

The biology and management considerations
of abundant large cyprinids
in Lake le Roux, Orange River, South Africa
by
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A THESIS
submitted to
Rhodes University

In partial fulfillment of
the requirements for the
degree of
Doctor of Philosophy
February 1983

ABSTRACT

The biology of three large cyprinid fishes, Barbus holubi, B. kimberleyensis and Labeo capensis, was studied in a large turbid man-made lake on the Orange River, South Africa. The influence of environmental fluctuations on population dynamics was examined in relation to biological adaptations. On this basis inferences were made about the effect exploitation would have on the populations, and management alternatives were considered.

Lake le Roux is situated in a semi-arid area, downstream from another large reservoir, Lake Verwoerd. In the pristine river, flooding is seasonal, and floodwaters carry a heavy silt load. Lake Verwoerd acts as a silt-trap and changes in turbidity in Lake le Roux (Secchi disc readings range from 15 to 160 cm) are influenced by hydrological management and are not necessarily seasonal. Water temperatures in the regulated river connecting the two lakes depend on the pattern of water release and fluctuations in lake levels depend on management practices.

Reproduction was studied by examination of gonads and from the distribution of newly hatched juveniles. Age and growth was interpreted from the reading of scales and otoliths. Relative year class strength, dispersal and mortality were monitored using catch data from a regular, standardized gillnetting survey.

The Barbus species spawn in the regulated river in spring or summer. Spawning is coordinated for a large part of the population and B. holubi spawn four to six weeks earlier than B. kimberleyensis. The juveniles are initially found along the shoreline, but later move into the pelagic zone and disperse throughout the lake. Year class strength is dependent on time of spawning and a late spawning results in a poor year class. For this reason, year class strength of B. kimberleyensis is generally poor, but there is a greater variation in year class strength of B. holubi, which is the dominant large Barbus.

The two Barbus species exploit the pelagic zone, visually preying on zooplankton. When turbidity increases large scale mortalities occur, especially in B. holubi. Mortalities more than compensate for the reduction in carrying capacity, and the size of the reduced population may be inversely related to initial abundance. Growth rate is similarly

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affected by turbidity and density, and size at sexual maturity in B. holubi is reduced when growing conditions deteriorate.

Labeo capensis do not form a homogenous population in Lake le Roux. Spawning occurs throughout the lake, but is erratic, probably depending on local rainfall. At each locality, more than one spawning may occur during spring and summer because of temporal variation in gonadal development. Juvenile survival appears to be mainly dependent on water level fluctuations, and strong year classes were formed when the lake was filling during the first two years. Subsequent year classes were weak.

Subadult and adult L. capensis are herbivorous and depend on autochthonous production for food. They are relatively sedentary, but when turbidity increases fish smaller than 200 mm disperse, probably in response to food shortages. Mortality rates may be accelerated but mortalities are not as high as in B. holubi. The growth rate of L. capensis is variable and depends on turbidity and population density. Size at sexual maturity remained relatively constant during the study period.

B. holubi has a relatively fixed reproduction cycle in Lake le Roux and exploitation is likely to dampen fluctuations in population density. Population growth and stability could be further promoted through hydrological management. B. kimberleyensis does not represent an exploitable population in Lake le Roux, although the large size obtained by this species (>3 kg) may be an attraction to anglers. L. capensis does not appear to have the potential to withstand sustained exploitation because of its erratic and generally poor reproductive success. However, the species is long-lived and can sustain relatively high densities under harsh conditions because of its relatively low mortality rates.

It was concluded that harvesting of B. holubi must be flexible to promote maximum benefits to commercial and recreational fisheries, but L. capensis which is not an angling species, should chiefly be exploited when catches of B. holubi are poor, but left to recover in between. An alternative management strategy would be to commercially exploit the fish populations of several reservoirs. A monitoring programme could be established to decide when each reservoir is to be exploited to see to the interests of commercial and recreational fishing alike.

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ACKNOWLEDGEMENTS



"This is the Orange River of sun and solitude, where people stagger under the dead weight of the summer heat. Yet it is a river of rare dawns and bright moonlights; and I am thankful that I have slept beside it in the open and seen the first amber light upon the water....."

(From Green, 1948, p. 85)

I am grateful for having had the opportunity to work on the fish populations of Lake le Roux. Many people from various disciplines were involved in the study, and it has been my privilege to get to know them and learn from their experience and expertise.

Mr P.B.N. Jackson was instrumental in getting this project off the ground (and into the water!). His interest and support during the study is much appreciated. Prof. M.N. Bruton was very helpful at all stages of the study and was an exacting, but friendly, supervisor. Prof. B.R. Allanson gave me constructive advice in his capacity as joint supervisor. David Eccles, Rob Hart and Tom Hecht made many helpful suggestions.

Members of the Cape Department of Nature Conservation have been extremely helpful by providing material and moral support. The long data series on the fish populations stem largely from their efforts

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and I benefitted from their knowledge of the lake and the fish fauna. Many were involved and I would, in particular, like to thank Jim Cambray, Kas Hamman, Stewart Thorne and Ian Gaigher.

The Department of Environment Affairs supplied data on river flows and lake levels. I am particularly indebted to Mr P.J. Louw and Mr P. Smit.

This study formed a part of a cooperative study and I am grateful to the CSIR for financial support. Material support was received from the Cape Department of Nature Conservation, Rhodes University and the J.L.B. Smith Institute of Ichthyology.

During my stay in Vanderkloof, near the lake, I experienced friendliness and hospitality from the people there and in the surrounding farming community.

Assistance during various stages of this study came from Debra Brown, Gerald Corsane, David Gilmour, Barend Harmse, Abe Mnweba and Carl van der Lingen. Special thanks must go to Elaine Grant whose varied tasks, skilfully executed, contributed much to the production of this thesis.

Robin Stobbs assisted in many ways throughout my work, including fieldwork and photography. The scale and otolith photographs were prepared by him.

Craig Beuthin and Hugh Murrell gave me valuable help with the computer. The staff of the printing unit helped with the photo-reduction of figures and tables and the reproduction of this thesis.

Beverley Stewart typed the first draft of this thesis. Jean Pote and Joan Wright typed the final version and suffered much inconvenience with a smile.

My families in South Africa and Iceland have been supportive throughout the study and my in-laws spent some of their Christmas holidays "doing numbers". Their assistance and encouragement I value greatly.

My little daughter, Marín, probably thinks that all fathers should be pale-faced, talk about fish and only pay distracted attention to their children. I hope she will accept me as a member of the family now that this thesis is complete.

The list of people helping in this study is long and incomplete, but nobody has worked harder and given up more than my wife, Allyson Macdonald. As editor, typist, proofreader, critic and a loving companion, she has made this thesis possible. It is hers too.

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The P.K. le Roux Dam



The height of the wall is 107 m, the highest of any dam in South Africa. The width is 765 m. The lake formed by the dam is 138 km² in area and has a storage capacity of $3\,185 \times 10^6 \text{ m}^3$.

THE BIOLOGY AND MANAGEMENT CONSIDERATIONS
OF ABUNDANT LARGE CYPRINIDS
IN LAKE LE ROUX, ORANGE RIVER, SOUTH AFRICA

I. INTRODUCTION

"Give me a fish and I eat for a day
Teach me to fish and I eat for a lifetime"

The present study arose from Jackson's (1977) recommendation that a commercial fishery be established on Lake le Roux to be managed by the local Griqua population, thus stimulating an economically depressed region. He realized that not only should a fishery be established, but that such a fishery had to be given management guidelines, derived through comprehensive research.

The Orange River Development Project (ORDP) has a long history. It is the largest of its kind in South Africa and includes the erection of several dams for flood control, power generation, diversion of water for irrigation, domestic and industrial water supply and extensive inter-basin transfer of water through a tunnel (Stallebras, 1963). Fish production and exploitation has in the past not been considered in water development schemes in South Africa (Jackson, 1976). However as the ORDP was becoming a reality, attention was focussed on the potential value of fisheries for recreation (du Plessis & le Roux, 1965) and commerce (Hamman, 1974b; Jackson, 1976).

The increased awareness of the potential value of freshwater fish has led to a multidisciplinary research project on the second man-made lake created on the Orange River, Lake le Roux. The project involves several agencies and research workers in the fields of physical and chemical limnology, primary production, zooplankton, fish feeding ecology, fish biology and gear suitability and effectiveness. The study reported on here forms a part of this research project and focusses on the biology of the major fish populations.

A. OBJECT OF STUDY

The overall objective of the present study is to examine the

biology and life history strategy of the abundant large cyprinids of Lake le Roux and to formulate management guidelines based on this research. It is not intended to recommend a specific policy but rather to make policy makers aware of the consequences of different management strategies on population growth and structure. More specifically, the objectives of this study are:

- i. To describe the biology and life history strategy of Barbus holubi, B. kimberleyensis and Labeo capensis, three important cyprinid fishes in the lake.
- ii. To determine how a fluctuating lake environment affects these populations.
- iii. To discuss the effect which varying intensities and modes of exploitation may have on the production and population structure of the fish species.
- iv. To discuss the influence hydrological management has on the life history of the fish populations.

B. ORIGIN OF AND NEED FOR THE STUDY

1. Importance of impoundments and their fisheries.

In 1978 the surface area of all the world's reservoirs was estimated to be about 600 000 km², and reservoirs constituted a prominent feature in the aquatic ecosystems of every continent (Bhukaswan, 1980). Although fisheries are rarely considered when a new reservoir is created, Lowe-McConnell (1973) concluded in a review article that the benefits derived from the use of this resource are often considerable.

The exploitation of fish populations in impoundments varies and is chiefly in the form of recreational angling in the more affluent societies, but in the form of subsistence or commercial fisheries in other parts of the world. Thus in North America management of reservoir fisheries is chiefly directed towards sport fishing (Jenkins, 1970), although commercial exploitation may also occur and is indeed often recommended to improve or maintain good angling (Thompson, 1955; Parsons, 1958). Angling is the most popular outdoor recreation in U.S.A. and numerous small impoundments and several large (>500 acres) reservoirs are specifically made for recreational fishing (Stroud, 1966).

In other parts of the world, emphasis is on commercial exploitation and this is the case in Russia (Butorin, 1980), which in 1978 had 122 000 km² of impounded waters (Bhukaswan, 1980). In Asia, commercial exploitation is similarly of greater importance than recreational uses (Bhukaswan, 1980). In Africa, commercial exploitation of the Great Lakes has played important roles in the economy of some countries and the several large reservoirs in this continent are also subject to commercial fishing. South Africa is an exception in that commercial exploitation of freshwater fish is negligible, but subsistence use of freshwater fishes is important in some regions such as Maputaland (Bruton & Kok, 1980).

Originally, South African drainage systems were characterized by seasonally flowing rivers, and natural lakes are relatively rare. It is not surprising therefore that large number of dams have been erected to ensure permanent water supplies. In 1978, South Africa had five reservoirs exceeding 100 km², 15 between 10 and 100 km², 15 between 5 and 10 km² and innumerable smaller ones (Davies, 1979).

Unlike most other parts of the world, little use is made of the fish populations in these reservoirs. Recreational angling is important locally, near large populations centres (e.g., Cadieux, 1980), and waters stocked with trout are much sought after but limited due to hydro-climatic reasons (Harrison *et al.*, 1963). Commercial exploitation is negligible and this may in part be attributed to superabundance of cheap, high quality sea fish and a good distribution system (Bross, 1981). South African waters are dominated by cyprinids which are not valued highly as eating fish due to their bony flesh. However, cyprinids are valued eating fish in other parts of the world.

2. Importance of cyprinids in man-made lakes

In North America, cyprinids are represented mainly by small species (minnows) and these are often important in reservoir fish management. They often provide the food for predatory angling fish (Jenkins, 1970), but more often their high population densities cause problems. Controlling their numbers is attempted using poison (e.g. King, 1953; Hooper & Crance, 1960), draining (Finnell, 1954) or partial drawdown during their breeding season (Shields, 1958). An ingenious way is to

introduce threadfin shad which multiply rapidly during the summer, effectively competing with other small fish species, and whose numbers in turn are controlled by their low tolerance to cold water, causing winter-kills (Parsons, 1958; Jenkins, 1970).

In Europe and Asia, cyprinids dominate in the commercial catches from floodplain rivers (Welcomme, 1979), and they frequently become an important part of the fish fauna in reservoirs. In Russia, they are considered to be a desirable component of a fishery and the filling up of reservoirs is often done stepwise to establish several strong year classes by inundating new land during the breeding season (Il'ina & Gordeev, 1981). In India, cyprinids form the major component of reservoir fisheries and reservoirs are normally stocked with 'major carps' (Jhingran, 1975; Sreenivasan, 1976).

In Africa, cyprinids are chiefly riverine species but they may also often inhabit lakes. Lake-dwelling populations are (or were) often the mainstay of important fisheries when they concentrate in in-flowing rivers during spectacular spawning migrations. Examples of this include Barbus altianalis and Labeo victorianus migrating from Lake Victoria (Whitehead, 1959), L. mesops from Lake Malawi (Lowe, 1952), B. tropidolepis from Lake Tanganyika (Poll, 1953) and L. altivelis from Lake Mweru (Matagne, 1950). The lake fisheries themselves are otherwise usually dominated by cichlids which are particularly well adapted to life in lakes, or as in the case in Lake Tanganyika, by clupeids and their non-cichlid predators (Fryer & Iles, 1972).

Cyprinids, mostly Labeo, often play an important role initially in the fisheries of man-made lakes in Africa, but tend later to be replaced by cichlids. The former are primarily river-fish and are very fecund (especially the Labeo species). High mortalities normally occur when the rivers recede but in the new lake favourable conditions for their survival are created. Thus, in the years of filling the new lake tends to be dominated by cyprinids and/or other riverine species (e.g. mormyrids). Subsequently species adapted to lake conditions, such as cichlids in inshore zones and clupeids in the pelagic zone (often associated with predators) become dominant, with cyprinids being confined to the 'riverine' parts of the lake. Examples of this are given below.

The Middle Zambezi River prior to the formation of Lake Kariba

was dominated by cyprinids. Labeo species dominated in the catches (up to 60%), but predators were also important (Jackson, 1961). In Lake Kariba, the Labeo species were soon replaced by cichlids in the inshore fishery, except in the two uppermost basins (Begg, 1974). In 1980 their importance had declined further still (Marshall et al., 1982), and although they still were the most abundant family in the two uppermost basins, their relative abundance there had declined over 50%. Considering that those two basins only represent about 10% of the total surface area of Lake Kariba, cyprinids are now of minor importance in the inshore fishery. A clupeid (Limnothrissa miodon) was introduced from Lake Tanganyika in 1967 - 1968 and by 1980 it supported an 8 000 tons/year fishery (Marshall et al., 1982). Associated with the increase in the sardine population was an increase in the tigerfish (Hydrocynus vittatus) population which is important in commercial and recreational fisheries (Marshall et al., 1982). In a pre-impoundment survey of Lake Cabora Bassa, Jackson & Rogers (1976) found that tigerfish were dominant, but that during the filling phase Labeo species dominated in the lake, and showed rapid individual growth. Unfortunately no subsequent studies on the fish fauna of this lake have been published.

Similar changes in Lake Kamburu, Kenya (Dadzie, 1980) and Nyumba ya Mungu, Tanzania (Bailey et al., 1978) have occurred with cichlids becoming dominant and cyprinids declining in importance, but maintaining a presence in riverine parts of the lakes. In Lake Volta, West Africa, mormyrids and cyprinids declined although the cyprinids maintained a presence in the riverine region, while cichlids and clupeids with associated predators became dominant (Evans & Vanderpuye, 1973). In Lake Kainji, Nigeria, there has similarly been a reduction in riverine species and cichlids now form a major component of the commercial catch (Blake, 1977).

