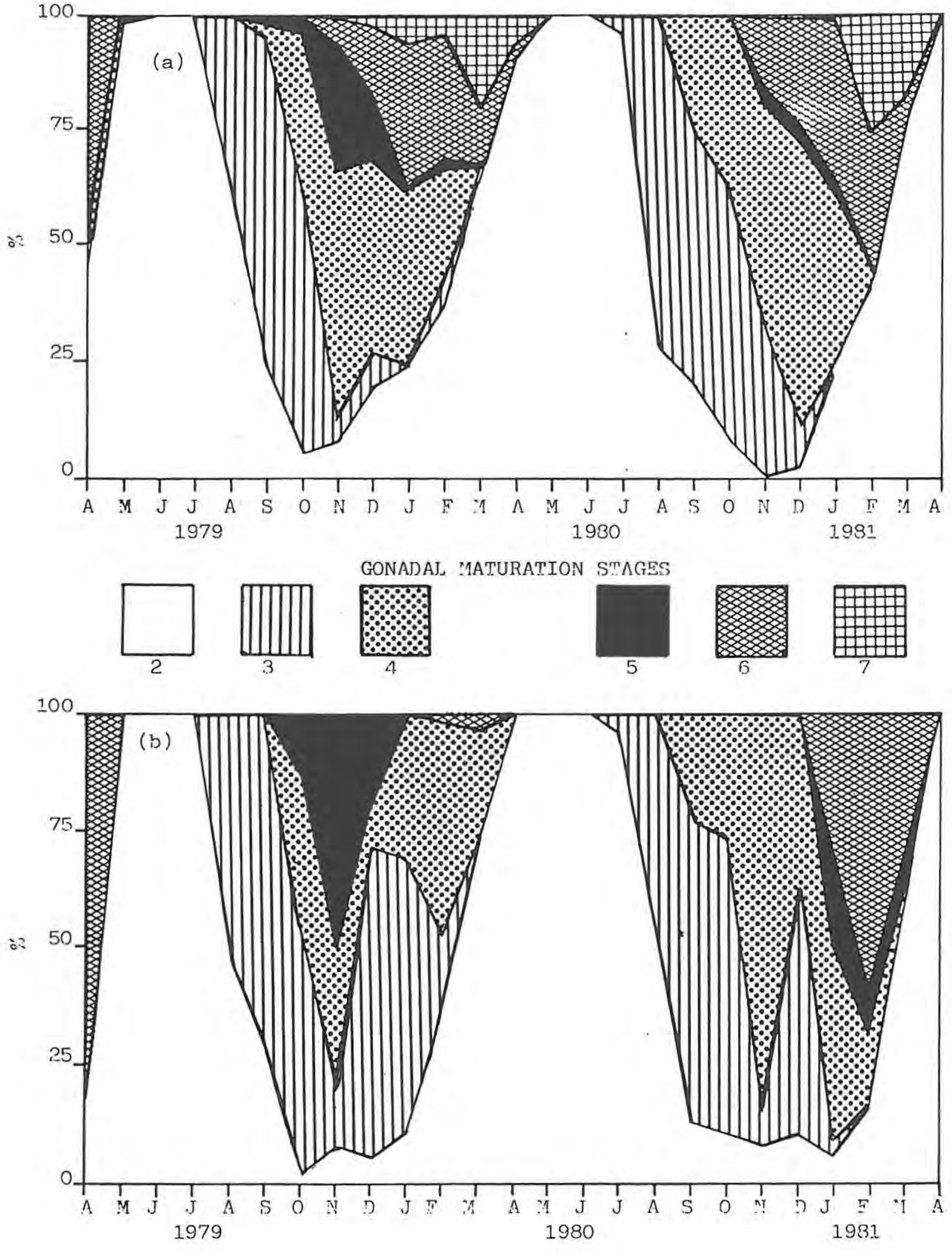


Fig. 16 Changes in the gonadal maturation stages of mature B. anoplus: (a) females, n = 3935; (b) males, n = 3300, April 1979 to April 1981 in the P.K. le Roux impoundment (Stages 2-7 explained in Table 10).

Gonad width:

The female and male gonad widths (Figs 17,18) indicate a similar seasonal pattern as did the GSI values, and subjective maturation stages.

Evidence of the prolonged spawning period is more evident in the gonad width graphs than in the GSI values for males, especially during the 1979/80 season. The first peak occurs in September to October followed by a decline after spawning with a second more modified peak in January 1980. This was especially evident in the fish over 45mm. After January in both years there is a noticeable decrease in gonad width until the gonads were in the resting condition.

Gonad width for both males and females appears to be a useful indicator of spawning times and possibly frequency. In field studies where an accurate chemical balance is not available, gonad width could be a simple and valuable alternative quantitative method of following gonad changes used with the subjective gonadal maturation stages.

Ova diameter frequency:

In August when the photoperiod increased (11h) and water temperatures increased, the ovaries began to swell and primary oocytes were readily observable under low magnification (8X). The oocyte size distribituion becomes distinctly more skewed after this period (Figs 19&20). By the end of September the ovaries had swollen, and females could easily be distinguished due to their distended abdomens. The primary oocytes had become well supplied with yolk and were yellow in colour. In September 1980 the larger ova form a discrete mode easily separated from the recruitment stock. The ovaries also contained many smaller (<0,7mm) less developed oocytes with yolky nuclei. The appearance of the ovaries remained fairly constant until spawning except for the increase in size of the primary oocytes.

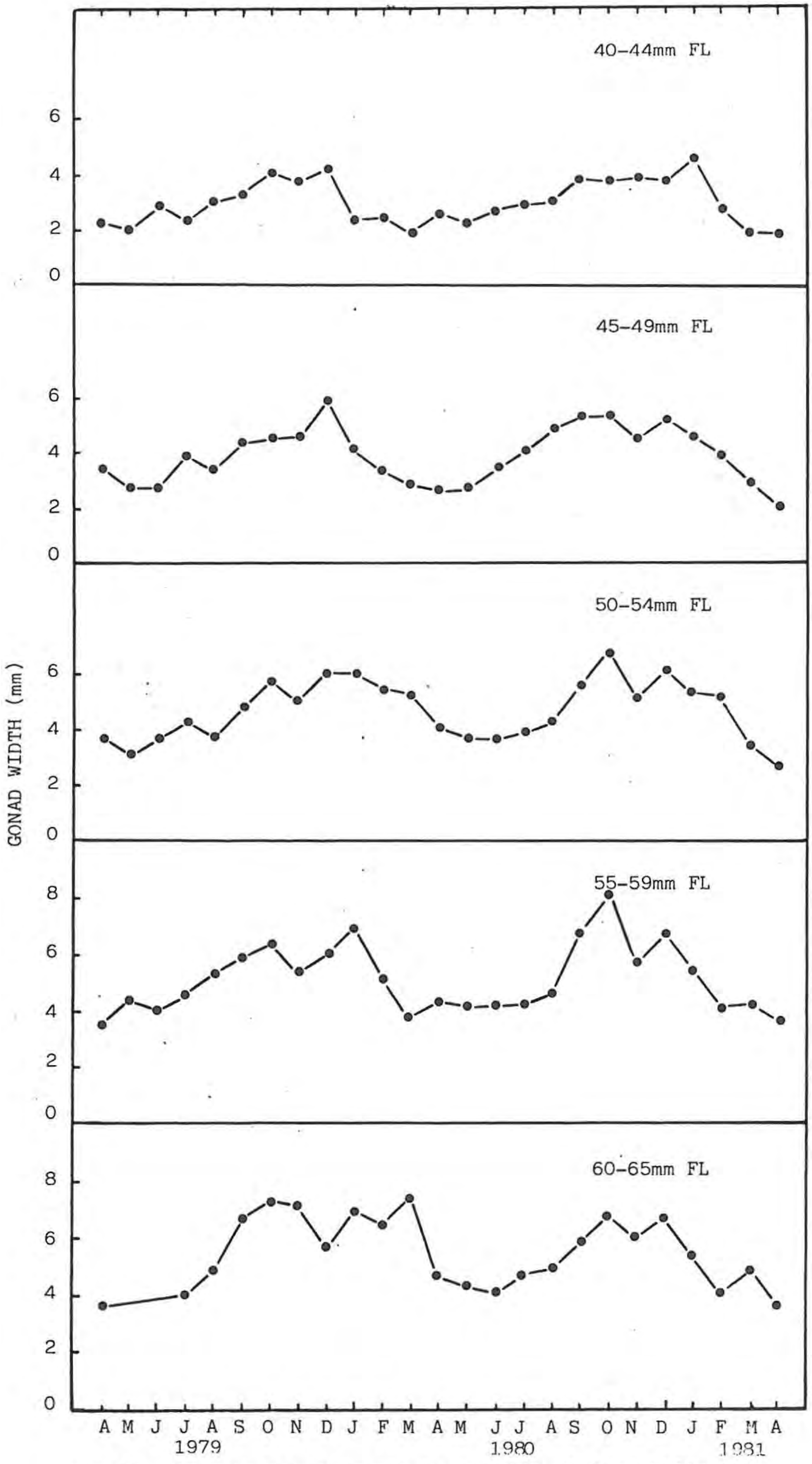


Fig. 17 Gonad width of female B. anoplus of five different length classes for a 25 month period in the P.K. le Roux impoundment.

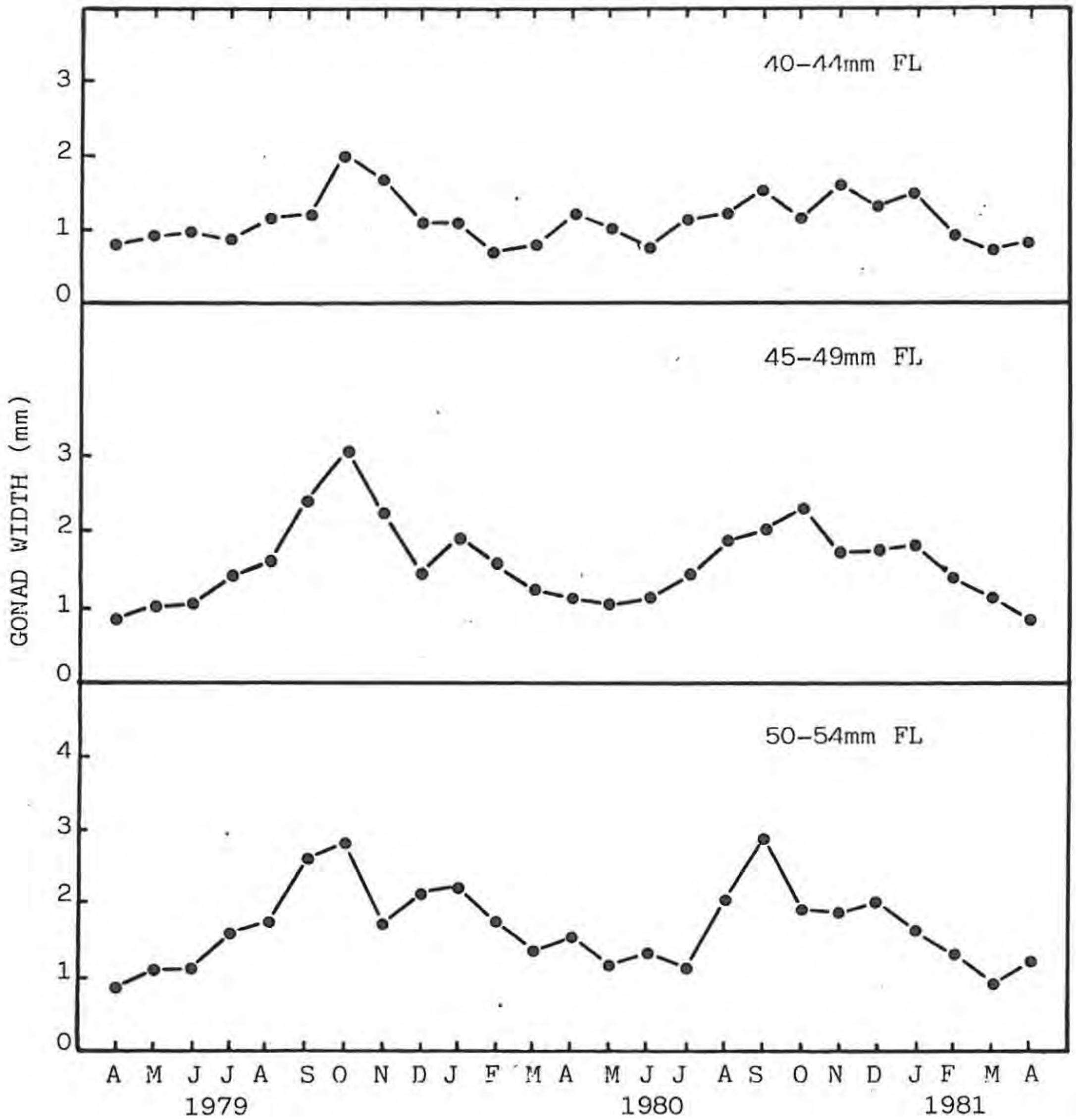


Fig. 18 Gonad width of male B. anoplus of three different length classes for a 25 month period in the P.K. le Roux impoundment.

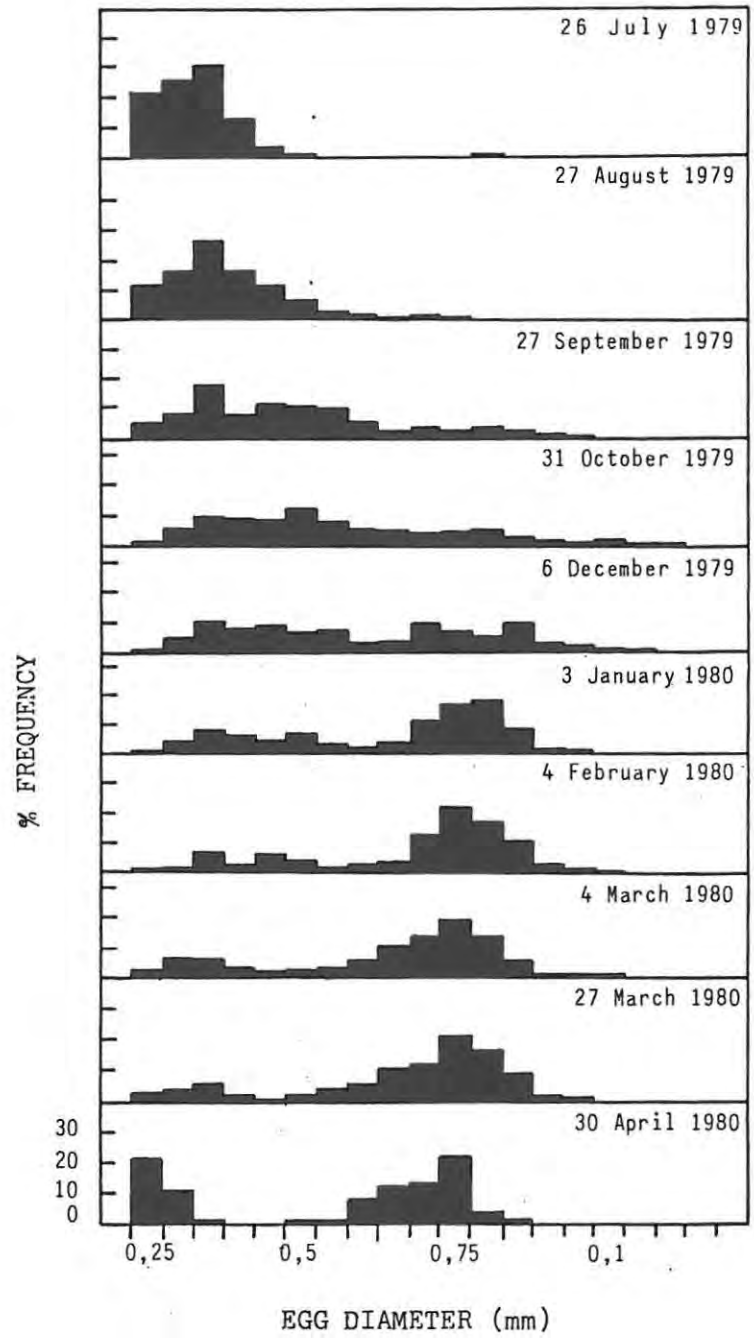


Fig.19 Monthly changes in size distribution of intra-ovarian eggs of mature B. anoplus in the P.K. le Roux impoundment (July 1979 to April 1980).

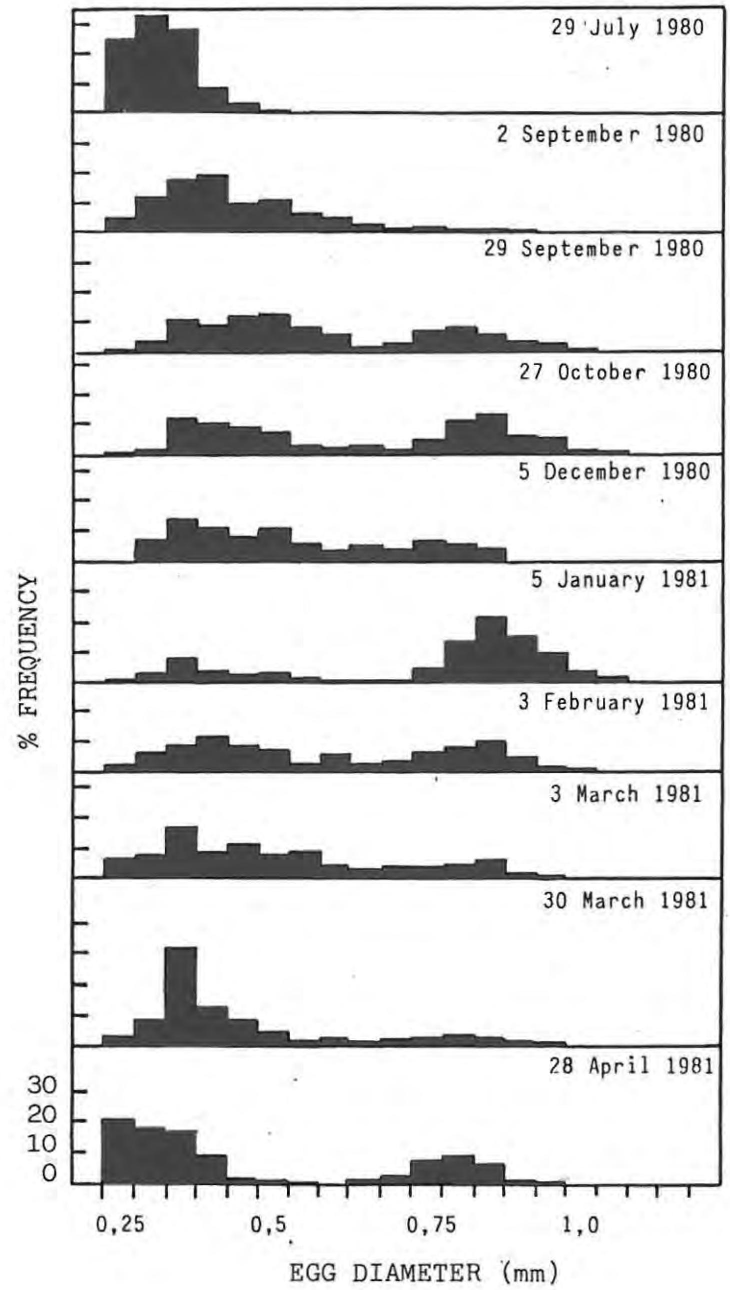


Fig.20 Monthly changes in size distribution of intra-ovarian eggs of mature B. anoplus in the P.K. le Roux impoundment (July 1980 to April 1981).

In January of both years there are discrete peaks of the two ova size groups with the mature ova dominating unlike the earlier (September) pattern.

In February to April 1980 the mature ova had a mode of 0,75mm in diameter whereas in the following year the eggs were slightly larger, with the mode at 0,85mm.

The apparent retention of the large ova at the end of the first reproductive season would indicate that these eggs would have to be resorbed. The second year clearly shows the pattern one would expect from a fish which spawns twice in a season (Fig.20). In April 1981, there are relatively fewer mature ova to resorb and the main stock of eggs measured were similarly distributed to the July 1980 pattern.

The retention of small (<0,7mm) yolky ova in the ovary after the first spawning, and their subsequent growth, indicates the possibility that individual females spawn more than once during the breeding season.

By the end of May the females were spent and the ovaries were thin and ribbon-like containing only a few resorbing ova. They remained in this state until the following spring.

Largest ova diameters:

Mean diameters of the largest ova in females from site six increased from late August to late October in both years (Fig.21). The pattern of development followed the trends observed in the increasing GSI values. The maximum size was reached in October, and this size was maintained until March, when the eggs started to resorb.

The primary ova in the second year were slightly larger than in the first

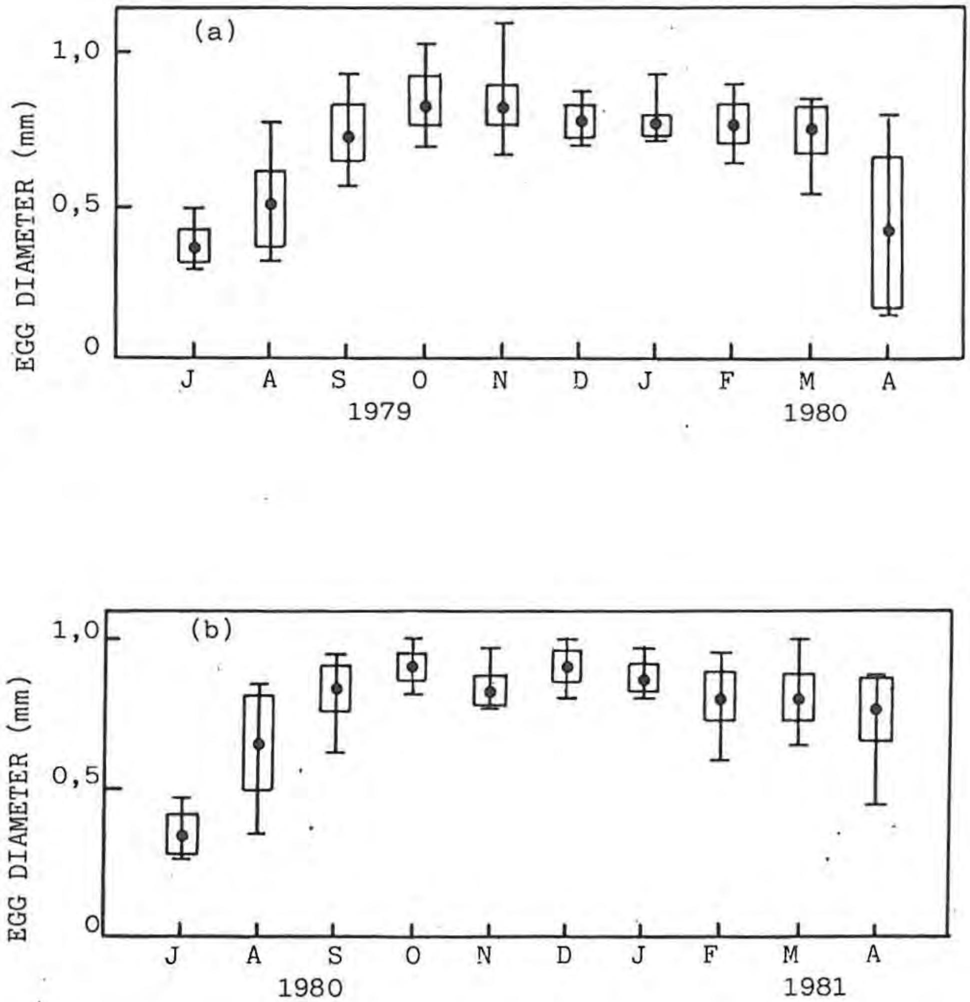


Fig. 21 Seasonal size changes in the diameter of the largest ova in mature B. anoplus females; (a) July 1979 to April 1980; (b) July 1980 to April 1981.

(means are dots, ranges vertical bars and ± 1s.d. are boxes) year of the study, which was also seen in the ova frequency data. The largest ovum measured in the study was 1,05mm in diameter collected in late October 1979. The unovulated mature ova ranged in size from 0,70 - 1,05mm in diameter.

Ova size frequency for different length groups:
The smallest fish (39mm) in the October 1980 sample shows a weak bimodal pattern of ova size compared to the four larger fish which have very similar bimodal frequencies (Fig.22). This would indicate that the smaller fish would possibly not participate in the first spawn of the year.

In the December 1980 sample (after the first spawn), the recruitment eggs in all fish are maturing, and it is quite evident that at least the three largest fish have spawned (Fig. 22b).

Tubercle development and breeding dress:
Breeding tubercles(secondary sexual characters) were noted on the males several months before the first spawning. The appearance of tubercles on the pectoral fins and the golden colouration constitute the most evident secondary sexual characters (Plates 15 & 16).

Table 12 summarizes the development of tubercles during early, middle and late periods of the spawning season. Development commences in July to August and reaches a peak by late October to November, which would coincide with the first spawning. The males at this time are a bright golden colour, and have sharp pointed tubercles (Plate 15a).

After January the tubercles become rounded and are not as prominent (Plate 15b) and in addition the golden colouring is not as brilliant. Small degenerating (rounded) tubercles were still present in large males during April, but were completely eroded by May (Plate 15c).

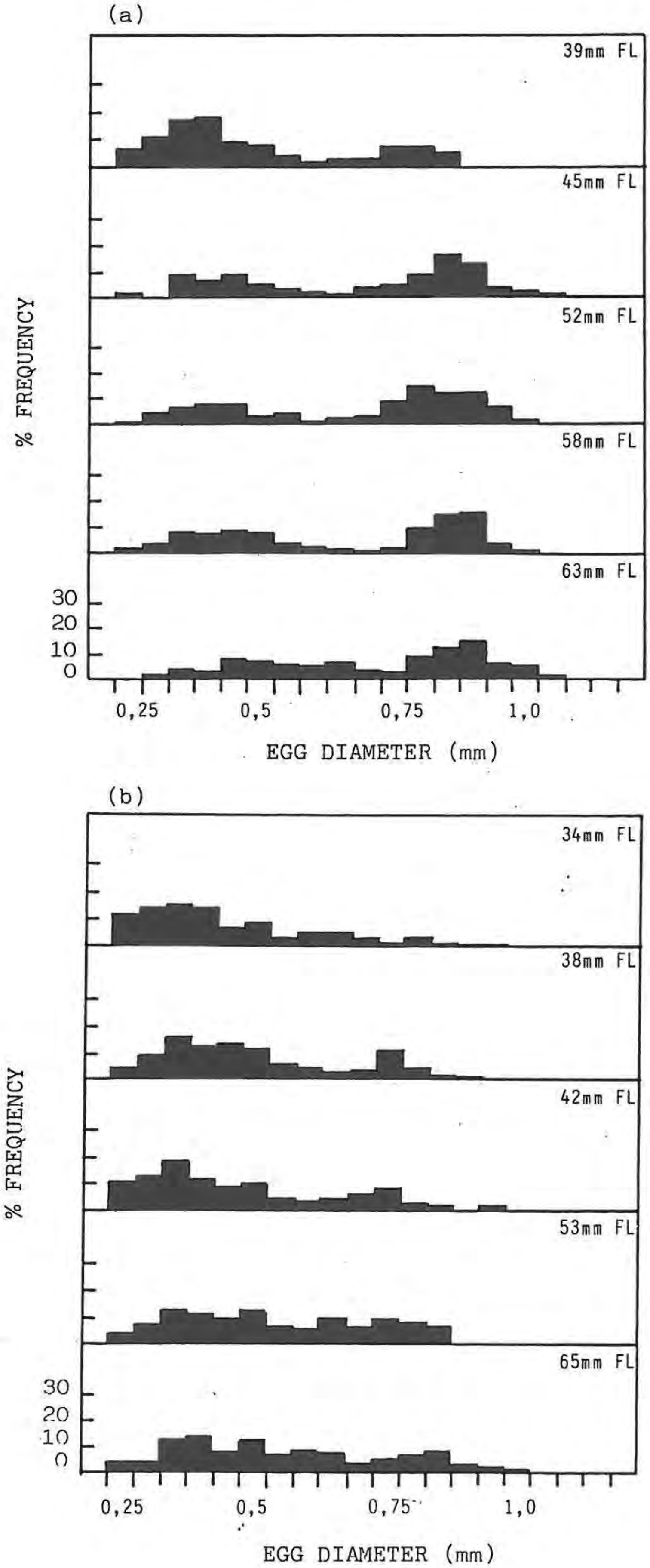
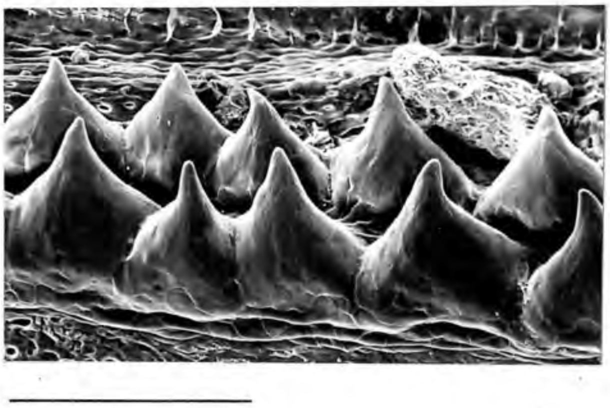
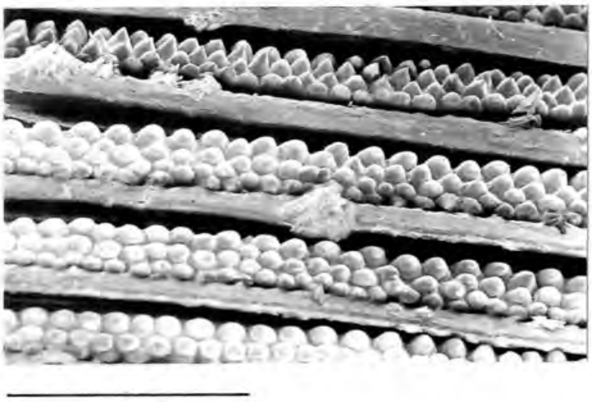


Fig. 22 Percentage frequency of intra-ovarian eggs of mature B. anoplus females of different lengths, collected at site 6 in the P.K. le Roux impoundment on (a) 27 October 1980 and (b) 5 December 1980.

(a)



(b)



(c)

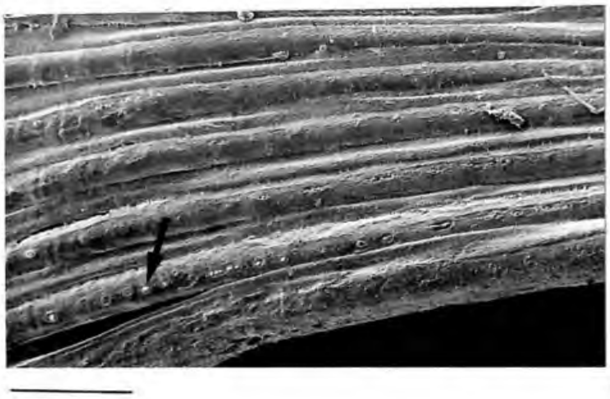


Plate 15 Tubercles on the pectoral fins of male B. anoplus collected in the P.K. le Roux impoundment.
(a) 55,8mm FL male, 1-11-79, scale bar = 0,1mm
(b) 49,3mm FL male, 3-1-80, scale bar = 0,5mm
(c) 50,0mm FL male, 27-5-79, scale bar = 0,5mm
arrow indicates eroded tubercles.

(a)

(b)

Plate 16 (a) Breeding colouration of two male B. anoplus in contrast to female (middle). Scale bar = 10mm
(b) Bright golden colour of freshly collected, migrating B. anoplus males, Berg River, November, 1980.

TABLE 12

Seasonal changes in the percentage of sexually matúre *B. anoplus* (40mm or larger) at given stages of tubercle development.

Date collected		Number examined	Percentage at given* stage of development			
			0	1	2	3
	25-6-79	3	100	0	0	0
	27-8-79	20	85	15	0	0
	27-9-79	20	0	35	65	0
1979/80	1-11-79	17	0	0	6	94
Season	6-12-79	20	0	0	0	100
	4-1-80	18	0	0	11	89
	29-7-80	20	75	25	0	0
	2-9-80	20	10	65	25	0
	29-9-80	20	0	0	5	95
1980/81	29-10-80	20	0	0	0	100
Season	4-12-80	13	0	0	0	100
	24-4-81	20	0	0	25	75

* 0 - no tubercles, 1 - little tuberculation, 2 - moderate tuberculation, 3 - maximum tuberculation. See text for descriptions.

Males with maximum tubercle development have very enlarged testes, and those lacking tubercles were found to be immature. Several males exhibit a few tubercles at a length of 32mm.

On the basis of tubercle development, males can probably successfully breed from late October to late April which again indicates a prolonged breeding season.

Fecundity:

The absolute fecundity of B. anoplus is related exponentially to fork length (FL) (Fig. 23) and linearly to weight (W) (Fig. 24) as is common in fish (Bagenal, 1973). The first curve was transformed to a straight line by a logarithmic transformation (Bagenal, 1973). The lines of best fit are described by the expressions:

October, 1979 $\text{Log AF} = 3{,}794(\log \text{FL}) - 3{,}458 \quad (r^2 = 0{,}86)$

$\text{AF} = 574{,}181\text{W} - 83{,}592 \quad (r^2 = 0{,}66)$

October, 1980 $\text{Log AF} = 4{,}364(\log \text{FL}) - 4{,}230 \quad (r^2 = 0{,}80)$

$\text{AF} = 785{,}671\text{W} - 79{,}087 \quad (r^2 = 0{,}87)$

where AF = absolute fecundity

FL = fork length

W = total weight

In October 1979 there is less of a relationship between absolute fecundity and weight than in October 1980 when the fish were in better condition (p.170) and had higher GSI values.

The lines of best fit for mature ova ($\geq$0,7mm) were also calculated for the fish collected in October 1979 and 1980, before the first spawn, and for fish collected before the second spawn, February 1980 and 1981 (Figs 25 & 26).

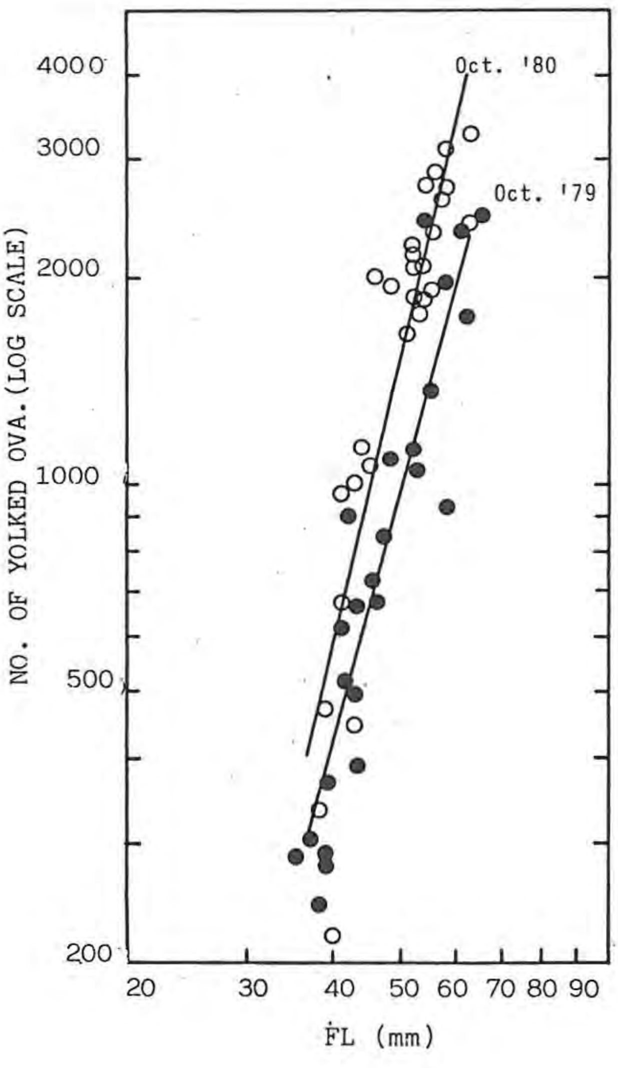


Fig. 23 The relationship between absolute fecundity (all yolked ova) and fork length (log-log scale) in 25 B. anoplus collected on October 31, 1979 (●) and 28 B. anoplus collected on October 27, 1980 (○) from site 6, P.K. le Roux impoundment.