While cyprinids do not appear to be important in the fisheries of man-made lakes in Africa, except perhaps for the first few years, the situation in South Africa is likely to be different. This is due to the increased proportion of species of this family with increasing latitude (Table 1). This is explained by their relatively high tolerance of lower temperatures so although there is a decline in the absolute number of all species with latitude, the percentage of cyprinids increases (Bowmaker et al., 1978).

Table 1. The composition of primary freshwater fish faunas (excluding exotics) of watersheds in southern Africa, arranged in order of increasing latitude (from Bowmaker et al., 1978).

		Fish Family						Total Spp.
Drainage		Mormyriiformes	Characoidaei	Cyprinidae	Siluriformes	Cichlidae	Others	
Zaire R.	Nos.	75	73	52	112	32	64	408
	%	18	18	13	28	8	16	
Lake Malawi and Watershed	Nos.	6	2	15	22	201	5	251
	%	2	1	6	9	80	2	
Zambian Zaire	Nos.	12	16	34	25	15	15	117
	%	10	13	29	21	13	13	
Upper Zambezi/Kafue/Okavango/Cunene R.	Nos.	5	8	32	18	25	12	100
	%	5	8	32	18	25	12	
Middle and Lower Zambezi R.	Nos.	5	8	22	12	11	9	67
	%	8	12	33	18	16	13	
East Coastal (1) Buzi/Pungwe/Save R.	Nos.	6	7	24	14	7	11	69
	%	9	10	35	20	10	16	
Limpopo R.	Nos.	1	2	25	8	5	6	47
	%	2	4	53	17	11	13	
East Coastal (2) (Inkomati/Pongolo)	Nos.	2	4	21	14	6	10	57
	%	4	7	37	25	11	18	
East Coastal (3) (Mkuzi to Mtamvuna R.)	Nos.	0	0	16	2	4	3	25
	%	0	0	64	8	16	12	
Orange/Vaal	Nos.	0	0	11	2	2	0	15
	%	0	0	73	13	13	0	
South Coastal	Nos.	0	0	16	1	0	4	21
	%	0	0	76	5	0	19	

The fish fauna of South African reservoirs is generally dominated by cyprinids. This is true for most reservoirs on the Orange-Vaal River system, such as Lake Verwoerd (Hamman, 1981), Lake le Roux (this study), Barberspan (Göldner, 1967) and Lake Boskop (Koch, 1975). A cichlid, Oreochromis mossambicus, was introduced into Lake Hardap (a reservoir on a tributary of the Orange River in South West Africa (Namibia)) where it is now well established (Bloemhof, 1974). In other impoundments where conditions are warmer, cichlids may dominate as in Lake Doornkraai (Batchelor, 1974), Lake Loskop (Göldner, 1969) and Lake Luphephu-Nwanedi (Hecht, 1980). In Lake Strijdom on the Pongolo River, a catfish, Eutropius depressirostris, made up 50% of gillnet catches but was not encountered in a pre-impoundment survey, whereas Labeo species have declined from 70% to 30% and surprisingly cichlids have also declined slightly in the catches (Kok et al., 1978).

3. Importance of cyprinids in South Africa.

Unlike other African reservoirs, fishing intensity is light in South African impoundments. It may well be that the relative importance of different species would change if they were to be exploited. It is therefore important to study their biology and life history, since these are the determinants of how a species will react to exploitation. Depending on the extent of exploitation and environmental conditions such changes may not be necessarily reversible.

Although some work has been done on the biology of the study animals (reviewed in the next chapter), long-term biological studies have not previously been performed. In view of the highly variable environment, long-term studies are called for if our understanding of adaptation of a fish to its environment is to improve.

The large Barbus and Labeo species are important components of most South African river systems and lakes. It is thus hoped that information gained in this study may have an application in the wider context of southern African fisheries management.

C. STUDY AREA

Most large African rivers experience seasonal changes, often

of considerable magnitude in such physical parameters as flow, turbidity and temperatures. The life histories of riverine fish are adapted to take advantage of these conditions (Welcomme, 1979; Daget & Durand, 1981). It thus becomes important to establish the characteristics of the rivers from which present fish faunas of man-made lakes have originated and how living conditions have changed. It is in this context that biological studies of fish faunas in reservoirs and their tailwaters must be seen. In this section the Orange River and the way in which conditions in the river entering Lake le Roux have changed are described and finally characteristics of the lake are discussed.

The Orange River is the largest South African river, 2 200 km long and draining a 650 000 km² catchment (Edwards, 1974). The variable flow in the river and relative scarcity of water led to the Orange River Development Project. This scheme, designed for large scale irrigation, flood control and power generation, included the building of three dams and diversion tunnels. In 1970 the H.F. Verwoerd Dam was closed forming a lake of 355 km² ($5\,950 \times 10^6$ m²) and in October 1976 the P.K. le Roux Dam was closed 120 km downstream (Fig. 1). Lake le Roux is 138 km² in area, with a storage capacity of $3\,185 \times 10^6$ m³ (Kriel, 1972; Davies, 1979). There is about a 35 km stretch of river connecting the two lakes. A third large dam downstream from the P.K. le Roux Dam is in the planning stage.

The Orange River originates in the Drakensberg mountains of Lesotho and drains westwards to the south Atlantic Ocean. Along its course it runs through increasingly arid country (Keulder, 1979). Flow is seasonal (Fig. 2), and highly variable within as well as between seasons. There are instances when the river has not flowed for several months. Annual variation in flow downstream of the present P.K. le Roux Dam from 1948 - 1970 (before river regulation) ranged from 17 to 267% of the mean (Kriel, 1972).

Daily variations in flow are even greater and flash floods, lasting for a few days occur. It is likely that the magnitude of such flash floods has increased considerably since the early 1800's due to erosion in the catchment (Jacot-Guillarmod, 1970). Flow in the tailwaters of Lake Verwoerd shows no seasonal trends, but has an assured minimum flow for riparian right owners downstream. Flow fluctuates in pulses lasting from a few minutes to several hours depending mainly on demand for

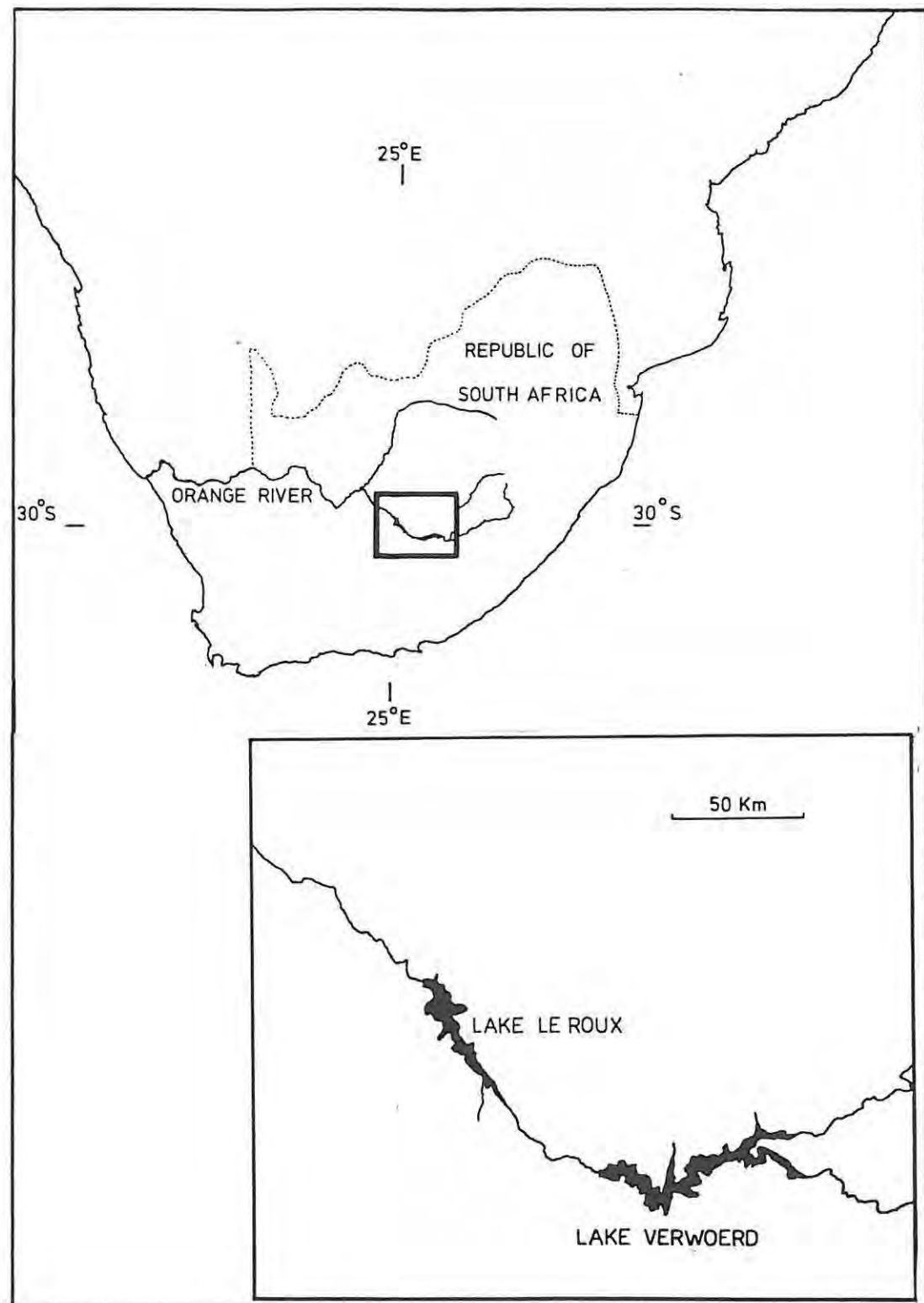


Figure 1. Geographical location of Lake le Roux and Lake Verwoerd.

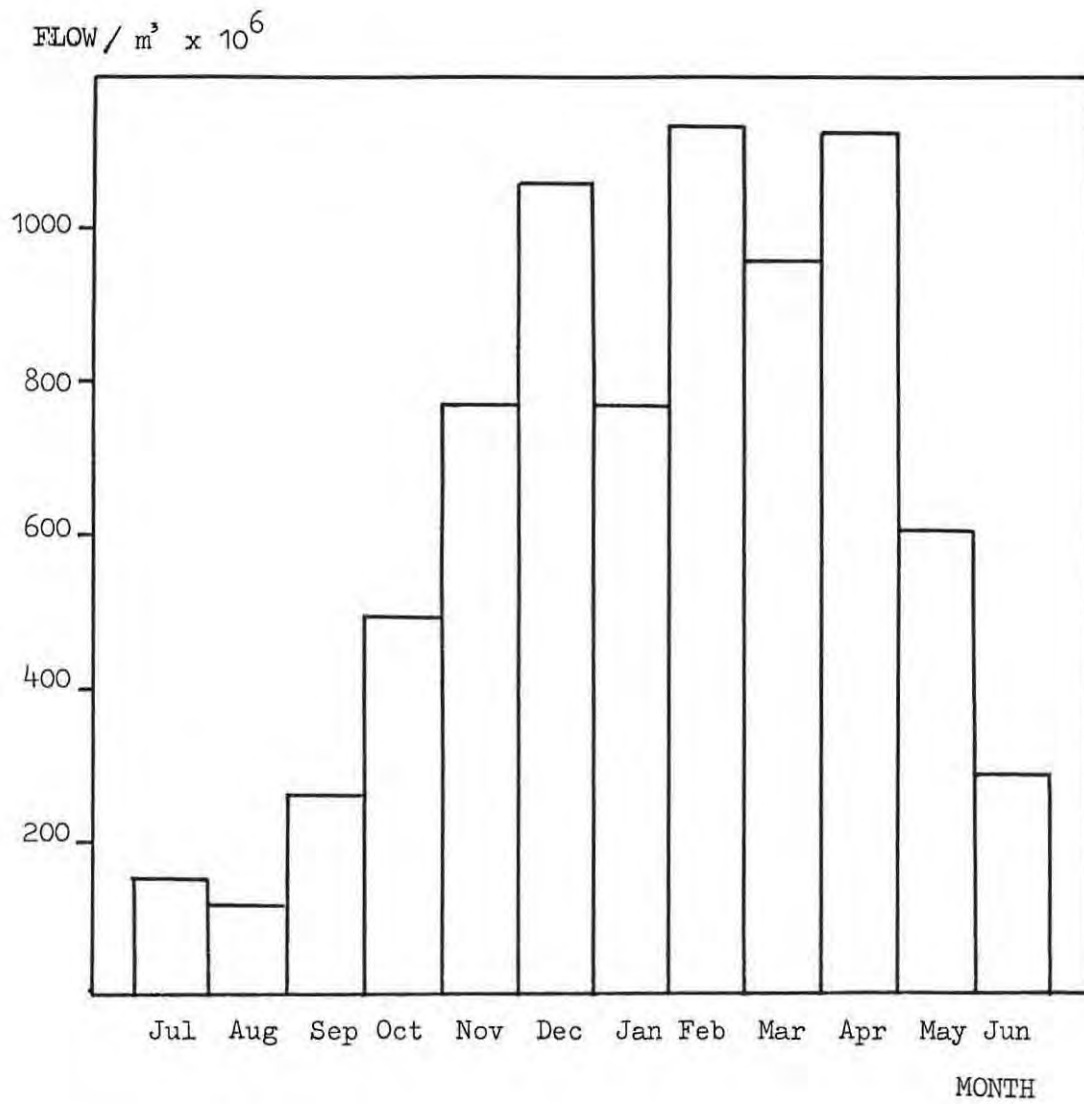


Figure 2. Average monthly flow in the Orange River (1922 - 1970).
(From Kriel, 1972).

electrical power.

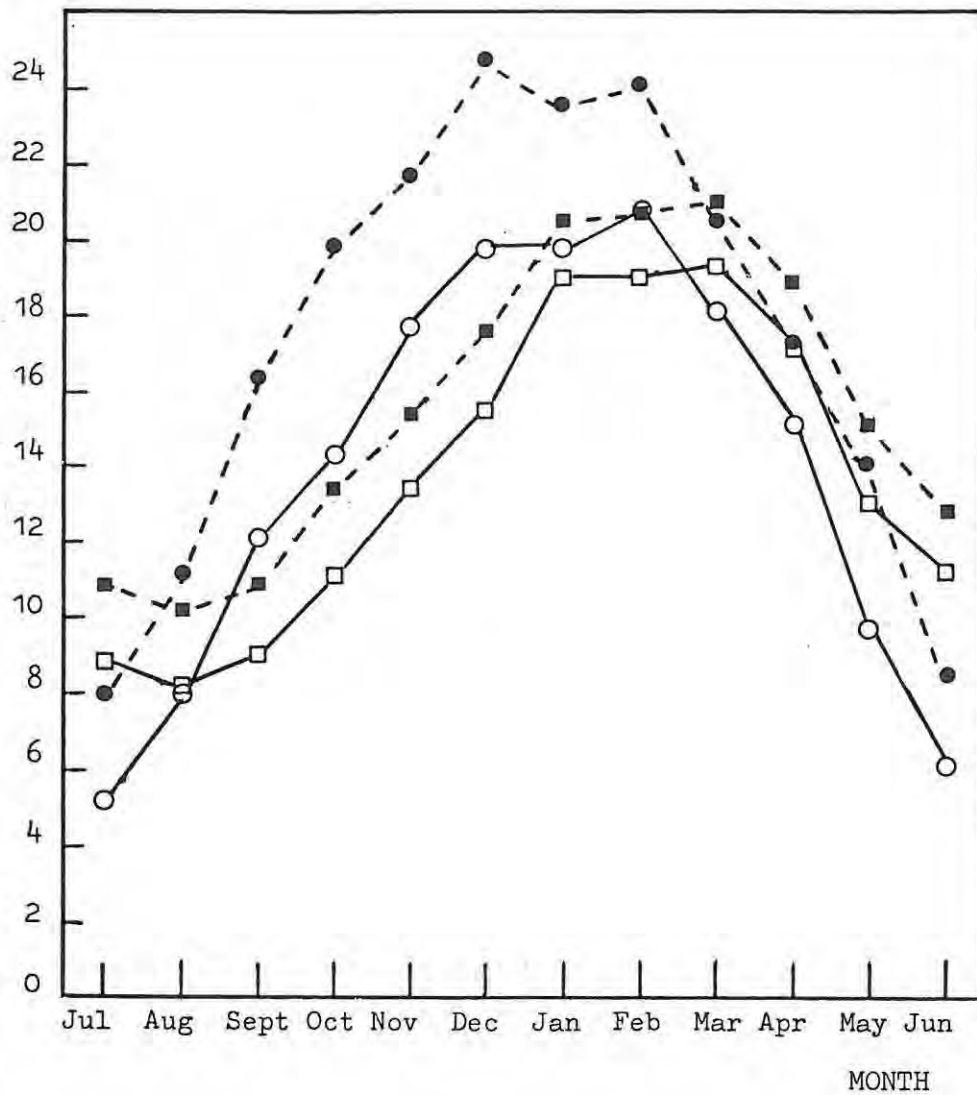
Water temperatures vary seasonally, but the creation of Lake Verwoerd has reduced seasonal differences in the river (Pitchford & Visser, 1975). Mean maximum summer temperatures in the river below Lake Verwoerd before it enters Lake le Roux have been reduced by up to 7°C (Fig. 3).