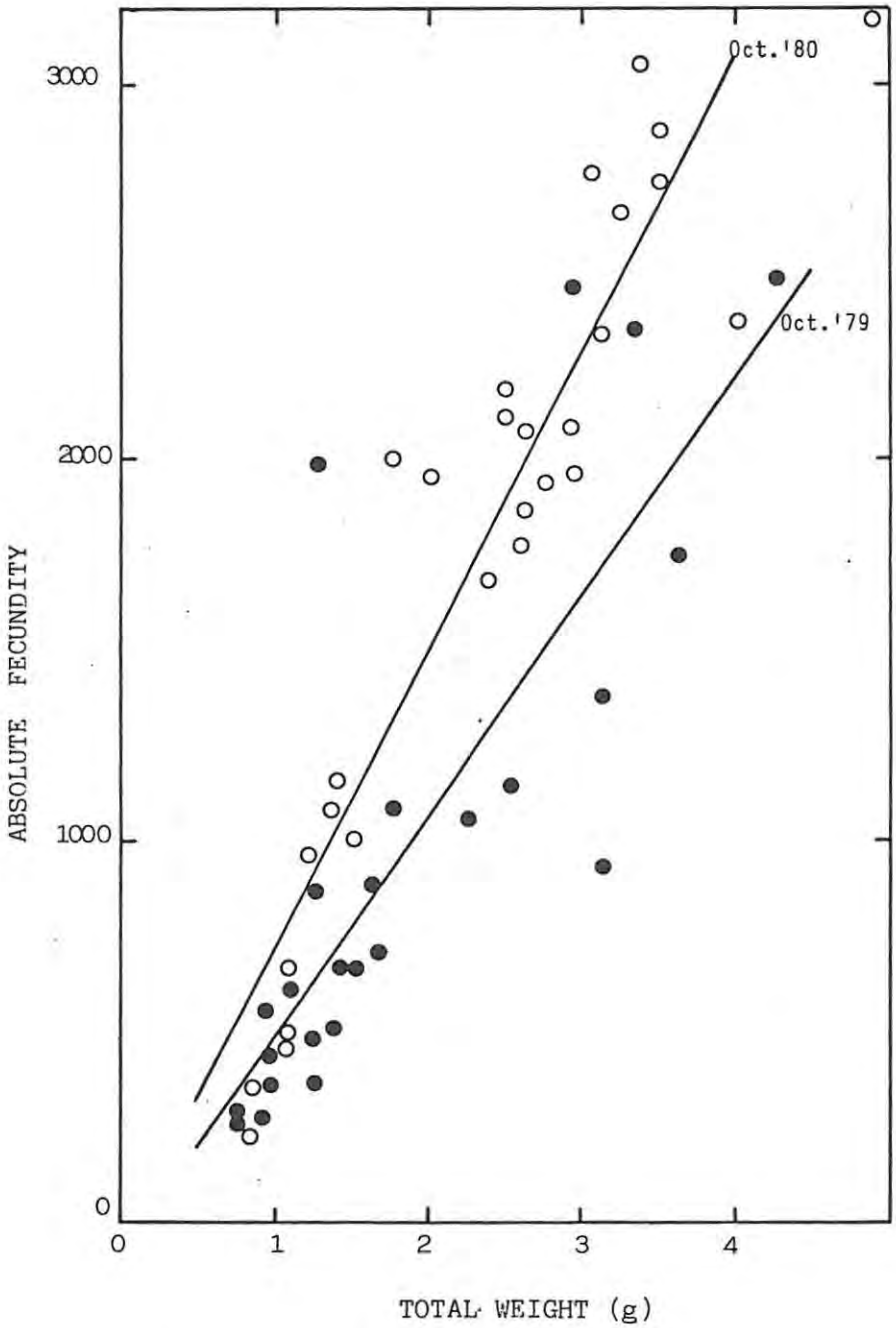


Fig.24 The absolute fecundity (total all yolked ova) of B. anoplus related to total weight for 25 fish collected on October 1979 (●) and 28 fish collected on October 1980 (O), P.K. le Roux impoundment.

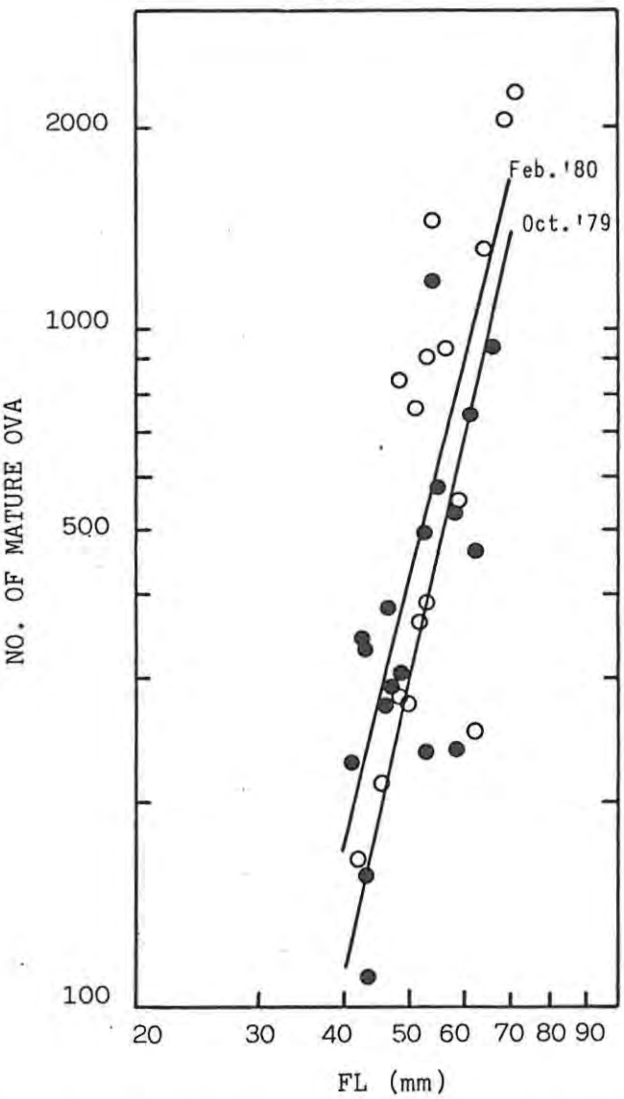


Fig.25 The relationship between the number of mature ova (≥0,7mm) and fork length (log-log scale) in 18 B. anoplus collected on October 31,1979 (●) and 16 B. anoplus collected on February 4, 1980 (○), from site 6, P.K. le Roux impoundment.

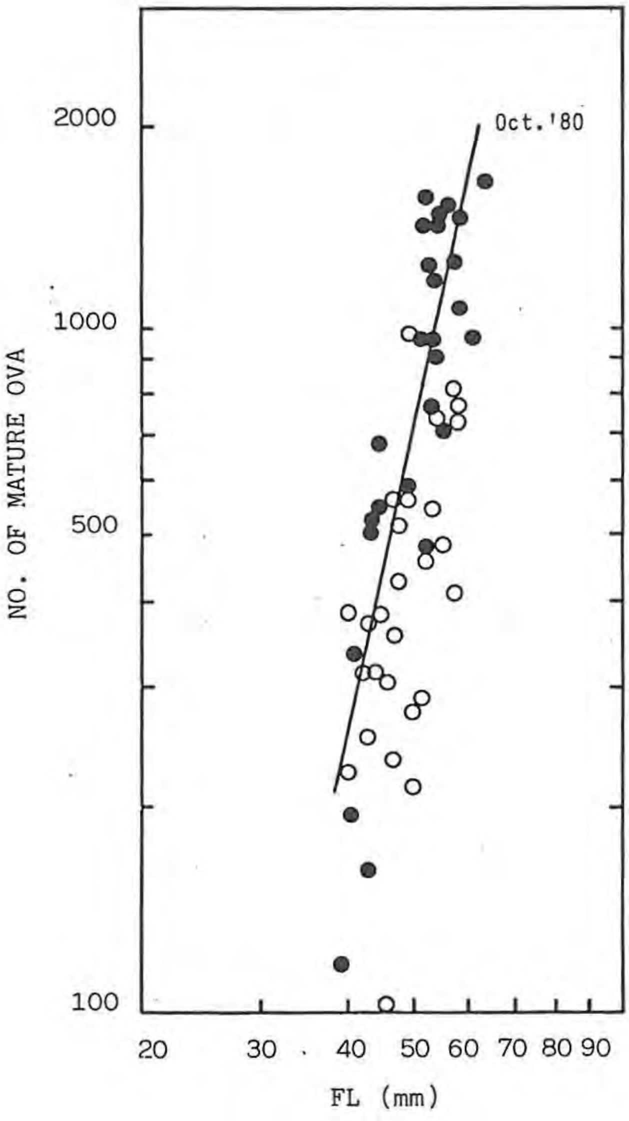


Fig. 26 The relationship between the number of mature ova (≥0,7mm) and fork length (log-log scale) in 27 B. anoplus collected on October 27,1980 (●) and 27 B. anoplus collected on February 3, 1981 (○) from site 6 P.K. le Roux impoundment.

October. 1979 log F = 4,433(log FL)-5,045 + (r^2 = 0,70)

February, 1980 log F = 4,057(log FL)-4,264 + (r^2 = 0,50)

October, 1980 log F = 4,543(log FL)-5,046 + (r^2 = 0,72)

February, 1981 - no relationship

where F = count of mature ova

FL = fork length

There is less (February, 1980) or no (February, 1981) relationship between the mature ova count and length after the fish have spawned once in the season. This might indicate that some fish participate to a greater degree than other fish in the same length group during the second spawn.

Pool breeding experiments:

B. anoplus bred in the still water pools and in the one small asbestos pool. Therefore B. anoplus do not have to undertake a spawning migration for a successful breeding. The first fry were seen on November 16, 1980, with a size range of 8,5 to 15,9mm FL. The largest fish was in the metalarval phase (Snyder, 1976) and from laboratory reared fish this developmental stage was reached after forty days from fertilization of ova. This would place the spawning date at approximately the time of introduction of the fish to the pools (October 7, 1980). Developmental rates are directly affected by food supply and temperature so that the spawning could have been several weeks later than indicated by the laboratory reared fish. In one pool, the fish spawned again in February 1981 and November 1981

Fry emergence:

From the length frequency graphs in section 7 p.152, the pattern of fry emergence can be seen. In late November 1979 the first fry are recorded from the impoundment site. The modal length of fry is 12mm (range 8-20mm). This wide range indicates that several spawnings have possibly occurred, although the modal length indicates one major spawning during this period. Possibly larval growth varies or that eggs of different sizes were released where larvae from the larger eggs would grow faster. At the end of March another spawning has occurred, but not as pronounced as the earlier spawning.

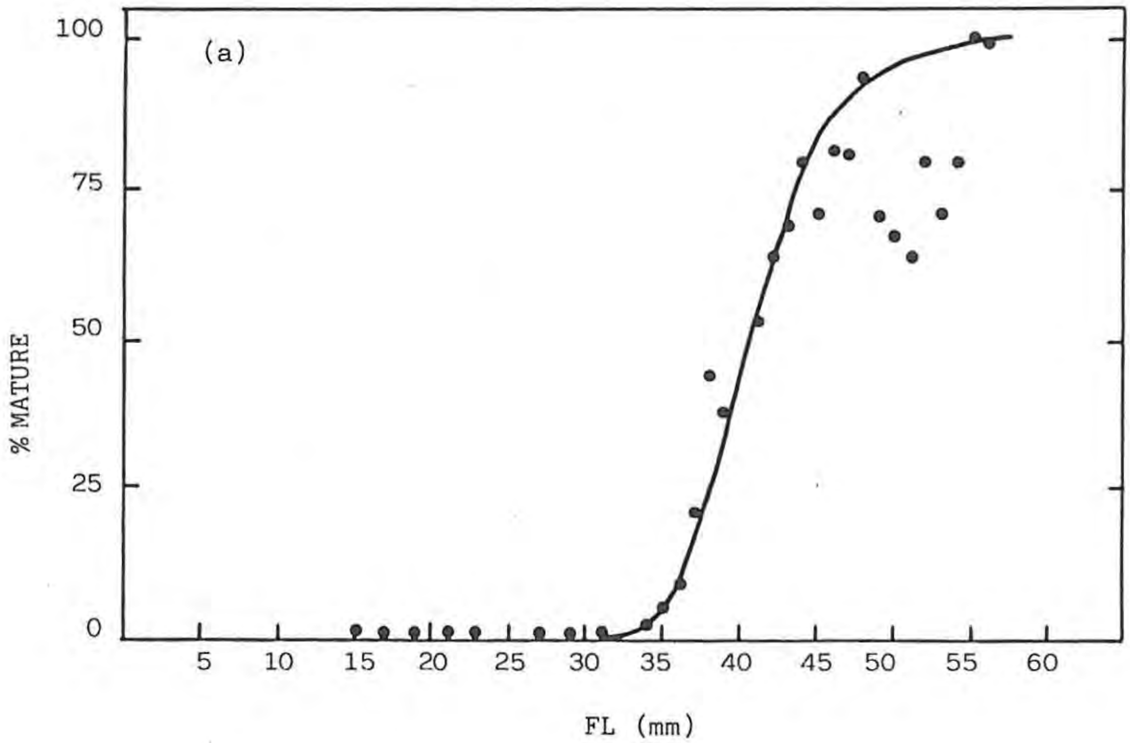
In the second year, the first spawning occurred in November, and fry have a modal length of 12mm (range from 7-15mm). Between the November and December collections the major spawning of the year occurred. The end of summer spawn occurs in February (see p.155).

The fry emergence pattern of these two reproductive periods confirms the prolonged reproductive season of this minnow species. Generally there is a major spawning between November and December when conditions were favourable, this is followed by a "back-up" spawn between February to April.

Median size at first maturity:
The median size at first maturity (length at which 50% of the catch is mature) was calculated from fish collected during the reproductive season (September to March) of both years. In the first year, the median size for males was 40-41mm and in the 1980/81 season the length was slightly smaller 38-39mm (Fig.27).

For females the median size was 39-40mm in the 1979/80 season and 38-39mm in 1980/81 season (Fig.28).

In this work the median length at sexual maturity has been taken as 40mm for both male and female minnows. From the length frequency data (see p. 152) it is seen that this length is attained by the end of April by fish spawned in November (6 months). These fish would therefore be ready to breed at the start of their second summer, that is within their first year of life.



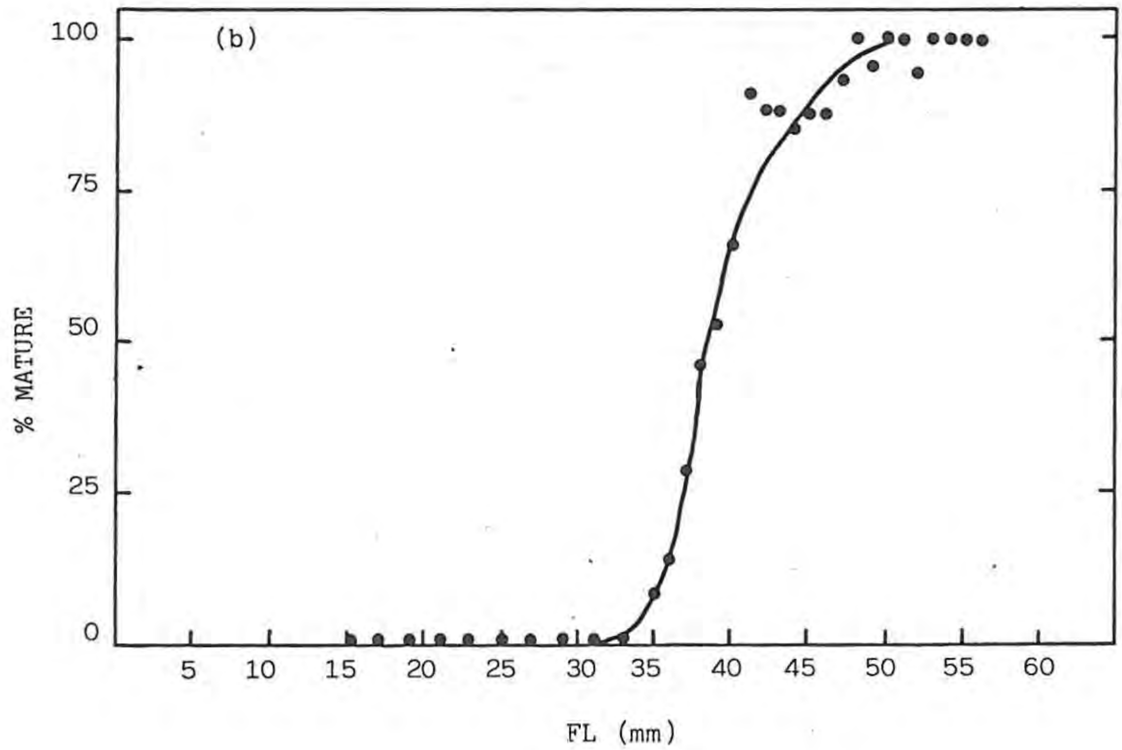
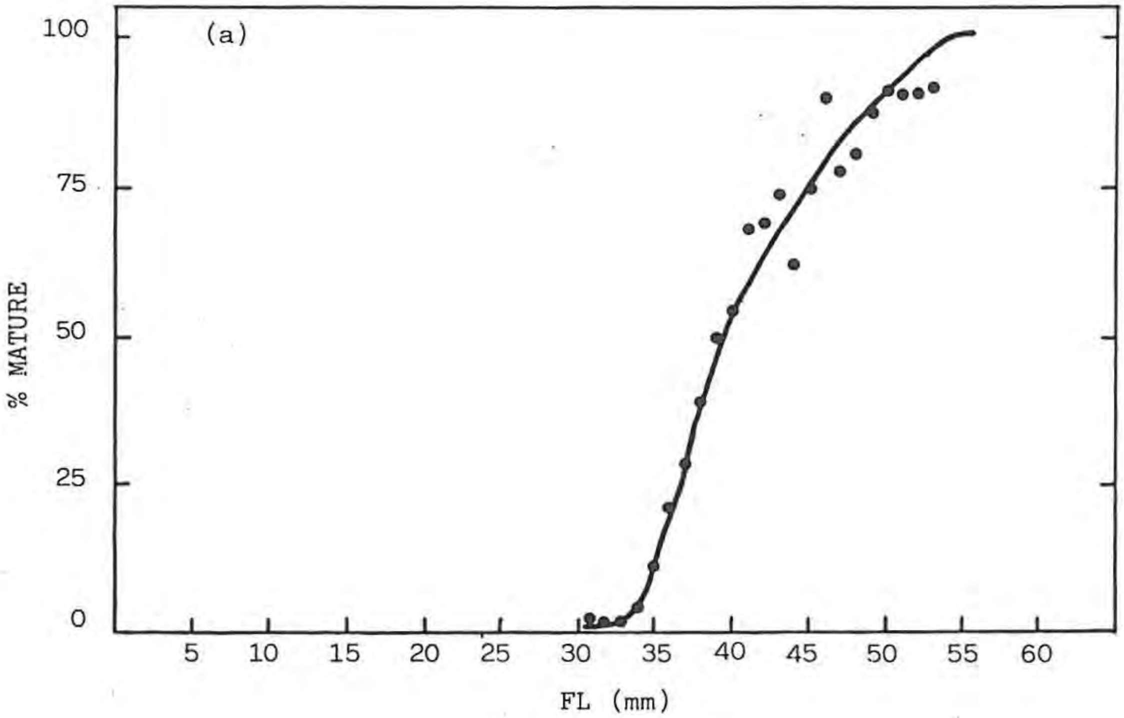


Fig. 27 Medium size at first maturity for B. anoplus males collected from the P.K. le Roux impoundment, (a) September 1979 to March 1980 (n = 2117) and, (b) September 1980 to March 1981 (n = 1603).



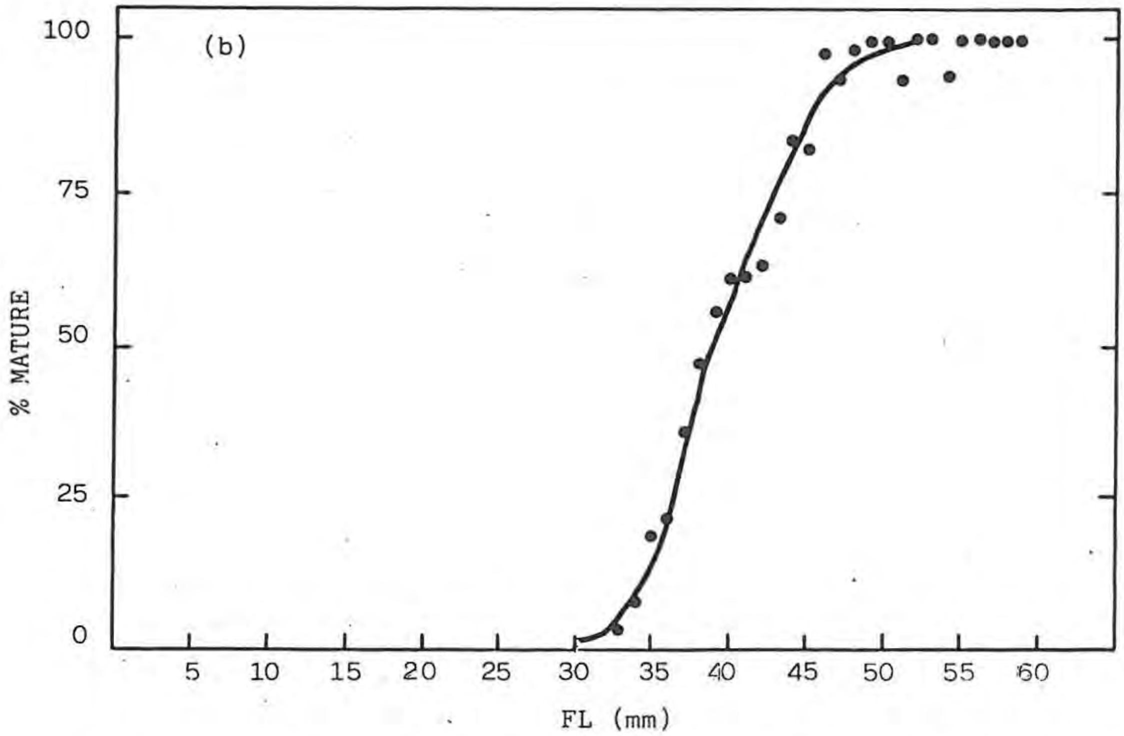


Fig. 28 Median length at first maturity for B. anoplus females collected from the P.K. le Roux impoundment, (a) September 1979 to March 1980 (n = 2341), (b) September 1980 to March 1981 (n = 1561).

Male and Female sex ratios:

The male:female sex ratio was followed at each of the five main collecting sites for the 25 month period. Insufficient data was available for the open shore locality (site 73) so this data has not been included (Fig.29). The overall male:female ratios for site 6 was 1:1; site 8 1:1,1; site 68 1:1; site 72 1:0,8 and for site 73 1:1,1. The ratio of all sexed fish (n = 22 920) was 1:1 for the 25 month period.

The sex ratio in the early part of the breeding season, November to December differs from the rest of the year (Fig.29). The difference is especially pronounced in the 1980 collections. In the three impoundment sites (6,8 and 68) the ratios vary from 1:1 relationship to 1:3,1 ; 1:4,4 and 1:2,1 during November 1980.

By contrast the riverine site (Site 72) had considerably more males in November (1:0,1) and December 1980 (1:0,3). These data would suggest a movement of males towards inflowing water during this period. Males in breeding colours were collected during migration runs up the Berg River at this time of the year (Plate 16b).

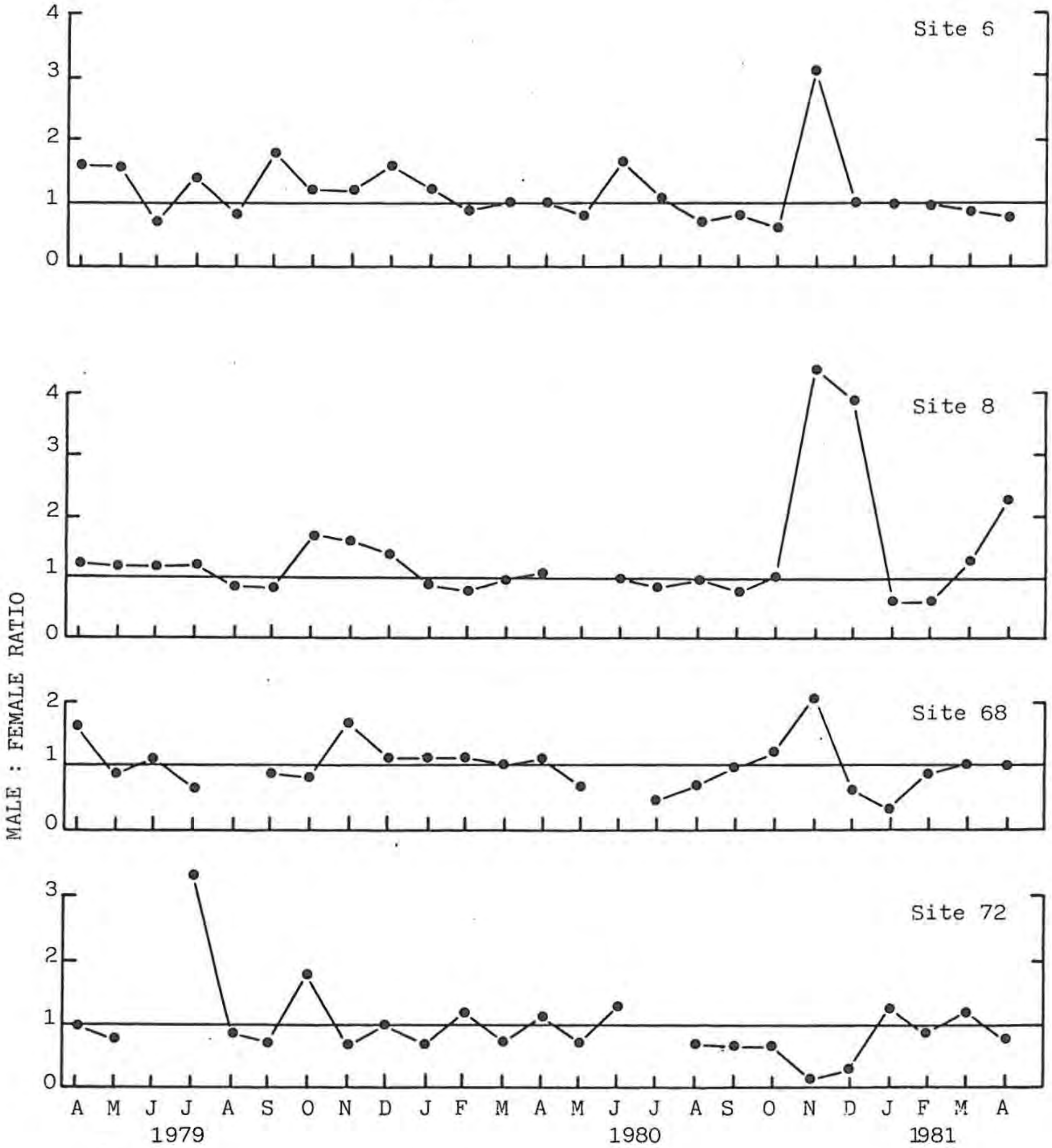


Fig. 29 The male to female sex ratios for B. anoplus over a 25 month period in the P.K. le Roux impoundment at four sampling sites (horizontal line indicates a 1:1 ratio, above line more females).

Discussion

It is usually found that some relation exists between time of breeding and the special needs of the organism (Bullough, 1939). Like the vast majority of teleosts (Scott, 1979), the reproductive cycle of B. anoplus is based on an annual periodicity. In the study area the range of cyclical environmental conditions is fairly extreme and it appears that the reproductive cycle of B. anoplus tends to be regularly recurring and fairly accurately repetitive from year to year. Further data over several years are needed to confirm this trend.

These regularly recurring reproductive cycles are typified by fish which live in freshwaters in the cold temperate zones. Here habitats are dominated by annual cycles of environmental variables such as daylength, temperature and food availability.

Between the tropical and temperate zones the environmental cycles are also regularly repetitive but less marked than in the colder areas and the spawning periods are therefore more prolonged. This would allow for such strategies as repeat spawning of successive batches of gonadal products.

The regularity of fish breeding seasons has attracted the attention of many investigators and lead to the search for some external environmental factor(s) which may regulate reproduction (Bullough, 1939). Scott (1979), in a recent review of the control of teleost reproduction, concluded that it is still not possible to give a comprehensive answer to the question "How do teleost fish time their reproductive cycle?" He notes that the correct timing confers a selective advantage and regularly recurring environmental events regulate the timing of the cycles, but the nature of these cues is far from clear, especially during the complex of activities called spawning.

Farringer et al., (1979) stated that the differences in stream physiognomy may explain the divergent observations regarding the effect of rainfall on reproduction in desert-dwelling cyrpinids in North America.

A review of the reproductive biology of several African small Barbus species is given in Table 13. There are two principal types of migration within a river system, longitudinal and lateral, with each of these requiring its own set of hydrological stimuli. In Africa there have also been divergent observations. In the Niger, B. occidentalis shows lateral migration associated with spawning (Daget, 1957), whereas in Nigeria B. occidentalis undertakes an upstream migration (Welman, 1948). It is possible that certain segments of the population can do either, depending on the system that they are in.

Small Barbus species in Lake Victoria and inflowing rivers have up-river spawning migrations coinciding with periods of flood (Whitehead, 1959; Welcomme, 1969). Welcomme (1969) found it difficult to isolate any one physical or chemical factor which induces longitudinal migration and Van Someren (1962) noted that it is probably the total flood condition which acts upon the fish. It has usually been found that large Barbus species are main channel spawners (Jackson et al., in prep.) The smaller Barbus species, in most cases would probably have to undergo lateral migration out of necessity, to shelter from the currents in the main channel. One exception is B. trevelyani which is a midstream spawner and does not undergo a lateral migration (Gaigher, 1975). Jackson (1961) stressed the importance of the potamodromous habit for the protection of the newly hatched fry from predation. Fryer (1965) noted that migration was important for the dispersal of the species over the whole river course.

TABLE 13

A review of the length of breeding season, fecundity, egg size and spawning habitats of some small African Barbus species.

Species	Locality	Breeding Season	No. of Months	Fecundity	Mature Egg Size (mm)	Spawning Habitat and Spawning Habits.	Reference
B. anoplus	Natal	September to March	7	-	-	-	Crass, 1964
B. anoplus	P.K. le Roux Dam	November to March-April	5-6	63FL-3250	1,0	-migration not necessary but some migrate -eggs adhere	This study
B. apleurogramma	Lake Victoria (stream)	-ripe fish present October to December and March to June.	-	36SL-818 58SL-1635	n.s.	-migrates upstream	Welcomme, 1969
B. kerstenii	Lake Victoria (stream)	-ripe fish present September to December and February to June	-	40-44SL-1170 70-74SL-2696	1,0	-migrates upstream -eggs adhere	Welcomme, 1969
B. liberiensis	Sierra Leone (stream)	June-July -single discrete season	n.s.	110TL-6-7000	1,0	-migrate upstream -eggs adhere	Payne, 1975
B. paludinosus	Natal	-mainly early summer	-	74FL-2200	1,0	-	Crass, 1964
B. paludinosus	Lake Victoria (stream)	-only ripe fish in rainy seasons	-	86SL-6100 112SL-11450	0,8-1,0	-migrates upstream	Welcomme, 1969
B. paludinosus	Lake Sibaya, Natal	October-February	5	-	-	-	Bruton, 1979
B. paludinosus	Lake Chilwa	-extended -throughout rainy season (November-April)	6	50-60TL-255-801 112TL-2513	-	-possibly a spawning migration	Furse, 1979
B. toppini	Kruger Park	-late summer	-	-	-	-possibly a spawning migration	Pienaar, 1978
B. trevelyani	Tyume River	-end of September to February/March	6-7	65-69FL-900 >100FL-4000-5000	1,0-1,3	-possibly spawns midstream -migration possibly not necessary	Gaigher, 1975
B. trimaculatus	Kruger Park	-	-	-	-	-migrates upstream	Pienaar, 1978
B. trimaculatus	Natal	-spring and summer	-	117FL-8000	0,9	-	Crass, 1964
B. unitaeniatus	Kruger Park	-late summer	-	-	-	-	Pienaar, 1978
B. viviparus	Natal	-throughout summer	-	53FL-8000	0,9	-	Crass, 1964
B. viviparus	Lake Sibaya, Natal	September-February	6	-	-	-	Bruton, 1979

The fact that some of the newly hatched fry of B. anoplus float (p.142) and some do not would add support to this suggestion made by Fryer. Also the role of physicochemical conditions in the upstream sites might be important in the development of the embryos (Greenwood, in Fryer, 1965). In addition, Welcomme (1969) found that in some species the final stages of maturation take place during upstream migration. In the Hendrik Verwoerd impoundment B. anoplus undertook seasonal spawning migrations up inflowing tributaries or undertook lateral migrations when the water level of the impoundment rose and flooded the terrestrial vegetation. Similarly, in the P.K. le Roux impoundment some of the minnow population undergoes upstream spawning migrations, even in the very small temporary inflowing streams. They also spawn in areas where upstream migrations are hampered by a barrier, over which water flows. Inundated emergent macrophytes along the Seekoei River were also possible spawning sites, indicating lateral migration. In this case, because of the positive buoyancy of early larval stages, it is possible that these fish were bred further upstream and transported downstream by water flow. The Verwoerd impoundment collections provide fairly strong evidence that no spawning migration in flowing water is required. Only a rise in water level to cover a suitable spawning substrate, plus the appropriate environmental cues, is necessary.

In the B. anoplus studied it is evident that not all of the population behaves the same; some undergo upstream migrations while others breed along the shoreline of the impoundment. Similar divergent observations have already been noted for B. occidentalis (Welman, 1948; Daget, 1957). In the still water pool breeding experiment, the minnows also bred. No inflowing water was available to the fish, although all pools were exposed to rainfall. It can therefore be concluded that a spawning migration is not necessary to initiate spawning in B. anoplus. No successful spawning was achieved in the indoor tanks, either in still or flowing water, with or without the addition of rainwater.

From February to the start of winter is the time of year for laying down a store of fat around the guts and indicates the end of the reproductive season. This fat reserve begins to disappear, most noticeably in the females, from August to October when the fish become ripe.

The protracted reproductive season exhibited by B. anoplus is also typical of many Notropis species (Cyprinidae) in the southern United States (Heins et al., 1980). There is also a similarity in the length of the reproductive season. For example, in studies on N. roseipinnis from the Mississippi (Heins & Bresnick, 1975), N. lutrensis in Central Texas (Farringer et al., 1979) and for an undescribed Notropis species in Alabama (Heins et al., 1980), the reproductive season was approximately five months for all species. The breeding period lasted from five to six months for the B. anoplus population studied in the Hendrik Verowerd and in the P.K. le Roux impoundments. B. trevelyani also has a protracted breeding season of five to six months (Gaigher, 1975). The breeding season of B. paludinosus in Lake Chilwa is an extended one through the months of the rainy season and sometimes longer (5-6 months; Furse, 1979). Similarly the breeding season of B. paludinosus and B. viviparus is an extended one in Lake Sibaya (Bruton, 1979).

In all the Barbus and Notropis species mentioned above the protracted reproductive season is probably facilitated by the long period of relatively high temperatures and the long day lengths experienced. Photoperiod and temperature are widely accepted as two important proximal factors regulating reproductive cycles in fishes (Schwassman, 1971; De Vlaming, 1972, 1974).

Payne (1975) noted that Barbus species from many parts of Africa, as well as other riverine fish, have a reproductive cycle geared to the early part of the rainy period, but he found several exceptions. For example, B. sylvaticus and B. lorenzi both show differential gonad development and spawn probably continuously all through the dry season, if not the whole year (Loiselle & Welcomme, 1971). In B. guildi spawning only occurs at the end of the rainy season (Loiselle, 1973). Welcomme (1969) found that B. magdalenae from Lake Victoria have become more or less adapted to a lacustrine existence and it does not seem to spawn in rivers, and fish are ripe throughout the year in the lacustrine environment.

The advantage of having a prolonged breeding season is that an individual fish or the population may have multiple clutches throughout this period. The ovarian development in all mature female chubbyhead barbs suggests that more than one clutch is produced by an individual female. This is also confirmed by the relatively few totally spent females compared to partially spent specimens collected after the first spawning. B. anoplus females probably cycle between stage 6 (partially spent) back to stage 4 (late maturing) then to stage 5 (ripe-running) when environmental conditions are suitable during the breeding season.

In studies of N. roseipinnis (Heins & Bresnick, 1975) and B. trevelyani (Gaigher, 1975), as well as this study of B. anoplus, there were no direct observations on multiple clutches. The gonosomatic values, ova frequency, ova size, gonad widths and emergence of fry demonstrate that there is a bimodal pattern with discrete peaks of major spawning activity in the early spring and late summer. It can therefore be concluded that individual B. anoplus females breed at least twice during a breeding season (November to April).

These major spawnings are possibly triggered and dependent on rainfall periods or water level fluctuations.

Heins & Bresnick's (1975) study of N. roseipinnis demonstrated that it would be possible for ovarian cycling to take place within a single month, since there was a rapid maturation of ovaries at the start of the season. In B. anoplus the maturation of ovaries follows a more leisurely pattern over three to four months (July to October), this would still allow for a second spawning even if it is relevant to consider this same time span (4 months). In fact I doubt whether this is a factor, considering that the early development occurs in the winter months and initially relies on fat reserves. The fat reserves have mainly been depleted by the first spawn, so a different energy source would have to be relied upon, i.e. the summer food supply. This food supply would have a very important influence on the second spawn, whereas the first spawn would have mainly relied on the previous summer's food reserves.

In the Barbus species of Lake Victoria and its inflowing rivers it is not certain whether individual fish spawn at only one or at both periods of flood (Payne, 1975).

Whitehead (1959) did not note any differential egg development. He suggested that since the flood periods were close together the two spawning periods resulted from sections of the population spawning at different times. The data of Welcomme (1969) for B. apleurogramma indicate that there is a possibility of a biannual cycle for this species (Payne, 1975).

B. ablabes in the Ivory Coast has a single spawning season in the early rains (Daget & Iltis, 1965), similarly Barbus species of Chad and from the Volta river system also have a single spawning season in the early rains (Blache, 1964; Hopson & Hopson, 1965). Payne (1975) found that _B. liberiensis_ living in forest streams of Sierra Leone and Liberia have a single discrete breeding season coinciding with the early part of the rains, during which the eggs appear to be shed all at the same time.

Female _B. paludinosus_ in Lake Chilwa may also spawn more than once a season (Furse, 1979).

Fractional spawning is a strategy that allows the small coelomic cavity of fish to be used to hold eggs more than once per season and in this way fecundity can be increased (Nikolsky, 1963). For example, a pair of spot fin shiners (_N. spilopterus_) spawned twelve times in one season, and the female spawned eggs which had a volume of three times that of the female (Gale & Gale, 1977).

Fractional spawning also decreases the chances of one or more entire generations being lost due to unfavourable environmental conditions (Nikolsky, 1963), but at the same time it reduces the chances of all eggs being spawned under optimal environmental conditions (Gale & Gale, 1977). Gale & Gale also noted that fractional spawners would tend to produce year classes of uniform strength by eliminating the chances of having very strong and very weak year classes.

Few species which are fractional spawners have been discovered in temperate climates. They are mainly tropical forms where there is "No clear seasonal variation in the supply of plankton," (Nikolsky, 1963). Gale & Gale (1977) indicate that it would have been more prudent to point out that few species which are fractional spawners have been discovered in the temperate climates. The point these two investigators make is simply that the breeding habits of many of the cyprinids are not known, and that since the cyprinids in general have long breeding seasons, many of them could be fractional spawners.

The long reproductive season of N. roseipinnis appears to be adaptive to unstable coastal stream environments (Heins & Bresnick, 1975). The more successful minnows in the Des Moines River in Iowa were late spawners (after floods) or were intermittent spawners (Starrett, 1951). The relatively long breeding season of B. anoplus probably evolved because of the effect on the successful spawning of the rapid increases in volume of flow and silt load in the Orange River and tributaries. If these conditions prevail throughout the spring of any given year, successful breeding could still take place in summer. It would be a distinct advantage in a relatively short-lived species (males 2-3 years; females 3-4 years) living in a harsh environment to have smaller than optimal broods. A small brood size decreases the chances of total failure on a given attempt.

The chances of an abrupt perhaps decimating decline in any given year class of the population would be reduced. Since both male and female B. anoplus are capable of breeding in the second, third and possibly a few females in their fourth summer of life, the chances that one or two years of poor recruitment could cause an extreme decline or extinction of the population or species is further reduced.

Age group 1^+ males and females of the first spawn of the previous year are very important to the population. They are the most abundant of the breeding stock and have the capacity to breed twice in the season. In terms of survival the late summer contribution of age group 1^+ of the second spawn may be of equal importance, especially when the mortality was high in the first spawn from the previous year.

The multiple spawning strategy might have developed to spread out the periods between spawning to reduce intraspecific competition between fry. It would also be beneficial to have the "back-up" spawn at a time of year when most species had completed the breeding cycle i.e. late February to March. This would reduce interspecific competition especially with the fry of the large Barbus & Labeo species. If spawning localities were limited, this strategy would allow more than one use of a site per season.

In a study of N. scepticus in South Carolina, Harrell & Cloutman (1978) found that this species had three ova diameter modes, indicating multiple spawnings. However, their gonosomatic values and visual observations did not confirm more than one spawn. Ova diameter frequency distribution in Phoxinus phoxinus from an upland Welsh lake also indicated the possibility of multiple spawning (Wooton & Mills, 1979).

The presence of eggs of various sizes in the ovaries of individual fish can indicate prolonged spawning, a phenomenon reported for other cyprinids including several North American minnow species (Reed, 1957; Griswold, 1963; Noble, 1965).

Gale & Buynak (1978) warned that fecundity estimates based upon only the largest eggs of some species are of little value and may be worse than none at all. They were able to study a minnow species in captivity where individual fish could be observed and the eggs removed after each spawn for counting.

The shiners had two major spawnings and other minor ones. Caution should also be applied to Gale & Buynak's (1978) results where there is a lack of inter- and intraspecific competition, lack of fry emergence and supposedly abundant food, which is unlike the natural environment. Their experimental set-up might, however, be similar to conditions faced by the early colonizer of a new habitat. Nonetheless this valuable work of Gale & Buynak (1978) points out the need to understand the full reproductive cycle of individual fish in a population before one attempts to calculate the absolute fecundity of multiple spawning fish. Even after noting that their study species is a multiple spawner, some workers have continued to obtain fecundity data by counting only the mature ova at one time of year (e.g. Heins *et al*., 1980).

In the present study there was considerable difficulty in trying to estimate the absolute fecundity for *B. anoplus* for the following reasons. Individual *B. anoplus* females probably have two major spawnings per reproductive season, however since there are mature ova in the ovaries for the entire breeding season (six months), there is still the likelihood of minor spawnings throughout the period. In addition, fecundity counts rely on the assumption that all mature ova are shed. It appears that this is not the case in this minnow species. Several minnows collected on 6.12.1979 (i.e. after the first spawn) had a high number of resorbing eggs, for example one 60mm fish had 538, and one 50mm fish had 374. An experimental approach similar to the Gale & Buynak's(1978) work on *Notropis* should be used. The shiners are crevice spawners and it is not known whether the chubbyhead barb would deposit all of its spawn in an artifical crevice.

In the two reproductive seasons followed in the present study, it was attempted to establish the "first fecundity" of the season and the "second fecundity" assuming that *B. anoplus* individuals spawn twice per season and that the majority of the minnows spawn all their mature ova each time. In this way an attempt was made to compare the number of mature ova available for spawning in one prolonged breeding season.

B. anoplus is similar to the Notropis species studied by Heins & Bresnick (1975), Heins & Clemmer (1976) and Heins et al., (1980), in that they exhibit some life history traits considered characteristic of a relatively r-selected species (Stearns,1976).

The r-strategists lie at one extreme, continually colonizing habitats of a temporary nature, with alternating "booms" and "busts" in population size. In this situation, natural selection will favour a short generation time, and allocation of available energy resources to reproductive activities. Since the habitats they colonize are often virtual ecological vacuums, high competitive ability is not required, and they will typically be small in size (Gunderson, 1980).

If the temporary nature of the habitat is changed into a more permanent one, then one would expect relatively more "boom" periods and less "busts" if there are few competitors. The impoundment environment offers B. anoplus such a situation. It is usually noted that r-strategists are not good competitors. Fortunately for B. anoplus, what appears to be one of the main fish competitors, B. holubi, spawns only in a relatively confined area of the impoundment (Cambray & Hahndiek, 1980; Tómasson, 1981).

Central to the understanding of the life history strategies of B. anoplus is a knowledge of the environment in which they evolved. As the environment in the Orange River changed in the past, the B. anoplus population evolved, and as the population evolved the individual fishes perception and definition of the environment changed.

The Orange River B. anoplus evolved in a river system which has very erratic flows and devastating floods with high silts loads (Kriel, 1972). In this environment the traits of maturing in the first year of life, large reproductive effort, quick growth, more than one clutch per year and an inter-brood interval timed for the most optimal times of year, would be advantageous for a small, short-lived species.

In a new habitat (e.g. an impoundment) the stratergy of early maturity within the first year and multiple spawning would be a distinct advantage to a colonizing species. The harsh, erratic environment of the Orange River has now been replaced by a relatively less hostile environment. Now all the multiple spawnings would have a comparatively high survival rate. This would lead to the rapid colonization of the impoundment, especially the more favourable marginal habitats for this species, the flooded erosion gullies, streams and vegetated areas.

Therefore B. anoplus has reproductive strategies (early maturity, a high reproductive effort i.e. multiple spawns) which would be advantageous to species colonizing a newly created habitat (i.e. the P.K. le Roux impoundment).

EARLY DEVELOPMENT

Introduction

There are very few published papers on the early development of African cyprinids. The notable exceptions are Labeo victorianus of Lake Victoria (Fryer & Whitehead, 1959), Barbus natalensis of Natal (Wright & Coke, 1975) and L. umbratus of the eastern Cape (Gaigher et al., 1975). Very few drawings of the developmental stages are given by Gaigher et al., (1975) and no drawings were presented for B. natalensis (Wright & Coke, 1975). Fryer & Whitehead (1959) provide the most detailed account supplemented with drawings of an African cyprinid.

The objective of the embryology section is to describe the gross embryogeny of B. anoplus and in particular to observe the behaviour, survival strategy and potential colonizing ability of embryos and larvae.

Methods

After a rainy period in early November 1980 a number of golden males and ripe females were collected on a daily basis from the P.K. le Roux impoundment with a minnow seine net. The fish were returned live to the laboratory. In the laboratory, eggs from several females were artificially stripped into a petri dish containing conditioned water. The males were then stripped, or in some cases the testes were dissected out and placed in the petri dish. The eggs and milt were then stirred with a glass rod for several minutes. B. anoplus have adhesive eggs so the wet method of fertilization was used. The eggs were then transferred to a shallow plastic container which had a small meshed plastic screen glued to the bottom. This container floated in a small aquarium which was continuously aerated.

When a successful fertilization was obtained, field collections were discontinued.

A sample of the fertilized eggs and larvae were periodically removed from the container and examined for development under a (8-80X) binocular dissecting miscroscope. The hatched larvae were released into the aquarium and the plastic container was removed. After the larvae changed from endogenous to exogenous nutrition, they were fed on cooked egg yolk, and a commercial fish food (Liqui-fry) twice a day (08h00 and 16h00).

Morphometric measurements were made with a dissecting microscope and an ocular micrometer accurate to 0,1mm. The diameter of eggs and lengths of larva were measured before preservation. Total length is defined here as the distance from the tip of the snout to the end of the caudal fin or fin fold.

A total of eighty stages were collected and the temperature of the water was recorded with a laboratory thermometer when each stage was collected. Behavioural observations of embryos and larvae were made in the aquarium. Live specimens were examined with a stereoscopic microscope before preservation. In addition to the behavioural notes, preliminary freehand drawings were made of each stage viewed. These sketches aided in drawing the final illustrations from preserved specimens, especially in the early stages of egg development. Final drawings were made with the aid of a camera lucida. Each drawing was based on a single specimen of the size indicated.

After viewing and making behavioural notes and sketches the specimen was fixed in 10% formalin and then preserved in 5% buffered formalin.

The parents and all preserved specimens of each development stage observed (total = 80) were deposited in the Albany Museum, freshwater fish section, catalogue numbers AMSA 8801-8881. The forty developmental stages of the second batch were deposited at the J.L.B. Smith Institute, Grahamstown, catalogue numbers 15691-15731.

Fryer & Whitehead (1959) cautiously noted that since very few African cyprinid embryos have been examined, it would be inadvisable to follow the numbered developmental stages suggested by Balinsky (1948). A similar state of affairs exists in 1981. In the early embryogeny (from fertilization to hatching) of B. anoplus I have not followed any of the currently used terminologies, nor have I proposed a new system, because I felt that more detailed work should be carried out on several African small barbs first.

The terminology of the larval phases follows Synder (1976). He reviewed the application of a number of other terminologies (360 references), including those of Hubbs (1943), Ahlstrom (1968) and Balon (1975). Synder (1976) modified selected portions of these and other existing terminologies in an attempt at standardization.

I have also chosen the terminology proposed by Synder (1976) because it has recently been applied successfully to the larval development of several North American minnows (Synder et al., 1977; Fuiman & Loos, 1978). Other workers have also successfully applied this terminology to other families (Cooper 1979, 1980 and Rasmussen, 1980). It is realized that this terminology might not be directly transferable from North American to African cyprinids. Synder (1976) was of the opinion that his extensively researched proposed terminology could be used for all fish species. It is hope that it will not be necessary to develop a new terminology of larval phases to add to the present lack of standardization throughout the world, and that future studies in Africa will follow Synder (1976).

Synder (1976) used three of the four types of developmental intervals proposed by Balon (1975): period, phase and stage. These terms are frequently misused in the literature.

The periods are the major and longest intervals and include the embryonic, larval, juvenile, adult and senescent periods. Each period can be divided into two or more phases. A stage is defined as the smallest most recently observed moment of development, and is frequently misused by fisheries biologists (Synder, 1976). The larval terminology proposed by Synder (1976) is as follows:

Larval: The period of bony fish development characterized by obvious fin morphogenesis following hatching. This period is terminated immediately before: 1 - the last fin fold and atrophying fins, if any, are absorbed beyond recognition; 2 - the full complement of distinct fin elements (spines and rays) becomes apparent in all fins and 3 - segmentation of principal rays in all fins becomes apparent.

Protolarva: The larval phase in which distinct median fin elements (dorsal, anal or caudal spines or rays) are not yet apparent.

Mesolarva: The larval phase in which at least one, but not all (full complement) of distinct rays in the median fins is apparent - or - if the full complement is present and the adult possess pelvic fins, the pelvic buds or fins are not yet apparent.

Metalarva: The larval phase in which the full complement of distinct principal rays in the median fins and, if the adult possesses pelvic buds or fins, these are apparent.

Results and Discussion

After several unsuccessful attempts in early November 1980, eggs were fertilized from fish collcted from the P.K. le Roux impoundment on November 7th, 1980. These eggs were followed through embryonic, larval and juvenile periods of development. The sequence and rate of development in these periods is given in Table 14 and shown in Fig. 30.

On January 28th, 1981 another batch of eggs was fertilized, and embryonic to protolarval phases were observed. The protolarvae developed fungus and could not be followed any further.

The egg:

The unfertilized ripe ovarian eggs of *B. anoplus* are approximately 0,8 to 1,0mm in diameter and a pale yellow colour. When the eggs were placed in water slight swelling occurred in the vitelline membrane of both fertilized and unfertilized eggs. The chorion of fertilized and unfertilized eggs firmly adhered to the substrate and the eggs were demersal. More than three-fourths of the families in Cypriniformes produce demersal and adhesive eggs (Breder & Rosen, 1966). The adhesive membrane could be stretched to over 10mm before breaking. After a few hours the eggs could not re-adhere if the original adhesive contact was broken. The strength of adhesion appeared to increase with time, and the eggs remained attached to the substrate until there were violent contractions of the embryo prior to hatching. Some of the eggs remained firmly attached until hatching occurred.

Early development:

At the one cell stage the width of the yolk was 0,8mm and the width of the entire egg was 1,1mm (n = 2). Development was more rapid in the eggs fertilized in January 1981 and observed at temperatures of 24° to 25°C than in the November 1980 batch (19-21°C). In January the

TABLE 14

Sequence and rate of development of the early developmental stages of Barbus anoplus at 20° to 25° C in an aerated aquarium from 7.11.80 to 3.2.81 at the Douglas Hey Limnological Research Station.

Age (hours then days)	Fig. no.30	Stage of development	Behaviour
0	A	Fertilized egg 1,0mm in diameter. Perivitelline space about 20% of egg diameter.	Adheres to substrate.
1h 35min.		2- and 4-celled phases. Second division perpendicular to the first.	Adheres
1h 50min.	B	8-celled phase. The eight large blastomeres are irregularly shaped and occupy the upper third of the yolk.	Adheres
3h 45min.	C	Many celled phase. Blastodermal cap in equatorial position giving characteristic acorn shape.	Adheres
17h 15min.		Embryo surrounds about 2/3 of yolk surface.	Stronger adhesion of eggs to substrate
22h 15min.		Optic vesicle, somite and notochord formation.	Adheres
28h		About 14 pairs of somites present. Enlarged caudal region; fin membrane apparent posteriorly. Yolk pear shaped, granular and pale yellow in colour.	Adheres
30h	G	Embryo completely surrounds the yolk. About 15 somites.Caudal fin fold well developed and spoon-shaped. Embryo clear.	Adheres. First muscular flexures noted.
33h		Coiling stage. Caudal region of embryo twists around yolk, and yolk indented. Frequent flexures. Lens placodes present.	Loss of adhesion in some eggs.
34h		Similar to 33h.	Violent contractions; embryo rotates 180° every 10 to 20 seconds.
41h	H	Heartbeat stage. Heart distinct and pulsating. Auditory placode apparent. Jaws started to form.	Violent 180° twisting of embryo continues.
43h		Auditory vesicle migrates forward. Both lapillus and astericus visible. Embryo clear; yolk granular, pale yellow, considerably reduced in size.	Embryo very active. Heart contracts at 69 pulses/min.
47h		Pigmentation first appears in eyes. Caudal region overlapped head.	Embryo active. Heart pulses 78/min.
49h		Pre-hatching stage. Eye more pigmented. Yolk more vacuolated. Remnant of adhesive membrane still visible.	Frequent twirling within egg. Heartbeat 90/min.

(Table continues)

(Table 14 continued)

Age (hours then days)	Fig. no. 30	Stage of development	Behaviour
53h		Protolarval phase. Late embryo prior to hatching. Tip of tail loose. While observing, larva hatched with one quick lash of tail. Larva, 3,1mm TL and dorso-ventrally 0,6mm. Larvae were melanophore-free except for the eyes. Yolk sac bulbous anteriorly and tubular posteriorly.	Heartbeat 108/min. Larvae rests on lateral surface. Moved with quick whip-like action, then rested on substrate.
55h	K	About 33-35 myomeres. Eye more pigmented.	Protolarvae move tail region up to eye and then rapidly flicked their tails, propelling themselves in a haphazard way on the substrate. Some of larvae float 1cm above substrate. Other larvae swim to surface (10cm) and then spiral down.
57h		Pectoral fin primordia present. Neurocranium area yellowing.	Some larvae cluster and float in aeration bubbles. Long periods without movement. Yolk dorsal, with the angle of body to substrate approximately 30°. Most of larvae positioned on side of container or free-floating.
67h		Uninflated single-chambered swim bladder observed. Body pigmentation appears dorsally to yolk sac over the developing vascular system. Dot-like isolated melanophores. Circulation observed on dorsal surface of yolk. Larvae 3,4mm TL. The increase in length is possibly due to the decrease in sharpness of the cranial flexure over the yolk.	Larvae more active, swimming, more dispersed, and move away from water movement. Float at about 20° to substrate. Some larvae on substrate.
77h		Auditory capsule migrates more anteriorly. Cranium more developed.	Larvae floating at surface or in water column. When larvae are disturbed they wriggle away to surface and then float downwards to rest.
89h	L	Pigmentation begins on dorsal surface under fin fold. Eye pale golden colour. Haemoglobin observed. 32 myomeres; and 4,0mm TL.	Larvae still floating or on substrate.
93h		Melanophores present on covering over brain. Head yellowish. Blood in heart obvious. General pigmentation make larvae easy to locate in aquarium.	Larvae difficult to collect. Floating about 80° to substrate.
97h		Rudimentary opercles and gill arches developing. Mouth more developed, antero-ventral in position. Yolk sac not visible from dorsal view. Larvae 4,1mm TL. Dorso-ventral width of yolk sac 0,4mm; of body plus yolk sac 0,7mm.	Swallowing action noted.

(Table continues)

(Table 14 continued)

Age (Hours then days)	Fig. no.30	Stage of development	Behaviour
105h		Pectoral fins loose, used in swimming.	Mouth opens and closes in gasps. Larvae more active, swim then float or lie on substrate.
4,5 days		One otolith larger. Gill slits more developed.	Mainly active swimmers now, only short rest periods.
4,7 days		Heart well developed, 2 distinct chambers. Eye movement noted for first time. Swimbladder increased in size and bulges into yolk. Larva length 4,5mm TL, dorso-ventral width of yolk 0,3mm, of body 0,6mm. About 32 myomeres.	Mouth remains open after gulps. Larvae very active and swim in a more horizontal position, in quick dashes.
5,2 days		Mouth terminal in position.	Use pectoral fins in swimming, flipper-like. Also use pectoral fins to remain upright on substrate. Some larvae still floating. Rapid eye movements.
5,7 days	M	Indentation of caudal fin fold, becoming a more paddle-shaped structure.	
6 days		Swim bladder very enlarged, almost full lateral width of body. Very little yolk remains.	Opercular movement obvious. Larvae very active, appeared to be visually searching for food.
6,7 days		Yolk absorption completed. Barbel rudiment present. Larvae 4,5mm TL, dorso-ventral width 0,6mm.	Free-swimming larvae, wriggle and glide, behave as juvenile fish.
7 days		Gut continuous from mouth to anus and functional. Vertebrae clearly observed.	Larvae feed actively. Food particles present in gut.
9 days		Eye movements more pronounced.	Do not swim against current but float with it.
11 days		Some caudal fin ray anlages present.	
		Mesolarval Phase	
28 days	N	Caudal fin rays present. Lateral line development.	Very active.
33 days	Q	Dorsal fin with ray development. Caudal fin with segmented rays and homocercal. Larvae 8,4mm TL and 1,5mm dorso-ventral width.	
43 days		Pigment along lateral line, blood in gills. Dorsal fin rays branching. Swimbladder dividing. About 32 vertebrae visible.	Active in midwater, feed at all levels in aquarium.
		Metalarval Phase	
51 days	T	Anal fin rayed. Swimbladder separated into two chambers.	
60 days	W	Gut convoluted. Pelvic fins forming with ray anlages.	

(Table continues)

(Table 14 continued)

Age (Hours then days)	Fig. no. 30	Stage of development	Behaviour
		Juvenile Period	
68 days	X	Pelvic fins rayed. Silvery peritoneum. Body opaque. Pigmented dorsal surface, with fine pigment spots. Length 15,9mm TL.	
88 days		Scales well developed. Most adult characteristics present. Pigmentation similar to adult.	

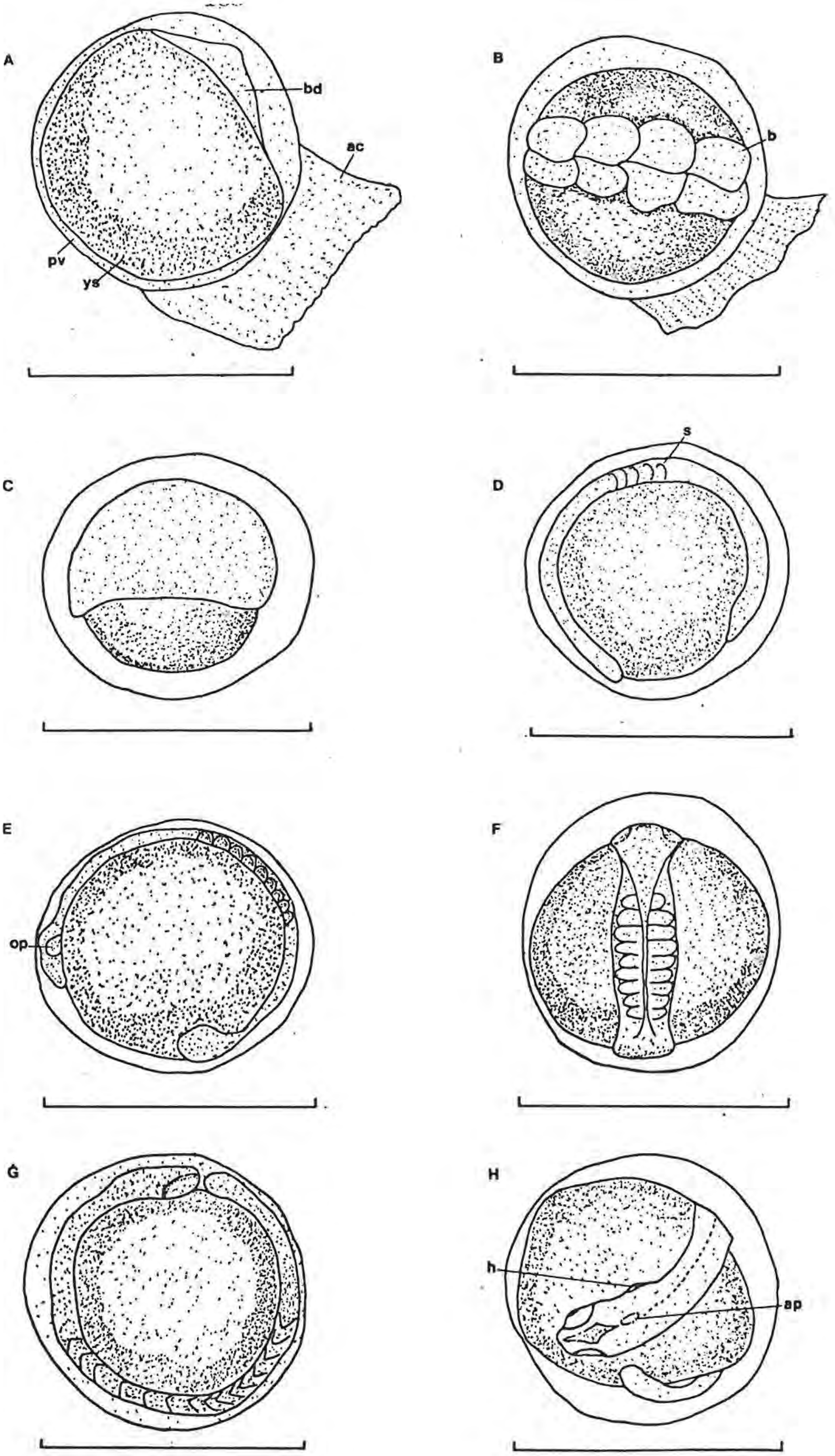


Fig. 30 The early developmental stages of B. anoplus, 20-25°C
A. One cell stage. B. Eight cell stage. C. Blastoderm. D. Five somite stage
E. & F. 14h embryo. G. 30h embryo. H. 41h embryo. ac: adhesive chorionic membrane.
ap: auditory placode. b: blastomere. bd: blastodisc. h: heart. op: optic placode.
pv: perivitelline space. s: somite. ys: yolk sac. (Scale bar = 1mm).

(Figure continues)

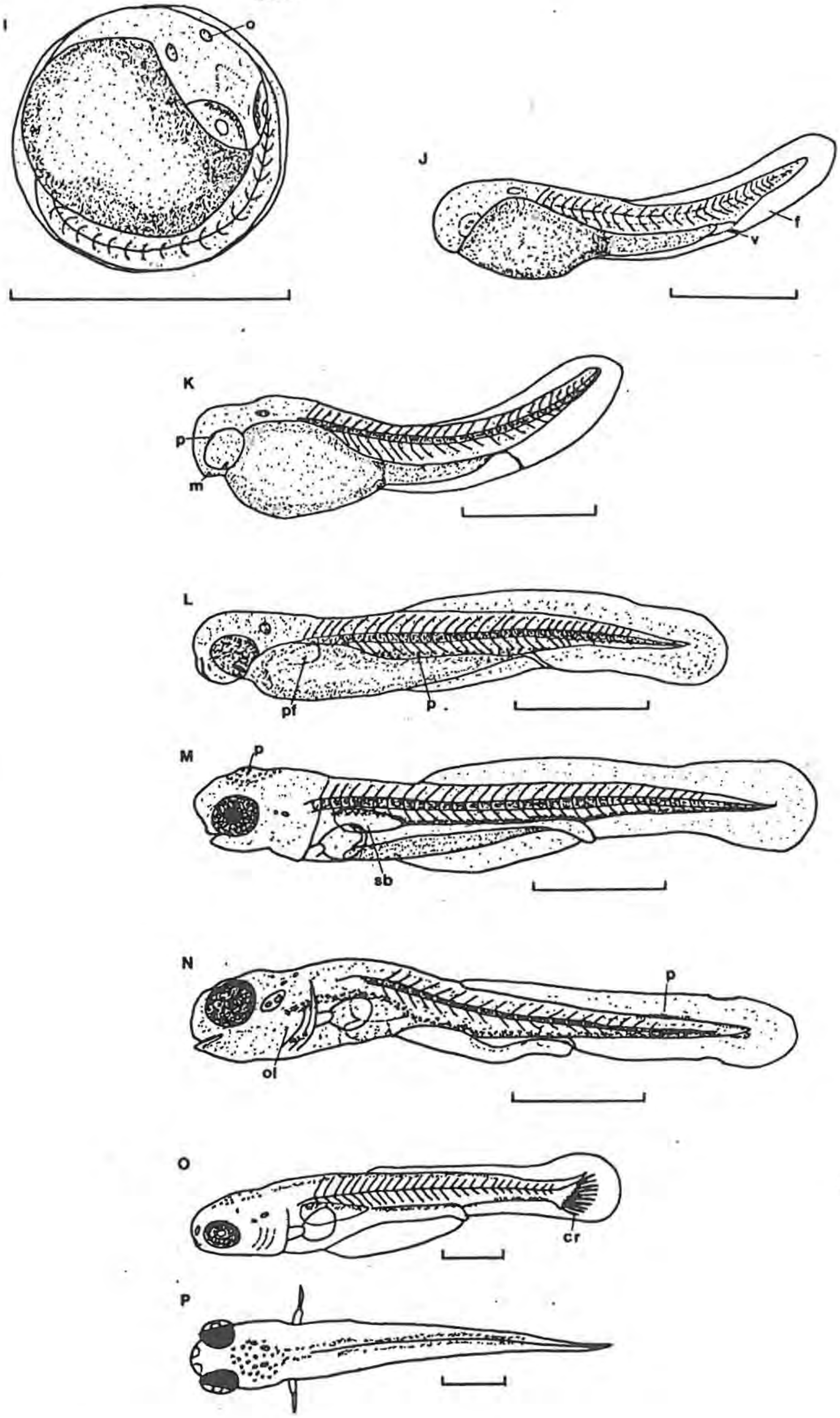


Fig.30 (contd.) The early developmental stages of B. anoplus at 20-25°C.
I. 51h embryo. J. Early protolarva. K. 55h protolarva. L. 89h protolarva.
M. 5,7 day protolarva. N. 10 day protolarva. O. 28 day mesolarva.
P. 28 day mesolarva, dorsal view. cr: caudal fin ray. f: fin fold.
m: mouth. o: otolith. ol: operculum. p: pigment. pf: pectoral fin.
sb: swimbladder. v: vent. (Scale bar = 1mm).

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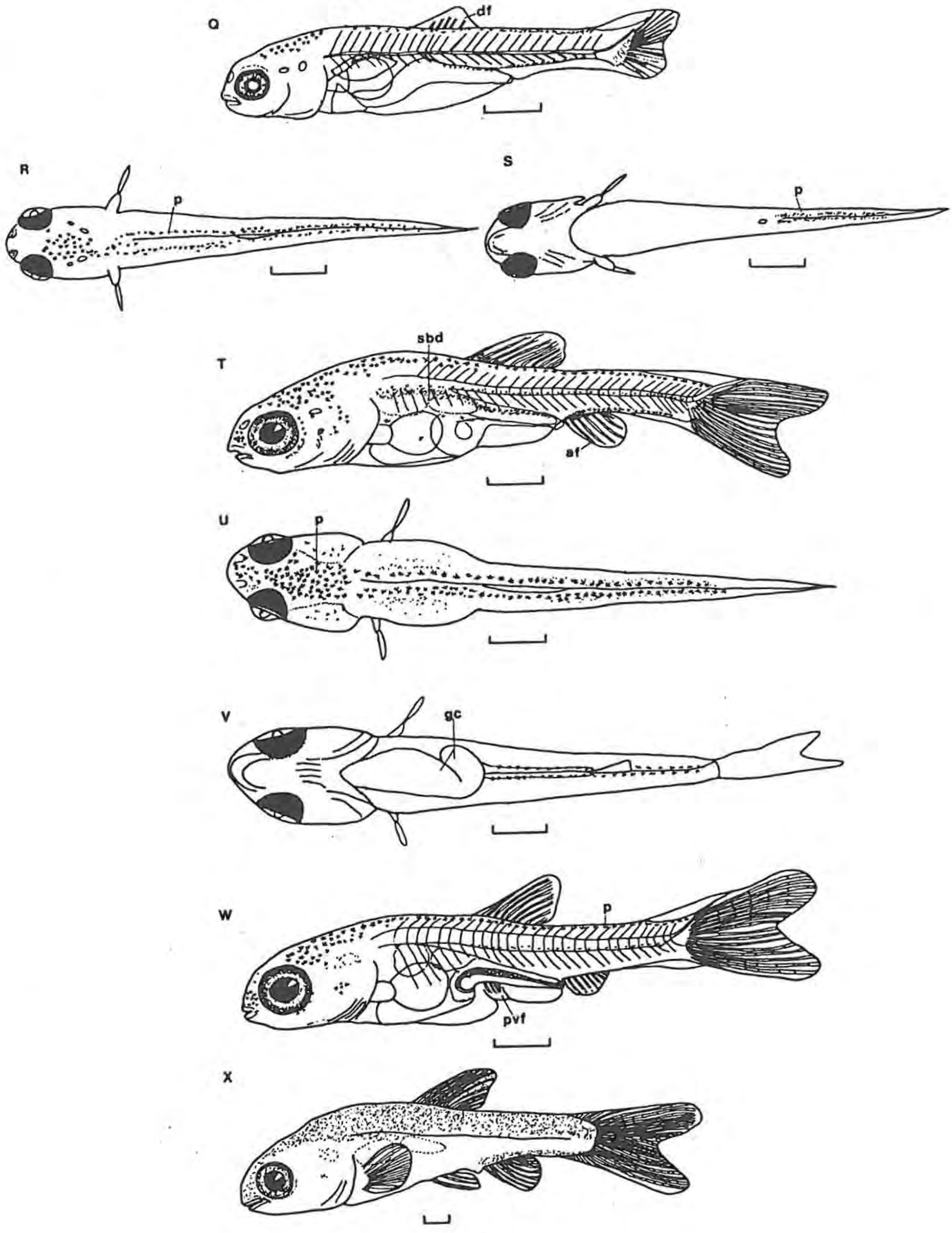


Fig.30 (contd.) The early developmental stages of B. anoplus at 20-25°C.
Q. 33 days, mesolarva. R. 33 days, mesolarva dorsal view. S. 33 days, mesolarva ventral view.
T. 51 days, metalarva. U. 51 days, metalarva, dorsal view. V. 51 days, metalarva,ventral view.
W. 60 days, metalarva. X. 68 days, juvenile. af: anal fin. df: dorsal fin.
gc: gut convoluted. p: pigment. pvf: pelvic fin. Sbd: swimbladder dividing.
(Scale bar = 1mm).

first larvae hatched at 28h whereas in the November batch the first larvae hatched at 53h.