The Orange River carries an average 0,6 vol % sediment load (Kriel, 1972), which depends on rate of flow (Keulder, 1979). This high load is largely attributable to unstable riverbeds. The upper catchment however has a stable riverbed, where increases in sediment load are unexpectedly high (Keulder, 1979), lending further support to Jacot-Guillarmod's (1970, 1971) observations of serious erosion in the upper catchment. Approximately 90% of the sediment is deposited in Lake Verwoerd (Kriel, 1972), leaving the river below relatively clear. However, siltload is variable and Secchi disc readings in Lake le Roux have varied from 10 to 160 cm at different times (Chapter IV).

Lake le Roux is relatively deep and narrow and has steep shorelines and limited littoral areas. The uppermost 20 km of the lake are in a narrow gorge (Fig. 4). Here the lake retains a riverine character in that currents are marked during times of water release from Verwoerd Dam and there is no thermal stratification. The average depth of the lake is 23 m, average breadth 1,74 km and the shoreline is 404 km long (Allanson, 1981). The lake is monomictic developing a thermal stratification in early summer which does not appear to be directly influenced by the inflow from Lake Verwoerd (Allanson, 1981).

Lake le Roux is situated in a semi-arid to arid area with average annual rainfall of less than 400 mm. Rainfall is highly unpredictable as to amount and timing (Dyer, 1981; Görgens & Hughes, 1982). Rain falls mainly during the summer months (December to March), and then largely as isolated thunderstorms, but usually becomes more general in February to March. The catchment between the two dams has an average annual runoff of about $110 \times 10^6 \text{ m}^3$ (Kriel, 1972). In contrast the catchment of Lake Verwoerd contributes 95% ($7\,180 \times 10^6 \text{ m}^3$) to the average annual runoff of the Orange River, excluding the Vaal River (Kriel, 1972). The tributaries of Lake le Roux have undependable summer flow and only two (the Seekoei and Berg Rivers) have enough permanent water to harbour

TEMPERATURE/ °C



KEY: ● Average maximum before 1970.
 ■ Average maximum after 1970.
 ○ Average minimum before 1970.
 □ Average minimum after 1970.

Figure 3. Average daily minimum and maximum temperatures in the Orange River before and after the erection of Verwoerd Dam. (Drawn from data by Pitchford and Visser, 1975).

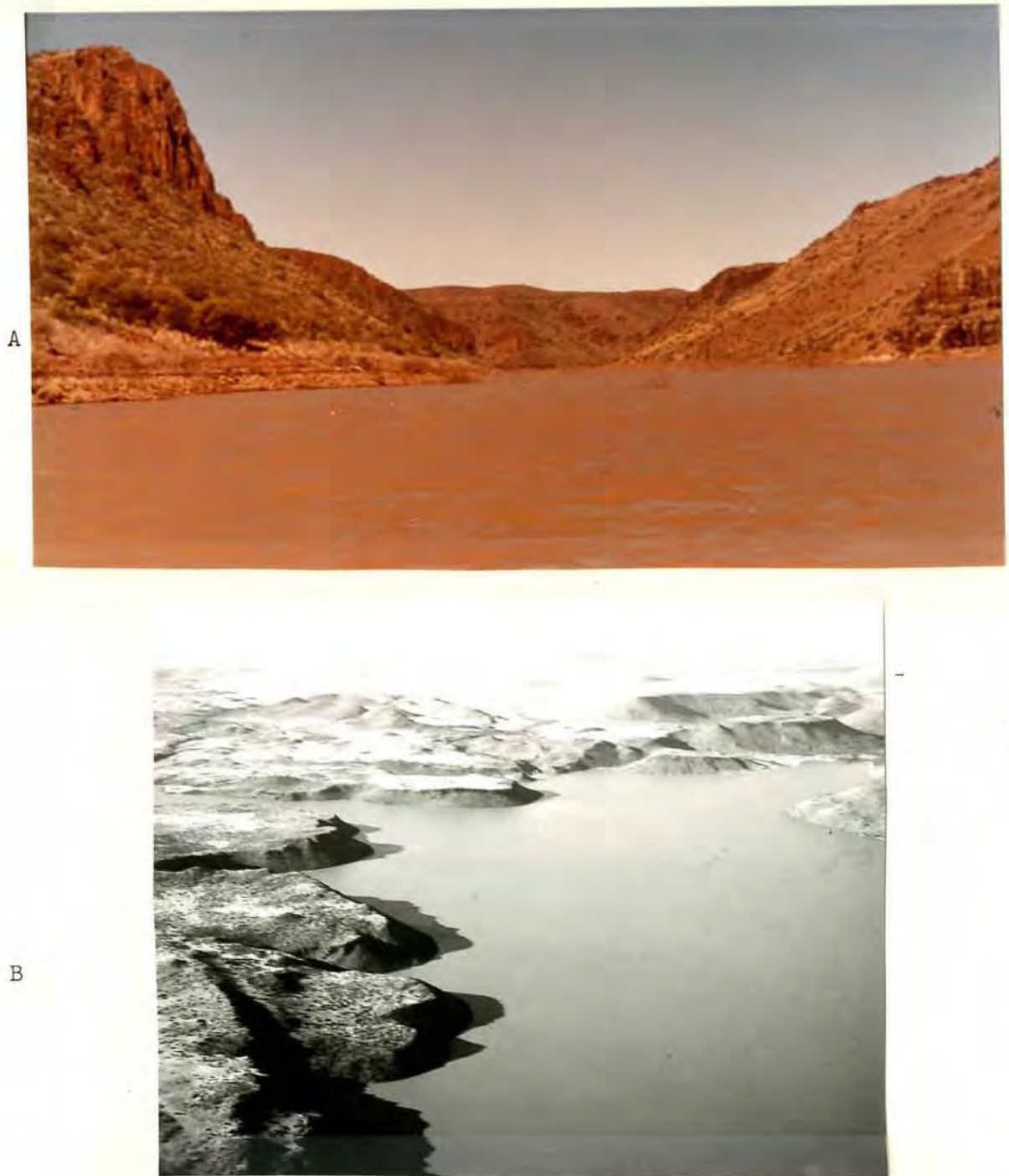


Figure 4. A. The uppermost basin in Lake le Roux looking towards the narrow riverine section. The shoreline is steep and rocky, and the water is heavily silt laden. A gang of floating gillnets can be seen along the left shore.

B. An aerial photograph of the largest basin in Lake le Roux, 15 km from the dam wall. Steep and rocky shorelines are common throughout the lake.

resident fish populations.

D. FISH POPULATIONS OF LAKE LE ROUX

The fish species now inhabiting Lake le Roux all originate from the river fauna prior to impoundment, and are dominated by cyprinids. To date ten species of fish have been collected from the lake (Table 2). The changes in relative abundance of these prior to and after impoundment have been discussed by Gaigher et al. (1981). Although sampling procedures on the CPA gillnetting surveys were not standardized until April 1978, the following general pattern has emerged:

- i. Labeo capensis has consistently been important in gillnet catches, both before and after impoundment.
- ii. Barbus holubi was well represented in the river catches and expanded rapidly in the new lake. This population crashed in 1978, but subsequently recovered.
- iii. B. kimberleyensis is relatively better represented in the lake as compared to the river. While not abundant, it is the third most important species in the gillnet catches.

These trends were examined further in the present study. Other species were only of minor importance in the gillnet catches, rarely contributing more than 10% of the catches and usually much less. Gillnet catches do not, however, necessarily reflect this relative abundance.

A minnow, Barbus anoplus, which reaches an adult size in the lake of about 70 mm, is abundant along the shores of the lake. Its life history has been studied in detail by Cambray (1982). He found that that this species rarely co-exists with juveniles of the larger cyprinids, but quickly colonizes newly created (or vacant) habitats, which is typical of an 'r' strategist.

A catfish, Clarias gariepinus, grows to a large size and may be the most marketable of the species in the lake. Although catches in the gillnets are poor this may be related to their ability to detect the nets with their long, sensitive barbels (Bruton, 1978). Occasional good catches are taken on longlines baited with fish. Growth rate and

Table 2. Fish species of Lake le Roux. Common names from Jackson (1975).

	Scientific name	Common name
Order Cypriniformes		
Family Cyprinidae		
	<u>Barbus anoplus</u> Gilchrist & Thompson, 1917	Chubbyhead barb
	<u>Barbus holubi</u> Steindachner, 1894	Smallmouth yellowfish
	<u>Barbus kimberleyensis</u> Gilchrist & Thompson, 1913	Largemouth yellowfish
	<u>Cyprinus carpio</u> Linnaeus, 1758	Carp
	<u>Labeo capensis</u> (Smith, 1841)	Orange River labeo
	<u>Labeo umbratus</u> (Smith, 1841)	Moggel
Order Siluriformes		
Family Bagridae		
	<u>Gephyroglanis sclateri</u> Boulenger, 1901	Rock-catfish
Family Clariidae		
	<u>Clarias gariepinus</u> (Burchell, 1822)	Sharptooth catfish
Order Perciformes		
Family Cichlidae		
	<u>Tilapia sparrmanii</u> Smith, 1840	Banded tilapia
Order Salmoniformes		
Family Salmonidae		
	<u>Salmo trutta</u> Linnaeus, 1758	Brown trout

relative condition of this species in the lake compares favourably with that from other water bodies (Quick, 1982).

Carp (Cyprinus carpio) were relatively abundant (10-15%) in the gillnet catches in summer 1978 to 1979 (Gaigher et al., 1980), but their numbers have subsequently steadily decreased. Occasionally, a large number of juveniles were caught in small beach seines, but they never appeared in the gillnet catches.

Of other species, L. umbratus normally makes up two to five percent of the total catches, but its distribution in the lake appears to be patchy. Gephyroglanis sclateri is rarely caught and its complete disappearance from Lake Verwoerd (Hamman, 1981) indicates that it is poorly equipped for life in lentic waters. Tilapia sparrmanii occurs around the shores of the whole lake, but not in large numbers. This species is territorial and this may limit their population growth (Jackson, pers. comm.). Their scarcity however indicates that other factors may be limiting their abundance. T. sparrmanii is a nest builder and water level fluctuations may adversely affect their reproduction. Relatively low water temperatures in winter may also cause mortalities. Only two brown trout have been caught since the lake filled (Gaigher et al., 1980) and none in the last three years.

E. DESIGN OF THIS STUDY

In this study, an empirical approach has been adopted. This approach seemed reasonable in view of the cooperative nature of this programme and recent views reflect that this may be a trend. Rigler (1982) advocated this (p.129):

".....I believe that the gulf between fisheries biology and limnology is unnecessarily wide. With a proper appreciation of the significance of empiricism in environmental science we will not only narrow this gap, but also accelerate the development of new predictive theories that are so essential to any society that intends to base its environmental decisions on predictions of science rather than on whim".

The data were collected in the field, from an environment over which the researchers could exercise no control. The response of the fish

populations to a variable biotic and abiotic environment was carefully monitored. The key questions address the response of fish populations of riverine origin to a variable environment with special emphasis on the effect which exploitation might have upon them.

Results often relate to two or more facets of the investigation. To facilitate the reading of this thesis, the main questions and avenues of research have been summarized in a schematic diagram (Fig. 5). The major areas of research are described in more detail below.

- i. Distributional patterns. The lake is large and the mobility of a fish species is important when decisions are made on exploitation. If local populations (or "stocks") are formed, then exploitation may lead to overfishing in one area of the lake while other areas may be unproductive due to high population density. Identification of a "unit stock" is a central concept in fish resource management (Cushing, 1981), and it has been suggested that even species of floodplain rivers which seasonally undertake long migrations may be made up of subpopulations (Welcomme, 1979). To determine the extent of mixing of fish between different areas of the lake, patterns of growth and recruitment were studied by locality.
- ii. Reproduction. The size of recruited cohorts is determined largely by reproductive success. It is therefore important to examine which factors may affect the reproduction and juvenile survival of each species. Time and locality of spawning were inferred from the occurrence of recently hatched juveniles in the marginal areas of the lake. The ultimate success of reproduction was measured as recruitment into a fleet of gillnets. This was then related to conditions during corresponding spawning seasons.
- iii. Growth and mortality. The combined effect of growth and mortality determine the optimal age at which fish should be exploited, all other factors (e.g. ease of capture, distribution and value of the fish) being equal. Growth

was determined using length-frequency distribution, ageing from otoliths and scales, and backcalculation to length at check formation based on scale measurements. Growth curves were constructed for different seasons using the von Bertalanffy growth equation to relate characteristics of growth to those of the environment. Mortality was inferred from catch per unit effort (CPUE) of year classes with time, as determined from the catches of a fleet of gillnets.