Development was followed from the first cleavage. At the eight cell stage the blastomeres were of various shapes and opaque, the yolk was pale yellow and granular (Fig. 30B)

The yolk sac remained spherical until the embryo almost completely surrounded the yolk. At this stage the yolk sac was pear-shaped. Fryer & Whitehead (1959) noted that the shape of the yolk sac in L. victorianus is distinctive with a posterior extension. The functional significance of the differentiation of the yolk sac into these two regions could possibly be to permit flexing movement of the body (Fryer & Whitehead, 1959). After 33h of development, when the B. anoplus embryo was very active, the yolk sac was indented where the embryonic head occurred over the yolk. Possibly this also facilitated movement of the embryo in the rapid 180° turns within the perivitelline space.

As in L. victorianus (Fryer & Whitehead, 1959), curvature of the developing B. anoplus embryo was necessary, as the egg width was only 0,8 to 1,0mm, but the hatched larvae were over 3,0mm in length.

Hatching time:

As in many fish there was considerable asynchrony in the hatching period of the larvae, within a single batch of eggs, under similar conditions. As already pointed out the hatching time can vary considerably with as little as 3-4°C difference in water temperature.

Newly hatched larvae:

The heart beat of the embryo was approximately 90 beats/min immediately prior to hatching. The newly hatched protolarvae had heart beats of about 108/min. Newly hatched larvae were 3,3mm TL (n = 3) with heads flexed sharply over the yolk sac (Fig. 30J). The larvae had pigmented eyes and straight urostyles. The mouths were incomplete and the gut posterior to the yolk appeared well developed and terminated at the anus, just anterior to the caudal portion of the fin fold. The yolk sac was still globular and began to elongate several hours after hatching. The finfold extended posteriorly from the yolk, around the caudal tip, and anteriorly in the dorsal region of the trunk to a point opposite the ventral origin, interrupted only by the posteriorly located anus. Pectoral fins had not yet developed. All body surfaces were devoid of melanophores.

Larval behaviour:

One of the most interesting aspects of larval behaviour was that some floated at different levels in the water column, while others remained on the substrate, yolk upwards. At first the floating protolarvae were in clusters later they were more scattered (Fig. 31). The protolarvae on the substrate periodically underwent a rapid undulation of the caudal area which propelled them upwards. When the swimming activity ceased, the larvae sank slowly to the substrate and landed in a dorso-ventral position with the yolk sac upwards. L. victorianus (Fryer & Whitehead, 1959) and L. umbratus (Gaigher et al., 1975) larvae also behaved in this manner. The swimming behaviour of the protolarvae i.e. active upward swimming and passive sinking, is characteristic of many species (Shelton & Stephens, 1980). This behaviour is possibly of adaptive significance in reducing the chances of suffocation in bottom mud. Similarly, the floating larvae would be a further adaptation to reduce suffocation.

In contrast, the B. natalensis larvae burrowed into the gravel substrate and succumbed to a heavy silt load which passed through the rearing trough (Wright & Coke, 1975). The differences in the larval fish behaviour deserves wider attention with regard to survival value of the large and small barbs under silty conditions.

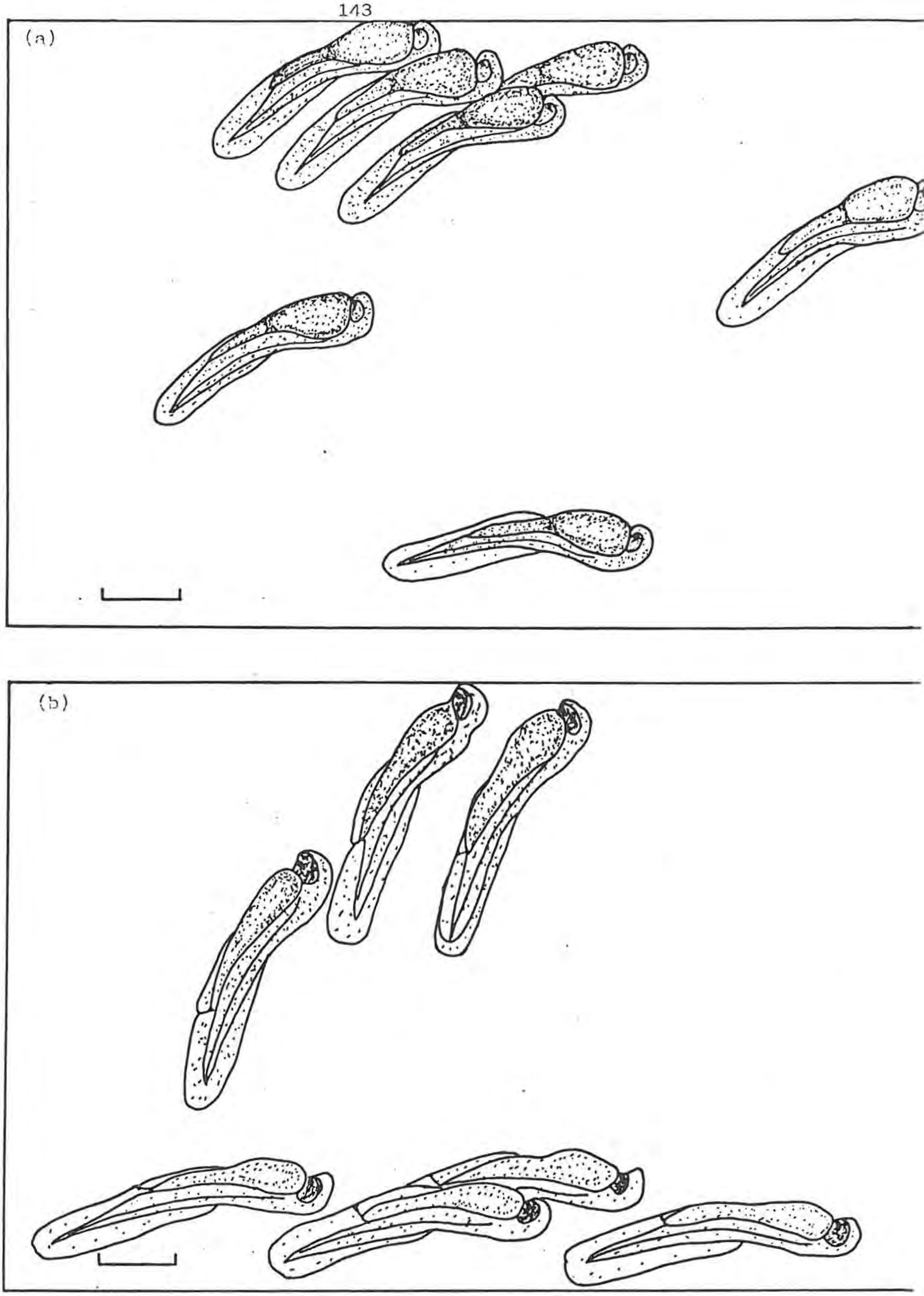


Fig. 31 Floating behaviour of B. anoplus larvae, (a) 57h protolarvae, (b) 77h protolarvae. (Scale bar = 1mm).

The floating protolarvae were mainly motionless even when they floated into the aeration bubbles. They did not actively avoid the bubbles.

The angle of the floating larvae to the substrate decreased with time, as the yolk sac was absorbed. The position of the yolk upwards and this change in angle of the larvae would suggest that the specific gravity of the yolk is responsible for the buoyancy. The difference between the substrate larvae and the floating larvae was probably the structure of their yolk which deserves further investigation.

The larval floating behaviour could also be an important downstream dispersal mechanism and could possibly be important during watershed exchange distributions. In the impoundment the floating larvae could possibly disperse throughout large areas carried by water movements. This adaptation could have aided in the rapid colonisation of the newly created P.K. le Roux shoreline. The substrate larvae would disperse at a more leisurely pace, and have more 'control' over their dispersal.

Another characteristic of the floating larvae was that some floated at the surface film while others were dispersed throughout the water column, with some only a few millimetres from the substrate. This could possibly be a predator avoidance trait or an aid to differential dispersal of the species.

B. anoplus adults migrate into very shallow areas prior to breeding. These shallow areas are temporary and the floating larvae would thus have a better chance of survival under severe conditions than the substrate larvae, which can only actively move a few centimetres at a time.

When the floating larvae were disturbed by the collecting pipette they swam away for several centimetres and then continued to float. The larvae that floated below the surface immediately swam to the surface, not to the substrate, and then remained motionless and sank to its previous level.

The development of pigmentation:

The first pigmentation occurs in the eye before the larva hatches. After hatching, pigment occurred immediately dorsal to the yolk sac and appeared to camouflage the rudimentary vascular system. Dorsal pigment occurred next under the caudal fin fold. Melanophores appeared on the dorsal region of the head, and the area gradually became heavily pigmented. The head region also became pale yellow at this stage (93h old). Pigmentation of the trunk continued in the two longitudinal rows. The third row of pigment occurred along the lateral line after 28 days.

At 68 days the juvenile fish had fine dot-like pigments on the dorsal surface and about half way down the lateral surfaces (Fig.30X). A few large melanophores were scattered on the head and along the dorsal surface.

Mouth and feeding:

The mouth was originally formed in a ventral position, from where it migrated to a terminal position as the yolk supply diminished. Barbel development was first observed after 6 days. After 6 days the larvae had good control of their jaw movements and appeared to search for food. After 7 days they actively took food from the water column and were visually orientating to small food particles and the gut was fully functional.

Growth rates:

All the growth rates (in Table 14) obtained in this study were made under laboratory conditions. Laboratory development of fish can, however, only be used as a rough indication of incubation and development under natural variable conditions.

Five of the November artificially spawned fish reached 30mm FL after 13 months, their comparable year class would be approximately 45 to 50mm FL in the impoundment. The fish have therefore been stunted under laboratory conditions.

CHAPTER 7

AGE, GROWTH, RELATIVE CONDITION AND POPULATION STRUCTURE

Introduction

Age and growth studies on *B. anoplus* were necessary to answer some of the questions raised in the reproduction chapter. Data on the longevity of *B. anoplus* was required to determine whether females live longer than males, and the significance of greater age in one sex to the population.

The trade-off between somatic growth and reproduction could play an important role in a colonizing species. A rapid growth rate and early age at sexual maturity would probably reduce the longevity of the species.

In addition, it was necessary to obtain a further understanding of the growth rates and longevity between the first and second spawn fish of one season and the significance to the population of the two spawnings.

A review of the age and growth of the small *Barbus* species is given and compared, when possible to *B. anoplus*.

Methods

Age and growth data were obtained from fish collected on a monthly basis throughout the study period, at sites 6,8,68,72 and 73 (Fig. 9 p.44). The minnow seine net (see p.50) was used as the main collecting gear.

Length frequency graphs and scale rings were used to interpret age and growth.

Length frequency distribution analysis may be used to age fish which have a limited spawning season. At any given time a population of such fish consists of a series of discrete age groups (Cadwallader, 1978). The size range of each age group tends to be distinct from that of adjacent groups and may be indicated by a mode in the length frequency distribution. This method of ageing is only applicable to B. anoplus in their first season of growth. Thereafter age groups one to three undergo a considerable overlap produced by individual growth variation and reduced growth rate compared to 0^+ fish.

Early collections of 4 key scales per fish had proved to be inadequate because of the large percentage of regenerated scales, especially in the older fish (Plate 17b). Approximately 10 scales were therefore removed from between the lateral line and the origin of the dorsal fin. The scales were mounted on a glass microscope slide under a cover slip.

Scales were examined with the aid of a microfiche reader at a magnification of 48X. Measurements of the magnified image of the scales were made with dial calipers with an accuracy of 0,05mm. The scale radius was measured from the focus to the posterior edge of the scales (Plate 17a). The distance to each annulus was also measured along the posterior axis.

The body: scale relationship was calculated by the method of least squares for 963 B. anoplus. This relationship is described by the formula:

$$L = 16{,}142 + 1{,}610R \quad (r^2 = 0{,}82)$$

where R = scale radius in mm x 48

L = fork length in mm

The regression is linear but not directly proportional. Back calculations were therefore made using Fraser's formula (Ricker, 1968):

$$Ln - c = \frac{Sn}{S}(L - c)$$

where Ln = length of fish when ring "n" was formed

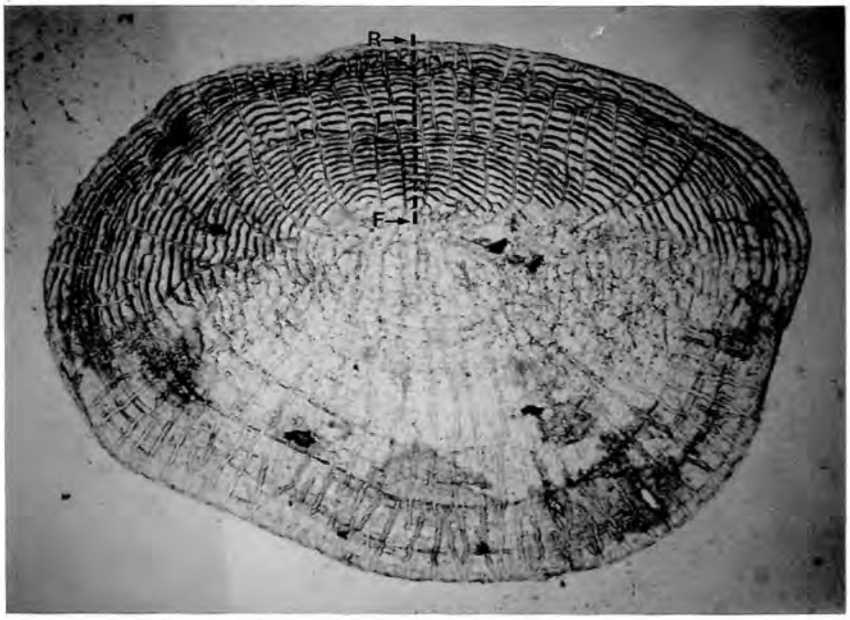
L = length of fish at capture

Sn = radius of ring "n"

S = radius of scale

c = intercept on length axis

(a)



(b)

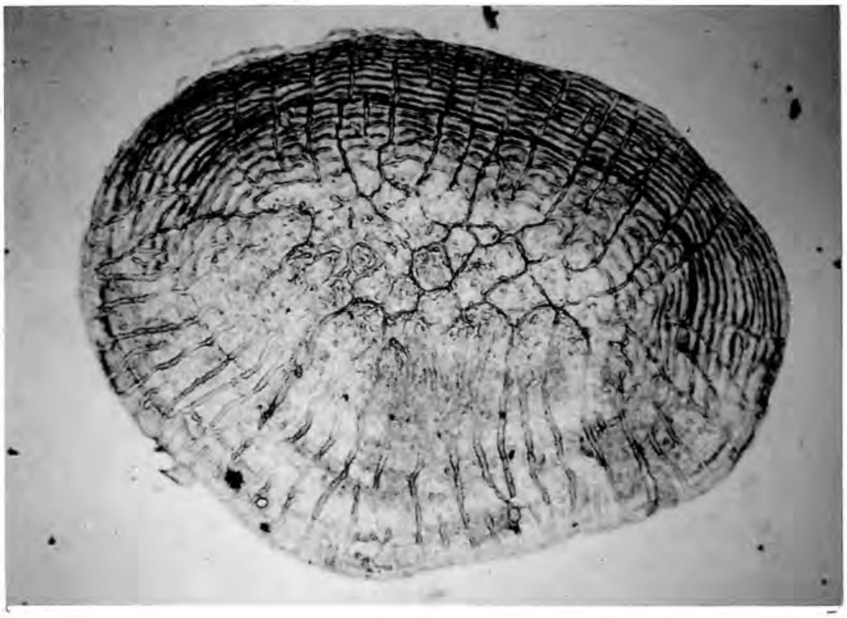


Plate 17 Scales from a 57,8mm FL male *B. anoplus*, showing (a) 2 rings, (b) regenerated scale. F-scale focus. F to R - scale radius. 1-ring one. 2-ring 2. (Scale bar = 0,5mm).

Otoliths were collected to aid the validation of the scale ring counts. Otoliths did not prove successful because a large percentage of 1^+ fish had no check on the otolith whereas some fish had up to 4 well defined rings. In some otoliths the ring number corresponded with the scale ring number.

The right opercular bone of a number of fish was collected and cleaned. No annular marks were visible on these structures.

The scale and length frequency methods were therefore the only two practical methods for age and growth studies of this species.

Annuli were validated by following the growth of the posterior edge of the scale on a monthly basis, and counting the number of circuli laid down after ring formation.

Relative condition

To follow changes in the length-weight relationship (condition) of the fish population throughout the year, the length-weight relationship of B. anoplus collected in May and June 1979 was used as a baseline. In May and June the gonad weight of both males and females is minimal, with the total body weight almost equal to somatic weight (see Fig.11). To the May/June baseline the weight for length of individual fish at other times of the year could be compared (Payne, 1975).

The length-weight relationships were calculated from double logarithmic transformations of the data. The mature males, females and the immatures were treated together (n = 170). The calculated regression line is:

$$\log_{10} W = -4,9458 + 3,0391 \operatorname{Log}_{10} L \quad (r^2 = 0,99).$$

where W = total weight (g)

L = fork length (mm)

The condition of each individual relative to the population in May-June was calculated as:

$$Kr = \frac{W_O}{W_E}$$

where Kr = relative condition factor of individual,

W_O = observed weight, either total or somatic,

W_E = the expected weight according to the May-June length/weight relationship (Payne, 1975).

W_E was obtained by substituting the length of the fish into the above regression equation for the population in May-June (Payne, 1975).

For each month the mean relative condition factor of both total and somatic body weight was calculated for immature females (21-30mm), maturing females (31-40mm), mature females (greater than 48mm), maturing males (31-40mm) and mature males (greater than 48mm).

Results

Length frequency:

Growth rate from length-frequency distributions (Petersen method):

The length frequency distribution of young-of-the-year minnows is given in Figs 32 & 33 for the two study years at site 6. Clear modes are apparent in both years, especially for the first spawning of the year. The first spawning occurs over an extended period during November and December 1979 and between December and January 1980 at both localities. The period between spawnings would account for some of the size range in this age group. The second spawn occurs in either February or March of both years.

Mean monthly lengths of the first and second spawnings were calculated for two localities, sites 6 and 8 (Tables 15 & 16 and Fig. 34). Male and female fish were lumped, as it was not possible to separate the sexes accurately below a length of 20mm.

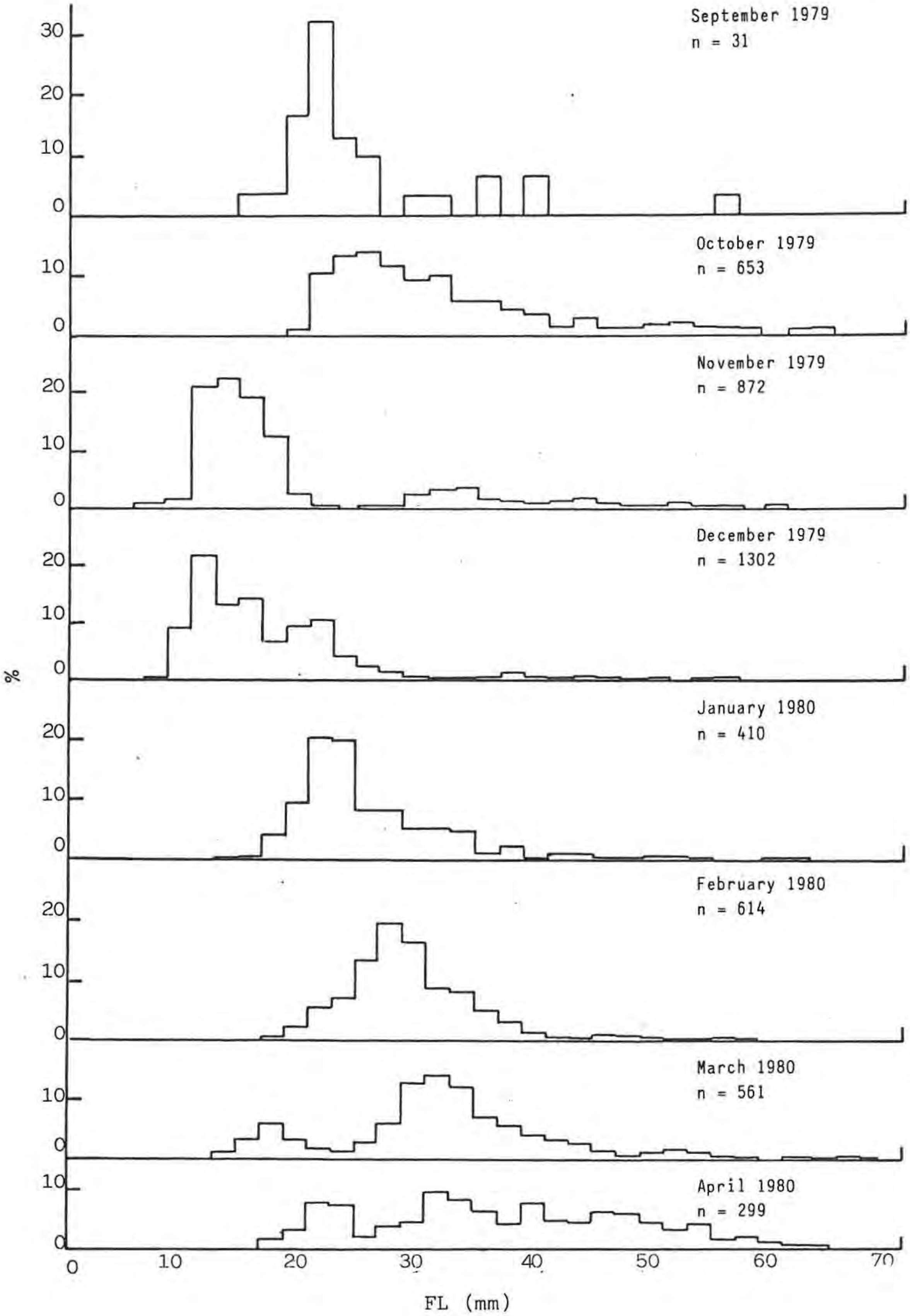


Fig. 32 The percentage length-frequency distribution of B. anoplus at site 6, P.K. le Roux impoundment, September, 1979 - April, 1980.

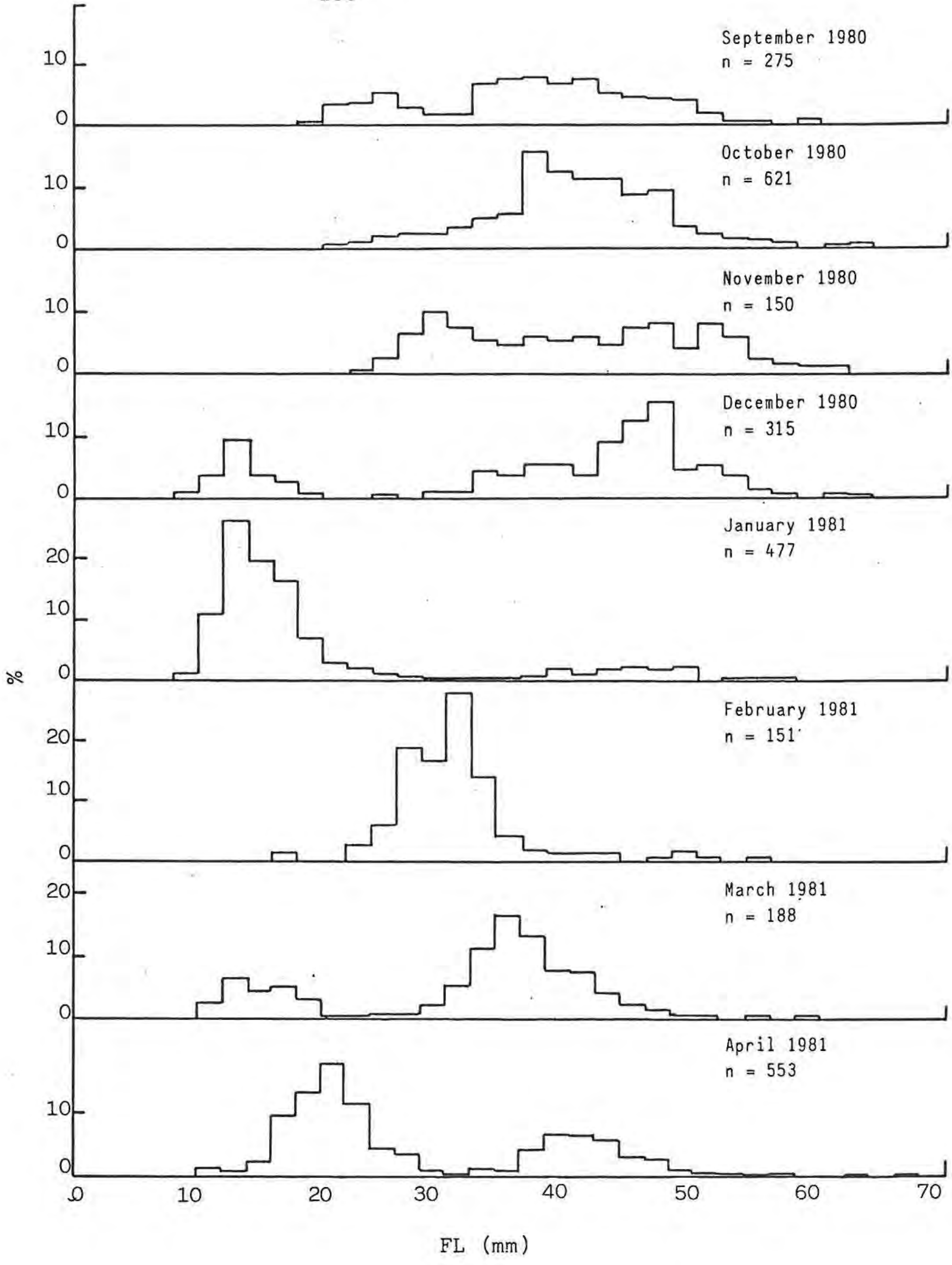


Fig. 33 The percentage length frequency distribution of B. anoplus at site 6 P.K. le Roux impoundment, September 1980 - April 1981.

TABLE 15

Growth of *B. anoplus* of the first and second spawnings at Site 6, P.K. le Roux impoundment for two summers.

Date	Mean F L (mm)	S.D.	Growth Increment (mm)	F L Range (mm)	n
First spawn					
1979 November	14,2	2,4	14,2	8-21	701
December	15,7	4,6	1,5	8-28	1229
1980 January	24,7	4,9	9,0	14-38	378
February	28,5	4,6	3,8	14-40	582
March	33,0	5,0	4,5	22-46	428
April	38,1	6,6	5,1	27-50	204
Second spawn					
1980 March	16,8	2,5	16,8	10-21	92
April	22,1	2,0	5,3	17-26	61
November	30,0	2,8	7,9	23-36	52
First Spawn					
1980 December	13,9	2,3	13,9	10-20	67
1981 January	15,6	3,2	1,7	9-27	417
February	30,1	3,3	14,5	18-37	140
March	37,1	4,1	7,0	28-44	138
April	41,5	3,7	4,4	33-49	178
Second Spawn					
1981 March	15,4	2,6	15,4	11-20	42
April	21,0	3,4	5,6	9-30	363

TABLE 16

Growth of *B. anoplus* of the first and second spawnings at Site 8, P.K. le Roux impoundment for two summers.

Date	Mean F L (mm)	S.D.	Growth Increment (mm)	F L Range (mm)	n
First Spawn					
1979 November	12,4	1,9	12,4	8-16	164
December	13,0	2,7	0,6	8-21	831
1980 January	25,5	4,5	12,5	17-36	226
February	32,6	4,1	7.1	25-42	225
March	39,2	1,1	6,6	33-46	168
April	38,1	4,7	-1,1	30-48	114
Second Spawn					
1980 February	17,3	3,9	17,3	10-24	71
March	20,0	3,7	2,7	9-28	75
April	23,4	3,3	3,4	14-29	212
November	32,8	2,8	9,4	25-38	50
December	36,1	1,8	3,3	33-38	26
First Spawn					
1980 December	19,8	3,3	19,8	14-26	18
1981 January	17,3	4,4	-2,5	9-28	398
February	31,0	3,4	13,7	22-39	335
March	36,0	3,4	5,0	27-43	247

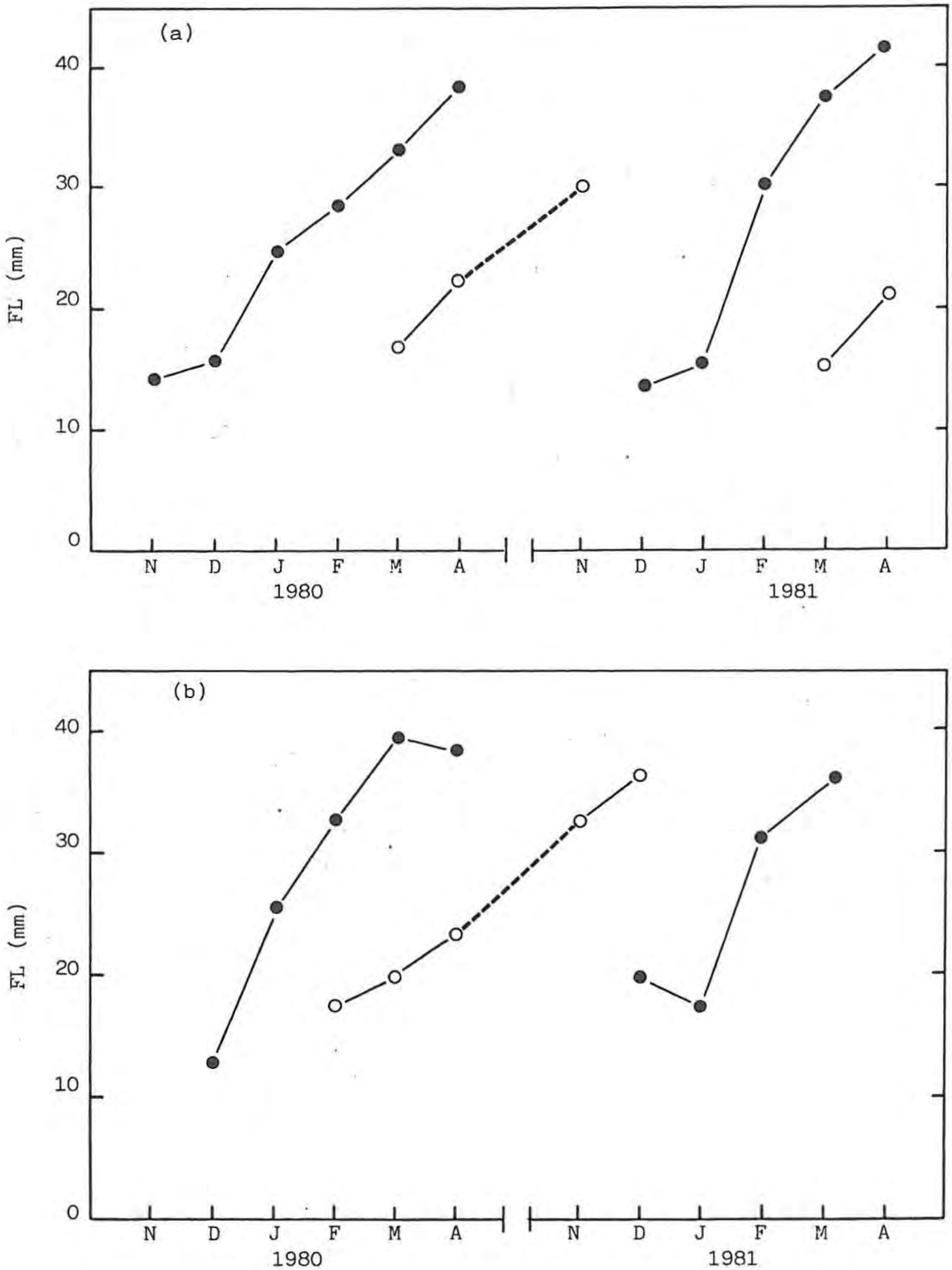


Fig. 34 Growth rate of B. anoplus of the first (closed circles) and second (open circles) spawnings at two localities in the P.K. le Roux impoundment for two years; (a) - 1979/80 and (b) - 1980/81.

At sites 6 and 8 the mean length of the first spawn was 38,1mm FL after approximately 6 months growth (in April, 1980).

In the second year, the first spawn at sites 6 and 8 were 37,1mm and 36,0mm FL respectively in March 1981 and 41,5mm at site 6 for April 1981 (approximately 5 months growth).

The spawning season occurred approximately one month later in the 1980/81 season, but the population mode had reached a greater size than in the previous season. At both localities the growth rate of the 0^+ group was greatest in January 1980 for the 1979/80 season, and in February 1981 for the second year. The fastest growth rate occurred in February 1981 which is the month in which the first spawn of the second season "compensated" for their later start.

The second spawn of the first season attained a mean length of 22,1mm (site 6) and 23,4mm (site 8) by the end of April 1980. These groups could be followed through to the next summer and attained mean lengths of 30,0mm (site 6) and 32,8mm (site 8) by the end of November 1980, which indicated a period of greatly reduced growth during the winter months.

In the 1980/81 season the second spawn attained a mean length of 21,0mm at site 6 by the end of April 1981, which is similar to the previous season. The asymptotic lengths obtained from Ford-Walford plots (see below) gave final lengths of 59mm for males and 67mm for females. The first spawned fish attained a length of approximately 40mm in 6 months which is 68% of male's and 60% of the female's total growth.

Age determinations from scales

(a) Annulus formation and validity of annuli:

Annuli were best distinguished in the posterior field beyond the closely spaced circuli laid down in winter. In addition to crowding of circuli, cutting over was often (but not always) observed in the lateral field of the scale (Plate 18a). The fish hatched late in the year (second spawn), had less growth to the first annulus and on these fish the annulus was not as clearly defined as in the first spawned fish (Plate 18b). In the 28-8-79 sample, 27% (n = 73) had developed a ring on the edge of the side and by 2-9-79, 94% of the sample (n = 49) had formed a ring. It appears that some of the smaller fish (<30mm of the second spawn) do not form recognisable rings after the winter season.

(b) Age determinations:

The length distribution of male (n = 301) and female (n = 409) B. anoplus for directly read scales is given in Table 17.

There is considerable overlapping and a wide length distribution for all age groups. The multiple spawning habit of B. anoplus would account for some of this variability, in addition to the fact that some fish probably do not lay down a ring in their first year as mentioned above.

Only one age group 3 male was found, whereas 10 of the females belonged in this age group, and one 70mm female was 4^+. In addition very few males were in age group 2 compared to the females. This would indicate a high mortality of males especially in the second year of life. The males would then have one-two seasons for reproductive activity whereas some of the females would have three reproductive seasons. Considering that females are probably multiple spawners they could therefore breed at least 6 times during their life span, and the one 4^+ female could possibly breed a total of 8 times.

(a)

(b)

Plate 18 B. anoplus scales, (a) a 45mm FL female (1^+) collected on 1-11-79 at site 6 and (b) a 25mm FL male (1^+) collected on 4-12-80 at site 6, P.K. le Roux impoundment. Scale bar = 0,1mm. (Arrow indicates cutting over).

TABLE 17

Length distribution of male and female B. anoplus from P.K. le Roux impoundment for different scale ring counts.