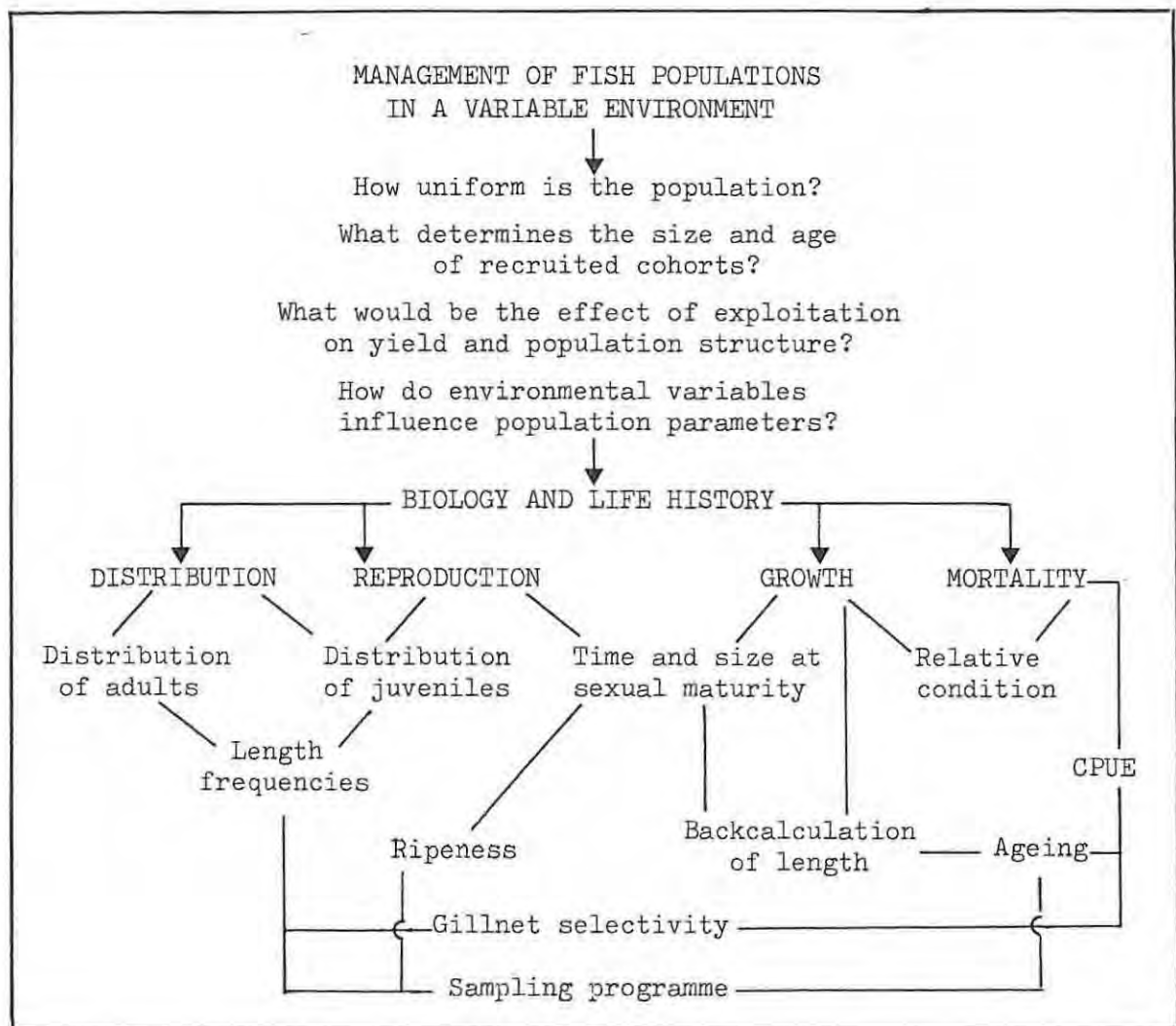


Figure 5. Inter-relationship between the objectives, research areas, analysis and sampling in this thesis.

II. BIOLOGY OF THE STUDY ANIMALS

The biology of Barbus and Labeo species in Africa is reasonably well documented, but consists largely of separate and short-term studies. Cyprinids are essentially riverine fish and because of the variable nature of their habitat, long-term studies are essential. A comparison of the biology of the study animals with that of related species should indicate the applicability of the results of the present study to other systems. The genus Barbus is exceptionally large and accommodates a wide variety of fish found in Europe, Asia and Africa. For this reason it is necessary to first identify groups within the genus which are made up of close relatives.

A. DISTRIBUTION AND TAXONOMY

Barbus holubi, B. kimberleyensis and Labeo capensis are all originally indigenous to the Orange-Vaal River systems (Barnard, 1943). B. holubi can occur at higher altitudes than the other species (Jubb, 1970). A valued angling fish, B. holubi has been bred artificially since 1949 (Groenewald, 1951) and subsequently introduced into several rivers in the Cape Province and to Zimbabwe (Jubb, 1968). L. capensis and B. holubi are known to have dispersed to the Great Fish River system through an 82 km tunnel constructed for irrigation purposes in 1975 (Cambray & Jubb, 1977).

It is probable that most of the cyprinid fauna of the Orange River resulted from invasions from the north (Farquharson, 1962; Lowe-McConnell 1975; Bowmaker *et al.*, 1978). The African Barbus are generally divided into two major groups based on scale characteristics (Banister, 1973): large forms (adults > 150 mm SL) with parallel-striated scales, and generally smaller forms with radiate-striated scales. The large African Barbus with parallel-striated scales occur predominantly in east, central and southern Africa. Their taxonomy has been reviewed by Groenewald (1958) and Banister (1973). The large Barbus of South Africa, including three species with radiately-striated scales are given in Table 3. Synonyms of these species are given by Jubb (1963).

The South African large Barbus are predominantly small scaled species. These show a gap in their distribution, occurring in the

Table 3. Large Barbus of South Africa (adults > 150 mm)

Species	Scale characteristics
<u>B. holubi</u>	small scales with parallel striae
<u>B. kimberleyensis</u>	
<u>B. capensis</u>	
<u>B. natalensis</u>	
<u>B. polylepis</u>	
<u>B. marequensis</u>	large scales with parallel striae
<u>B. serra</u>	scales with radiate striae
<u>B. andrewi</u>	
<u>B. mattozi</u>	

Limpopo River (B. polylepis) and then again only in Lake Malawi (Jubb & Farquharson, 1965) (Fig. 6).

The large Barbus show a high degree of phenotypic variability and Banister (1973) has suggested that small scales may be an adaptation to lacustrine environments. However, the South African species are all riverine. It is doubtful that size of scales is a good phylogenetic indicator (Skelton, pers. comm). Eggs of B. holubi have been fertilized by sperm from B. kimberleyensis and B. polylepis with over 99% success (Mulder, 1971). A cross between female B. holubi and a male B. marequensis yielded similar results (Hecht, pers. comm.). This is indicative of the close relationship among the South African large Barbus. In this study the biology of the two Barbus species will be compared firstly to other South African large Barbus and secondly to east and central African species.

The taxonomy of the Labeo has been much less studied than that of the Barbus and classificatory work is scanty. Reid (1978) has revised this genus, but his work is in thesis form and is not generally available. Unlike the large Barbus, this genus is well

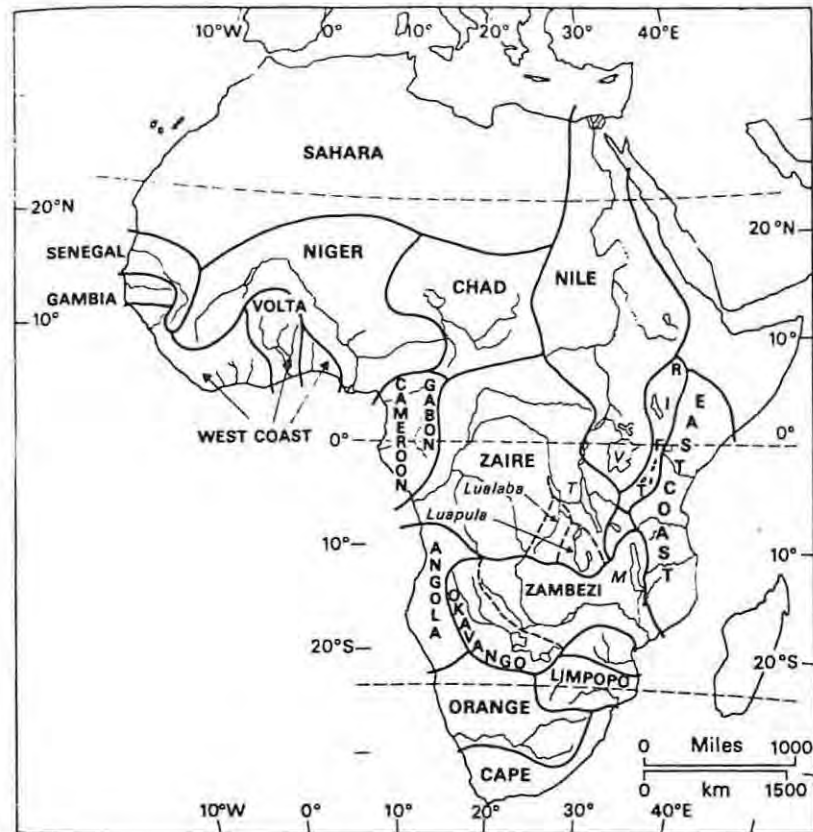


Figure 6. The Orange River basin in relation to other major river basins on the African continent. The Great Lakes (Victoria (V), Tanganyika (T) and Malawi (M)) are shown on the map. (Figure reproduced from Lowe-McConnell, 1975).

distributed throughout the continent (Banister, 1973). Its world distribution is limited to Africa and Asia. The Labeo appear to form a fairly homogenous group. In this study the biology of L. capensis will be compared separately to that of African and Asian species.

B. BREEDING

The large Barbus and Labeo are primarily riverine fish, and while they may occupy lakes at some stage of their life history, spawning generally takes place in rivers or their floodplains during flood.

Large Barbus, as a rule, deposit their eggs in gravel beds in flowing water following a spawning migration. Shortt-Smith (in Jubb, 1967) reported that B. holubi migrated upstream in first floods and spawned in gravel beds. In the Vaal River they spawned in spring to summer (Mulder, 1973a). Louw (1970) observed a spawning in February of large fish in a gravelly area in a small slowly flowing tributary to a reservoir in the Gouritz River system where they had been introduced 17 years earlier. No evidence was found which indicates that this population has reproduced successfully since their introduction. In captivity, B. holubi bred in a pond with strongly circulating water, making a nest ± 5 cm deep in gravel beds (Groenewald, 1951). Here breeding behaviour was first observed when water temperatures exceeded 18°C. However, spawning was not always successful under these circumstances since many eggs died due to poor oxygenation of the gravel beds (le Roux, 1968). Groenewald (1957) described what he considered could be the nests of B. holubi in gravel banks in two impoundments on the Vaal River. However, this species is regarded as ideal for stocking small farm reservoirs, since it will not breed successfully in standing water, and so will not overpopulate small habitats (le Roux, 1968; Straub & Combrinck, 1973a). In captivity a fish may spawn more than once in a season, but in the wild one spawning per season is probably the rule (Mulder, 1973a).

The spawning of B. kimberleyensis has never been observed, but their breeding habits are probably similar to those of other large Barbus. Their juveniles (up to a size of 80 mm) cannot easily be separated from those of B. holubi. After examining the ripeness of the gonads of these two species, Mulder (1973a) concluded that

B. kimberleyensis spawn later in the year than B. holubi. His observation is further supported by growth rates of these two species in the Vaal River, where B. holubi reaches a greater length by the end of their first and second growing season than B. kimberleyensis (Mulder, 1973a). Similar results were obtained in Lake le Roux (this study). Gaigher (1976) reported that B. cf. kimberleyensis, now confirmed to be B. kimberleyensis (Butler, pers. comm.) spawned in standing water probably in the gravelly shores of Lake Hardap on the Fish River, Orange River system in South West Africa/Namibia. It was inferred from the results that spawning had taken place twice, the first time in late summer and the second time in early spring. However there is a possible alternative interpretation of Gaigher's data, i.e. that there is only one spawning which occurs in late summer, coinciding with the flooding of the dammed river.

Other large Barbus of South Africa conform to the pattern outlined above. Barbus capensis ascend rivers and spawn in clear gravel beds in relatively shallow water (Hey, in Breder & Rosen, 1966). B. natalensis migrate upstream to spawn and are unable to breed in still water (Crass, 1964). They are known to spawn in clean well-circulated gravel in fast-flowing water when the water temperature exceeds 19°C (Wright & Coke, 1975a). B. marequensis make nests in gravelly areas of the river (Crass, in Whitehead, 1959) and are known to have a spawning migration at times of heavy flood (Donnelly, 1980). Of the South African large Barbus with radiate striae on their scales, B. mattozi (Donnelly, 1980) and B. andrewi (Harrison, 1952) also migrate up river to spawn, the latter doing so over gravel and rocks.

The large Barbus of Lake Malawi (Lowe, 1952; Banister & Clarke, 1980), Lake Tanganyika (Poll, 1953; Banister, 1973), Lake Victoria (Whitehead, 1959) and Lake Mweru (de Bont & Maes, 1956) all migrate up major affluent rivers in flood to spawn. Large Barbus of West Africa also migrate up rivers seasonally (Daget & Durand, 1981). In Asia similar examples may be found. Al-Hamed (1972) studying the reproduction of three Barbus species in the Euphrates-Tigris system, found that the smallest of the three species (males maturing at 250 mm) spawns in lakes, whereas the two larger species (males maturing at 410 to 500 mm) migrate up rivers in flood and spawn on beds of fine gravel. Similarly in India the tor mahseers (Tor species) spawn in rivers on gravel substrates after a

migration (Jhingran, 1975; Chaturvedi, 1976). Tor species have previously been classified in the genus Barbus (Jhingran, 1975).

In contrast to the large Barbus, Labeo generally leave the main river channel and spawn in newly inundated areas. They are renowned for their longitudinal spawning migrations (Jubb, 1967), but these have never been reported for L. capensis. They do, however, have a lateral migration, spawning among inundated vegetation in times of flood (Mulder, 1973b; Gaigher et al., 1980^b). Individual females apparently shed all their eggs at once (Gaigher et al., 1980^b) but the spawning season may begin in early spring and continue throughout the summer (Göldner, 1967; Mulder, 1973b; Baird, 1976; Gaigher et al., 1980^b). Similar spawning behaviour has been observed for L. lunatus in the Upper Zambezi River (Bell-Cross, 1976). Other species of the genus Labeo have also been reported to leave the main channel and spawn on the flooded banks and floodplains e.g. L. congoro in the Zambezi River (Jackson, 1961a). L. cylindricus in the Incomati system (Gaigher, 1969) and L. rosae in the Pongolo River (Kok, 1980). The latter also has an extended breeding season although each female only spawns once in a season (Kok, 1980), in the Pongolo River. L. cylindricus in Lake Malawi may spawn on rocky substrates in the lake (Jackson et al., 1963) and this is the only Labeo in Africa which has been reported to do so.

L. umbratus migrates upstream and spawns on a floodplain (Jackson & Coetzee, 1982) as well as over gravelly and rocky substrates where weirs hinder their upstream migration (Gaigher et al., 1975; Mitchell, 1982). Bowmaker (1973) similarly reports that four species of Labeo migrated up a tributary of Lake Kariba to spawn, although no inundated vegetation was available. Jubb (1967) states that L. umbratus are prolific breeders in impoundments, but this is not supported by reports in the literature. L. umbratus will migrate long distances during times of flood. This has been observed in the heavy floods in summer 1980/1981 in the Gouritz River system (Hamman & Thorne, 1982). Skelton (in press) has observed that this species is a major component of the fish fauna in secondary tributaries to the Orange River which may occasionally dry up. This is in sharp contrast to observations in the main channel of the Orange River, where L. umbratus appear to be scarce (Skelton & Cambray, 1981). The occurrence of this species in seemingly isolated farm reservoirs also indicates that they may undertake long migrations.

Here, lack of interspecific competition and predators gives rise to dense populations. This may result in individual growth being highly variable (Nikolskii, 1969), which without careful study may give the impression that many year classes are present. These populations deserve further attention though, especially if they are to be exploited.

Spectacular spawning runs up flooded rivers have been observed for L. victorinus from Lake Victoria (Fryer & Whitehead, 1959), L. mesops from Lake Malawi (Lowe, 1952) and L. altivelis from Lake Mweru (Matagne, 1950). All resulted in spawning on the floodplain among inundated vegetation. In West Africa, Labeo species are similarly reported to undertake spawning migrations up flooded rivers (Daget & Durand, 1981) and the spawning of L. coubiei was observed on the flooded bank of a river in Gambia (Svensson, in Jackson & Coetzee, 1982). In India, Labeo species are invariably reported to spawn during the monsoon on newly flooded ground although vegetation may be absent (Sinha et al., 1974; Jhingran, 1975; Khan & Jhingran, 1975).

C. FECUNDITY AND SIZE AT SEXUAL MATURITY

Fecundity is generally related to the size of the female, usually adequately described by a power function (Bagenal & Braum, 1978), but there is a large individual variation. Relative fecundity, i.e. fecundity in relation to size, varies from species to species and may also vary among populations of the same species, and this may be related to size at sexual maturity. In this section, variations in fecundity in the large Barbus and Labeo are examined. Males generally mature at a smaller size than the females. Hamman (1981) has summarized what is known of size at sexual maturity (Table 4).

It is evident that size at sexual maturity is variable. As a consequence minimum observed length at maturity may be a poor measure of what the population as a whole is doing. Judging by the size of females from which eggs were taken, the population of Barbus in Lake Hardap (Gaigher, 1976) was maturing at a markedly smaller size than the other Barbus populations. The same applies for the Labeo populations in the Caledon River (Baird, 1976) and the Tyume River (Gaigher et al., 1975). Egg counts from these species have been done by several authors and the relationships are given in Fig. 7. The following main conclusions

Table 4. Minimum length (cm) at sexual maturity in B. holubi, B. kimberleyensis, L. capensis and L. umbratus. (Adapted from Hamman, 1981)

Locality	<u>B. holubi</u>		<u>B. kimberleyensis</u>		<u>L. capensis</u>		<u>L. umbratus</u>		Source
	Male	Female	Male	Female	Male	Female	Male	Female	
Lake Verwoerd	21	31	40	44	22	29	24	32	Hamman, 1981
Vaal River	28	34	35	46	26	31	22	30	Mulder, 1971
Vaal River	20	24			22	24	33	33	Groenewald, 1957
Barberspan	20	25			26	32	32	34	Göldner, 1967
Lake Hardap			17	25					Gaigher, 1976
Caledon River					16	20			Baird, 1976
Tyume River							14	20	Gaigher <u>et al.</u> , 1975

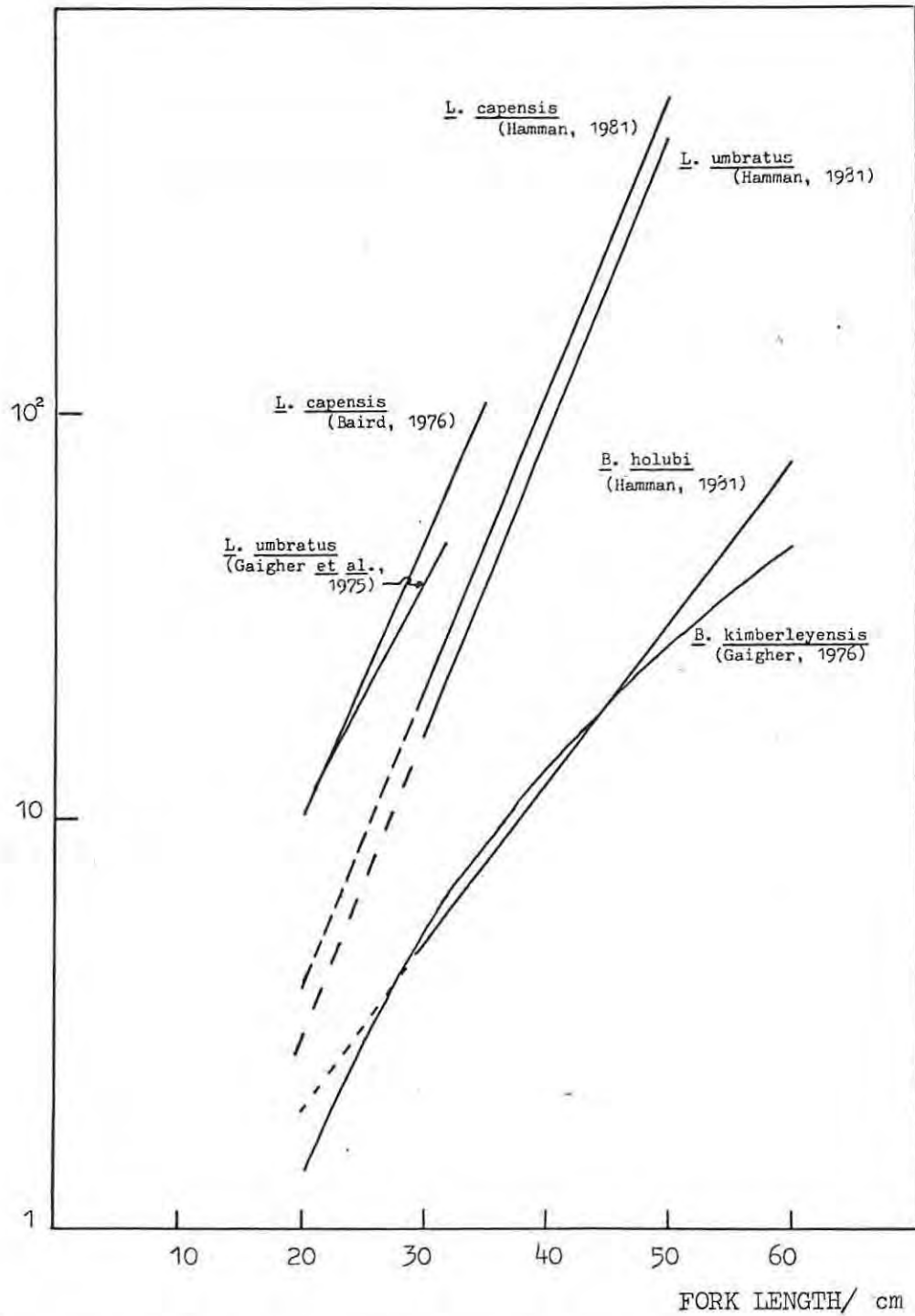
FECUNDITY $\times 10^3$ 

Figure 7. Fecundity of various *Labeo* and *Barbus* populations in South Africa.

can be reached:

- i. The two Barbus species have approximately the same relative fecundity although size at maturity is different (Gaigher, 1976; Hamman, 1981).
- ii. Relative fecundity of the two Labeo species appears to be related to size at sexual maturity. The populations maturing at a small size are relatively more fecund than those maturing at a large size. Hamman's (1981) relationship is in good agreement with results obtained by Groenewald (1957), Göldner (1967) and Mulder (1973b).
- iii. There is a much greater relative increase in fecundity with size in the Labeo species than in the Barbus. For every 10 cm increment in length of Barbus, fecundity is increased two to three times as compared to a five to six times increase for the Labeo (Fig. 7).

No further information appears to be available on fecundity of different populations of the same species. However, the general difference in fecundity between Labeo and Barbus, as well as the relative increase in fecundity with length is supported by observations of other members of these genera. Examples are given below.

In Iraq, the fecundity of three Barbus species (Al-Hamed, 1972) closely resembles that of those under study. The same is true for the large Tor species of India (Jhingran, 1975; Chaturvedi, 1976). The relatively high fecundity and rapid increase with length of Labeo has been observed in L. rosae (Kok, 1980), L. mesops (Anon., 1964), L. altivelis (Matagne, 1950) and L. victorianus (Cadwalladr, 1965b). In India, the same holds true for L. rohita (Khan & Jhingran, 1975) and L. gonius (Siddiqui et al., 1976).

D. INCUBATION AND EARLY LIFE HISTORY

Incubation time depends on temperature, but there appear to be marked differences between Labeo and the large Barbus species in this regard as well as in the early larval behaviour.

The fertilized eggs of B. holubi incubate for three to eight days at 18° - 21,5°C, but the larvae do not become motile until four to six days after hatching (le Roux, 1968; Mulder & Franke, 1973).

B. kimberleyensis has been bred artificially. The incubation period was two to three days and the larvae became motile in three to four days at 23° - 25°C (van der Merwe, 1981). B. natalensis eggs hatched in six to eight days in the relatively cold water of a trout hatchery and the larvae burrowed into the gravel (Wright & Coke, 1975b). Similar observations were made on B. andrewi (Harrison, 1952).

When observing spawning of L. capensis, Mulder (1971) collected eggs which hatched after 30 hours at 22°C. The larvae were about 4 mm in length and moved repeatedly up and down the water column by swimming upward then remaining still and sinking downwards. The relatively short incubation period and swimming behaviour of the larvae has been observed several times in Africa e.g. for L. mesops in Lake Malawi (Anon., 1965), L. victorianus in Lake Victoria (Fryer & Whitehead, 1959) and L. umbratus in the Tyume (Gaigher *et al.*, 1975) and Modder (Mitchell, 1982) rivers in South Africa. In India, L. rohita exhibits the same characteristics (Khan & Jhingran, 1975). The fertilized eggs are relatively buoyant since upon fertilization they swell to over double the diameter of an unfertilized egg (Fryer & Whitehead, 1959; Anon., 1965). In India there is a large trade in collecting spawn (fertilized eggs and larvae) of the 'major carps'. (including Labeo species) as these drift downstream after spawning (Jhingran, 1975).

E. FEEDING

B. holubi can best be described as an opportunistic omnivore. Enslin (1966) studied the feeding of this species in Barberspan, a lake in the Vaal River system, and found that the smallest individuals (up to 120 mm FL) fed on zooplankton. As they grew larger, more benthic invertebrates and plant material were eaten (vascular plants, filamentous algae and detritus). The switch from one type of food to another occurred at different sizes at different times. Groenewald (1957) found that B. holubi in the Vaal River is carnivorous to a length of 200 mm and thereafter, depending on the availability of animal protein, increasingly included vegetable matter in its diet. These observations are further supported by an analysis of gut length to fish length ratio. This ratio shows an increase in the larger fish, indicating that ability

to accommodate plant material is acquired as the fish grows larger (Kruger & Mulder, 1973).

In Lake le Roux, B. holubi initially remains close to the shore but at 50 - 70 mm FL they enter the pelagic zone and feed mainly on zooplankton (Tómasson, 1981). Eccles (1980) has shown that B. holubi feeds on zooplankton during daytime, visually selecting its prey. At night some benthic food is eaten. The progression of carnivorous habits at a small size leading into an omnivorous-herbivorous diet as the fish grows larger was also observed (Eccles, 1980). Since B. holubi hunt their prey visually in the pelagic zone, turbidity has a profound effect on their feeding habits. B. holubi switch from a zooplankton dominated diet to a benthos-dominated diet, and the size at which this change takes place appears to be governed largely by turbidity. This has important consequences for the population as shown by Tómasson (1981) and explained by Eccles (1980, p. 6):

"The fact that larger fish feed to a greater extent on benthic organisms and algae may not reflect an innate preference for these items but, rather, the difficulty of detecting sufficient planktonic food in turbid water. In water where the range of vision is limited by turbidity, the volume effectively searched by a fish will bear a linear relationship to its swimming speed, which varies with the square root of the length, while food requirements will vary with the cube of the length. In such situations the fish may reach a size at which plankton feeding can no longer supply their requirements and are forced to exploit benthic resources."

B. kimberleyensis in the Vaal River are carnivorous throughout their life cycle with an increasing tendency towards piscivory (Mulder, 1971). In Lake le Roux, B. kimberleyensis initially has a similar diet to B. holubi, but when B. holubi turns to omnivory, B. kimberleyensis becomes piscivorous.

In general, the diet of the two Barbus, especially B. holubi, can be said to be characteristic of the large Barbus. Large Barbus are typically facultative feeders and while they may have a preferential diet, under normal circumstances they may readily adapt to a different diet (Matthes, 1963). Sometimes these adaptations include morphological changes in the formation of so-called "rubber lips". This is frequently found in B. holubi and is thought to be an adaptation to feeding amongst rocks in riffles (Groenewald, 1957). Rubber lips disappear within a

year in a lentic environment (Groenewald, 1958). They are common in many species of large Barbus in South Africa (Jubb, 1963) as well as in East and Central Africa (Banister, 1973).

Unlike the large Barbus, Labeo are highly specialized feeders. Matthes (1963) recognized two main groups in this genus:

- i. Those living on the bottom in muddy rivers and quiet backwaters. These have a small head and compressed body. They feed on the carpet of algae and debris on the bottom, and have a long intestine, although its relative length is shorter than that for the second group.
- ii. A group with a more cylindriform body. These are common in rapids and eat algae off the rocks. The intestine is long and undifferentiated. Intestine length to standard length ratio is high (150 - 200) and increases with the size of the fish.

Of the two Labeo species in Lake le Roux, L. umbratus belongs to the first group and L. capensis to the second. L. capensis is very common in riffle areas of the Orange River (Skelton & Cambray, 1981) whereas L. umbratus prefers quiet waters (Mulder, 1973b). The relatively high abundance of L. capensis in Lake le Roux may be due to its high initial abundance in the river and the long rocky shoreline of the lake. L. umbratus is scarce in the lake, reflecting low initial abundance and relatively limited areas of muddy shallows favoured by this species.

A study of the feeding of L. capensis and L. umbratus in Barberspan (Enslin, 1966; Schoonbee, 1969) shows that they are both bottom feeders with a predominantly herbivorous diet, but the resolution of their data allows no further inferences to be made.

It is well known that the gut length to fish length ratio is a good indicator of diet. Reviewing this subject Bond (1979) found that the higher the intake of plant matter and indigestible material, the higher the ratio. The ratio of gut length to fish length of the fish in Lake le Roux further confirms their diet as outlined above (Table 5).

Feeding during early life history may be more crucial than subsequent feeding patterns in determining the relative success of a species. Detailed work on L. calbashu in India shows an early dependence on animal protein which gradually disappears. The ratio of gut length

to fork length changes from 0,5 - 1,0 in the fry (carnivorous, sight feeders), to 1,1 - 2,0 in fingerlings (omnivorous, sight and taste feeders) and 2,1 - 13,0 in adults (herbivorous, taste feeders; Sinha, 1976). Apart from the increase in relative gut length with size, there is also a relative increase of the absorptive surfaces of the gut (Sinha, 1976). Similar findings have been made with other 'major carps' in India (Kamal, 1967; Khan & Jhingran, 1975). There is a need for the study of ecological requirements of South African Labeo during their early life history.

Table 5. Mean gut length to fork length ratio of the large Barbus and Labeo found in Lake le Roux (from Kruger & Mulder, 1973).

Species	n	ratio	shortest fish in sample (mm)	correlation coefficient (r)
<u>L. capensis</u>	27	14,90	103	0,954
<u>L. umbratus</u>	22	10,00	70	0,980
<u>B. holubi</u>	39	1,70	92	0,954
<u>B. kimberleyensis</u>	32	1,14	95	0,920

During the egg and larval stages fishes are most dependent on their immediate environment and hence vulnerable to change (Bagenal & Braum, 1978). Their tolerance limits to variability in environmental factors subsequently increase.

F. AGE AND GROWTH

Research into age and growth of the study animals has usually relied on the use of scales, but little has been done to validate the results. B. holubi is an exception in that age has been accurately known in a few cases when reservoirs have been stocked and reproduction has not been successful. Age and growth studies on other species of large Barbus and Labeo in South Africa are scarce and have mainly been done by the same authors as have aged the species under study. They are left out of this discussion since their basic shortcomings are similar to those discussed here.