Males				Females				
F L mm	1^+	2^+	3^+	F L mm	1^+	2^+	3^+	4^+
16				16				
18				18				
20				20				
22				22				
24	2			24	2			
26	2			26	2			
28	7			28	7			
30	5			30	9			
32	13			32	16			
34	9			34	11			
36	13			36	17			
38	11			38	22			
40	11			40	17			
42	30			42	20			
44	30	2		44	18			
46	45	4		46	18	2		
48	35	15		48	36	12		
50	21	13		50	24	14		
52	8	9	1	52	10	16		
54	4	3		54	11	28		
56	2	2		56	6	25	2	
58	1	2		58	7	14	1	
60	1			60	1	12	2	
62				62		13	2	
64				64		3		
66				66		2	2	
68				68		2		
70				70		1	1	1

Tables 18 & 19 summarize the average back-calculated fork lengths of both sexes for the different scale ring counts. The data has been separated into fish which were spawned during November to December (first spawn) and those which were spawned at the end of the breeding season (February to March).

The back-calculated lengths for age one fish (Tables18 &19) agree with the mean lengths given in Tables 15 & 16; approximately 40mm for the first spawn fish and 30mm for the second spawn fish, at time of ring formation.

Ford-Walford plots (Ford, 1933; Walford, 1946) of length at age "t" against length at age "t + 1" were drawn by regression analysis using the method of least squares (Fig.35). The data points are arranged in a straight line which bisects the 45° diagonal. In B. anoplus males (first spawn, Table 18) there are not enough data points to calculate a Ford-Walford plot. In this case, the mean length of a "third" age group was obtained from the 6 two-ringed males collected at the end of their third summer of growth, April 1981, which were over 47mm (mean length at age II). It appears that the two-ringed males of the first spawn do not live through to the next season (3^{+}). The mean length for the 6 fish was 52mm.

The von Bertalanffy's parameter, t_o (the theoretical time when length is zero) was calculated for male and female B. anoplus using Ricker's (1975) method in which log (L_∞ - t) is plotted against age in years. L_∞ is the asymptotic (final) length obtained from a Ford-Walford plot. (Fig. 35) (details below). Values of t_o which are close to 0 indicate a good fit to von Bertalanffy's growth model, and values close to 1 or -1 indicate a poor fit.

TABLE 18

Back calculated fork lengths (mm) for the first and second spawn males of B. anoplus in the P.K. le Roux impoundment obtained from measurements of scale rings.

First Spawn (November, December)
Males

No. of rings at capture	n	Length at age I	II	III
1	96	40		
2	11	38	47	
3	0	-	-	-
No. of fish	107	107	11	0
Mean F L		39	47	-

Second Spawn (February, March)
Males

No. of rings at capture	n	Length at age I	II	III
1	154	30		
2	39	29	44	
3	1	25	43	46
No. of fish	194	194	40	1
Mean F L		28	44	46

TABLE 19

Back calculated fork length (mm) for the first and second spawn females of B. anoplus in the P.K. le Roux impoundment, obtained from measurements of scale rings.

First spawn (November, December)

Females

No. of rings		Length at age			
at capture	n	I	II	III	IV
1	76	41			
2	33	40	52		
3	1	45	59	67	
4	1	37	50	57	64
No. of fish	111	111	35	2	1
Mean F L		41	54	62	64

Second Spawn (February,March)

Females

No. of rings		Length at age			
at capture	n	I	II	III	IV
1	178	31			
2	111	31	46		
3	9	31	47	55	
4	0	-	-	-	-
No. of fish	298	298	120	9	0
Mean F L		31	47	55	-

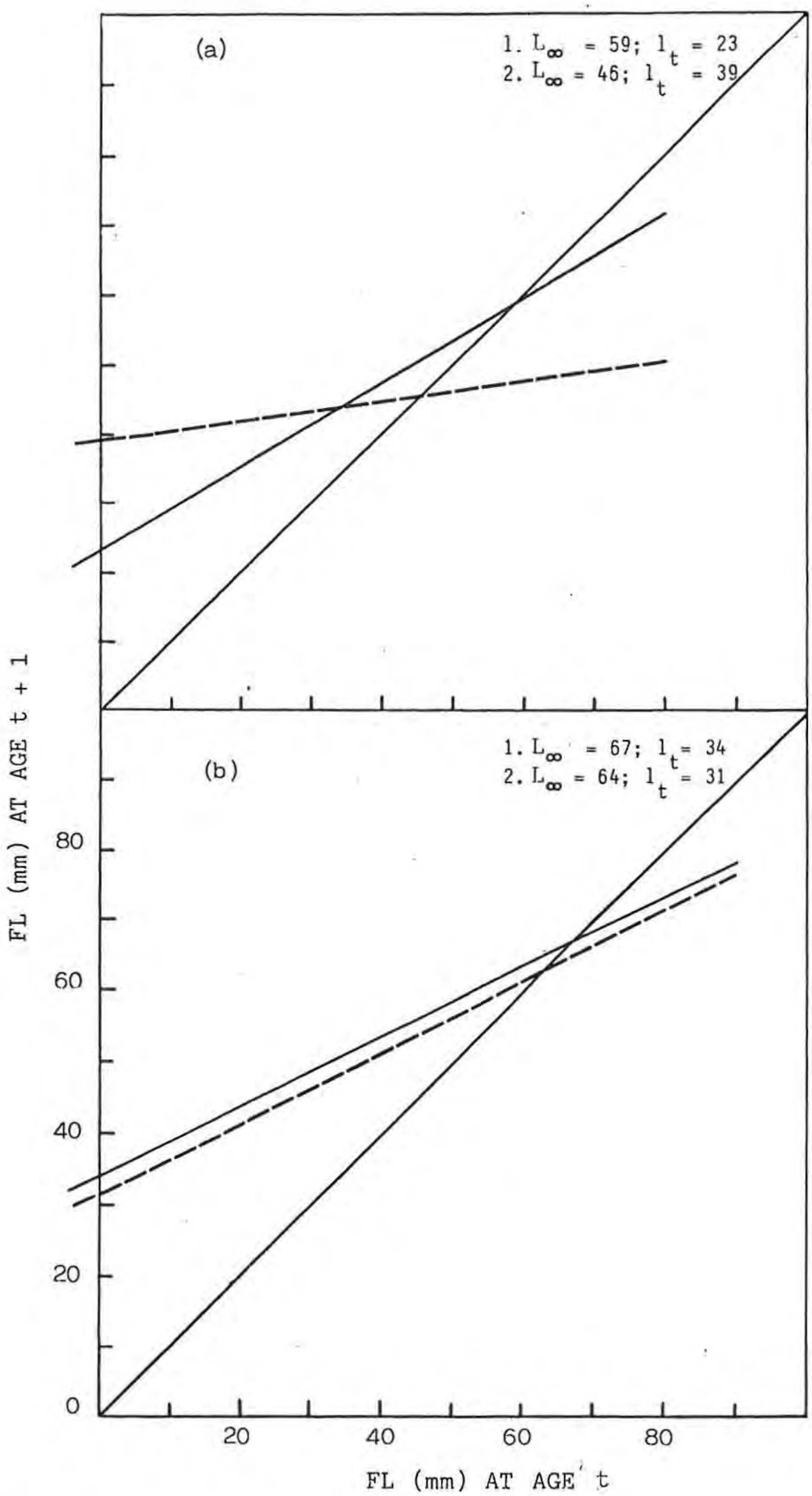


Fig. 35 Ford-Walford plots for (a) male and (b) female *B. anoplus* for two separate spawns (first spawn-solid line, second spawn broken line).
L_∞ = asymptotic length (intercept on diagonal)
l_t = length at one year (intercept on y-axis)
1 & 2 = first and second spawns.

The values of t_o for males and females are shown in Table 20. A poor fit (t_o = -1,053) was obtained for males, possibly due to the assumed length at age 3/3 . A somewhat better fit was obtained for females (t_o = -0,283).

The Ford-Walford plots (Fig. 35) are typical of a growth curve which shows an initial period of rapid increase (see Table 18 & 19) and then a decrease, as described by von Bertalanffy's model (Ricker, 1975). This pattern of growth suggests a limiting size, the asymptotic length, which is read off a Ford-Walford plot as the intercept on the 45° diagonal.

Ford-Walford plots of the first spawn B. anoplus give asymptotic length of 59mm and 67mm for males and females respectively. The asymptotic lengths for the second spawn fish are 46mm and 64mm respectively. The postulated asymptotic lengths of the first spawn fish agree with the 22 265 B. anoplus measured in this study, of which only 15 (0,1%) females were greater than 67mm and the largest male was 60mm. Nine per cent (n = 1011) of the males exceeded a length of 46mm (postulated asymptotic length of the second spawn), but the majority of these males might be first spawn fish. The theoretical length at one year is read off a Ford-Walford plot as the intercept on the y-axis. From Fig.35 these values are: males, first spawn 23mm, second spawn 39mm and females 34mm and 31mm. These lengths do not agree with the calculated values (Tables 18&19) with the exception of females of the second spawn. For example the first spawn males attain a length of 39mm not 23mm attained from the Ford-Walford plot, and the second spawn males attain 28mm not 39mm.

TABLE 20

Calculation of t_o from von Bertalanffy's growth equation for male and female *B. anoplus* of the first spawn from the P.K. le Roux impoundment using Ricker's (1975) method. All lengths in mm.

Males

Year	F L	L_∞ -1t	$Log_e(L_\infty$ -1t)
1	39	20	3,00
2 *	47	12	2,48
3 *	52	7	1,95

L_∞ = 59mm

y = 3,527 - 0,525 x (r^2 = 0,99)

$$t_o = \frac{3,527 - 4,08}{0,525}$$

= -1,053

Females

Year	F L	L_∞ -1t	$Log_e(L_\infty$ -1t)
1	41	26	3,26
2	54	13	2,56
3	62	5	1,61
4	64	3	1,10

L_∞ = 67mm

y = 3,990 - 0,743 x (r^2 = 0,99)

$$t_o = \frac{3,990 - 4,20}{0,743}$$

= -0,283

where y = Log_e (L_∞ -1t)

x = age in years

L_∞ = asymptotic length

1t = length at time t (years)

$$t_o = \frac{\text{y axis intercept} - Log_e(L_\infty)}{\text{Slope of plot x:y}}$$

* see text for explantaion

Knight (1968) has noted that the asymptotic length obtained from the Ford-Walford plot, is a descriptive summary of data for a population, not a law of Nature. Ford-Walford plots cannot be used for fish which have near linear growth throughout life, a group in which B. anoplus is not included. The minnows attain nearly 60 to 70% of their final length in their first six months of life, and thereafter the growth rate slows down and reaches a plateau. The theoretical length values at one year read off the Ford-Walford plots indicate that the growth pattern of B. anoplus does not follow the classical growth pattern and the intercept on the y-axis is unreliable.

Description of growth:

Growth rates for males and females of the first and second spawn were calculated. Mean weight was determined from the length-weight regression used for the relative condition (see p.150) of B. anoplus (n = 170), and is expressed as follows:

$$\log_{10} W = -4,9458 + 3,0391 \ \mathrm{Log}_{10} \ F\,L \ (r^2 = 0,99)$$

where W = weight in grams

FL = fork length in mm.

Growth in weight for the first and second spawn females is almost linear for the first three years, and then decreases (Fig.36). The weight increments were highest in the second year for both age groups of females and both spawns.

In males growth in weight decreases after the second year. The weight increments were greatest in the first year of the first spawn and the second year of the second spawn.

Growth in length of the males and females was similar in the first year after which the females grew faster (Fig. 37). The annual length increment was highest in the first year for both sexes and then decreased progressively.

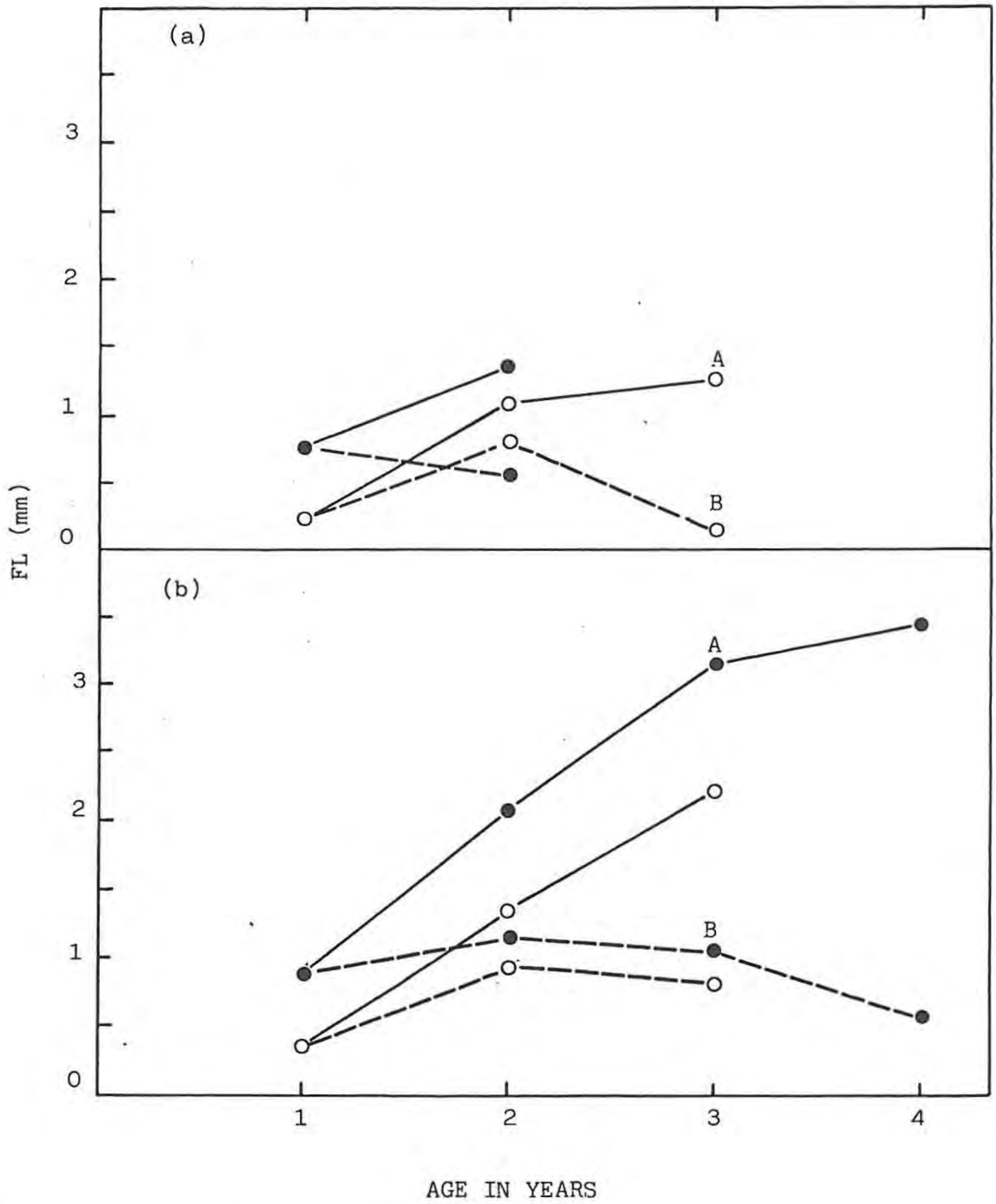


Fig. 36 Growth in weight of B. anoplus (a) males and (b) females of first spawn (●) and second spawn (○) in the P.K. le Roux impoundment, (A - growth rate of population; B - weight increments).

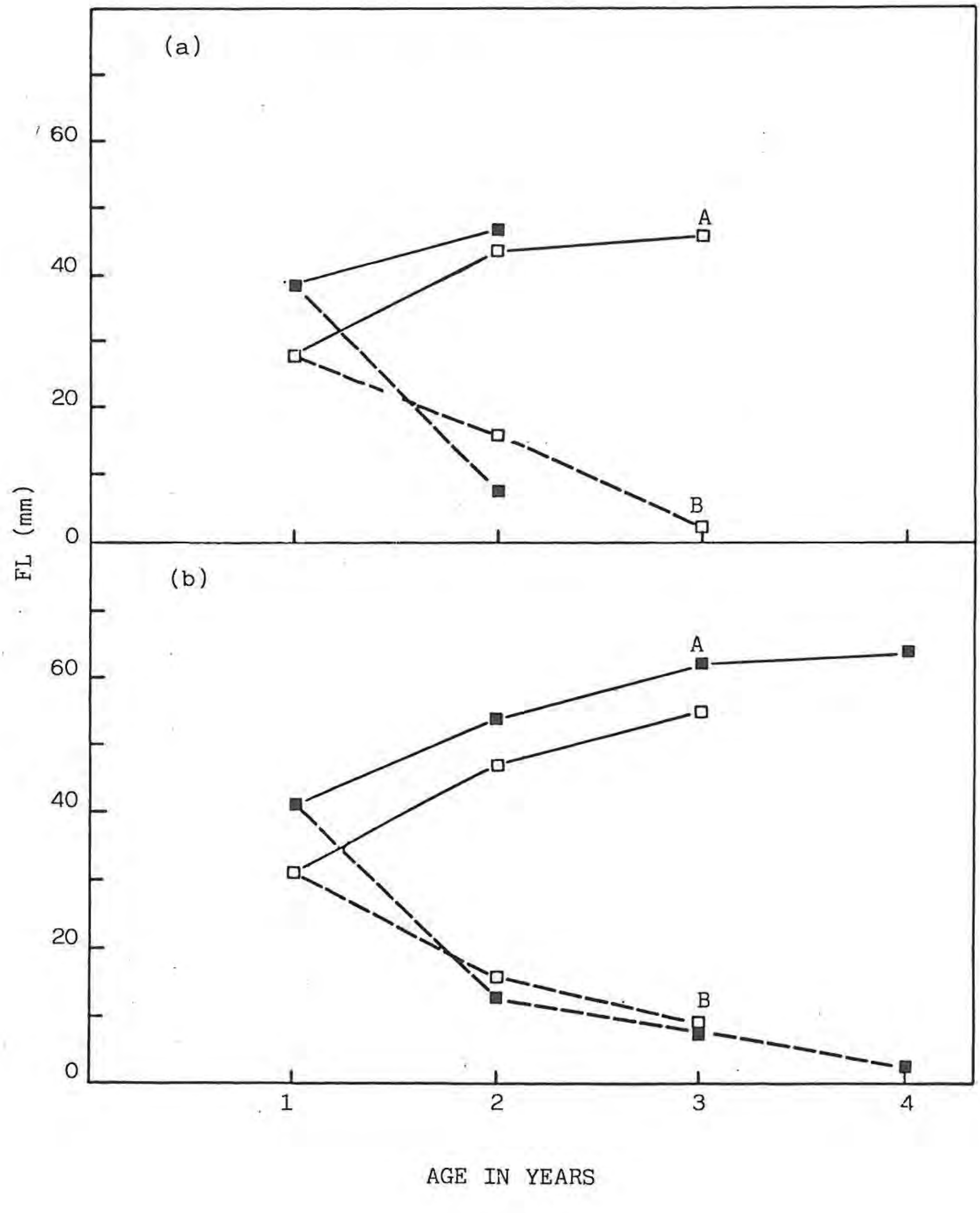


Fig. 37 Growth in length of B. anoplus (a) males and (b) females of first spawn (■) and second spawn (□) in the P.K. le Roux impoundment. (A - growth rate of population, B - length increments)

Relative condition:

In the mature females (Fig.38) the somatic body condition (K_S) and total condition (K_T) begin to diverge in August 1979. There is an increase in both condition factors during this period. As was observed in the GSI values (Fig.11), the ovaries are the largest in October, which is the period when there is a large gap between the two conditions factors, but the somatic condition has not been diminished and showed a slight increase from August. Spawning occurs in November 1979 and the December 1979 data show a sharp drop in both the K_T and K_S values. The drop in K_T after spawning is caused by shedding of eggs. The similar drop in K_S values for both years after a spawning has occurred could indicate several occurrences. Condition is either lost due to spawning activity or the cessation of feeding during spawning, or both. In the second year a similar decrease is only seen after December 1980.

Somatic condition steadily improves after December 1980 and is back to 1,0 by May June 1980. The K_T undergoes a slight increase in February (2nd spawning) and then decreases. In the second year, the fish undergo a similar pattern, but there is a marked increase in both conditions.

The maturing males (31-40mm) (Fig.38b) show less divergence between the two conditions, but they follow a similar pattern. The greatest divergence is seen in October 1979, October and December 1980 (the period before the first spawning). The smallest females (21-30mm) (Fig.38c) which do not take part in reproduction, also show distinct seasonal trends in condition. The peak in 1979 was reached in October, but in the second year there was only a peak in February.

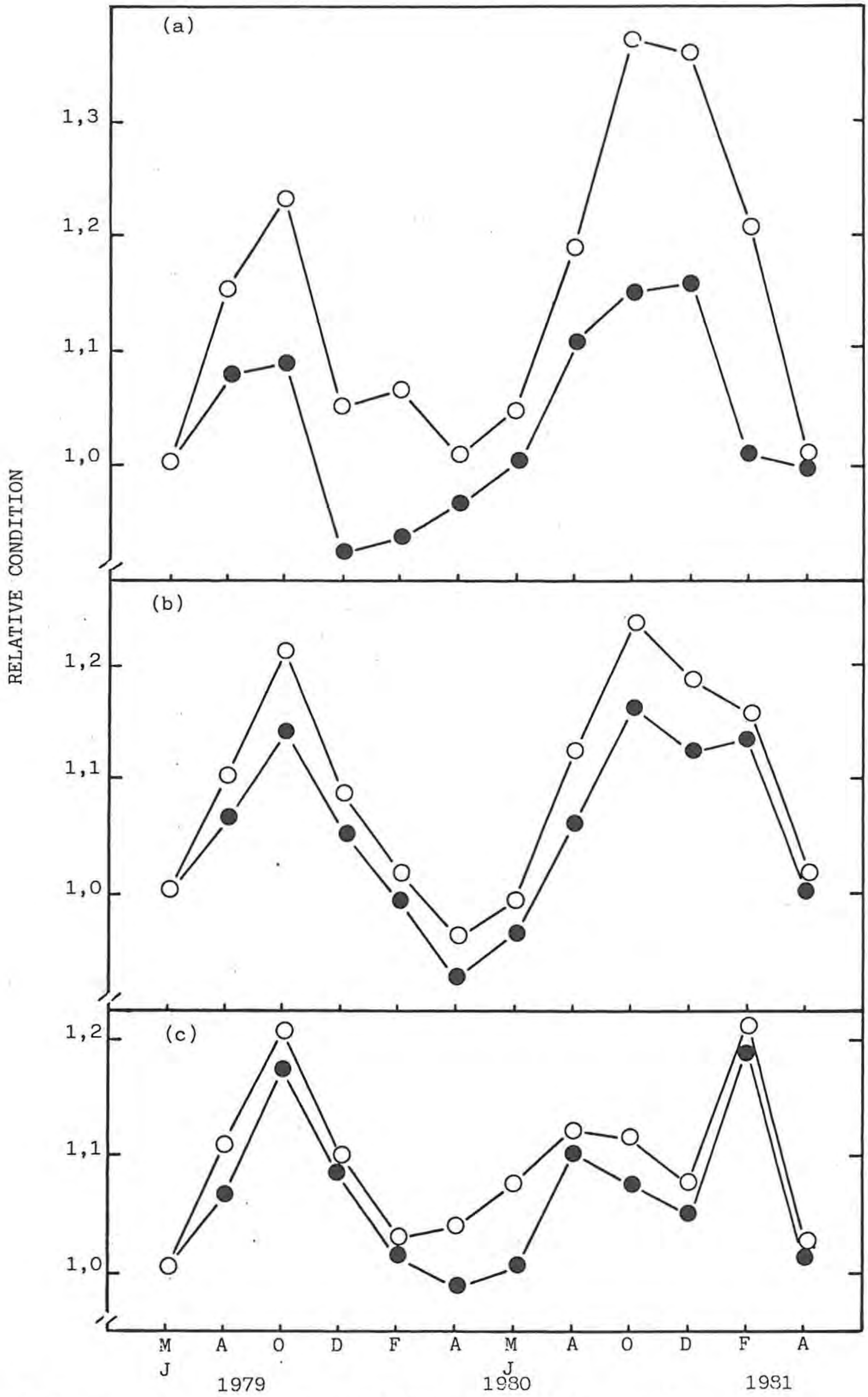


Fig. 38 Two monthly changes in condition of female B. anoplus: (a) greater than or equal to 48mm FL; (b) 31-40mm FL; (c) 21-30mm FL, relative to the condition of the fish collected in May and June 1979, (open circles - mean total condition, closed circles - mean somatic condition).

The pattern of change in relative condition of mature males (Fig. 39) was very similar to mature females. There is less divergence between K_S and K_T as would be expected. The main divergence occurs between August and October of both years. There is a second increase in February 1980, which was not seen in February 1981 for either sex. The males are in a better condition in the second year which was also indicated for females.

The maturing males (31-40mm) (Fig.39b) show very little divergence between K_T and K_S. The fish are in their best condition during October 1979 and October 1980 to February 1981.

The improved condition of the second year was only seen in the mature females (Fig.38a) and males (Fig.39a), and was not observed in the smaller fish (Figs 38b,c & 39b,c).

In both the immature and mature fish a monophasic cycle of condition occurred, with the fluctuations in the total condition followed very closely by somatic condition.

Population structure:

The length frequency of 11277 males, 10988 females and 8894 juvenile and unsexed fish caught at sites 6,8,68,72 and 73 for the 25 month period (April, 1979 to April, 1981) is given in Fig. 40 . The length mode of the males is similar to females (34-38mm). Females grow to a greater length (73mm) than males (60mm) (Figs 40 & 41).

Sex determination of the pooled sample of 22265 fish over 20mm in length showed no deviation from a 1:1 sex ratio. Males numbered 11277 (50,6%) and females 10988 (49,4%). The male to female sex ratio decreases with age (Fig. 41). The graph of the percentage of the total population

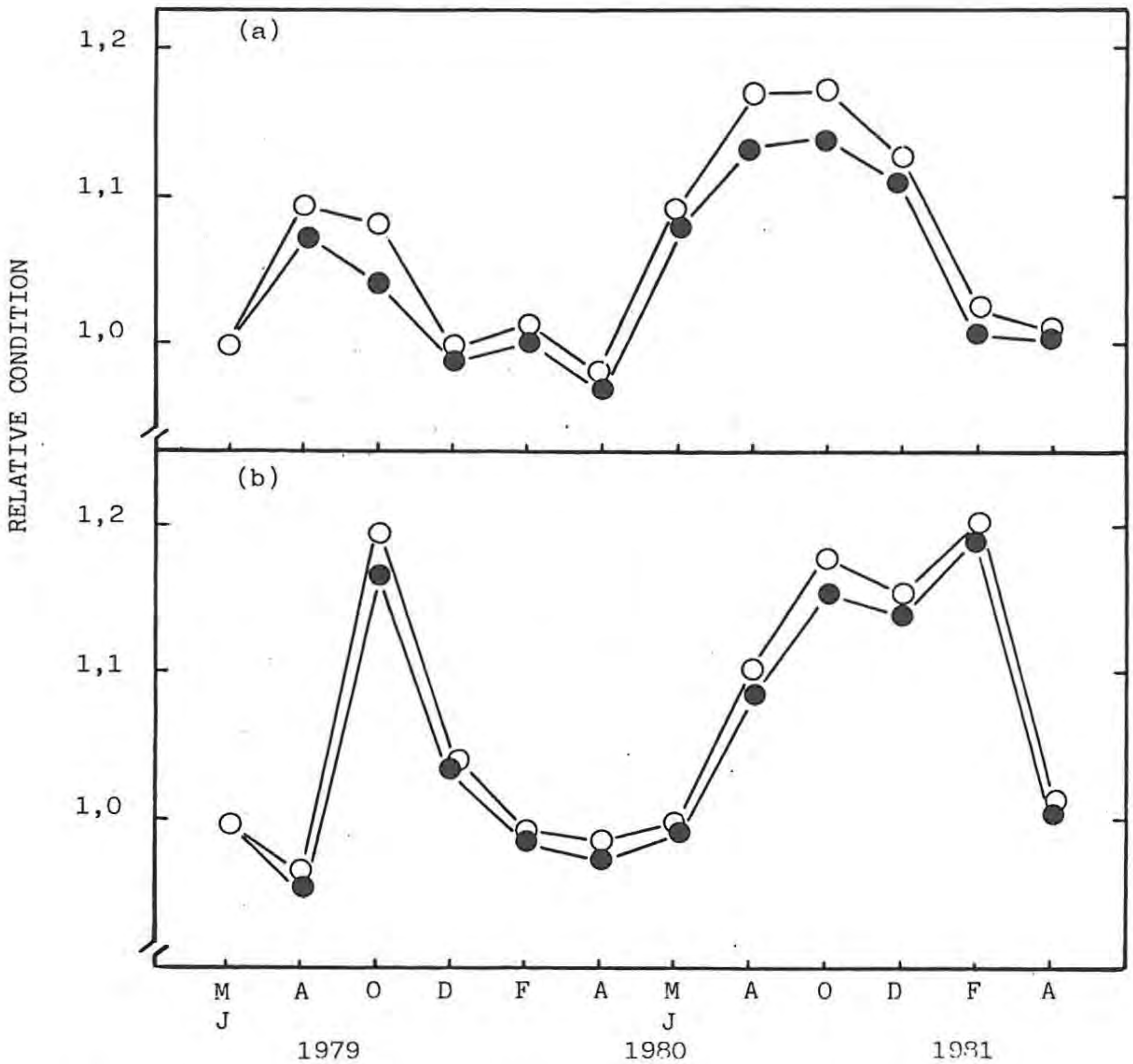


Fig. 39 Two monthly changes in condition of male B. anoplus: (a) greater than or equal to 48mm FL; (b) 31-40, relative to the condition of fish collected in May and June 1979, (open circles - mean total condition, closed circles - mean somatic condition).

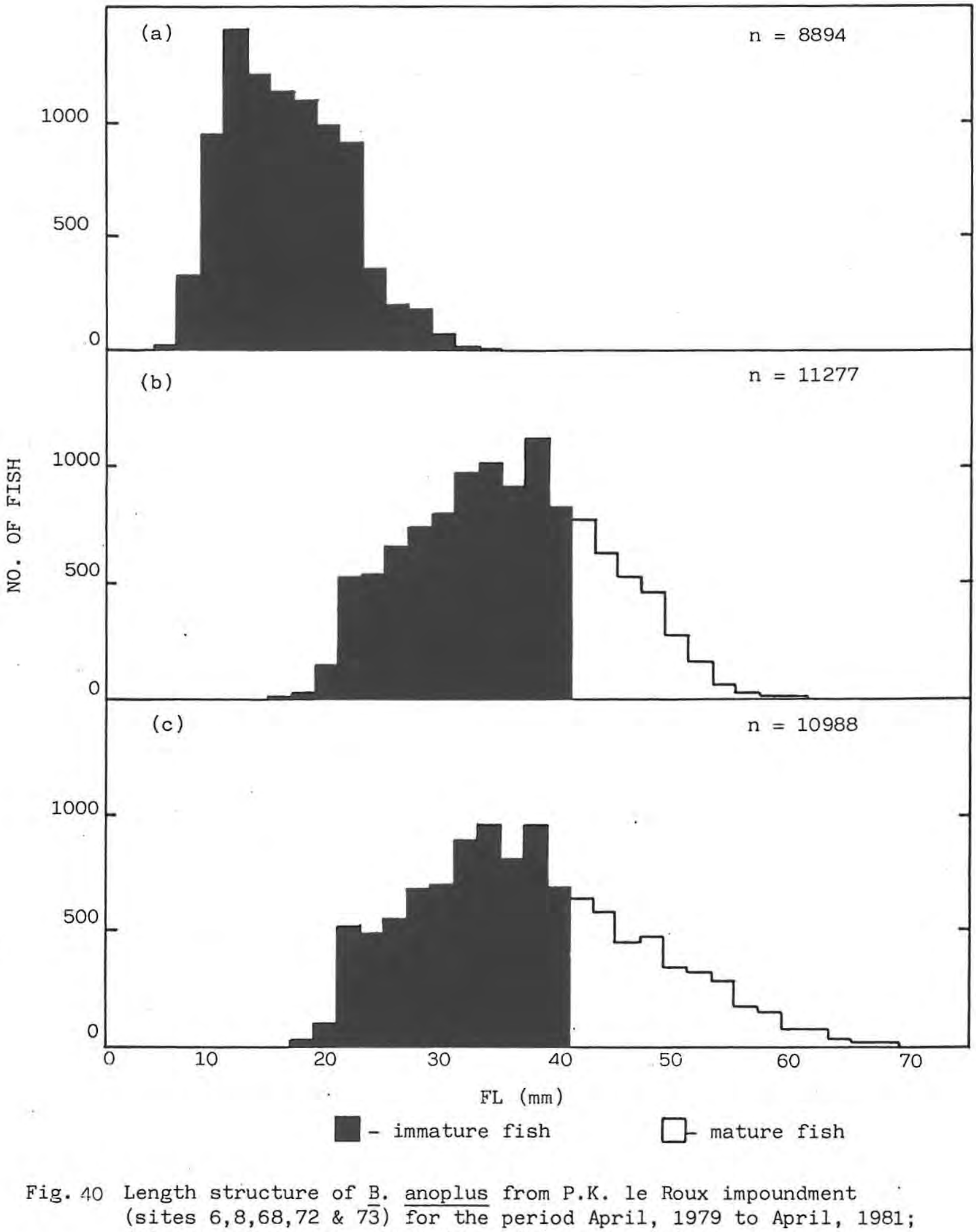


Fig. 40 Length structure of B. anoplus from P.K. le Roux impoundment (sites 6,8,68,72 & 73) for the period April, 1979 to April, 1981; (a) juveniles and unsexed fish; (b) males; (c) females.

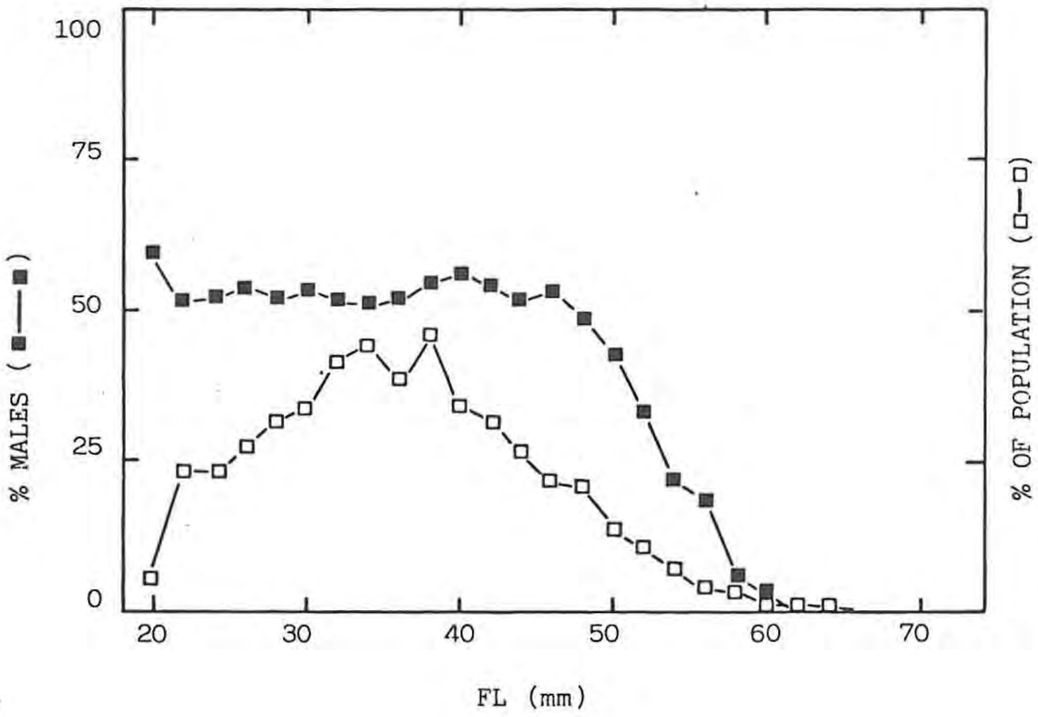


Fig. 41 Percentage of male B. anoplus at different lengths in fish collected throughout a 25 month period (April 1979 to April 1981) in the P.K. le Roux impoundment (males, n = 11277; females, n = 10988).