Le Roux (1963) reports on an introduction of 50 fingerlings into a three ha pond. In 2 1/2 years these fish reached an average length

of 30 cm and three years later reached 40 cm. After 12 years when the pond was drying up 37 (74%) of the original stock were captured, measuring on average 53 cm (49 - 59 cm; 1,8 - 3,6 kg). In 1964 80 fingerlings were released into Settlers reservoir ($\pm$ 90 ha) near Grahamstown. In March 1972 three of these were caught (age 8+) averaging 51 cm and 2 kg (Skelton, 1972). In May 1953, 200 fingerlings were released into a reservoir ($\pm$ 95 ha) on the Gouritz River system. In January 1959 (age 6+), 13 of these were caught in a 15 x 3 m gillnet, 100 mm stretched mesh set overnight (Harrison, 1959). These ranged from 50 - 56 cm in length and 2,1 to 3,1 kg. Eleven years later, Louw (1970) caught 5 yellowfish there, 50 - 67 cm in length. With one exception (50 cm male, 1,7 kg) these fish were extremely deep bodied with a 57 cm fish weighing over 5,5 kg. It would appear that in eleven years little growth in length was achieved, whereas the weight had almost doubled. These growth rates may not be paralleled under normal circumstances but the following conclusions may be drawn:

- i. B. holubi appears to be long-lived and grows rapidly in length for a few years, but subsequent annual length increments are small but weight increments may be large.
- ii. Because scales grow in relation to body length it may be difficult or even impossible to correctly age old members of a population, even if growth is seasonal and regular.

Bearing this in mind, the literature on the growth of B. holubi and B. kimberleyensis will be examined.

Straub & Combrinck (1973c) attempted to determine time of annulus (check) formation of B. holubi from Barberspan. In this study material collected from 1950 to 1965 (Straub & Combrinck, 1973b) was lumped by month. The total sample was 794, but no scales had been collected in December, January or June. From their results it appears that a check may be formed in the youngest fish (with one 'annulus') in spring (September), but results for fish with two or more checks on their scales are inconclusive. This may be due to their lumping of material, since conditions in the lake appear to be highly variable (Göldner, 1967). In no other growth studies of B. holubi have attempts been made to verify the results and in no case have results been related to environmental conditions (i.e. the environment is treated as constant).

Hamman (1981) found that females of B. holubi grow faster than

the males for the first four years (when males were 20,3 cm and females 22,3 cm) whereafter rate of growth was comparable for the sexes (Table 6). This is an unusual pattern of growth and can probably be explained by small sample sizes but no statistical tests were reported. The author found that 50 - 60% of his scale samples were unreadable. This was particularly common with scales from the larger fish. The unreadable portion may not represent a random sample. Thus the more material that is left out, the more likely it is that the results become biased, for it is possible that slow growers could only be aged when they are still relatively young, whereas only the faster growers could be aged of the larger fish. It is thus doubtful whether Hamman's growth estimates for the two large Barbus species reliably reflect the growth characteristics of these populations. Mulder (1971) found that the annulus may not be formed in the first year on the scales of Barbus species, but made no further attempts to validate his results. He gives no information on the number of scale samples rejected, but does say that scales from large fish were often regenerated. It is likely that the relatively small decrease in growth rates with size (Table 6) reflect a similar bias to that in Hamman's (1981) study. Göldner (1967) determined size at age for B. holubi in Barberspan by examining length frequencies. The modes he identified were indistinct and alternative interpretations would be easy to find. Size at age did not agree with Straub & Combrinck (1973c) using scale samples, some of which were collected during Göldner's (1967) study. Koch (1975) studied the growth of B. holubi in Lake Boskop, a small tributary on the Vaal River. The results of his study with those discussed above are given in Table 6.

The growth of L. capensis has been studied in the Vaal River (Mulder, 1973b), the Caledon River (Baird, 1976) and in four reservoirs, i.e. Barberspan (Göldner, 1967), Lakes Hardap (Bloemhof, 1974), Boskop (Koch, 1975) and Verwoerd (Hamman, 1974a, 1981). Scales were used in each of these studies and although an annulus was assumed to form during the cold months, this was never demonstrated. Time and frequency of check formation were never studied, nor could they have been, due to insufficient sampling. Gaigher (1977) did preliminary investigations, comparing the number of checks on vertebrae and scales. He found that checks on scales were of varying clarity and obtained only 58% agreement between the two methods. Hamman (1981) found 10 - 15% of his scale

Table 6. Age and growth of B. holubi and B. kimberleyensis, based on backcalculation of lengths from scale measurements.

<u>B. holubi</u>		Fork length in mm											Source
	Age	1	2	3	4	5	6	7	8	9	10	11	
Male	95	151	205	258	311	359	395						Vaal River (Mulder, 1973a)
Female	94	146	198	251	301	351	390	432	474	501			
Male	67	108	156	203	256	303	340	372					Lake Verwoerd (Hamman, 1981)
Female	61	113	166	223	276	322	364	391	416				
Male	68	112	151	189	217	248	261	267					Lake Boskop (Koch, 1975)
Female	75	118	153	198	242	293	339	349					
Total	91	131	191	224	256	288	311	361	394	400	462		Barberspan (Straub & Combrinck, 1973c)
<u>B. kimberleyensis</u>													
Male	81	133	184	235	284	327	372	406	446				Vaal River (Mulder, 1973a)
Female	83	137	189	240	292	336	379	425	460	507	555		
Male	66	110	157	204	249	295	350	389	440	491			Lake Verwoerd (Hamman, 1981)
Female	60	111	158	208	263	317	371	419	458	484			

samples of this species to be unreadable and this may have introduced some bias into his results. None of the other authors reported the percentage of unreadable scales.

Göldner's (1967) results are contradictory. He converts a length-frequency distribution of L. capensis to a probability plot on which he identifies five points of inflexion, indicating that the length-frequency distribution is a composite of five normal curves (see Harding, 1949). He then uses the percentage representation of each mode to compute annual mortalities between year classes (assuming constant recruitment). However, he indicates 9 (+) age groups (using an unspecified method) in the same length range. He fails to explain this discrepancy in the results and it is not clear what he is trying to show.

Other results have been summarized in Table 7. If differences in size at first annulus formation (age 1) are taken into account, the growth rate for the different populations show a remarkable similarity. These populations come from a variety of habitats and would be expected to show different rates of growth. In the present study, growth was found to vary considerably among seasons. In view of Gaigher's (1977) comments on the clarity of checks and the short duration and limited sampling done in these studies, the results must be regarded with reservation.

The study animals were originally indigenous to the Orange-Vaal River System and the above investigations were mainly done in reservoirs on this system. Exceptions are Mulder's (1973a, 1973b) and Baird's (1976) work on the Vaal and Caledon Rivers respectively. The system typically has highly variable streamflow, carrying heavily silt-laden waters at times of flood (indeed the Vaal River derives its name from its turbid waters). Because of high inter-and intra-seasonal variations in the aquatic environment, interpretation of checks on scales and otoliths are difficult. Assumptions about time and frequency of check formation may be invalid and need to be carefully evaluated. This is demonstrated in the present study (Chapter IV) and results from investigations other than long-term ones perhaps should be regarded with caution.

Table 7. Age and growth of L. capensis based on backcalculations of lengths from scale measurements.

Sex	Age	Fork length in mm											Source
		1	2	3	4	5	6	7	8	9	10	11	
Male		52	97	143	184	234	274	311	343	368			Caledon River (Baird, 1976)
Female		52	97	144	185	238	280	320	353	381			
Male		69	107	146	180	210	250						Barberspan (Koch, 1975)
Female		71	107	154	193	232	293	331	345				
Male		75	115	155	205	236	277	317					Lake Verwoerd (Hamman, 1981)
Female		78	119	163	210	225	301	344	362	391	427		
Total		52	115	174	225	273	310	354	380	396			Lake Hardap (Bloemhof , 1974)
Male		90	145	197	251	304	338	372					Vaal River (Mulder, 1973b)
Female		87	139	195	249	302	363	377	398				

III. METHODS

To obtain samples of the fish populations, two distinct programmes were undertaken. Juveniles and small fish were collected along the shores of the lake using fine mesh beach seines and rotenone, whereas adults and subadults were primarily sampled with gillnets. Although there were numerous sampling localities, for the purposes of this thesis they have been grouped into eight stations (Fig. 8).

Extensive sampling was done quarterly by the Cape Provincial Administration (CPA) from April 1978. In July 1979, I joined the CPA programmes and started a gillnetting and seining programme between the quarterly sampling. In this chapter the sampling programmes, the selectivity of the sampling gear and the way in which material collected was worked are described in detail.

Environmental variables were monitored by other researchers in the co-operative programme. Their sampling concentrated around station 1, sampling less frequently the entire length of the lake. Data on Secchi disc transparencies, temperature, chlorophyll and zooplankton concentrations were either drawn from research reports by Allanson (1981) and Hart (1981), supplied by these authors directly or personally gathered for the present study. Information on lake levels, flow regimes and rainfall were supplied by the Department of Environment Affairs, Pretoria. A summary of the environmental data is presented in Chapter IV.

A. SAMPLING PROGRAMMES

1. Adults

CPA used a gang of seven floating multifilament nylon gillnets, set at 28 sites over a period of 14 days. Nets were set during the afternoon, usually between 15:00 - 17:00 and taken up in the morning usually 07:00 - 09:00. The nets were always set parallel to the shore. Nets of different twine thickness and colour were used from April 1980 (Table 8). Each net was 100 m long.

In April 1982 CPA discontinued sampling at eleven sites and three new ones were added (Fig. 8). In 1980 a new sampling programme

was started once or twice between the CPA surveys. For this programme, a gang of sinking light green monofilament nylon gillnets were set parallel to the shore in shallow water (1 - 2 m). These were of 20, 30, 40, 50, 65, 80 and 100 mm stretched mesh, each 30 m long and approximately 1,2 m deep. The three smallest meshes were made of 0,15 mm nylon and the larger ones were of 0,20 mm diameter. During the latter half of 1979 occasional samples were also collected with a variety of gear. Sampling dates, stations and gear are summarised in Table 9.

Table 8. Specification of gillnets used by CPA during quarterly surveys on Lake le Roux.

Mesh size (mm stretched mesh)	Black nets April 1978-January 1980		Brown nets April 1980-October 1982	
	Depth (m)	Twine thickness (den.)	Depth (m)	Twine thickness (den.)
35	2,50	210/9	2,22	210/4
45	2,49	"	2,20	"
57	2,46	"	2,19	210/6
73	2,46	"	2,22	"
93	2,46	"	2,23	210/9
118	2,46	"	2,17	"
150	2,52	"	2,16	"

Originally CPA workers measured the fish to the nearest cm (FL) and recorded sex and maturity using Nikolskii's 6 point scale (Nikolskii, 1963). From July 1979 the two Barbus species were measured to the nearest mm and weighed to the nearest gram. Triple beam, spring and electronic balances were used and these were checked for internal consistency. From January 1980, length to the nearest mm and mass to the nearest gram of all species caught were measured.

Scales and otoliths were collected for analysis of age, growth and the computation of year class abundance. These methods of analysis will be described in later sections. Comparative age and growth material was obtained from the sister impoundment upstream in December 1980 and 1981 when CPA did a routine gillnetting programme

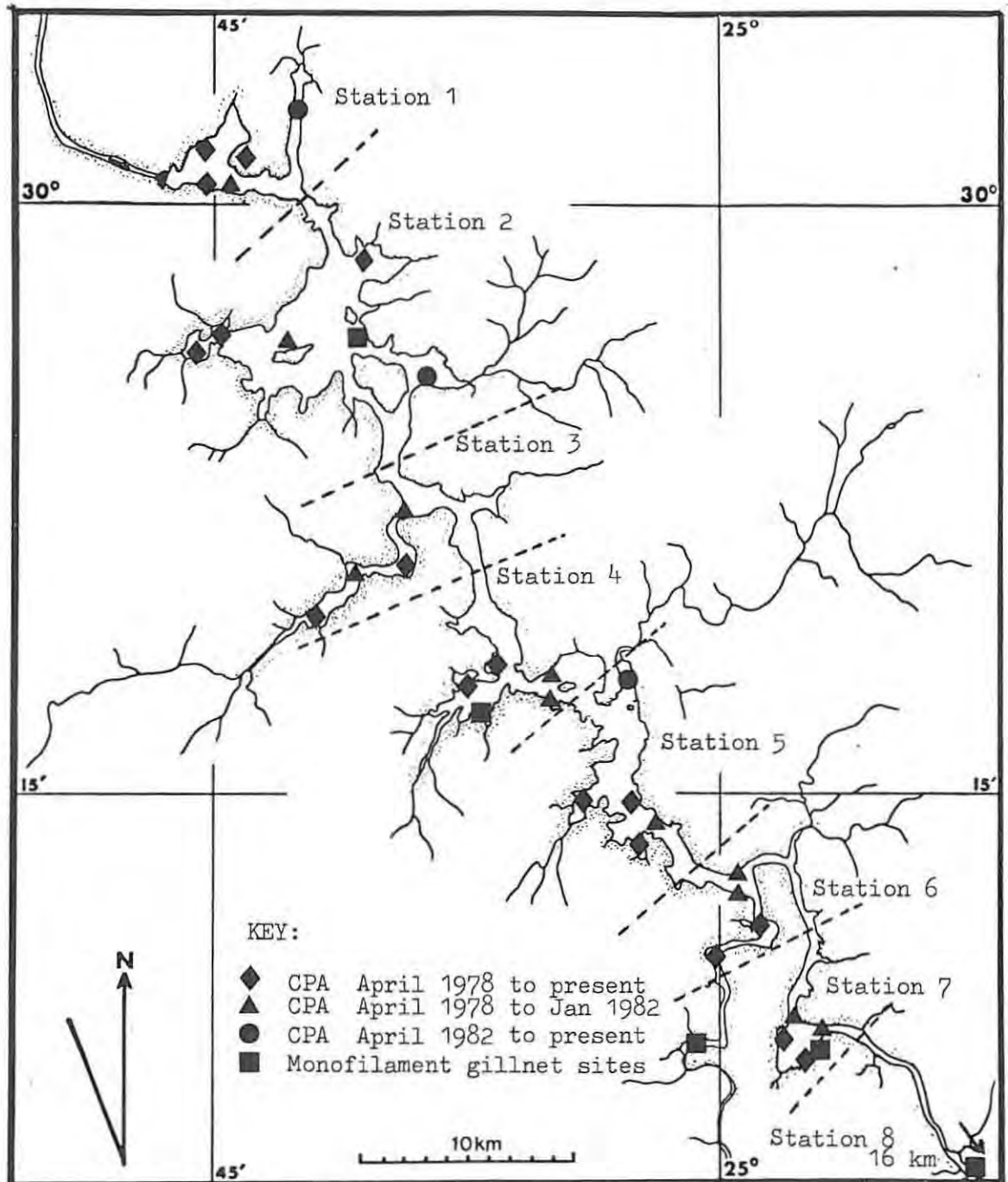


Figure 8. Gillnet sites in Lake le Roux and the division of the lake into stations.

Table 9. Sampling dates, gear and stations for adults used in this study.

Date	Gear	Station							
		1	2	3	4	5	6	7	8
4-17/4	1978 Multi series	x	x	x	x	x	x	x	
2-15/7	Multi series	x	x	x	x	x	x	x	
2-15/10	Multi series	x	x	x	x	x	x	x	
9-23/1	1979 Multi series	x	x	x	x	x	x	x	
17-30/4	Multi series	x	x	x	x	x	x	x	
5-19/7	Multi series	x	x	x	x	x	x	x	
26-27/7	57 mm gillnet, Purse seine	x							
14-21/8	Purse seine, Beach seine	x							x
11-26/9	Purse seine, 57 mm gillnet	x					x	x	
	Beach seine, Trawl								
13-26/10	Multi series	x	x	x	x	x	x	x	
20-23/11	Trawl, Purse seine	x					x		x
9-22/1	1980 Multi series	x	x	x	x	x	x	x	
29/2-3/3	Mono series		x		x		x	x	x
27-30/3	Mono series		x		x		x	x	x
15-28/4	Multi and Mono (Stn 8) series	x	x	x	x	x	x	x	x
21-24/5	Mono series		x		x			x	x
20-21/6	Mono series		x		x			x	x
29/6-12/7	Multi series	x	x	x	x	x	x	x	x
24-25/7	Mono series		x		x			x	x
26-28/8	Mono series,		x		x			x	x
2-3/10	65,80 & 100 mm mono gillnets							x	x
12-25/10	Multi series	x	x	x	x	x	x	x	
19-25/11	Mono series		x		x			x	x
15-17/12	Mono series		x		x			x	
15-29/1	1981 Multi series	x	x	x	x	x	x	x	
24-25/2	Mono series		x		x				
26/3-8/4	Multi series	x	x	x	x	x	x	x	
17-20/5	Mono series		x		x			x	
1-20/7	Multi series	x	x	x	x	x	x	x	
3-5/9	Mono series		x		x				
7-20/10	Multi series	x	x	x	x	x	x	x	
25-28/11	Mono series, Trawl	x	x		x			x	
9-22/1	1982 Multi series	x	x	x	x	x	x	x	
9-12/3	Mono series	x	x		x			x	
21/4-1/5	Multi series	x	x	x	x	x	x	x	
5-14/10	Multi series	x	x	x	x	x	x	x	

on Lake Verwoerd.

Gonads from ripening fish were weighed and relative gonadal weight was calculated as a percentage of total weight (Gonado-somatic index, GSI). Changes in GSI were used to describe the reproductive cycle and the reproductive effort was taken to be reflected by the GSI.

The number of modes in a size distribution of ova are often taken to represent the number of spawnings individual females are capable of within a season (Bagenal & Braum, 1978). Female gonads were preserved in 4% formalin. A subsample of preserved ova were measured using the method described by Gaigher (1976). The ova were put into a petri dish across which a straight line had been drawn. All ova touching the line were measured, using a micrometer. Ova diameters were always measured perpendicular to the line, since after the preservation, the ova were not always perfect spheres.

The information gained from the weighing and measuring of gonads complemented information obtained from the capture of juveniles.

2. Juveniles

Since 1978, CPA has conducted a quarterly 3 day survey of the juvenile and small fish populations along the shores of the lake. Depending on lake levels, 30 - 40 sites were sampled covering a variety of habitats. The main gear used was a seine net made out of monofilament shade cloth, with a stretched mesh size not exceeding 2 mm. The localities and gear used are described in detail by Cambray (1982). Cambray also sampled stations 1 and 2 for juveniles monthly from April 1979 to April 1981. From October 1979 the upper reaches (Stn. 6 - 8) of the lake were sampled at 4 - 6 weekly intervals. Other stations were sampled after rains or when evidence of recent spawning had been found in the extensive surveys. It was suspected that rainfall might trigger spawning, especially in the Labeo which normally spawn on newly flooded river banks.

The juveniles caught were preserved in 4% formalin. When catches were high, an effort was made to take a random subsample and release the rest. Normally however, high catches only occurred in warm (30° - 35°C) shallow water and the juveniles died before they could have been released.

B. SELECTIVITY OF FISHING GEAR

Most gears used to capture fish are selective to some extent. Selection refers to any process which causes the composition of the catch of a given species to deviate from that of the population (Hamley, 1975; Pope et al., 1975). Selectivity is a quantitative measure of the deviation of relative representation in the catch, usually of a size class, from that of the population (Hamley, 1975). In most studies of fish populations an estimate of the selectivity of the gear is necessary, especially when parameters such as length-weight relationship, growth and mortality which usually require unbiased sampling are estimated.

Selectivity of a gear may depend on extrinsic factors (e.g. construction and method of operation) and intrinsic factors (associated with the biology of the fish) or an interaction among these (Lagler, 1978). It follows that successful sampling is thus highly dependent upon the operators' knowledge and experience, a point emphasized in connection with seines by Hendricks et al., (1980).

Several methods exist for estimating gillnet selectivity, which are reviewed and discussed fully by Hamley (1975), on which the following remarks are based. The most commonly used are so-called indirect methods, which rely on comparing the catch of some size class of fish in nets of different mesh sizes. These methods all assume the relative height (catchability of optimally sized fish for a given mesh size) to be the same for all mesh sizes. Of the indirect methods, Holt's (1963) method is the most commonly used. This method assumes that the selectivity curves for any mesh follow a normal distribution.

In this section, the selectivity of the CPA gillnets will be examined, followed by a short discussion on the selectivity of the beach seine used to sample juvenile fish.

1. Gillnet selectivity

It is generally accepted that gillnet catches can be used to indicate temporal and spatial changes in a population, but may not

accurately reflect the relative abundance of species (Powell et al., 1971). However, Jester (1973, 1977) has found that colour and mesh size as well as setting locality and season deployed may greatly influence the species composition of the catch.

Selectivity estimates for the CPA gillnets have been calculated by Hamman (pers. comm.) and kindly made available for this study. The results are presented graphically in Fig. 9. Holt's method was used based on the entire CPA gillnet catch from April 1978 to January 1982. In lumping all the data, the assumption is made that selectivity of the nets used before and since April 1980 (see Table 9) was the same.

The validity of this assumption may be in doubt since stretchability and flexibility of a twine are inversely related to its thickness (Hamley, 1975). The optimum size of fish caught in a mesh of thinner twine may then be marginally larger than that of fish caught in a mesh made of a thicker twine.

The two assumptions inherent in Holt's method i.e. the shape of the curve being normal and being of the same relative height for each mesh size, are frequently violated (Hamley, 1975).

Violations of the first assumption are most serious in fish which are likely to become tangled in the nets (by teeth, spines etc.) as well as gilled and wedged. The resulting curve is likely to have more than one mode. This has been found for walleye (Hamley & Regier, 1973) and Clarias species (Gulland & Harding, 1961; Hamman, 1981). However, all the species studied have a fusiform body shape and were usually caught by wedging and less commonly by gilling. Gaigher et al., (1980)^b compared fitted selectivity curves to the actual length frequency distribution of the catch of the CPA gillnets in Lake le Roux from April 1978 to July 1979. Their results show a good agreement between the fitted and actual curves. Similarly, Hamman (1981) obtained good agreement between fitted normal curves and length frequency of the same species caught in Lake Verwoerd, in different size nets. Since the nets used were the same or similar, catching the same species under the same or similar conditions, this indicates that the first assumption is valid for the study animals. In consequence, the relatively smooth correction factor curves in Fig. 9 show that the catch will accurately reflect the position of modes in the size distribution of the population. This is especially true for

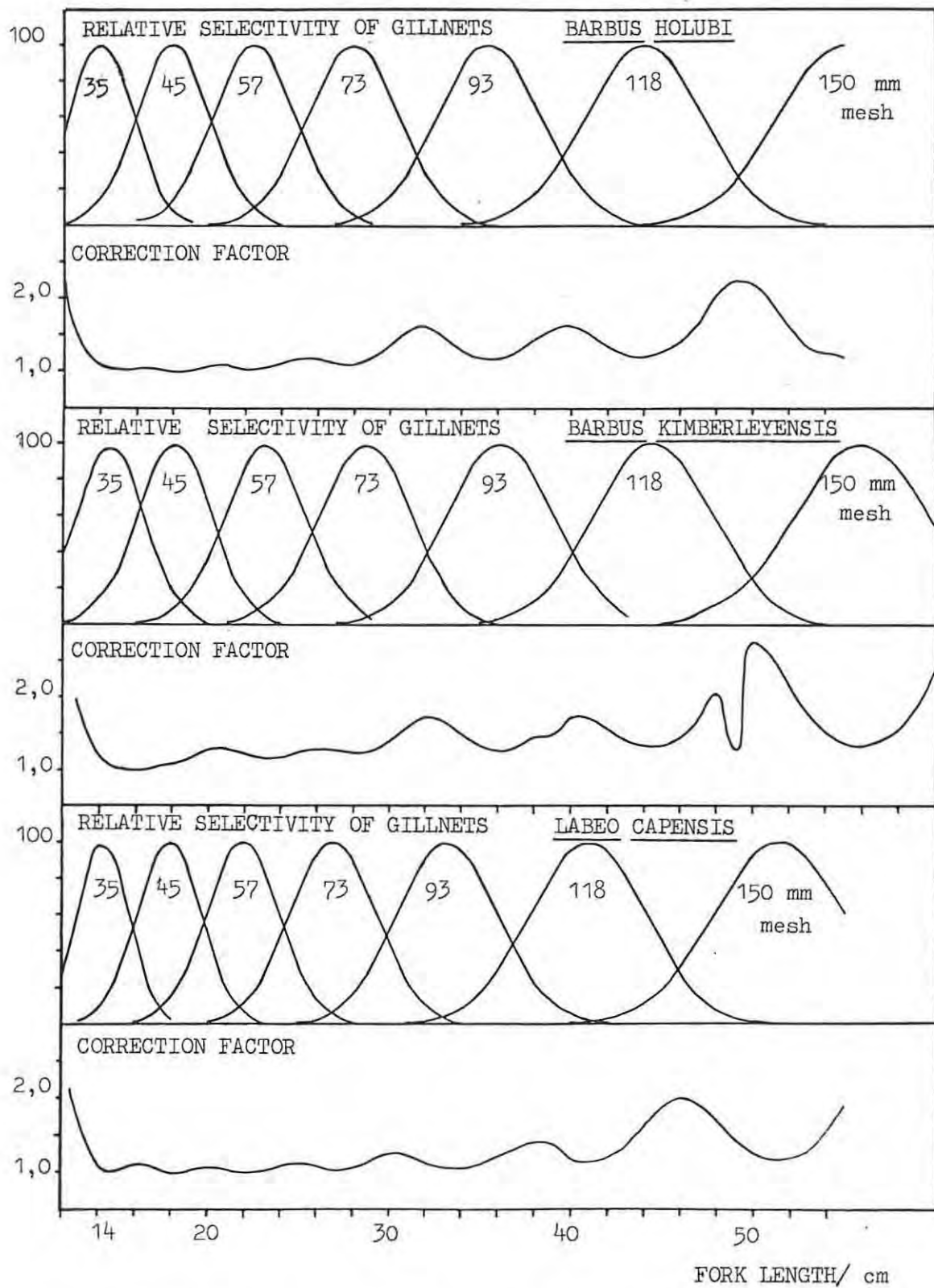


Figure 9. Relative selectivity of CPA gillnets of different mesh sizes for different length fish, and the correction factor used to adjust catches to actual relative abundance. (Based on data from Hamman, pers. comm.).

B. holubi less than 30 cm FL and L. capensis below 40 cm, which includes over 90% of the catch of these species.

The second assumption that selectivity curves for individual nets all have the same height is often broken in that several studies have shown the amplitude of selectivity curves to increase with mesh size (Hamley, 1975). The validity of this assumption can be examined by comparing catches of gillnets with catches in gear of known selectivity or from a known (e.g. tagged) population. Neither method could be used in Lake le Roux. Large beach seines, often considered to be relatively unselective, were extremely difficult to use except in one small area (depending on lake levels) and no gear tried yielded enough live fish to make a tagging programme a viable alternative. Hamman (1981) compared catches in Lake Verwoerd, made in the same series of gillnets as used in the present study, to the catch in a large beach seine (122 x 5,5 m). The centre portion "bag" of the seine was made of 10 mm stretched mesh. The nets and the seine were used in the same area within 24 hours. He found, after correcting for selectivity, that the beach seine caught a relatively greater number of small (< 20 cm) B. holubi and B. kimberleyensis than did the gillnets when all the gillnets were made of twine of the same thickness. After April 1980 (when the nets were changed) relative frequency estimated by the two methods was similar, except that fish larger than 30 cm were only caught in the gillnets. The portion of the catch larger than 30 cm constituted only a small percentage of the catch though and the discrepancy may be related to the increased ability of the larger fish to evade the seine (Hamman, 1981). Similar results were obtained for L. capensis.

It is concluded that the selectivity of the gillnets used has changed during the course of the study due to differences in material used in the nets. Until April 1980, smaller fish were underrepresented in the catches, but the use of a thinner twine in the smaller meshes from that date has increased the vulnerability of smaller fish to capture. The magnitude of change cannot be quantified from comparisons of catches by gillnets and seines for the following reasons :

- i. The relative frequency of the seine catch is presented for fish down to 10 cm, whereas the nets do not capture fish smaller than 12 - 13 cm. Thus the two curves are not directly comparable.
- ii. The sample size was too small, especially since a major portion of the fish caught in the seine were not vulnerable to capture in the gillnets.
- iii. The seine net may be subject to bias.

Unfortunately, no comparative observations were made using the two gangs of nets at the same time. In addition, highly variable environmental conditions, especially turbidity (see the next section) may have affected the relative selectivity of the gillnets for any of the species. This is one of the main limitations of this study and calls for caution in interpreting some of the results.

2. Selectivity of the beach seine

A small beach seine was used to sample the marginal shallow areas only. Catches in an open-water trawl often included large numbers of B. holubi from 6 cm, indicating that a pelagic mode of living is assumed about that size, if conditions are suitable. Only occasional fish were caught in the trawl in the riverine section (Stn. 8), where zooplankton were found to be scarce in the water column (Chapter IV, A).

It was found that handling of the seine net had a direct influence on the size composition of juvenile Barbus, while the habitat sampled could greatly influence the size composition of the Labeo caught. If juvenile B. holubi (or B. kimberleyensis) were caught, and the seine operation was successful, all size groups would be represented in the catch. If there were snags or escape routes, large juveniles escaped. Major problems were the abundance of snags (rocks and roots) which could not be seen because of the high turbidity of the water. Fluctuating water levels meant that the habitat sampled changed from time to time at each locality.

Juveniles of L. capensis were more readily caught than those of Barbus species, but the size distribution of the sample could be totally different from two adjacent hauls (Fig. 10) suggesting that they may swim in schools in which individuals are of similar size.

NUMBER

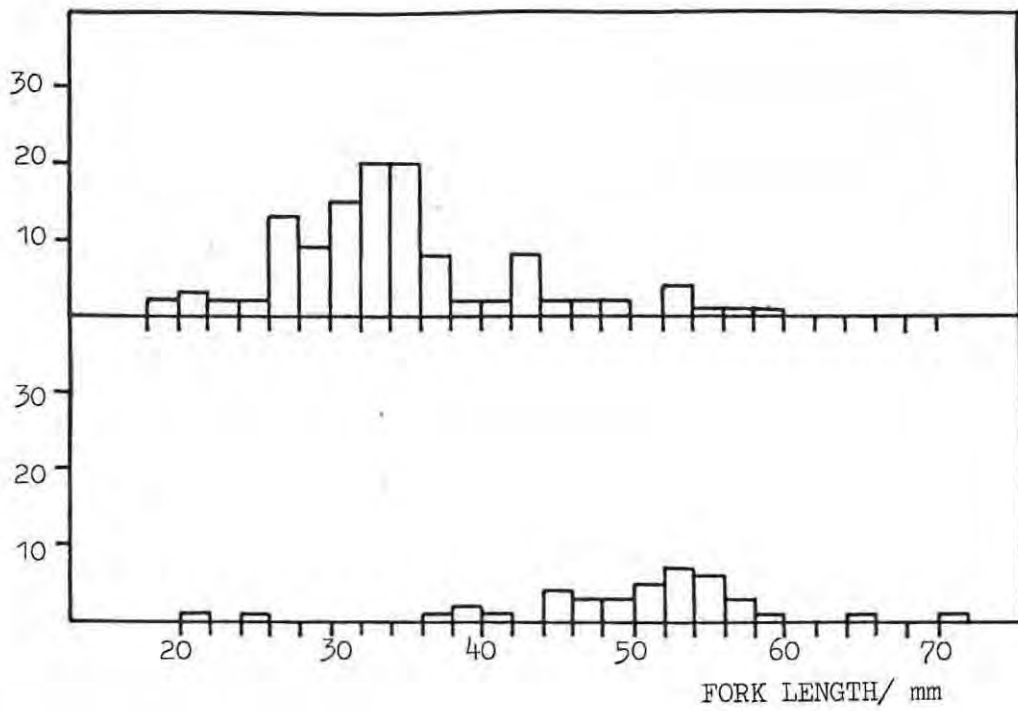


Figure 10. Length frequency distribution of juvenile *L. capensis* caught in a flooded river channel, station 8, 27/4 1980. The two hauls were each about 10 metres and had virtually the same starting point, but were taken to different parts of the shore. The two samples were collected within ten minutes. The substrate was covered with mud, but in the upper haul it was over vegetation.