In the Hendrik Verwoerd impoundment the 122m net, which was used in Grassridge Dam, was used as a control to see if the minnow seine net was sampling the entire population of chubbyhead minnows. There was a similar length distribution of large fish in catches from both nets, therefore the minnow seine was sampling the entire population in the Verwoerd reservoir. Due to the rocky substrate in the P.K. le Roux impoundment the large seine net was not used, but it is reasonable to assume from the 15m anchovy mesh seine net, purse seine and trawl net catches that very few B. anoplus of 60mm or longer occur in the impoundment. sexed for each length group, in combination with the male to female sex ratio provides a more thorough picture of the population structure of fish over 35mm. After 38mm ($0-1^+$) there is a fairly rapid decrease in the numbers of both sexes. Very few fish occur in the length group over 60mm, which are 2^+ or 3^+ fish.

Similarly in the Hendrik Verwoerd reservoir very few fish over 60mm in length were collected (Cambray et al., 1978). B. anoplus have also been collected from Grassridge Dam (31°45'S, 28°28'E) on the Great Brak River. Grassridge Dam is the first reservoir below the outlet of the Orange-Fish River Tunnel scheme. In a sample of 716 B. anoplus collected with a 122m seine net, with a cod-end of 28mm stretched mesh, minnows of 50 to 70mm were common in the catch. The largest male was 71mm whereas the largest female was 101mm (Cambray et al., 1977). Collections were also made with the minnow seine net. In the total catch of B. anoplus for both nets (n = 966), 52% were males and 50% of the catch was between 51-70mm.

Discussion

Temperature plays an important role in the length of the growing season of most fish (Van Oosten, 1944 in Cadwallader, 1978), and this relationship of growth to temperature is an accepted phenomenon in fishes (Brown, 1957). Most of the growth of B. anoplus occurred when the highest water temperatures were recorded and growth slowed down when water temperatures were low.

Temperature affected the length of the growing season, particularly after the second spawn. Fish hatched from the first spawn had a longer growing season (5-6 months) than the second spawn (2 months).

B. anoplus males attain a maximum age of only 3 years, but it appears that the majority of the adult male population die after their second summer (1^+). Females live to a maximum of 4 years and have a higher growth rate than males after the first summer. The majority of adult females also die after their second summer, but more attain an age of 2^+ than males. There is therefore a rapid turnover of the population.

Of the 39 small Barbus species reviewed in Table 21, basic life history traits such as age and length at sexual maturity and maximum length and age are only known for four species, B. anoplus, B. liberiensis, B. paludinosus and B. trevelyani.

B. trevelyani of the Tyume River in the Eastern Cape grow rapidly in their first year of life to a maximum of 40 to 50mm FL. The growth rate then decreased and remained approximately linear until the sixth year (80-100mm FL; Gaigher, 1975). Gaigher found that females may grow faster than males, and reach a length of 103mm FL. Sixty-three per cent of the population over 70mm FL were females. All males were found

TABLE 21

Review of the length and age at first sexual maturity and maximum length of various small African Barbus species.

Species	Locality	Length at sexual maturity (mmFL)		Age at sexual maturity		Maximum		Reference
		♂♂	♀♀	♂♂	♀♀	Length FL (mm)	Age	
B. afer	Cape	n.s.*	n.s.	n.s.	n.s.	102	n.s.	Jubb, 1967
B. afrohamiltoni	Natal	<76	<76	n.s.	n.s.	127	n.s.	Crass, 1964
B. afrohamiltoni	Zimbabwe	n.s.	n.s.	n.s.	n.s.	115TL	n.s.	Bell-Cross, 1976
B. afrohamiltoni	-	n.s.	n.s.	n.s.	n.s.	127	n.s.	Jubb, 1967
B. afrovernayi	Zimbabwe	n.s.	n.s.	n.s.	n.s.	45	n.s.	Bell-Cross, 1976
B. afrovernayi	-	n.s.	n.s.	n.s.	n.s.	57	n.s.	Jubb, 1967
B. annectens	Kruger Park	n.s.	n.s.	n.s.	n.s.	75	n.s.	Pienaar, 1978
B. annectens	Zimbabwe	n.s.	n.s.	n.s.	n.s.	76TL	n.s.	Bell-Cross, 1976
B. annectens	-	n.s.	n.s.	n.s.	n.s.	76	n.s.	Jubb, 1967
B. anoplus	P.K. le Roux Dam	40	40	1	1	60♂ 73♀	4	This study
B. anoplus	Grassridge Dam	n.s.	n.s.	n.s.	n.s.	101 ♀.	n.s.	Cambray et al., 1977
B. anoplus	-	n.s.	n.s.	n.s.	n.s.	89	n.s.	Jubb, 1967
B. anoplus	Natal	38	38	n.s.	n.s.	89	n.s.	Crass, 1964
B. apleurogramma	Lake Victoria	32SL	32SL	1	1	n.s.	n.s.	Welcomme, 1969
B. argenteus	-	n.s.	n.s.	n.s.	n.s.	197	n.s.	Jubb, 1967
B. argenteus	Natal	70	70	n.s.	n.s.	197	n.s.	Crass, 1964
B. argenteus	Kruger Park	70	70	n.s.	n.s.	197	n.s.	Pienaar, 1978
B. asper	Cape	n.s.	n.s.	n.s.	n.s.	117	n.s.	Jubb, 1967
B. aurantiacus	Zambezi	n.s.	n.s.	n.s.	n.s.	76	n.s.	Jubb, 1967
B. barnardi	Zimbabwe	n.s.	n.s.	n.s.	n.s.	76TL	n.s.	Bell-Cross, 1976
B. bellcrossi	Zimbabwe	n.s.	n.s.	n.s.	n.s.	89	n.s.	Jubb, 1967
B. burgi	Cape	64	64	n.s.	n.s.	121	n.s.	Jubb, 1967
B. brevipinnis	Incomati R.	n.s.	n.s.	n.s.	n.s.	51	n.s.	Jubb, 1967
B. burchelli	Cape	n.s.	n.s.	n.s.	n.s.	95	n.s.	Jubb, 1967
B. calidus	Olifants R.	n.s.	n.s.	n.s.	n.s.	95	n.s.	Jubb, 1967

*n.s. (not specified)

(Table continues)

(Table 21 continued)

Species	Locality	Length at sexual maturity (mm FL) ♂♂	Length at sexual maturity (mm FL) ♀♀	Age at sexual maturity ♂♂	Age at sexual maturity ♀♀	Maximum Length FL (mm)	Maximum Age	Reference
B. eutaenia	-	n.s.	n.s.	n.s.	n.s.	127	n.s.	Jubb, 1967
B. eutaenia	Kruger Park	n.s.	n.s.	n.s.	n.s.	100	n.s.	Pienaar, 1978
B. eutaenia	Zimbabwe	n.s.	n.s.	n.s.	n.s.	140TL	n.s.	Bell-Cross, 1976
B. fasciolatus	-	n.s.	n.s.	n.s.	n.s.	57	n.s.	Jubb, 1967
B. fasciolatus	Zimbabwe	n.s.	n.s.	n.s.	n.s.	60TL	n.s.	Bell-Cross, 1976
B. gurneyi	Tugela	n.s.	n.s.	n.s.	n.s.	102	n.s.	Jubb, 1967
B. gurneyi	Natal	<51	<51	n.s.	n.s.	102	n.s.	Jubb, 1967
B. haasianus	Zambezi	n.s.	n.s.	n.s.	n.s.	32	n.s.	Jubb, 1967
B. kerstenii	Lake Victoria (stream)	34SL	34SL	n.s.	n.s.	68 ♂ SL 75 ♀ SL	n.s.	Welcomme, 1969
B. liberiensis	Sierra Leone (stream)	50-60TL	50-60TL	1	1	119TL	4	Payne, 1975, 1976
B. lineomaculatus	-	n.s.	n.s.	n.s.	n.s.	76,2	n.s.	Jubb, 1967
B. lineomaculatus	Natal	n.s.	n.s.	n.s.	n.s.	83	n.s.	Crass, 1964
B. lineomaculatus	Zimbabwe	n.s.	n.s.	n.s.	n.s.	76TL	n.s.	Bell-Cross, 1976
B. manicensis	Zimbabwe	n.s.	n.s.	n.s.	n.s.	152	n.s.	Jubb, 1967
B. manicensis	Zimbabwe	n.s.	n.s.	n.s.	n.s.	153TL	n.s.	Bell-Cross, 1976
B. motebensis	Limpopo	n.s.	n.s.	n.s.	n.s.	97	n.s.	Jubb, 1967
B. multilineatus	-	n.s.	n.s.	n.s.	n.s.	64	n.s.	Jubb, 1967
B. multilineatus	Zimbabwe	n.s.	n.s.	n.s.	n.s.	45TL	n.s.	Bell-Cross, 1976
B. neefi	Limpopo	n.s.	n.s.	n.s.	n.s.	51	n.s.	Jubb, 1967
B. paludinosus	-	n.s.	n.s.	n.s.	n.s.	127	n.s.	Jubb, 1967
B. paludinosus	Natal	51	51	n.s.	n.s.	102	n.s.	Crass, 1964
B. paludinosus	Kruger Park	50	50	n.s.	n.s.	n.s.	n.s.	Pienaar, 1978
B. paludinosus	Zimbabwe	n.s.	n.s.	n.s.	n.s.	130TL	n.s.	Bell-Cross, 1976
B. paludinosus	Lake Chilwa	50TL	50TL	1	1	120TL	3	Furse et al., 1979

* n.s. (not specified)

(Table continues)

(Table 21 continued)

Species	Locality	Length at sexual maturity (mmFL)		Age at sexual maturity		Maximum		Reference
		♂♂	♀♀	♂♂	♀♀	Length FL (mm)	Age	
B. paludinosus	Lake Chilwa	n.s.	48	n.s.	n.s.	n.s	n.s.	Kirk, 1972
B. paludinosus	Lake Victoria	48SL	54SL	n.s.	n.s.	n.s	n.s.	Welcomme, 1969
B. pallidus	Cape	44	44	n.s.	n.s.	70	n.s.	Jubb, 1967
B. pallidus	Natal	n.s.	n.s.	n.s.	n.s.	51	n.s.	Crass, 1964
B. phlegethon	Olifants R.	n.s.	n.s.	n.s.	n.s.	70	n.s.	Jubb, 1967
B. poechii	-	n.s.	n.s.	n.s.	n.s.	152	n.s.	Jubb, 1967
B. poechii	Zimbabwe	n.s.	n.s.	n.s.	n.s.	110TL	n.s.	Bell-Cross, 1976
B. puellus	Zambezi	n.s.	n.s.	n.s.	n.s.	38	n.s.	Jubb, 1967
B. radiatus	-	n.s.	n.s.	n.s.	n.s.	102	n.s.	Jubb, 1967
B. radiatus	Kruger Park	n.s.	n.s.	n.s.	n.s.	95	n.s.	Pienaar, 1978
B. radiatus	Zimbabwe	n.s.	n.s.	n.s.	n.s.	80TL	n.s.	Bell-Cross, 1976
B. tangandensis	-	n.s.	n.s.	n.s.	n.s.	76	n.s.	Jubb, 1967
B. tangandensis	Zimbabwe	n.s.	n.s.	n.s.	n.s.	65TL	n.s.	Bell-Cross, 1976
B. thamalakanensis	Zimbabwe	n.s.	n.s.	n.s.	n.s.	50TL	n.s.	Bell-Cross, 1976
B. toppini	-	n.s.	n.s.	n.s.	n.s.	38	n.s.	Jubb, 1967
B. toppini	Natal	n.s.	n.s.	n.s.	n.s.	38	n.s.	Crass, 1964
B. toppini	Kruger Park	n.s.	n.s.	n.s.	n.s.	40	n.s.	Pienaar, 1978
B. trevelyani	-	n.s.	n.s.	n.s.	n.s.	89	n.s.	Jubb, 1967
B. trevelyani	Tyume R.	40-50	65-75	1	3	103 ♀	6	Gaigher, 1975
B. trimaculatus	-	n.s.	n.s.	n.s.	n.s.	152	n.s.	Jubb, 1967
B. trimaculatus	Natal	<76	<76	n.s.	n.s.	152	n.s.	Crass, 1964
B. trimaculatus	Kruger Park	75	75	n.s.	n.s.	155	n.s.	Pienaar, 1978
B. trimaculatus	Zimbabwe	n.s.	n.s.	n.s.	n.s.	140TL	n.s.	Bell-Cross, 1976
B. unitaeniatus	-	n.s.	n.s.	n.s.	n.s.	140	n.s.	Jubb, 1967

*n.s. (not specified)

(Table continues)

(Table 21 continued)

Species	Locality	Length at sexual maturity (mmFL)		Age at sexual maturity		Maximum		Reference
		♂♂	♀♀	♂♂	♀♀	Length FL (mm)	Age	
B. unitaeniatus	Kruger Park	n.s.	n.s.	n.s.	n.s.	105 TL	n.s.	Bell-Cross, 1976
B. viviparus	-	n.s.	n.s.	n.s.	n.s.	64	n.s.	Jubb, 1967
B. viviparus	Natal	38	38	n.s.	n.s.	76	n.s.	Crass, 1964
B. viviparus	Kruger Park	n.s.	n.s.	n.s.	n.s.	65	n.s.	Pienaar, 1978
B. viviparus	Zimbabwe	n.s.	n.s.	n.s.	n.s.	55TL	n.s.	Bell-Cross, 1976

*n.s. (not specified)

to be sexually mature at the end of the first year of life, unlike females which only reached sexual maturity in the third year of life. This delayed age at sexual maturity is unlike any of the other small Barbus recorded in Table 21.

In Lake Chilwa male and female B. paludinosus reach sexual maturity in their first year of life (50mm TL). Females grow faster than males and females appear to mature at a slightly smaller size (Kirk, 1972; Furse, 1979). Females outnumber males above 45mm TL and very few males exceed 75mm TL (Furse, 1979). B. liberiensis in Sierra Leone also reach sexual maturity in the first year (50-60mm TL), (Payne, 1975).

It is interesting to note that in the four species for which length at the end of the first year and maximum length are known, over 40% and in several species up to 67% of the total growth in length occurs within the first year (Table 22).

Females of the small Barbus usually live longer and attain a greater length than the males, and would therefore have a longer reproductive life. Males of the four small Barbus species appear to be more 'r-selected' than the females. That is, the males are smaller, have a more limited reproductive life and in the case of B. trevelyani mature at an earlier age than do females.

What would be the advantage to the population, of males being more 'r-selected' than females? Payne (1975) suggests that the early demise of male B. liberiensis, which live in headwater streams where resources are scarce, is to conserve the food supply. Furse (1979, p.188) notes that in B. paludinosus of Lake Chilwa the decrease in males after 45mm TL is a, "significant factor in maintaining a high reproductive effort", but he does not elaborate further.

TABLE 22

Approximate percentage of total growth obtained in the first year of life by four small *Barbus* species.

Species	Approximate length at end of first year		Approximate percentage of total growth obtained in the first year.		Reference
	♂♂	♀♀	♂♂	♀♀	
B. anoplus	39mm FL	41mm FL	65	59	This study
B. liberiensis	69mm TL	69mm TL	62	62	Payne, 1975
B. paludinosus	50mm TL	50mm TL	67	42	Furse, 1979
B. trevelyani	±45mm FL	±45mm FL	46	48	Gaigher, 1975

Why do B. anoplus females live longer and attain a greater size than males? Large females can benefit the population because they are physically capable of carrying more eggs than smaller females. For example, in October 1980, the absolute fecundity of a 40mm (1^+) female was 220 and a 63mm (2^+) female had 3252 yolked ova. In the above example a 1,6 fold (23mm) increase in length meant a 15 fold increase in fecundity. The breeding behaviour of B. anoplus is not known, but we can assume here that the size of a sexually mature male has a limited influence on his reproductive success. Therefore a 60mm FL (2^+) male is of little value to the population, except when there is a poor year class of 1^+ males. The 2^+ and 3^+ males would compete with the females for food (Payne's resource conservation argument), therefore it would be advantageous for the population if the majority of the males die off after one reproductive season. The limited fall and winter resources could then be used by the females for survival and laying down a nutrient store in preparation for the next reproductive season, when they will breed with mainly 1^+ males not 2^+ males. Therefore, it is advantageous to the population if males are relatively more r-selected.

The multiple spawning strategy of B. anoplus is very important in understanding the age and growth adaptations in the chubbyhead barb. The first and second spawns were treated as two separate age groups, which is acceptable considering their difference in length attained at the end of the first summer (e.g. 1979/80 season, first spawn 38,1mm, second spawn 22,1mm). The significance to the population of the 'double spawn age groups' can be obtained from the back calculation tables 18 & 19. In the males, 78% (n = 40) of the two year old fish and the only three year old male are from the second spawn. In the female sample a very similar pattern appears, of all the females two years or older, 77% (n = 120) are second spawn fish. (However, the only four year old fish was from a first spawn).

The significance of the second spawn to the population is now more obvious. The delay of the second spawn is probably an adaptation to defer their first breeding, which would in turn prolong the number of summers they would live to reproduce. The benefit to the population of second spawn fish would occur in years when there were few survivors from the first spawn of the previous year. I suggest that the above-mentioned adaptations evolved because of the unstable environment (Orange River) in which B. anoplus live.

The somatic condition (K_S) of B. anoplus follow the total condition (K_T) pattern very closely. When K_T increased there was a corresponding increase in K_S. Neither ovary nor testes development took place at the expense of somatic body weight, possibly indicating that food was readily available in the August to December periods. le Cren (1951) working on Perca fluviatilis and Payne (1975) studying B. liberiensis found that there was a fall in somatic body weight (W_S) with ovary development. The decrease in W_S represents the mobilization and transfer of body reserves to the ovaries during development. Payne (1975) noted that in B. liberiensis females the loss of somatic condition was understandable because the ripe ovaries constituted some 9,04% of the total body weight. In the B. anoplus population studied some females had ripe ovaries of over 20% of their total body weight, and yet there was no loss in somatic condition. The difference between the condition changes of the two Barbus species is probably due to the availability of food during gonadal development. In the P.K. le Roux impoundment there is enough food to replenish any resources that are needed for testes or ovary development.

There is a lack of recovery in relative condition of *B. anoplus* after spawning. Mann (1980) suggested that the balance between reduced somatic growth in *Gobio gobio* from the River Frome, and increased reproductive effort was supported in his study by the lack of recovery in relative condition after spawning. A similar pattern was also observed for *B. anoplus* which like *G. gobio* is an r-strategist.

The reproductive strategies of both *B. anoplus* and *G. gobio* support the thesis (Svärdson, 1949) that any diversion of energy resources away from somatic growth and maintenance towards a high reproductive effort might be at the expense of increased parental mortality.

CHAPTER 8

FEEDING BIOLOGY

Introduction

Very little is known about the feeding biology of small *Barbus* species in South Africa. Most studies have been superficial, and only a small number of guts were examined (Gaigher, 1979).

The principle objective of the present gut analysis study was to establish whether or not *B. anoplus* is euryphagous. Trophic adaptability would be an important asset for an r-selected fish in a harsh environment. This adaptability would have to occur in all size groups of the minnow.

The following hypothesis was tested: *B. anoplus* of all size groups are opportunistic feeders, which would aid this species in colonizing new areas.

Methods

The use of stomach contents in food preference studies can be criticized because small and soft-bodied prey may be digested before recovery. In the present study this point has to be considered. Even though care was taken to collect during the peak feeding period of the minnow, and fish were preserved within minutes (following suffocation) after capture, the possibility of rapid digestion of soft food matter exists. Digestion of soft insect parts was evident with chironomid larvae in the foregut analyses. The larvae are masticated by the raptoral pharyngeal teeth which appears to greatly facilitate rapid digestion, and in many foreguts only the well chitinized head was present. Therefore organisms without chitinized sections are probably underestimated in this study.

Gut contents were difficult to analyse for several reasons: the pharyngeal teeth fragment food items into small pieces; the foregut volume is very small, and there were relatively few fish with more than 50% of their gut full. Care had thus to be taken to choose a method or combination of methods to best represent the feeding habits of B. anoplus.

Lagler (1956, in Windell & Bowen, 1978) noted that stomach contents may not reflect the consumers diet accurately. Karpwitch & Bakoff (1937 in Swenson & Smith, 1973) described digestion as a process comprised of an "effection phase" during which up to 90% of the food is digested rapidly and a "residual phase" in which hard parts are softened and passed slowly. This point is also noted by Windell & Bowen (1978) in that some important components of the diet may be processed so rapidly that they leave little or no recognisable remains. There are also different rates of food progression for various items which lead to selective accumulation of food items which are digested slowly.

Care was therefore taken to collect the fish quickly (seine net), the fish were then suffocated before preserving to prevent regurgitation and in analyzing foregut contents separately from hindguts. Windell & Bowen (1978) recommended that a study of the food and feeding habits of a fish population should begin with a series of collections made at regular intervals over one or more 24h periods. Three such collections were made at the start of the present study to reveal the best time of day for collection of regular monthly samples.

The three diel feeding periodicity studies, each covering a 24h period, involved the collection of minnows with a minnow seine net at two hourly intervals. Five specimens from each collection time were analyzed with regard to fore- and hindgut fullness, based on an arbitrary fullness points system. The assessment of fullness was made after viewing the sections under 10 - 20X magnification. Points were allocated as follows:

Visual estimate of fullness		Points
Full	-	5
75%	-	4
50%	-	3
25%	-	2
Trace	-	1
Empty	-	0

Three separate studies were completed, because food intake and the digestive rate of fishes are influenced by many factors (Windell, 1968). These factors may have influenced the findings of a single diel study. It was not practical to do a 24h study each month, which would allow for changes in seasonal feeding periodicity. The principle aim of the three studies was to ascertain the best time to collect specimens to be used for dietary analysis.

Choice of method.

There are two main categories of diet studies: firstly those which examine the diet with a view to assessing the species nutritional standing in the fish community and the second category consists of studies which attempt to estimate the total food consumed by a fish population, which may involve calculation of daily ration or energy budget (Hyslop, 1980). The present B. anoplus study falls into the first category, and the main objective was to compare the adaptability of the species feeding habits in several different habitats.

Any one of the normal techniques of analysing gut contents is a compromise, and usually a combination of methods is necessary to avoid a biased picture of the importance of the items in the diet (Hynes, 1950). In a recent review Hyslop (1980) holds a similar view and states that the prudent investigator should employ at least one method measuring the amount and one measuring the bulk of the food material present. Windell & Bowen (1978) note that the goal of the study will determine the methods to be used. With this in mind the following methods were chosen for the reasons outlined. Other methods are not given here as the criticism of each technique is outlined in Hynes (1950), Windell & Bowen (1978), Butler (1980) and Hyslop (1980), and their discussions are applicable to the present study.

(a) Frequency of occurrence.

The number of stomach (fore and hindgut) samples is recorded in which one or more of a given food item is found. It is expressed as a percentage of all non-empty stomachs examined (Windell & Bowen, 1978). This is obviously an important method as it gives a qualitative picture of the food spectrum and is used by the majority of fisheries biologists, but it is usually not used alone, for it gives little indication of the relative bulk of each food category present in the stomach (Hyslop,1980).

(b) Numerical method.

The numerical method was also used for part of this study. The number of recognizable individuals in each food category was recorded for all stomachs and expressed as a percentage of the total individuals in all food categories. This method overemphasizes the importance of small prey items taken in large numbers (see Hyslop, 1980, for list of references).

Hyslop (1980) notes that in cyprinids it is difficult to estimate numbers in each category because of mastication of the food or the effects of digestive processes. Both these problems occurred in the present study and possibly caused underestimation of some food items.

(c) Volumetric.

The third method used was an indirect estimation of the volume of each food item. A direct method was not used because of the small volume of each food item and the fact that in many chironomids only the head capsule could be used, which would underestimate the volumetric value of this food item. Again Hyslop (1980) notes the difficulty in cyprinid studies, where the food is masticated and categories are largely inseparable. In the present study the food items were sorted into recognizable taxa on a petri dish. Millimetre graph paper had been glued to the bottom of the petri dish. The area covered by the group was recorded. The volume of items which had been very masticated or digested was compared to whole specimens which were collected from the same habitat. In this way a crude estimate of the volume of each category of food item was obtained. Windell & Bowen (1978) note that errors in estimated volume are usually trivial when compared to errors in enumeration.

The volumetric data for each category was expressed as a percentage of the total volume of all stomach contents examined. Hyslop (1980) notes that the volumetric techniques probably give the most representative measure of bulk and may be applied to all food items.

Collection techniques

B. anoplus dietary analysis samples were taken from the regular monthly minnow seine netting programme at sites 6,72 and 73.

Additional specimens were collected with an open-water trawl (Jackson, 1979) and during the 24h diel feeding periodicity studies.

After collection with the minnow seine, the fish were allowed to suffocate to prevent regurgitation before they were placed in 10% formalin. Considering the small size of the minnow it was not thought necessary to inject a preservative into the gut to retard digestive processes.

In the laboratory the fork length (nearest mm), mass (10^{-3}), date, location, sex and sexual maturity were recorded for each fish. The entire digestive tract was removed and placed in a separate labelled bottle with 4% neutralized formalin. Most cyprinids do not have a true stomach, but a dilated section of the anterior intestine which is histologically similar to the rest of the gut except that secretory cells are more numerous (Abban,1972, in Payne, 1975). In minnows the anterior third before the first loop of the intestine is usually called the foregut (Payne, 1975; Crisp, Mann & McCormack, 1978).

In B. anoplus the foregut consisted of the digestive tract from the oesophagous to the first loop of the intestine. Incision was made directly anterior to the first constriction, the anterior section was termed the foregut, the remainder of the tract was the hindgut (Fig. 42).

The contents of the foregut and hindgut were analyzed separately. Assessment of each sections' fullness was done as outlined in the 24h study section (see p. 189).

The contents of each section was rinsed into a petri dish, with the attached grid for volumetric analysis. The contents were then transferred to a grooved tray for counting.

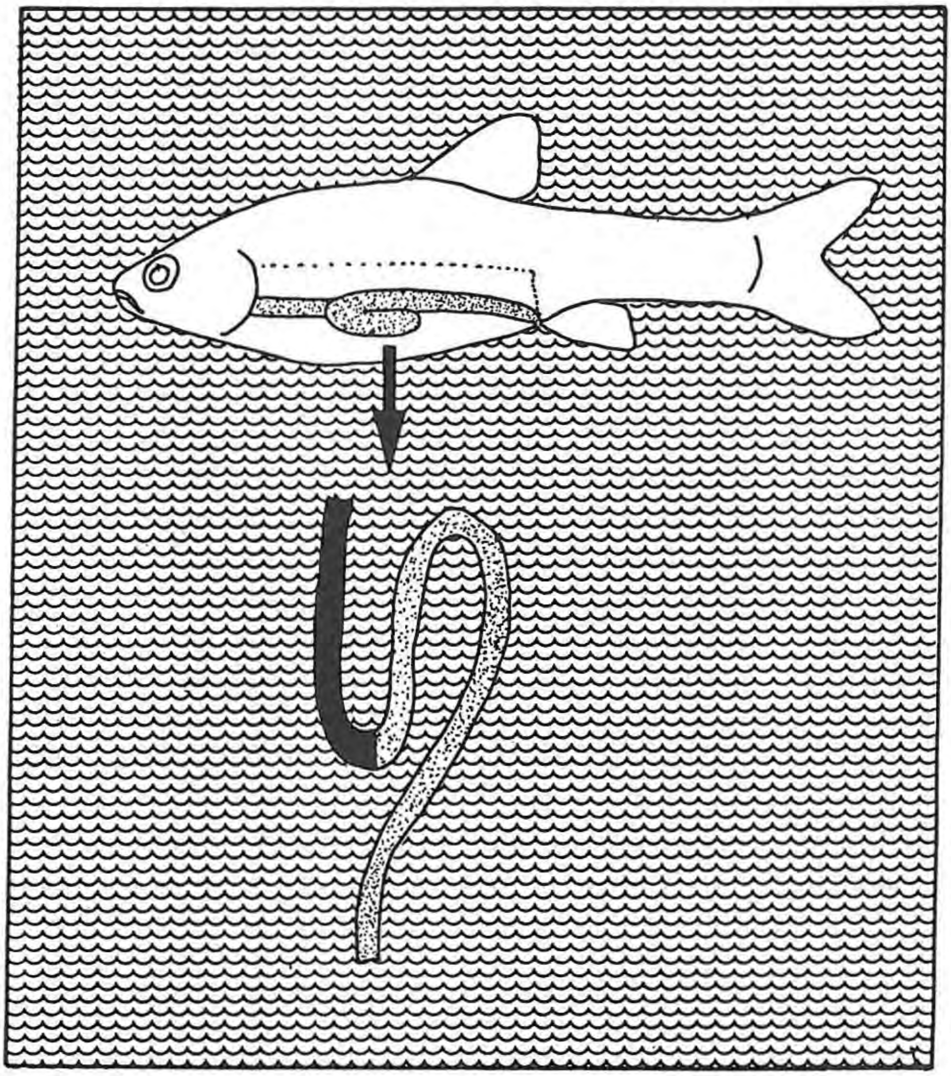


Fig. 42 Short S-flexured intestine of B. anoplus (■- forgut; ▦- hindgut).

Zooplankton samples were identified from a collection supplied by Professor R.C. Hart of the Institute for freshwater studies, Rhodes University. Notonectidae and Corixidae were identified by Mlle. F. de Sallier Dupin of the Université de Rennes, France. Ostracoda were identified by Dr. K. McKenzie, Riverina College of Advanced Education, Wagga Wagga. Chironomid larvae were sent away for identification, but a reply has not been received to date.

The zooplankton population consists of the copepods, Metadiaptomous meridianus, Lovenula excellens, and cyclopoid copepods. Cladocerans include, Daphnia gibba, D. barbata. D. longispina/pulex, Moinia brachiata and chydorids. Corixidae were Anisops poweri and A. graciloides, and one notonectid, Micronecta scutellaris. The Ostracoda were Ilyocypris cf. australiensis, Candonopsis nama and Herpetocypris chevreuxi. Items in the final analysis were classified into convenient major groups such as chironomid larvae, copepods etc. to obtain a more concise picture of the feeding habits. Complete tables of each organism taken would be cumbersome and provide very little additional information for the goals of this particular study.

The data obtained were analyzed for the following information:
(i) diel feeding pattern to establish a food collection time; (ii) average index of fullness of foreguts and hindguts on a monthly basis; (iii) the seasonal feeding pattern of five different length groups; (iv) a comparison of the feeding habits of fish collected from 4 habitats.

Monthly collections of minnows were made between 10h00 and 12h00 at station 6 throughout 25 months. Only specimens from the first 12 month period were analyzed. Fish were grouped into arbitrary size categories:

less than 24mm; 25-34mm; 35-44mm; 45-54mm and greater than 54mm. When possible 10 fish from each length group were analyzed each month with regard to fore and hindgut fullness, frequency of occurrence, estimated volume and numerical abundance of each food item. The data were pooled for each length group into 4 seasons; spring (September, October, November); summer (December, January, February); autumn (March, April, May) and winter (June, July, August). These data provided information on the seasonal trends of food for each length group as well as the difference in diets between the groups during each season.

Finally, a study was undertaken to assess the feeding pattern of the minnow population in 4 different habitats. One habitat represented the natural, unaltered environment of the minnow, Site 72, a clear flowing river which flows into the main basin of the impoundment. A collection site was chosen approximately 1km above high impoundment level. Fish from the impoundment would obviously enter this area, however their diet would be a riverine one. The other three habitats occurred within the impoundment. One was an open-shore locality (site 73), fish from this area were collected during the regular monthly sampling. The specimens from site 6 used in the previous study were also used in this study. The last habitat was the open water, specimens were kindly supplied by Mr P.B.N. Jackson from his open-water trawl net study of the fish population of the impoundment.

All sizes and dates of collection were pooled for this analysis. A total of 506,60,152 and 100 specimens were analyzed, as previously outlined, from sites 6,72,73 and open water, respectively.

Morphology

It is generally known that the length of the intestinal tract is closely related to the feeding behaviour and size of prey (Kruger & Mulder, 1973). Since little previous work has been done on B. anoplus, except for Skelton (1980) the gut length of a number of fish from different length groups was measured.

The gut was severed immediately behind the transverse septum and at the anus. Connective tissue and organs were dissected away, and the alimentary tract was straightened, without stretching, and measured. The regression of gut length to standard length was then calculated by the method of least squares.

The pharyngeal teeth of the minnow were dissected out and photographed to illustrate tooth shape and distribution.

Results and Discussion

Morphology.

Skelton (1980) found that the majority of the small and moderately sized radiately-striated, scaled Barbus species have a short intestine equal to or less than the standard length. The tract in B. anoplus is a single recurved S-pattern and the length is less than SL (Fig. 43) which would indicate that the minnow is carnivorous (Kruger & Mulder, 1973). The pharyngeal teeth of B. anoplus consists of small teeth in the minor row with sub-cylindrical stems and bent depressed cusps (Plate 19). The middle row teeth are larger but are basically the same pattern. The outer, major row teeth are heterodont. Skelton (1980) found that the above-mentioned pharyngeal tooth pattern was common in Barbus species. The raptoral pharyngeal teeth are well adapted to masticate the larger food items taken by B. anoplus.

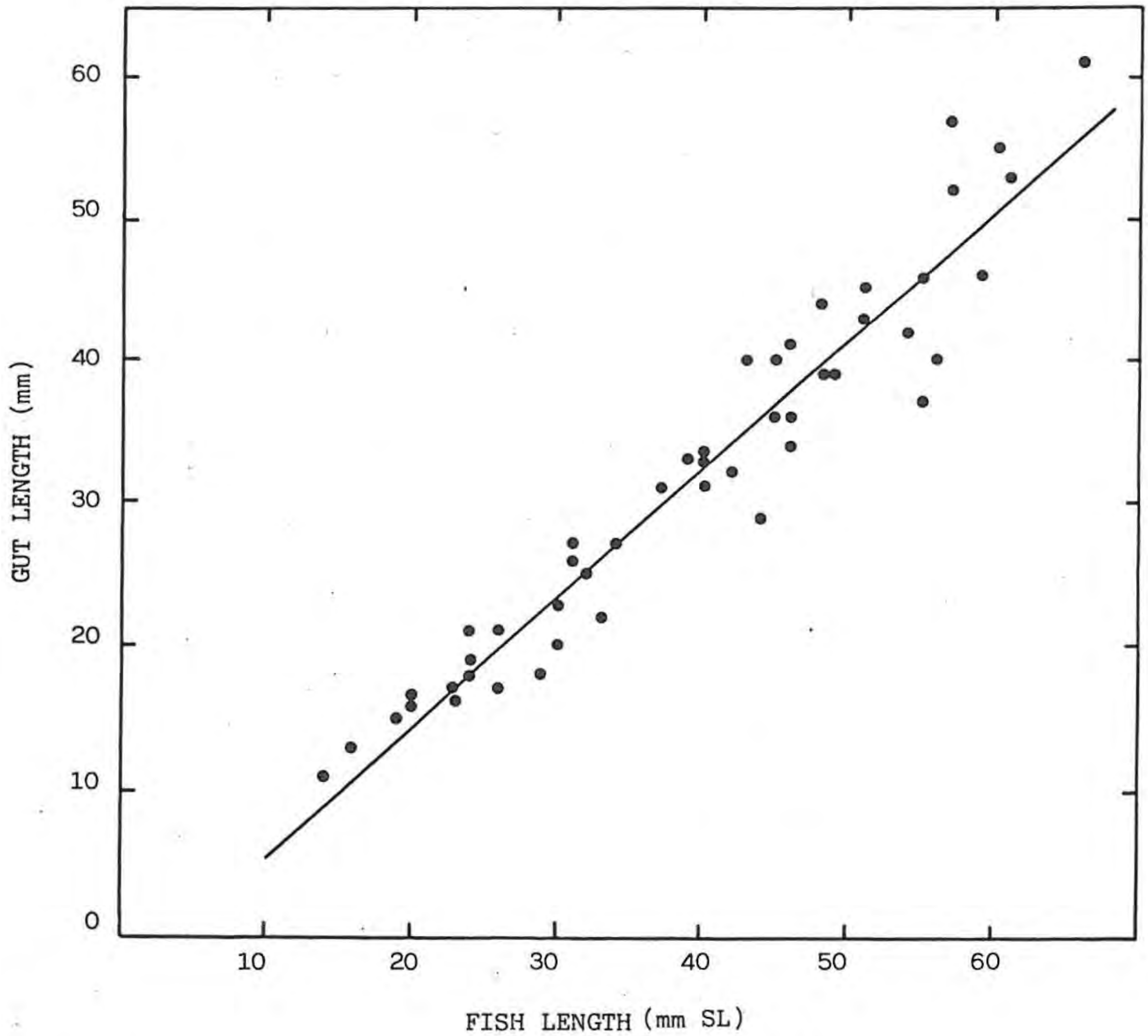


Fig.43 Relationship of the length (SL) of B. anoplus to total gut length (n = 48). $y = 3,5446 + 0,9068\,x$ ($r^2 = 0,93$) where y = gut length (mm) x = fish length (mmSL).

Plate 19. Occlusal view of pharyngeal teeth of B. anoplus (65,1mmFL) from the P.K. le Roux impoundment. Scale bar =0,5mm.

Food habits at four localities.

A comparison was made of the feeding habits of the chubbyhead barb at four different habitats. The localities were site 6 (small temporary stream), site 72 (in the Berg River), site 73 (open-shore) and several open-water sites along the main axis of the impoundment. Fore and hindgut contents have been pooled.

Copepoda were abundant in the guts of minnow collected at both site 6 and in open water (Figs 44 & 45). The majority of the copepods eaten at site 6 were cyclopoid whereas in the open water calanoid copepods (Metadiaptomus meridianus and Lovenula excellens) were the main prey species. Very few copepods (by volume) were found in the fish collected from the river (a few cyclopoids) or along the open shore although copepods occurred in 25% and 22% respectively of the guts examined (Fig.45). The frequency of occurrence of copepods in fish from site 6 and open water was 81% and 71% (Fig.45).

The cladocera show a similar pattern to the copepods, although there were more cladocerans (mainly Daphnia species) in the fish collected along the open-shore. At station 6 many of the cladocerans in the gut contents were chydorids whereas in the open water the majority were Daphnia species. In the open water habitat 82% of the fish had cladoceran remains, compared to 20% (site 72), 22% (site 73) and 55% (site 6). Ostracods were not a major part of the diet at any of the four localities. At site 6 ostracods constituted 4% of the volume of all food items compared to 0,3% (site 72), 0,1% (site 73) and none were found in the open water collections. The highest frequency of occurrence of ostracoda was found at site 6 (30%) and site 72 (28%).

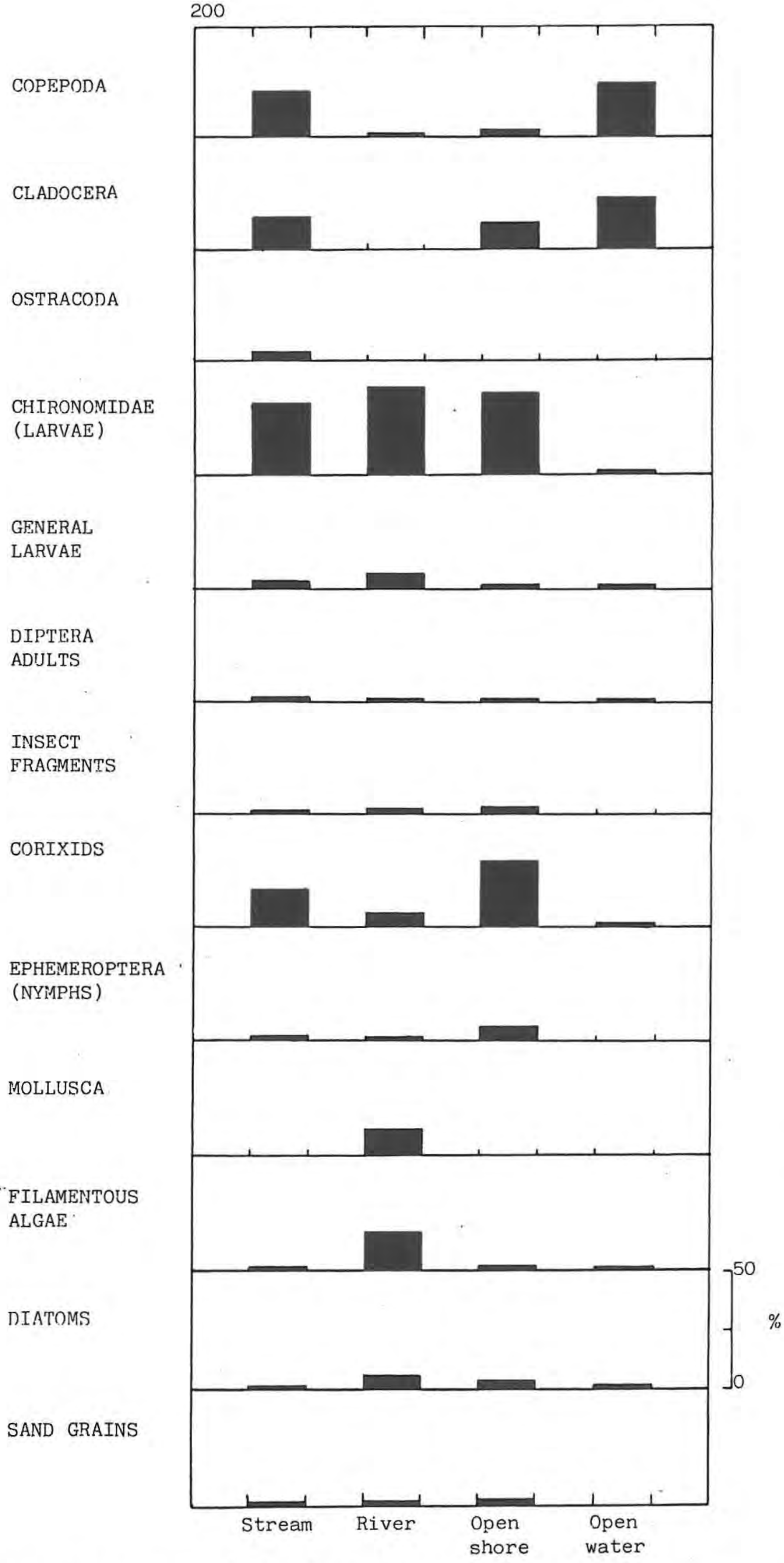


Fig. 44 Percentage composition (volume) of different items in the diet of *B. anoplus* at four different habitats in the P.K. le Roux impoundment.

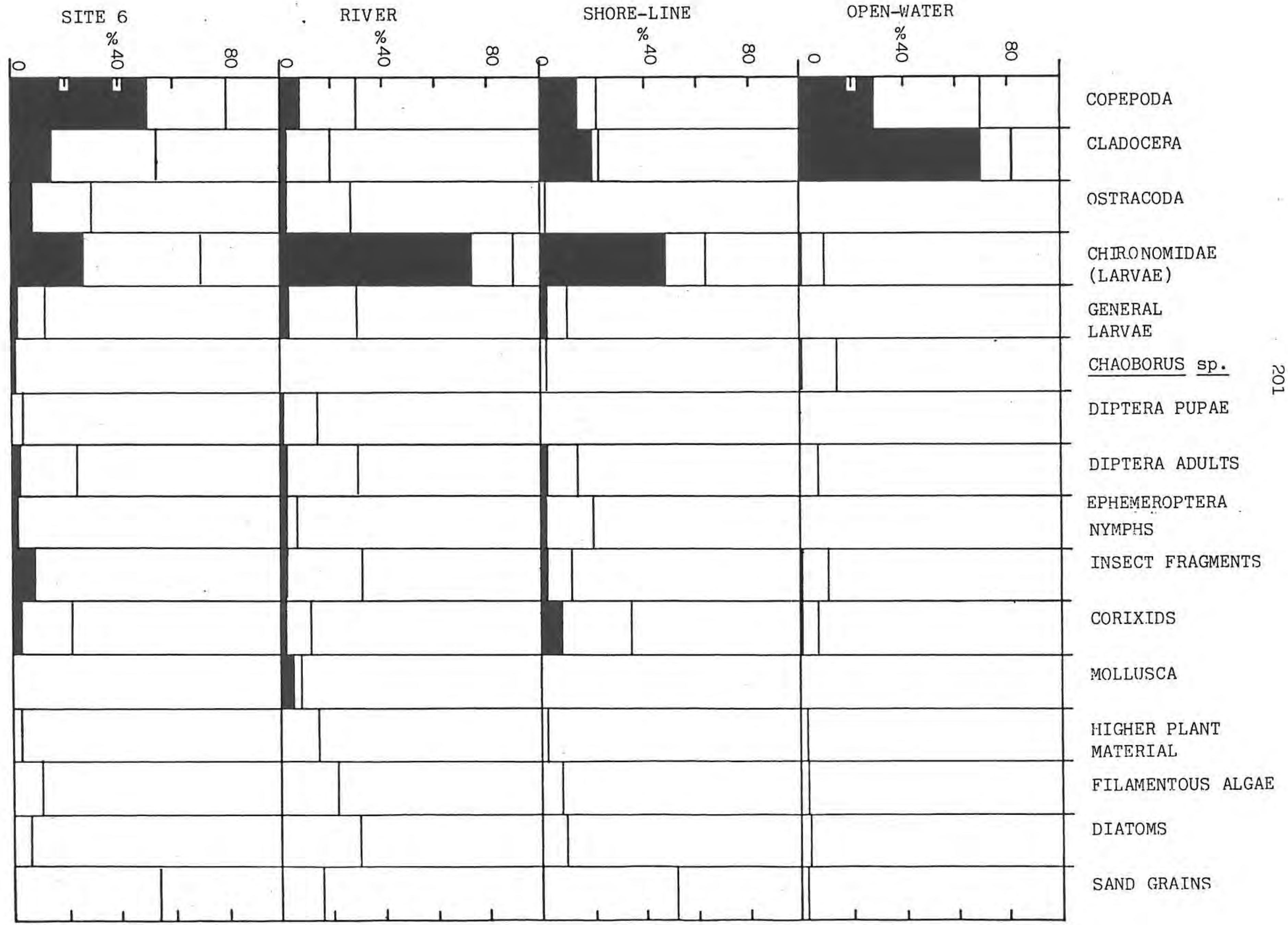


Fig. 45 Frequency of occurrence (■) and numerical percentage (□) of items in the diet of *B. anoplus* at four different habitats in the P.K. le Roux impoundment.

Chironomid larvae were important at all localities except the open water collections. In the river locality chironomid larvae formed the bulk of the diet (44%), compared to only 0,2% from the open water specimens. The various dipteran larvae were most important in the diet of the riverine fish.

Dipteran adults occurred at all localities and could probably be labelled chance food items.

Corixids formed an important portion of the diet at all localities except open water. The highest percentage volume occurred along the open shore (30%) and they were present in 36% of the fish. Ephemeroptera nymphs were more important in the diet of minnows inhabiting the open shore than at the other three localities. Ephemeroptera nymphs represented the main food item during one 24h study. Further analysis of more specimens collected throughout the year indicated that the minnows were only being opportunistic on an abundant food source at the time of the diel study. Frost (1948) also gives a good example of how a single collection can lead to erroneous interpretations of diet.

No molluscs were found in the fish collected from the three impoundment sites. In the river locality molluscs represented 11% of the volume found in 8% of the fish. The larger fish had a higher proportion of molluscs than did the smaller length groups.

Fish from the river locality also had a higher percentage of filamentous algae than the other habitats. The algae does not appear to be digested. Algae is probably taken in accidently when the fish are feeding on aquatic insect larvae in the algae. Diatoms were mainly utilized by the larger fish but did not form an important portion of the diet at any of the localities.

Higher plant material mainly consisted of grass and tree seeds which formed 2,0% by volume of the diet in the river population and less than one percent at the other localities.

Sand grains in the guts was most abundant at the open-shore locality (4,0% of the volume) whereas the frequency of occurrence indicated that in all localities (except the open water habitat) the fish were benthic feeders during the day, by virtue of the presence of sand in the foregut. The frequency of occurrence of sand for the sites was: site 6 - 54%, site 72 - 17%, site 73 - 53%, open water - 0%.

In general the most important food items for the fish from the two shoreline localities (sites 6 & 73) were chironomid larvae, corixids and copepods (site 6 only).

In contrast chironomids, molluscs, dipteran larvae, corixids and filamentous algae formed the bulk of the diet of the riverine fish. The guts of the river fish also had the most varied diet, indicating the opportunistic feeding habits of this basically riverine minnow.

In contrast to the other three localities, fish collected from the open water sites had a more rigid diet. This is of course directly related to the habitat in which they occur where the main food items for planktivorous fish are copepods and cladocerans (Hart, 1981). A few of the fish had benthic organisms, but these fish were collected from tributaries and had obviously moved away from the littoral area to feed in the open water when they were collected.

A wide variety of miscellaneous items were found in stomach contents. These items occurred infrequently and included a variety of egg masses, sticks, snails, ants, spiders, beetles and a number of unidentifiable insect fragments.

Monthly gut fullness

Very few fish collected at site 6 between 10h00 and 12h00 had empty fore or hindguts (Fig.46). Very few foreguts were full but in contrast relatively more hindguts were full. Very little seasonal pattern is evident over the 12 month period (Fig.46). One would expect a more pronounced pattern between the summer and winter collections considering the changes in temperature in the littoral zone (Fig.11).

Diel feeding pattern

In the three diel studies during March and April, the fish fed throughout the afternoon with a peak period at dusk (Fig.47). Very little food was found in either the fore or hindgut between 24h00 and 06h00. Feeding resumed again between 06h00 and 08h00 and increased to 12h00. At the start of the first two collections the 12h00 collection is lower than the 12h00 collection of the following day. Peak feeding times appear to be at sunset and a few hours after sunrise. In the three studies the mean foregut fullness index was low in all but two collection periods, which possibly indicates a quick passage of food items through the foregut The diel feeding pattern data suggests that the collection time should be between 10h00 and 12h00 for the regular monthly collections at site 6.

Food habits of different length groups

All the minnows examined for diet at site 6 were divided into 5 length groups.

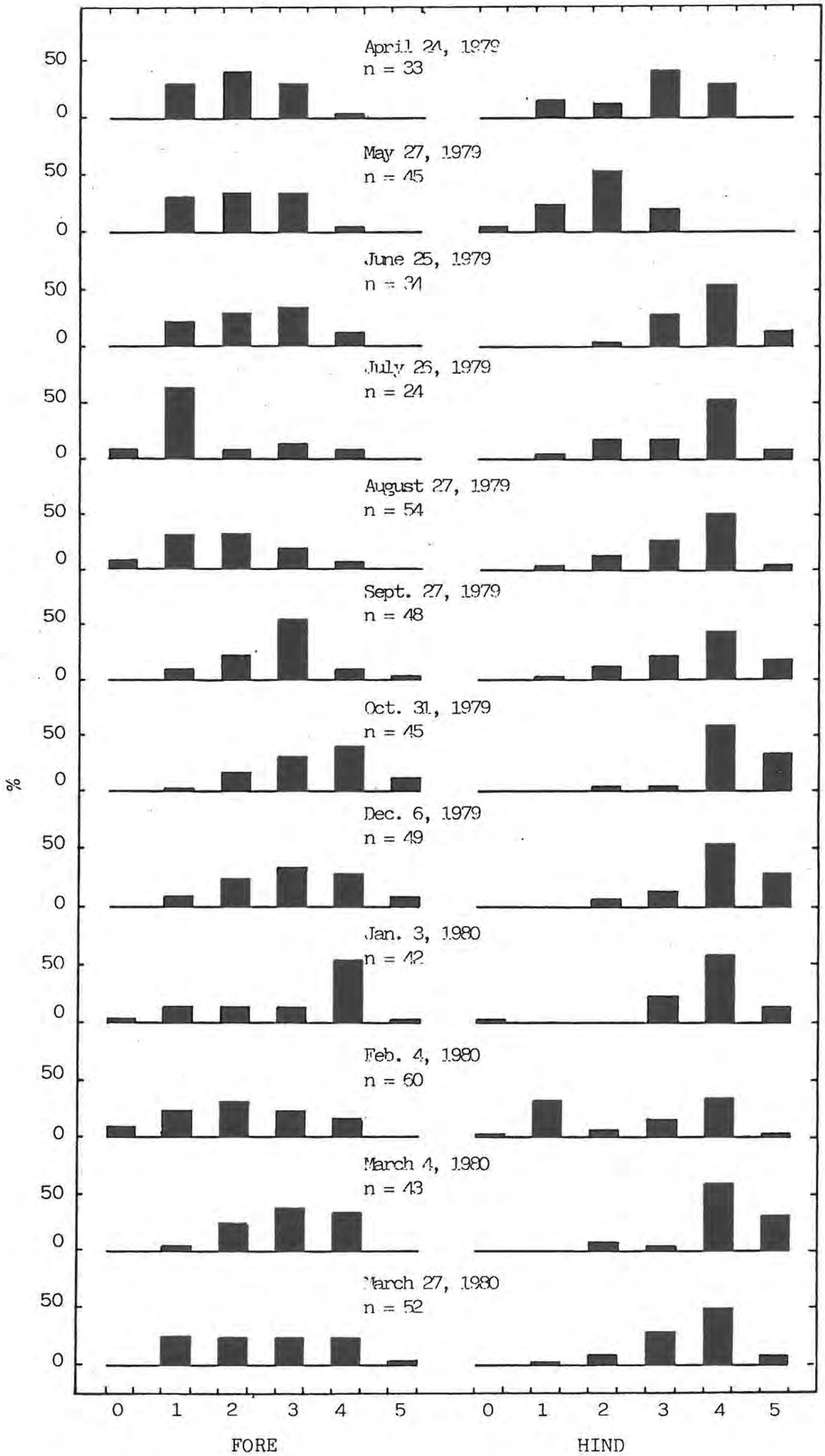


Fig. 46 Percentage of B. anoplus fore and hindguts in each fullness index ranking (see text) for a 12 month period (April 1979 to March 1980). Fore and hindguts treated separately.

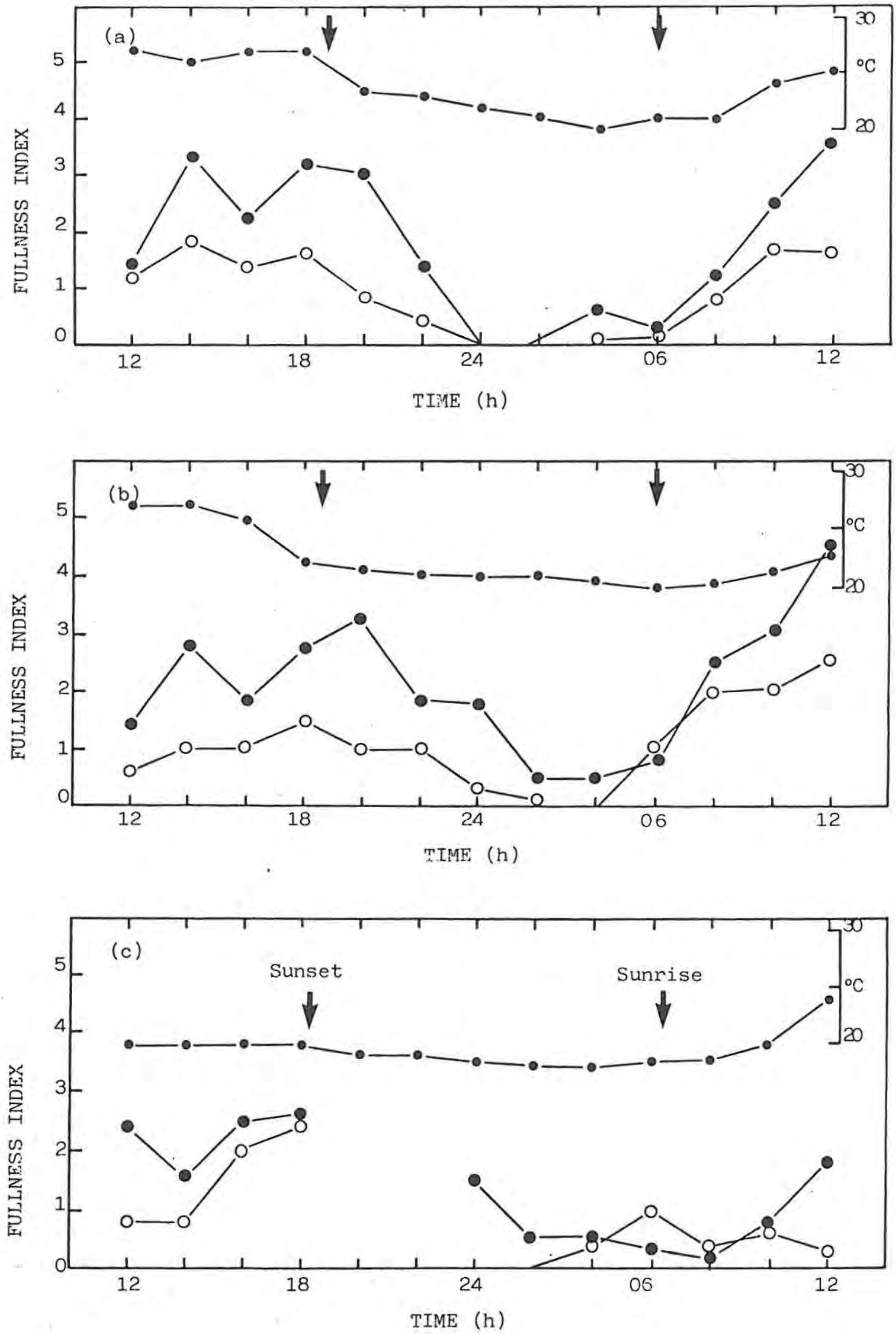


Fig. 47 Diel feeding pattern of B. anoplus on:
(a) 1-2 March, 1979, Site 73;
(b) 15-16 March, 1979, Site 8; and
(c) 5-6 April, 1979, Site 73.

(O-O) foregut fullness, (●-●) hindgut fullness.

Length (mm)		Approx. age (years)
0 - 24	-	0^+
25 - 34	-	$0^+ - 1^+$
35 - 44	-	$0^+ - 1^+$
45 - 54	-	$1^+ - 2^+$
54	-	$2^+ - 3^+$

An equal number of fish from each length group was not available each season for analysis, especially in the larger fish. The number of fish examined per season per length group is given in Table 23. The diet of each length group, as shown by frequency of occurrence and estimated volume is shown in Figs. 48 to 51. Fore and hindgut contents were combined.

TABLE 23

Number of fish examined per season in five different length groups for diet analysis (see Figs 48-51).

Length group (mm)	Spring	Summer	Autumn	Winter	Total
24	30	34	38	23	125
25-34	29	30	26	22	107
35-44	31	28	30	23	112
45-54	32	29	31	31	123
54	19	11	16	13	59
TOTAL	141	132	141	112	526

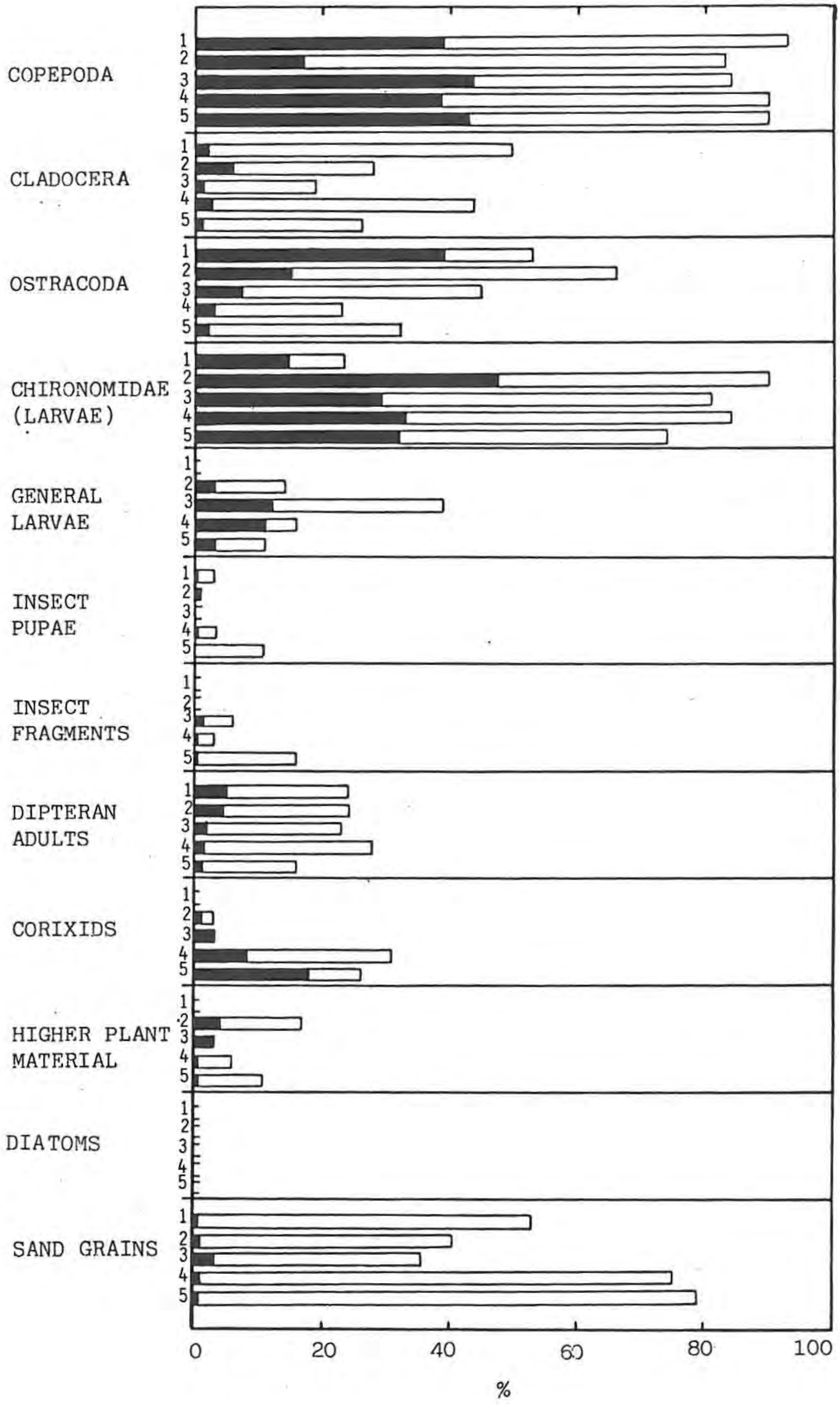


Fig. 48 The feeding habits of five different length groups of B. anoplus during spring in the P.K. le Roux impoundment (Site 6), with each length group treated separately.

Size groups 1 - fish less than 24mm FL
2 - fish - 25-34mm FL
3 - fish - 35-44mm FL
4 - fish - 45-54mm FL
5 - greater than 54mm FL

□- frequency of occurrence ■- percentage of volume

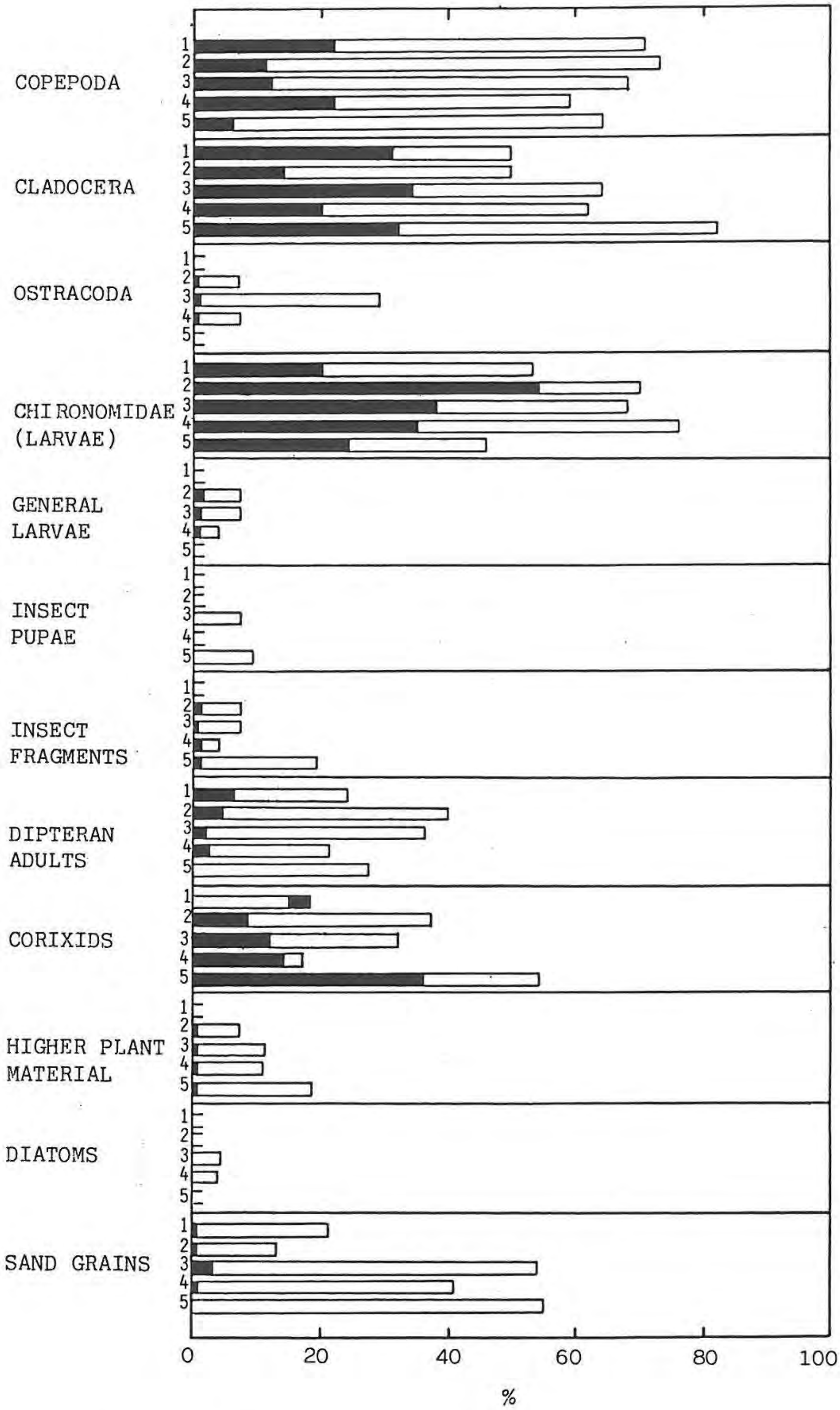


Fig. 49 The feeding habits of five different length groups of B. anoplus during summer in the P.K. le Roux impoundment. (Key as in Fig 48).

The previous section (Figs.44 &45) has shown that for the pooled data of all length groups throughout the year the four most important food items at site 6 were chironomid larvae, copepods, corixids and cladocerans, respectively.

(a) Spring (Fig.48)

In Spring (September, October, November) chironomid larvae and copepods were important in the diet of all length groups. Ostracods occurred in a relatively high percentage of fish of all length groups, but were more dominant in the smaller fish.

Insect larvae were fairly important in all groups except in fish under 24mm in length. Dipteran adults were present in all length groups. Corixids were more important in the diet of the larger fish. Corixids represented 18% of the bulk of the diet in fish over 54mm in length.

The presence of sand grains in a high percentage of all length groups indicated a bottom feeding habit, especially in fish over 54mm in length.

(b) Summer (Fig.49)

In Summer (December, January, February), chironomid larvae, cladocerans, copepods and corixids formed the major part of the minnows diet. In contrast to Spring, the cladocerans were well represented in all length groups by volume. The ostracods have decreased in importance, possibly indicating a shift in feeding patterns from bottom to mid-water. The frequency of sand grains has decreased, which also suggests a shift in feeding to mid-water.

Corixids were now important to fish under 24mm in length and represented 36% of the bulk of the diet in fish over 54mm. The density of these insects were clearly evident in the minnow seine hauls at this site. Sometimes it was difficult to find the smaller fish because they were covered in corixids (plate 20). In aquarium studies it was noted that

Plate 20. Corixids abundant in a collection of B. anoplus at Site 6,P.K. le Roux impoundment, in summer, 1980.

this minnow had difficulty in catching corixids but, in the high densities in which the insects occur in nature this difficulty would be somewhat offset.

(c) Autumn (Fig.50)

In Autumn (March, April, May) the major food items were again chironomid larvae, copepods, cladocerans and corixids.

The copepods were most important in the smaller fish and their percentage volumes ranged from 27% in fish less than 24mm to only 7% in the largest fish, although copepods occur in over 60% of the fish in each length group. Cladocerans indicate a similar trend with a range of 37% by volume in fish less than 24mm to only 0,5% in fish over 54mm.

One of the major changes in diet from the previous season was the increased number of insect larvae in the diet of all fish, which is similar to the Spring data. Corixids were once again the main food item of the larger fish. Sand was frequently found in all fish over 25mm in length, indicating that the smaller fish were feeding in mid-water on copepods and cladocerans.

(d) Winter (Fig.51)

In Winter (June, July, August) the major food items were chironomid larvae, cladocerans and copepods. The main changes from the previous season are that the smaller fish are feeding on the bottom as indicated by the frequency of occurrence of sand grains. There was an increase of cladocerans in larger fish, and ostracods were again an important part of the diet, as they were in Spring. The volume of insect larval material had decreased as had the number of corixids in the diet. The winter seine hauls also indicated low numbers of corixids during the season. The larger fish have therefore switched from corixids to chironomid larvae.

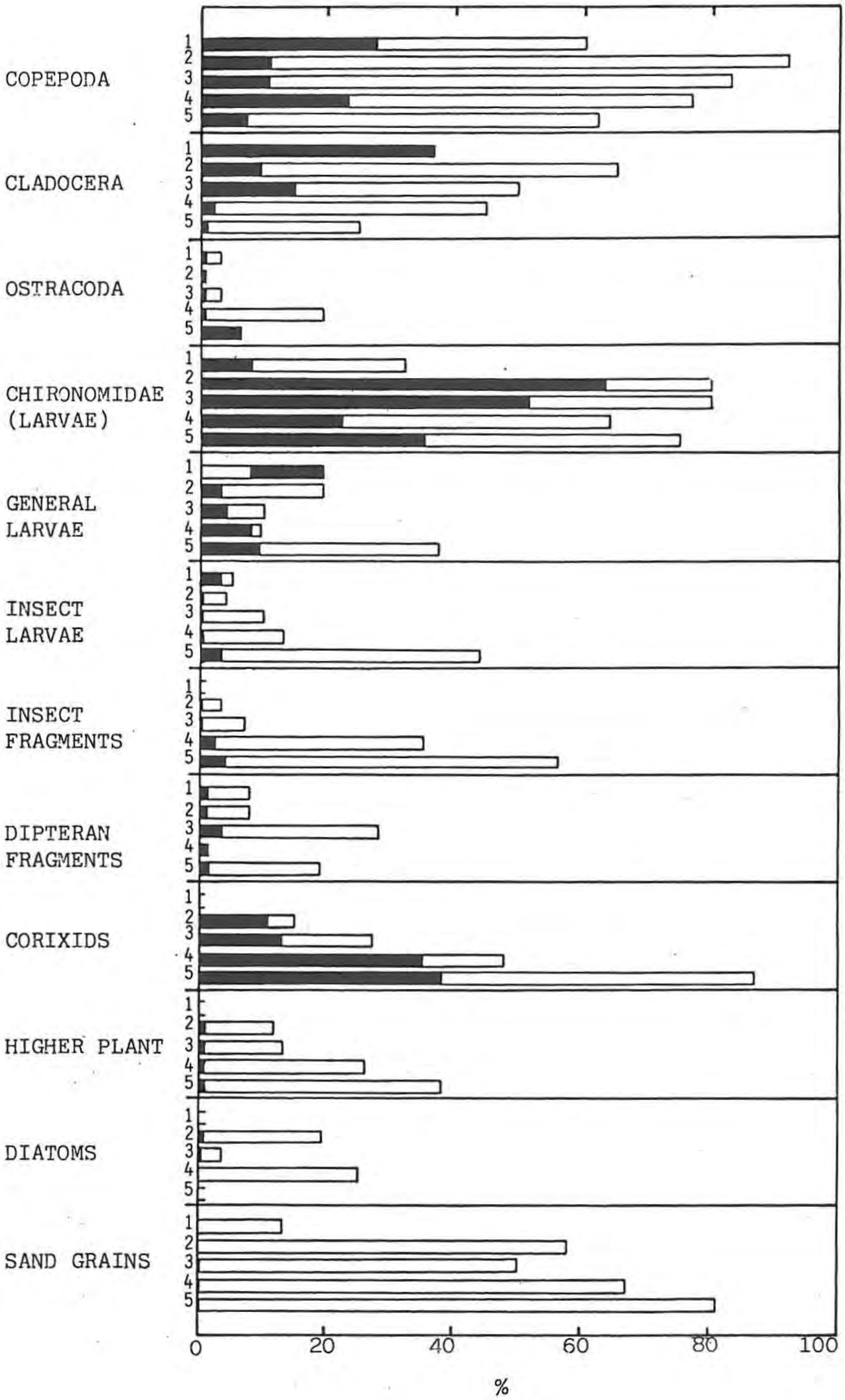


Fig. 50 The feeding habits of five different length groups of B. anoplus during autumn in the P.K. le Roux impoundment. (Key as in Fig.48).

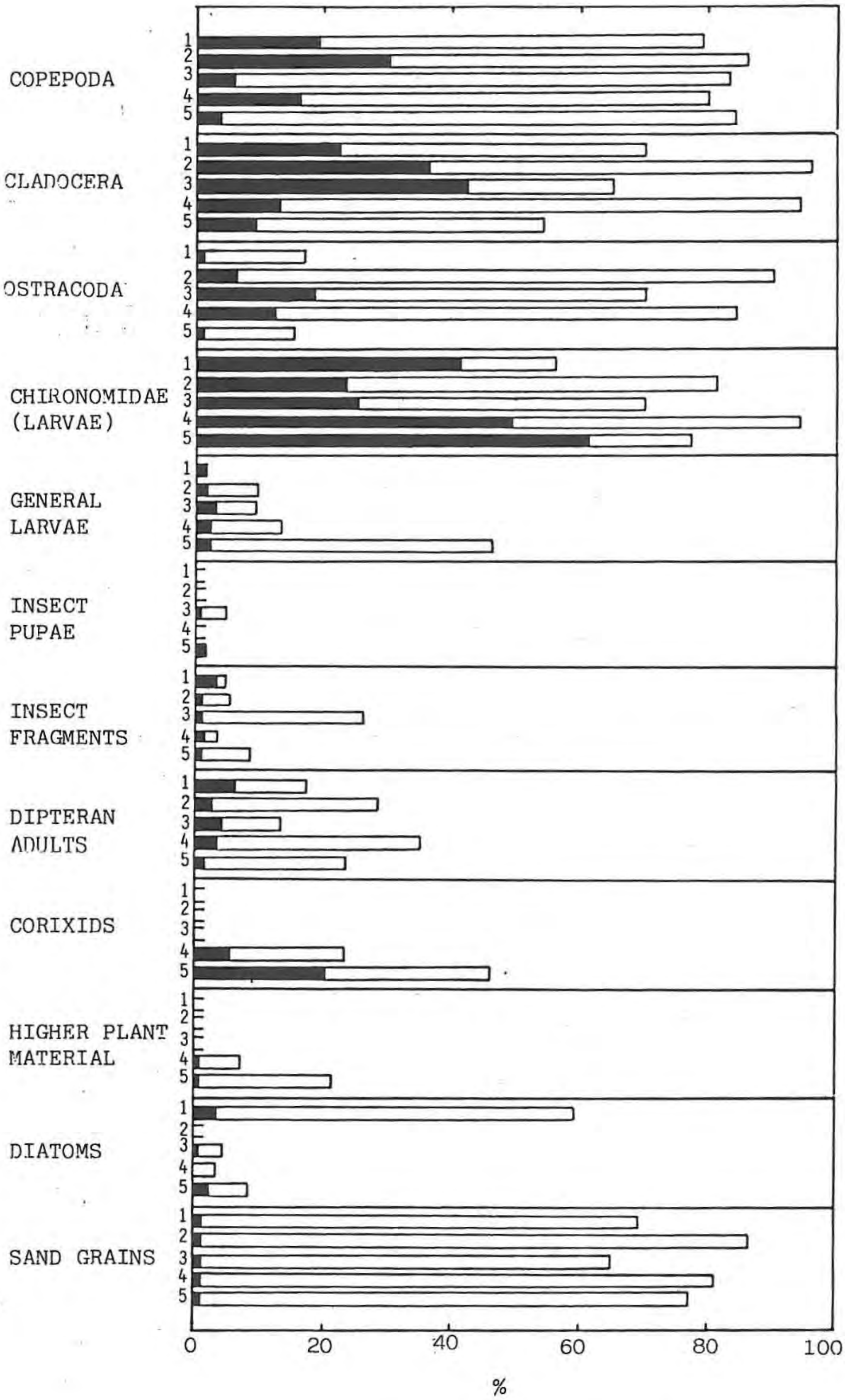


Fig. 51 The feeding habits of five different length groups of *B. anoplus* during winter in the P.K. le Roux impoundment. (Key as in Fig.48).

Discussion

Like the other minnows studied in Africa, the bulk of the diet of B. anoplus was found to be animal matter.

In an open water habitat B. anoplus fed mainly on copepods and cladocerans whereas in the riverine locality the fish fed on a wide range of food items. Along the shore line corixids were important in the diet. The minnows fed throughout the water column. One specimen can have benthic organisms, mid-water organisms and adventitious insects in its gut at the same time. It was also noted that the larger fish have a more diverse diet than the smaller size groups. More terrestrial insects and corixids were taken by the larger minnows. This is attributed to age-specific differences in feeding behaviour and the inability of young fish to ingest relatively large food items. This is a general phenomenon, that larger fish are better able to use larger and harder food items (Hynes, 1970, in Heins & Clemmer, 1975).

Gaigher (1979) pointed out that the genus Barbus mainly consists of facultative feeders or species which exist largely on aquatic invertebrates. He also maintains that most species show changes in food habits with increase in size and are seasonally dependant on availability. Europhagy therefore enhances the fish's chances of survival under unfavourable conditions.

This trophic adaptibility of B. anoplus is an important asset for an r-selected fish in a harsh environment. The Orange River is characterized by large variations in turbidity and runoff. It is therefore reasonable to assume that there would also be a large variation in certain food sources such as terrestrial insects and plankton at different times of the year.

The flexibility in diet would also be advantageous to a colonizing species. This factor and the reproductive strategy of B. anoplus probably combined to enable this minnow to rapidly colonize the man-made lake in the early productive phases. The wide distribution of this minnow both within the impoundment and throughout South Africa confirms its adaptability to diverse environments, and a wide range of food items.

Review of the feeding habits of small *Barbus* species

In general, it has been found that small *Barbus* species feed on zooplankton and aquatic and terrestrial insects. They also ingest plant material (Table 24).

In a synthesis on the feeding biology of indigenous freshwater fishes, Gaigher (1979) noted that virtually all the information on food habits of South African minnows was based on superficial examinations of small samples. No detailed study of the food habits of any species had been done. Similarly, Bell-Cross (1976) noted that there is very little known of the feeding biology of minnows in Zimbabwe.
Gaigher's (1975) study of 40 *B. trevelyani* "stomach" contents was the most detailed study. This species was found to feed on aquatic insect nymphs and larvae, with Ephemeroptera nymphs occurring in 88% of the stomachs examined (Table 24).

Groenewald (1957), Crass (1964), Jubb (1967), Bell-Cross (1976) and Pienaar (1978) describe the food habits of several barbs, but as Gaigher (1979) notes these studies were based on relatively few specimens, or an unspecified number of specimens.

In Barberspan, *B. paludinosus* fed on ostracods, chironomids, Ephemeroptera nymphs and organic debris, which indicated a bottom feeding habit (Groenewald, 1957). In contrast, *B. anoplus* and *B. trimaculatus* in the same habitat fed mainly on microscopic cladocerans when macroscopic organisms were

TABLE 24

Review of the food preferences of small Barbus species in Africa.

Barbus species	Locality	Method of "stomach" analysis	Predator length range (mm)	Main prey (% frequency)	Other prey	No.of "stomachs" examined	Reference
B. afrohamiltoni	Kruger Park	not specified (n.s.)	n.s.	Insects - n.s.	n.s.	n.s.	Pienaar, 1978
B. anoplus	Barberspan	n.s.	n.s.	Small cladocerans (approx. 100%) -(n.s.)	n.s	n.s.	Groenewald,1957
B. anoplus	Natal	n.s.	n.s.	Insects (midge,mayfly and blackfly larvae) -(n.s.)	Small flying insects, diatoms, algae, vascular plants.	n.s.	Crass, 1964
B. apleurogramma	Lake Victoria	Frequency	Mean length 52mm SL	Diatoms (100%) Ostracoda (100%) Copepods and Cladocerans (100%)	Insect remains, chironomids, Rhizopoda, plant debris,mineral particles	25	Welcomme, 1969
B. apleurogramma	Kafunta River (Uganda)	Frequency	Mean length 27-48mm SL	Rhizopoda (80%) Ostracoda (65%)	Filamentous algae, diatoms,insect remains, chironomids, mites, copepods, cladocerans,plant debris and mineral particles	40	Welcomme, 1969
B. argenteus	Sabie River	n.s.	n.s.	Terrestrial insects -(n.s.)	n.s.	n.s	Pienaar, 1978
B. cercops	Riber Nzoia	Frequency	n.s.	Insects (72%)	Algae, higher plant matter,insect larvae, debris	58	Balirwa, 1979
B. eutaenia	Zimbabwe	n.s.	n.s.	Small animals and insects of fast waters -(n.s.)	n.s.	n.s.	Bell-Cross,1976
B. gurneyi	Natal	n.s.	n.s.	Insects -(n.s.)	Tadpoles	n.s.	Crass, 1964
B. kerstenii	Kafunta River (Uganda)	Frequency	Mean length 18-42mm SL	Insect larvae (100%) Adult insects (84%)	Adult Coleoptera, Hymenoptera, Isoptera, Diptera, copepods, cladocerans, ostracods, diatoms, filamentous algae, higher plant material, sand grains	67	Welcomme, 1969
B. kerstenii	Lake Victoria	Frequency	n.s.	Insect larvae (60%) Ostracods (50%)	Adult Coleoptera, Hymenoptera, Isoptera, Diptera, diatoms, sand grains	20	Welcomme, 1969
B. kerstenii	River Nzoia (Uganda)	Frequency	n.s.	Debris (80%) Higher plant material(66%)	Algae, insect larvae, insects	26	Balirwa, 1979
B. kerstenii	Bugungu stream (Uganda)	Frequency	n.s.	Algae (66%) Insects (66%)	Higher plant materials, insect larvae, debris, molluscs	29	Balirwa, 1979

(Table continues)

(Table 24 continued)

Barbus species	Locality	Method of "stomach" analysis	Predator length range (mm)	Main prey (% frequency)	Other prey	No. of "stomachs" examined	Reference
B. liberiensis	Forest stream in Sierra Leone	Frequency	n.s.	Insects (51%)	Vascular plants, filamentous algae, oligochaets,diatoms	72	Payne, 1975
B. lorenzi	Dahomey (stream)	n.s.	n.s.	Aufwuchs	Mid-water particles	n.s.	Loiselle & Welcomme, 1971
B. paludinosus	Barberspan	n.s.	n.s.	Ostracoda,chironomids, Ephemeroptera nymphs -(n.s.)	Organic debris	n.s.	Groenewald,1957
B. paludinosus	Natal	n.s.	n.s.	Insects (e.g. midge larvae) -(n.s.)	Small crustaceans	n.s.	Crass, 1964
B. paludinosus	Kruger Park	n.s.	n.s.	Insects (e.g. midge larvae) -(n.s.)	Small crustaceans, plant material, diatoms	n.s.	Pienaar, 1978
B. paludinosus	Lake Sibaya	n.s.	n.s.	Chironomid larvae, Copepoda, amphipods -(n.s.)	Other small aquatic insects, crustaceans, diatoms	n.s.	Bruton, 1979
B. paludinosus	Zimbabwe	n.s.	n.s.	Zooplankton -(n.s.)	Aquatic larvae, small crustaceans	n.s.	Bell-Cross,1976
B. paludinosus	Lake Chilwa	% of contents		Crustacea	Higher plants, green algae (filamentous and non-filamentous),blue-green algae, diatoms, aquatic insects, rotifers, fish eggs	586	Bourn, 1973
B. paludinosus	Lake Victoria	Frequency	Mean length 92mm SL	Ostracoda (80%) Copepoda (60%) (bottom feeder)	Insects, gastropods,diatoms, mineral particles	20	Welcomme, 1969
B. paludinosus	Kafunta River	Frequency	Mean length 38-95mm SL	Filamentous algae (92%) Plant debris (70%)	Insects, ostracods, copepods, arachnids, diatoms, mineral particles	40	Welcomme, 1969
B. paludinosus	River Nzoia (Uganda)	Frequency	n.s.	Algae (50%) Debris (44%)	Higher plant matter, insect larvae, insects, debris, molluscs	46	Balirwa, 1979
B. profundus	River Nzoia (Uganda)	Frequency	n.s.	Insect larvae (69%)	Algae, higher plant material, insects, debris, molluscs	21	Balirwa, 1979
B. radiatus	Kruger Park	n.s.	n.s.	Vegetable matter -(n.s.)	n.s.	n.s.	Pienaar, 1978
B. sylvaticus	Dahomey	n.s.	n.s.	Copepoda, Ostracoda -(n.s.) (bottom feeders)	Detritus	n.s.	Loiselle & Welcomme, 1971

(Table continues)

(Table 24 continued)

Barbus species	Locality	Method of "stomach" analysis	Predator length range (mm)	Main prey (% frequency)	Other prey	No. of "stomachs" examined	Reference
B. trevelyani	Tyume River	Frequency % by weight	n.s.	Ephemeroptera nymphs (88%)	Chironomid larvae, plant material, terrestrial insects, Simulidae larvae	40	Gaigher, 1975
B. trimaculatus	Barberspan	n.s.	n.s.	Small cladocerans-(n.s.)	Small cladocerans were approx.100%	n.s.	Groenewald,1957
B. trimaculatus	Kruger Park	n.s.	n.s.	Midge, mayfly and caddisfly larvae -(n.s.)	Terrestrial insects	n.s.	Pienaar, 1978
B. trimaculatus	Natal	n.s.	n.s.	Aquatic larvae - (n.s.)	Terrestrial insects	n.s.	Crass, 1964
B. unitaeniatus	Zimbabwe	n.s.	n.s.	Aquatic larvae, small Crustacea -(n.s.)	n.s.	n.s.	Bell-Cross,1976
B. viviparus	Lake Sibaya	n.s.	n.s.	Chironomid larvae, copepods, amphipods -(n.s.)	Other small aquatic insects, diatoms	n.s.	Bruton, 1979
B. yongei	River Nzoia (Uganda)	Frequency	n.s.	Debris (86%)	Algae, higher plant material, insect larvae, insects	22	Balirwa, 1979

available in quantity on or near the bottom. This feeding behaviour is in contrast to the B. trimaculatus studied by Crass (1964), Table 24. Groenewald (1957) also noted that B. paludinosus numerically dominates B. anoplus and B. trimaculatus which is possibly related to the feeding habits in Barberspan.

More detailed studies have been done on small Barbus species in other parts of Africa.

In Lake Chilwa, Bourn (1973) looked at several different size groups of B. paludinosus and compared fish from different habitats. In Chilwa, B. paludinosus fed mainly on zooplankton (56%) with non-filamentous green algae (19%) and higher plant material (14%) forming a substantial part of the diet (Bourn , 1973).The smaller B. paludinosus (less than 4,0cm) fed predominantly on zooplankton whereas the larger fish had a more varied diet. Kirk (1967) noted that B. paludinosus from Chilwa, contained sand grains indicating some bottom feeding. Bourn (1973) also found that this species fed less actively during the night than during daylight hours. Welcomme (1969) working on one of the stream/swamp systems which flow into Lake Victoria, found that B. paludinosus guts indicated a bottom feeding habit on small arthropods. The fish from the river ingested more plant matter than fish from Lake Victoria.

Bell-Cross (1976) pointed out that due to the wide distribution of B. paludinosus in a multiplicity of habitats, it must be able to utilize a wide variety of food items.

The studies of Cockson & Bourn (1973) on the digestive enzymes of B. paludinosus indicated that this species was able to utilize a wide spectrum of foods, and is capable of digesting plant matter. B. paludinosus, like other Barbus species, has no true stomach. Amylase activity was demonstrated throughout the length of the intestine, while trypsin was confined to the posterior end. The anterior intestine gave an average pH of 5,8 compared to 7,8 for the posterior section.

In a study of the feeding habits of non-cichlid fish in Lake Victoria, Corbet (1961) found that the main food item for B. portali was insects, although plants were also eaten. There was a frequent occurrence (17%) of sand grains in the gut which indicated a bottom feeding habit but they also took insects from the surface. Ephemeropteran larvae were the most common insects taken (24%). The food of other small Barbus species in Lake Victoria are similar to B. portali with insect larvae the common food, augmented with surface insects and molluscs in some cases (Garrod, in Corbet, 1961).

In Lake Victoria B. kerstenii contained more ostracods and sand grains than the minnows sampled in the river (Welcomme, 1969). The juvenile fish had a varied diet as well, with insect larvae and chironomid larvae playing an important role. Welcomme (1969) notes that the filamentous algae, which occurred in up to 41% of the fish from the river (0% from the lake), appeared to pass undigested through the gut. The epiphytic and bottom living diatoms were digested.

Payne (1975), working on the biology of B. liberiensis in a forest stream in Sierra Leone, found that insect material was the most important source of food. He suggested that the fragmentary nature of the insect remains was not only due to the pharyngeal teeth, but also a result of the fragmentary nature of the insect remains which fell from overhanging trees. He also observed the minnows moving over the bottom taking mouthfuls of silt and blowing it out again. In this way they were probably searching for pieces of organic material. Generally he found that this species can utilize a wide range of food types probably dependant on availability. The fish can feed through the 24h cycle, and the food is processed rapidly. The quick passage of food through the digestive system may compensate for the high percentage of non-digestable chiton and cellulose in the diet (Payne, 1975).

Payne (1975) noted that B. liberiensis, like many other small Barbus species for which I can now include B. anoplus, is an unspecialized, facultative feeder. This is a common attribute of riverine fishes (Lowe-McConnell, 1969). The adaptive significance of being able to switch from one source of food to another, as the seasons change or as the environment changes (e.g. floods) is an important strategy for any fish living in a harsh environment.

CHAPTER 9

GENERAL DISCUSSION

B. anoplus, an r-strategist.

The minnow, *B. anoplus*, has successfully colonized the shoreline of the P.K. le Roux impoundment. This small barb evolved in a highly variable riverine environment (Orange River) and is adapted to survive periods of 'booms or busts'. The impoundment of the Orange River has offered a boom situation for the minnow species.

In terms of current life history theories, *B. anoplus* is on the r side of the r and K continuum when compared to a large *Barbus* species (e.g. *B. kimberleyensis* in the frontispiece). The minnow's life history strategies include: early maturity, rapid growth in first year, high fecundity, low asymptotic length and short generation time. A further characteristic is that the minnows appear to be poor competitors. *B. anoplus* is not a characteristic r-strategist, because it is not semelparous. The minnow has evolved a multiple spawning habit, and some individuals can reproduce for several reproductive seasons. Multiple spawning enables one female to produce more eggs in one season than she could physically carry at any one time, reduces the risk of losing all the spawn of one year, reduces intraspecific competition among fry, enables fish to use the same breeding area more than once a season and produces two separate age groups (see below).

In the course of this study it became evident that not only males and females should be treated separately, but that first spawn fish (November-December) should be treated separately from the second spawn (February-March). The first spawn grow to a sexually mature length (38-40mm FL) within the first summer, they will therefore be able to participate in the first and second spawnings in their second year of life. In their first summer they allocate resources to growth and survival, but in their second summer growth is of less importance, and the allocation is now mainly to reproduction, with some females having gonads which weight over 20% of their total body weight. Even this figure of 20% would underestimate their total seasonal commitment to reproduction because of the double spawning habit. After the males have spawned once or twice they gradually die-off leaving more resources for the females, which continue to grow and reproduce. The larger females are valuable to the population because of their high reproductive effort: a difference in length of 1,5 fold can mean a 15 fold increase in fecundity.

In contrast to the first spawn, the majority of the second spawn fish are not able to reproduce in the following November-December period, and instead they continue to allocate resources to growth until they attain the sexually mature size of 38-40mm in time to reproduce in March or April. In the following season, when they are 2^{+}years old, they will participate in the first spawn, and are the larger fish in the breeding population. After reproducing once or at both spawns they will in turn die-off, leaving the cycle of first and second spawn fish to continue. I have represented part of this cycle in a simple diagrammatic form (Fig. 52).

Whenever there is a trade-off between adult survival and reproductive effort, and the environment is variable, an adult that decides not to reproduce may have a better chance of surviving to the next breding season than would the young produced if the adult had breed. In B. anoplus the first spawn fish can reproduce, but the insurance lies in the back-up fish (second spawn).

In each spawn there is a size hierarchy. It is possible that the slower growing males and females from the first spawn would behave as second spawn fish, and the delayed time of their first reproduction would enable them to live through another summer, which in turn would be important when the second spawn had limited success.

In general, there is a rapid turnover of the B. anoplus population and the standing populations are mainly dependent on 1^+ males and egg production from 1^+ and 2^+ females.

Stearns (1976) suggests that measurements in the field are now needed to determine the actual trade-offs between adult survival and reproductive effort to generate the shapes of the curves necessary to test the graphical arguments put forward by Gadgil & Bossert (1970) and by Schaffer (1974).

Stearns (1976) notes that the most exciting 'recent' theoretical models make the assumption that reproduction costs something in terms of subsequent survival and future possibilities for reproduction (Williams, 1966; Gadgil & Bossert, 1970; Schaffer, 1972, 1974; Charnov & Krebs, 1973). Predictions based on this idea depend on the shape of the relationship between reproductive effort at time t and survival from to to time t + 1. The double spawning nature of B. anoplus adds support to this body of theory. The first spawn B. anoplus commit a portion of their resources to reproduction at the start of their second summer (1^+), and this in turn reduces their potential for future growth and survival (Fig. 52). The second spawn appears to be an adaptation to prolong the reproductive potential of the species as the result of an unstable environment. They have a higher potential to survive into the next reproductive season (t + 1) as previously outlined.

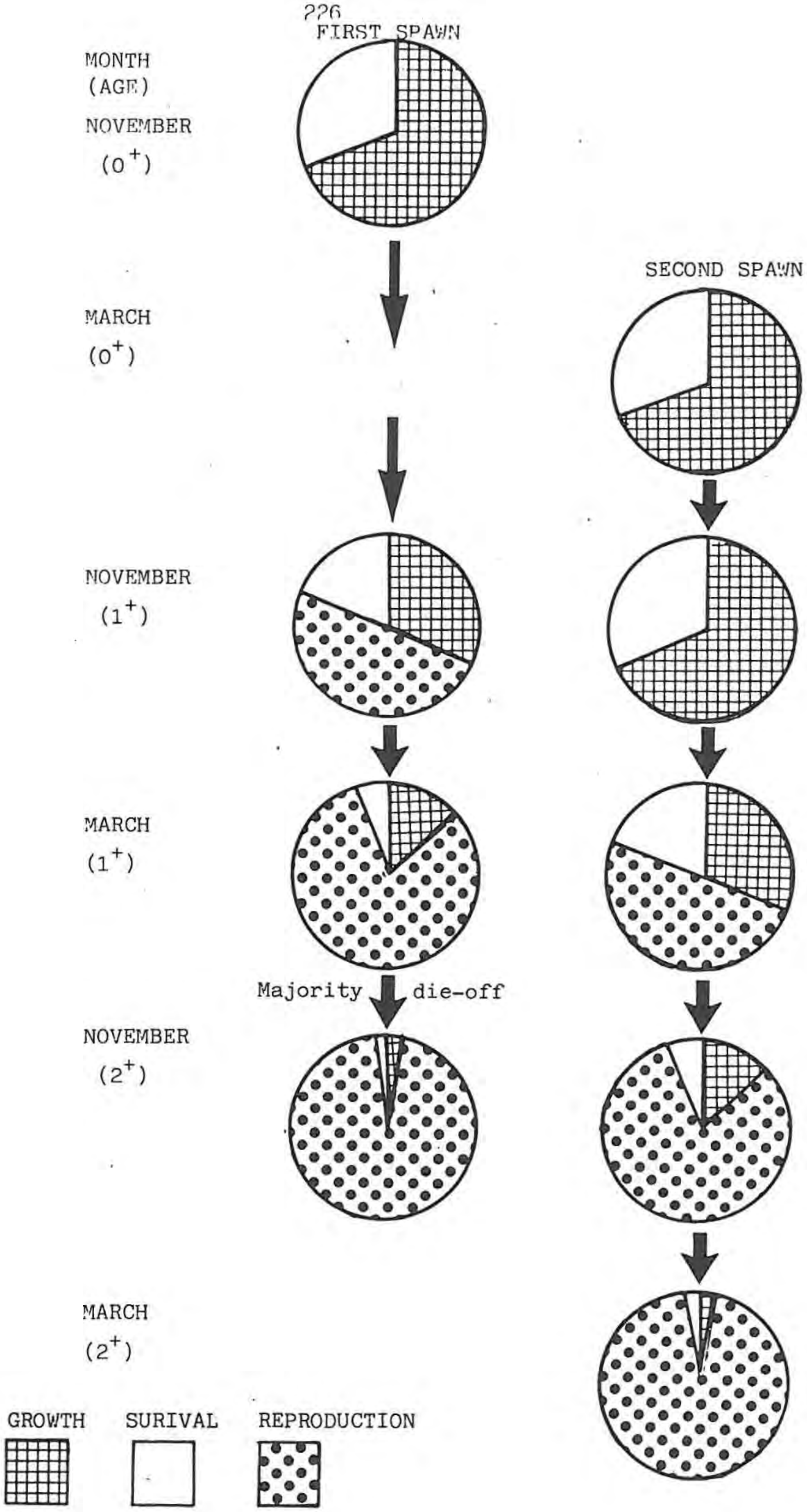


Fig. 52 Diagrammatic representation of the allocation of resources of the first and second spawns of the female portion of a *B. anoplus* population.

The genepool of any species contains within it some range of variation of both r- and K-selected traits. This range is not fully shown in the simplistic frontispiece diagram, however some indication of variability is shown between sexes of the same species. Most theorectical models reviewed by Stearns (1976) deal with females only and assume stable age distribution. Natural populations are rarely in a stable age distribution (Caughley, 1966) and the selective forces operating on males can be quite different from those operating on females (Darwin, 1859). B. anoplus males are more r-selected than females and I propose that it is more advantageous to the population if the males have a shorter life span, are smaller and correspondingly would reproduce less often than females.

Even where species are closely related, it is difficult to gain insight into the development of life history tactics and account must be taken of too many variables to make such comparisons meaningful. A more promising approach is to examine one species living under different environmental conditions (Svärdson, 1949; Stearns, 1976; Mann & Mills, 1979). There is a need for carefully controlled field experiments on short-lived plants and animals (Stearns, 1976). Stearns (1976) recommended the use of a poeciliid fish in the tropics for the difficult practical study of life history evolution. In South Africa, the ideal freshwater teleost candidate is B. anoplus. It has a wide distribution and occurs in a number of environments.

The continuum on the frontispiece has now been redrawn. Instead of one small and one large Barbus species, four separate populations of B. anoplus (three are hypothetical at this stage) have been placed on the continuum, to compare several life history parameters (Fig. 53).

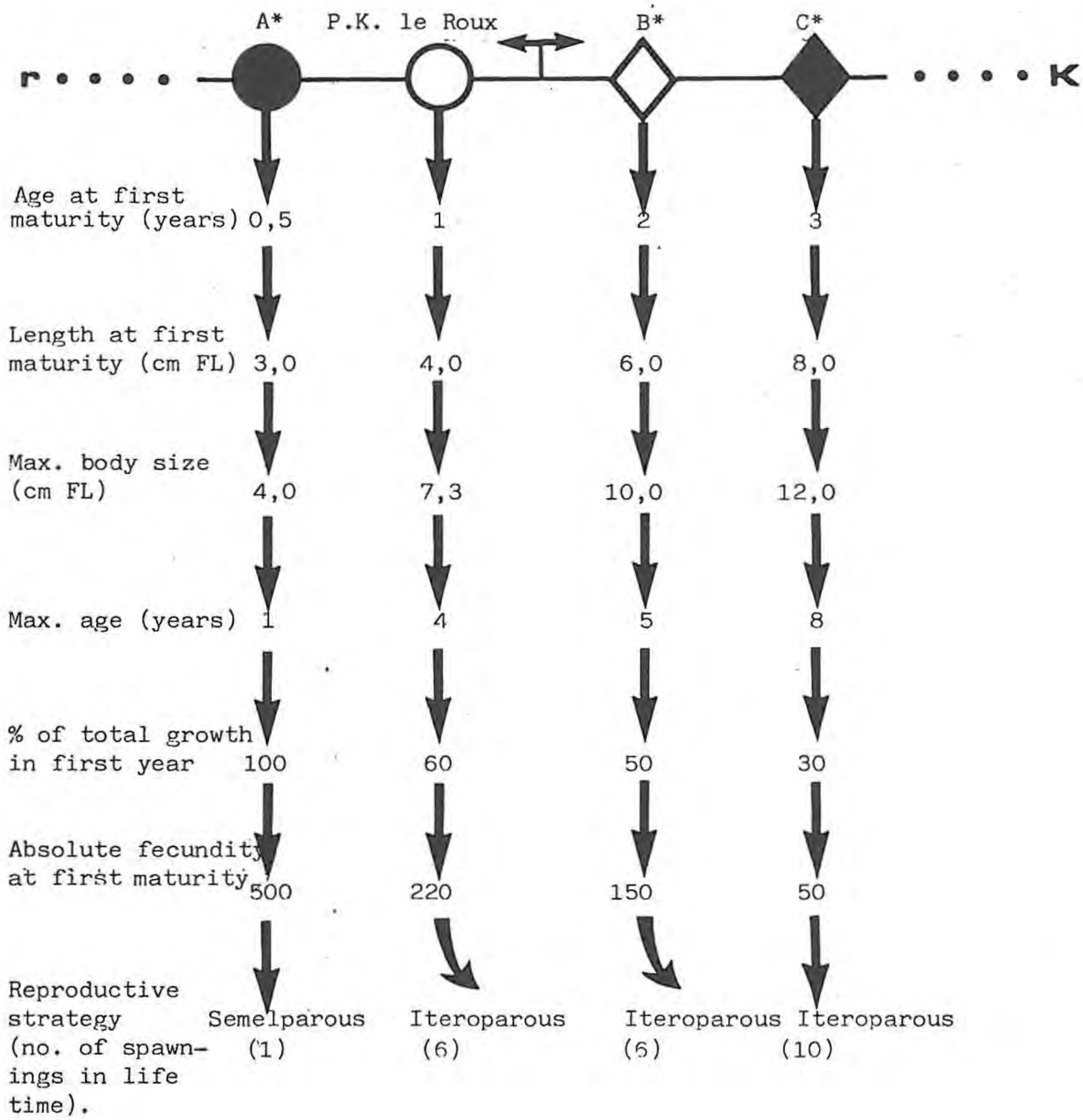


Fig. 53 r and K correlates in the life history parameters for four populations of B. anoplus females (*values for populations A,B & C are hypothetical).

By using a single species from several different environments we can be more certain what is causing an evolutionary trend (Stearns, 1976).

Population A is an annual species which grows rapidly, reaches sexual maturity within 6 months at a length of 3,0cm FL, reproduces once and dies within one year. Population A is therefore an r-selected species and is located on the left of the continuum. In contrast the other three populations reach sexual maturity later at a greater size, grow to a greater length, attain a greater age, have a slower growth rate in their first year, a lower annual absolute fecundity and are repeat spawners. They span the r & k continuum. Population C is the most K-selected of the four populations. They only reach sexual maturity after 3 years at a length of 8,0cm FL. They have a low annual reproductive potential of 50 eggs in their first reproductive season, compared to 500 eggs in the smaller, r-selected population A.

The theory of life history tactics tries to predict the best decisions to make in the face of the problems posed by different situations. These B. anoplus populations have made varying life history adaptations to the environments in which they live. Once there is a sound data base then the sets of adaptive traits can be mathematically analyzed.

Success of small cyprinids in southern Africa:

In southern Africa there are 52 Barbus species of which 81% (n = 42) reach a maximum size of 150mm FL or less. Why has this group of small cyprinids been so successful in this region? Small size is an obvious adaptation to a variable environment. The evolutionary trend towards smaller size would make new sources of food available by allowing access to spacially restricted habitats (Miller, 1979).

Smith (1978) viewed the environment as offering the fish community a linear series of ecotopes, with characteristic food dimensions, shelter sites and hunting territories, each one available only for fish of a certain size. Then within each ecotope, differences in morphology, physiology and behaviour would allow for spatial overlap of similar size fish (Zaret & Rand, 1971).

The river systems in southern Africa are mainly shallow and have erratic seasonal flow patterns. Small fish were probably selected for in many of the river systems because large fish species would not be able to find suitable shelter from predation or sufficient water for efficient feeding and breeding activities.

Cyprinids are a significant component of the fish fauna of southern Africa because they are more tolerant of lower temperatures than the many fish families which have dispersed to this region (Bowmaker *et al.*, 1978). Similarly, I suggest that within the cyprinid family the small *Barbus* species have been successful because they are more tolerant of lower temperatures than the large species.

The small *Barbus* species were probably pre-adapted to survive a wide range of temperatures when they originally colonized the shallow river systems of southern Africa. The minnows are relatively r-selected species (poor competitors) which are continuously under pressure from the more competitive K-selected species. To avoid competition, the small barbs inhabit shallow waters from which large fish are excluded. These marginal waters undergo extreme daily and seasonal temperature fluctuations compared to the deeper pools or swift-flowing waters occupied by the larger species.

Several field observations add support to this argument. *B. anoplus* is the only species which overwinters in the shallow inflowing streams of the Hendrik Verwoerd impoundment. Juveniles of the larger cyprinid species migrate to pools or to the impoundment during winter, probably because of prevailing temperatures.

A large Barbus species (B. holubi) was introduced into the Old Thomas River in the eastern Cape as a sport fish. In the winter of 1974 there were heavy mortalities of B. holubi due to low water temperatures, but no small barbs, which naturally occur in the river system, died (personal observations). Further work is required on the temperature tolerance of the small and large Barbus in order to obtain a fuller understanding of their present day distribution in southern Africa.

The relatively short generation time of the minnows enables them to make a quick recovery after a poor year. The small barbs grow rapidly in their first year and thereafter channel resources into reproduction which enables them to have a high reproductive effort in their second summer. A good example is B. paludinosus in the shallow (± 2m deep) Lake Chilwa in Malawi. Between the years 1965 to 1968 the lake dried out. Catches of B. paludinosus from the lake and adjoining swamps plummeted from 2800 tonnes per annum in 1965 to 7 tonnes in 1968. Two years after the lake refilled, 1460 tonnes of B. paludinosus were harvested (Morgan, 1979). The minnow population which had survived the dry period in the adjoining swamps had re-invaded and colonised Lake Chilwa in a two year period. This provides an excellent example of a 'boom and bust' situation, for which r-strategists are adapted. The high reproductive potential (rapid maturity, multiple spawning) enabled the B. paludinosus to make a rapid recovery. In the fluctuating environment of the shallow rivers in southern Africa these same life history traits would have been advantageous.

Until more intensive studies, similar to the present one, are completed we can only speculate on the reasons for the success of the small barbs in southern Africa.

The minnows have successfully colonized the shallow river systems of southern Africa. The main reasons for their success may be summarised as: small size, early age at sexual maturity, rapid growth rate in the first year, migration not necessary for spawning, high fecundity, floating larvae, and tolerance of low water temperatures.

It is clear that small r-selected species have been well adapted to inhabit the unstable riverine habitats in southern Africa.

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