Alternatively, different size groups may have distinct preferences in their microhabitats.

During each sampling period an attempt was made to obtain samples of the whole size range of juveniles present, but this was difficult at some localities, depending on lake level. Results were analysed according to locality and no attempt was made to calculate CPUE since it was felt that this could not be adequately standardized. Similar conclusions were drawn by Hendricks et al. (1980) about the use of small seines in streams.

C. PREPARATION AND INTERPRETATION OF SCALES

Scales have been used for ageing and the backcalculation to length at check formation since the turn of the century (Ricker, 1977). It has been shown that scales form at different times on different parts of the body (Clutter & Whitesel, 1956).

Scales are frequently lost and these are replaced by new scales which are unsuitable for ageing. These replacement scales (regenerated scales) are found in different proportions on various parts of the body. Consequently, there are some areas on the fish body which are more suitable for collecting scales than others. This has led some authors to advocate the use of a single scale from a fixed locality of the body or "key" scale (e.g. Hile, 1970; Bagenal & Tesch, 1978). However, the use of the single scale may adversely affect the study in that it may be a regenerated scale. Some scales may also form checks which are not annuli. Such checks may be caused by the loss of a neighbouring scale (La Lanne & Safsten, 1969). Scarnecchia (1979) found that the collection of a "scrape" sample, i.e. the collection of several scales from a well defined area of the body gave the same results as obtained from a "key" scale.

In this study 5 - 10 scales were collected from the first two rows above the lateral line, just anterior to the dorsal fin. Studying scales on Barbus holubi, Straub & Combrinck (1973a) found scales from this area to be most suitable for ageing. The scales were scraped off using a scalpel and placed in a paper envelope (Fig. 11). From the sample three good scales were selected. These were soaked in a KOH solution and then brushed off in clean water.

J. L. B. SMITH INSTITUTE OF ICHTHYOLOGY		
Number		
Species		
Place		
Locality		
Date		
Gear		
Length mm.	Weight gm.	
Sex	Maturity	Gonad weight
Remarks		

Figure 11. Envelope used to store scales and otolith samples. When scales were read, distance from focus to each annulus was marked off along the right edge and later measured. It would have improved efficiency to have had a metric scale printed along that edge.

After wiping them off on a paper towel, the scales were returned to the envelope and pressed to prevent warping as they dried. The scales were read in a microfiche reader at 24x magnification.

Criteria for determining checks or annuli on scales are given by several authors (e.g. Chugunova, 1963; De Bont, 1967; Bagenal & Tesch, 1978). There are, however, no absolute criteria which can be applied. Scale reading is by nature ambiguous, but this ambiguity can be reduced to acceptable levels if certain procedural rules are followed:

- i. The researcher must examine a large number of scales and compare the results to other information such as marks on otoliths and length frequency distribution. From this one decides what constitutes a check.
- ii. Scales must be sampled on a regular basis from fish of all sizes for at least one year, or if the environment is unstable, for several years. Time and frequency of check formation can be determined and this may differ between size groups, species etc., as life history characteristics in conjunction with environmental conditions determine patterns of growth in fish.

This is contrary to the belief that "objective" methods are the most accurate way to interpret scales. In these the reader does not know the time or locality of sampling (size of the fish is easily inferred from the size of the scale although some authors ignore this).

The main characteristics of checks were:

- i. In small fish the widening of circuli followed a band of relatively closely spaced circuli. The first annuli or two are often hard to identify. The thickening of the centre portion in large scales obscured these checks which are often indistinct. In some cases the first annulus is not registered on the scale. This is commonly found when young-of-the-year fish are small when entering their first winter (Brown & Bailey, 1952; Nordeng, 1961; Regier, 1962), and has previously been observed in B. holubi from the Vaal River (Mulder, 1971).
- ii. In larger scales, checks generally become more distinct due to lateral resorption of scales in winter which then caused "cutting over" laterally as growth was resumed.
- iii. Often a dark band on the posterior unsculptured part of the

scale would be associated with a check. This was especially true for L. capensis.

A sample of scales is shown in Figs. 12 and 13.

D. PREPARATION AND INTERPRETATION OF OTOLITHS

Otoliths have been used to age fish since 1899 and next to scales are the structures most commonly used to determine the age of fish (Ricker, 1977).

Otoliths are considered by many to be more reliable for age determinations than scales (Jonsson, 1976; Hecht, 1979). Otoliths do not resorb during periods of starvation or spawning (Simkiss, 1974) and this is understandable in terms of their function as balance organs. Otoliths are less likely to register "false checks" than are scales (Hecht, 1979) and it seems that random (within season) changes in the environment are less likely to affect otoliths (protected structures) than scales (protection structures). Williams & Bedford (1974) give detailed accounts of the collecting, preparation and interpretation of otoliths.

There are three pairs of otoliths in teleost fish, and different pairs are used for ageing in different orders. In the Cypriniformes, the lapillus pair is best suited for ageing (Hecht, 1979). Otoliths were collected by making a cut across the head between the opercular and preopercular bones (or just posterior to that in large fish). They were then removed, using fine forceps, from the posterior section of the fish, ventro-laterally around the brain. In larger fish the brain was removed using the rounded handle of the forceps, prior to collecting the otoliths. After removing remnants of the membranous otolith sac (capsula auditiva) the otoliths were stored in an envelope. The otoliths were placed in a black glass dish submerged in methyl salicylate BP, and observed in reflected light through a microscope at 30 - 40x magnification.

Otoliths from the two Barbus species were generally clear, showing narrow hyaline (dark), and broader but more variable opaque zones (white) (Fig. 12). These usually agreed well with the patterns of checks seen on the scales. In older fish, the clarity of rings was often indistinct towards the centre of the otoliths. This was

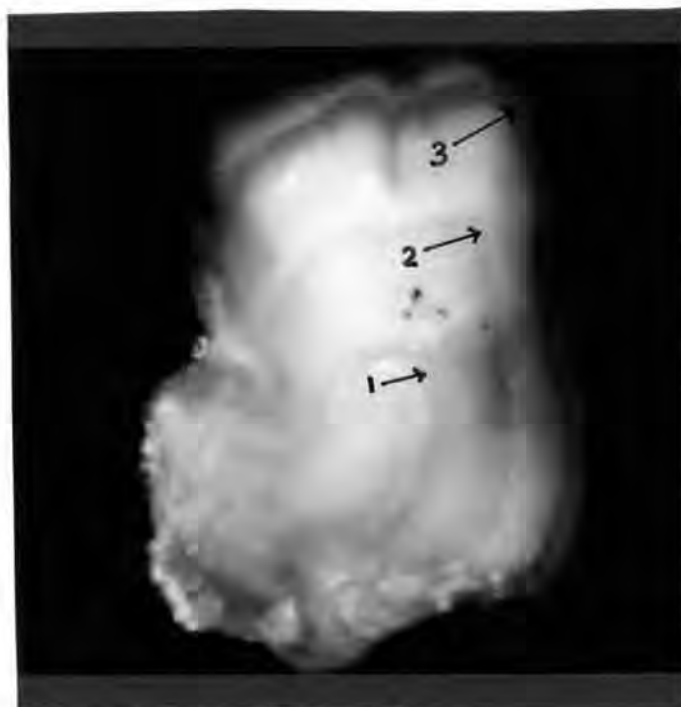


Figure 12. Otolith and scale from Barbus holubi, 248 mm, caught at Station 3 30/3/1981. The fish is in its fourth growing season (3+). The annuli are clear in the otolith, but the first one is missing from the scale.

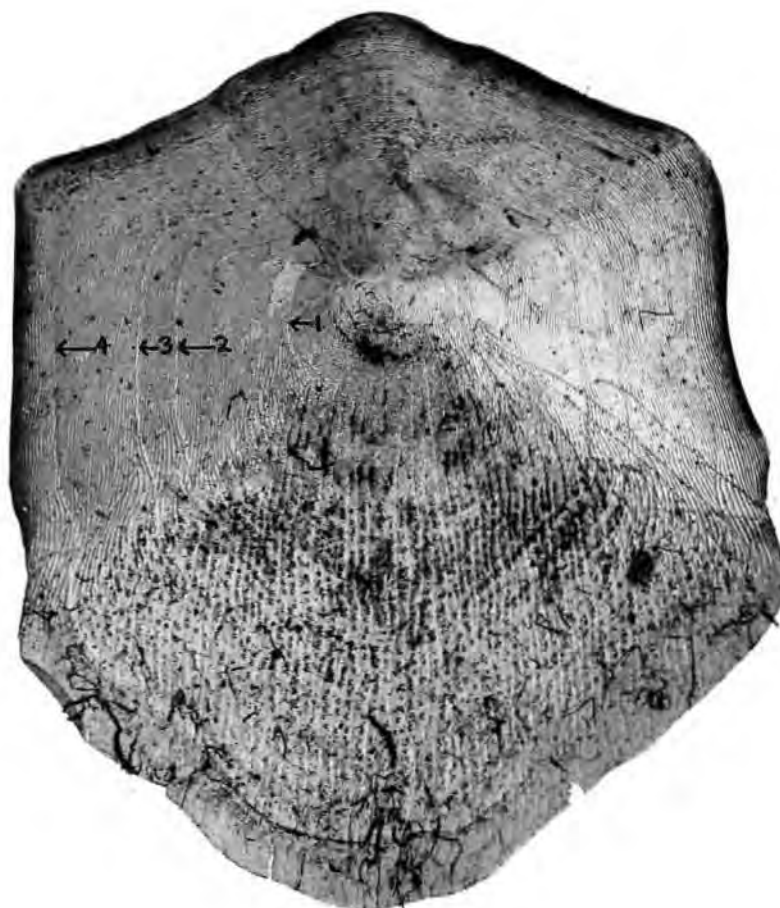
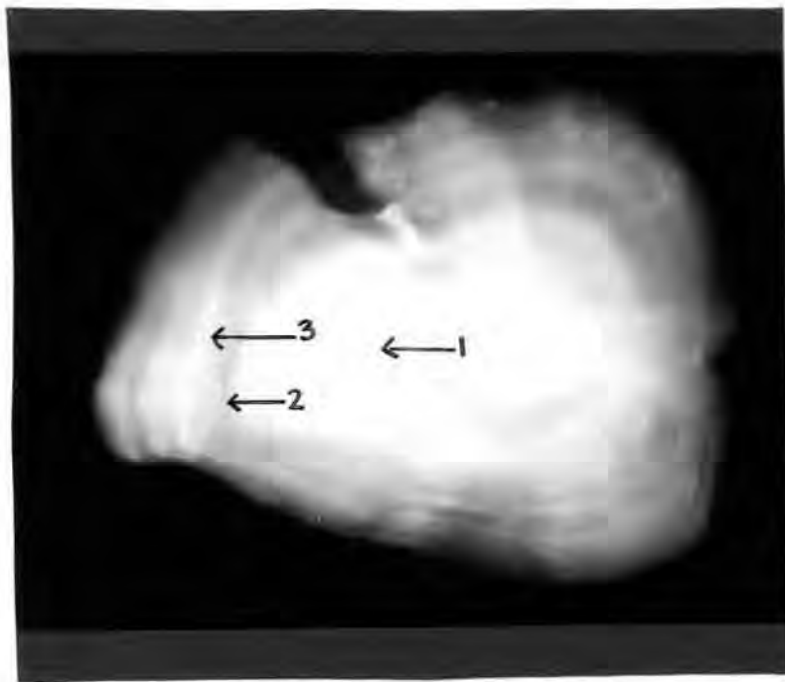


Figure 13. Otolith and scale from Labeo capensis, caught at Station 2 29/3 1981. The fish is in its fifth growing season (4+). Annuli are distinct on the scale, but the otolith is indistinct after the third annulus.

remedied by sanding the otoliths lightly on a fine wetstone. On sanding, some of the outer checks could be eliminated so one of the otoliths was always kept intact.

Otoliths from L. capensis generally showed the same pattern of alternating opaque and hyaline zones, but some ($\pm 15\%$) were indistinct and of little use (Fig. 13). Grinding the otolith did not help.

E. BACKCALCULATION OF LENGTHS

If a relationship between the size of a structure used for ageing and the length of the fish is established, then the length of a fish at the time of previous check formation may be calculated. The major advantage of this is the data it generates. Backcalculation of length from scales was first done by Lea (1910). Hile (1970) has reviewed the methods used and concludes that body-scale relationships from the same species may differ between populations and even between years in the same populations. More recently, Carlander (1982) has suggested that such variation may be due to variation in measurements and insufficient sampling and that body-scale relationships are constant within a species. Certainly differences in the relationship may be found when the actual relationship is not linear and all size groups are not represented.

In this study scales were measured from the focus along the anterior median radius. This was done since scales often resorbed laterally and thus would have affected backcalculation of lengths if lateral measurements had been made. Scales commonly resorb laterally (Regier, 1962; Buchholz & Carlander, 1963) and excessive scale resorption in anadromous salmonids during spawning gives rise to spawning checks (Bagenal & Tesch, 1978). Comparisons of body-scale relationships in B. holubi from different seasons are given in Table 10. This comparison was done at a time of dramatic environmental changes which greatly reduced the population. However, no differences between the relationships are revealed.

In this study, a random selection of 10 body-scale measurements per cm-group were made from the entire collection. Scales form when the juveniles reach 25 - 30 mm in all three species. It was found that they all had curvilinear relationships which could be adequately

described by a power formula, $y=ax^b$ (Table 11; Figs. 14 and 15). It appears that after the scale is formed it grows at a slow rate relative to the fish initially but its growth rate gradually increases until the body-scale relationship approaches a straight line. Vork (in Chugunova, 1963) showed that body-scale relationships are curvilinear. This is because the body form of a fish changes during its lifetime. Such changes may be associated with growth stanzas which occur commonly in the early life of a fish (Ricker, 1975). It is likely that this is the reason for the curvature in the body-scale relationship which is so pronounced in the lower size ranges of the cyprinids under study. The relationships for the three species are given in Table 11.

Table 10. Linear relationships between anterior median scale radius (x 24) mm and fork length* (mm) of B. holubi in Lake le Roux.

Time	Relationship	r^2	n	p
Jan 1981	FL = 0,44 SR - 29	0,95	168	< 0,00001
July 1981	FL = 0,45 SR - 33	0,94	109	< 0,00001
Oct 1981	FL = 0,46 SR - 33	0,94	218	< 0,00001

* Length range 120 - 430 mm.

Table 11. Relationship between fork length (mm) and anterior median scale radius (mm x 24) for some cyprinids in Lake le Roux

Species	Relationship	r^2	n	p
<u>B. kimberleyensis</u>	FL = 0,044 SR	0,97	421	< 0,00001
<u>B. holubi</u>	FL = 0,038 SR	0,98	421	< 0,00001
<u>L. capensis</u>	FL = 0,041 SR	0,97	411	< 0,00001

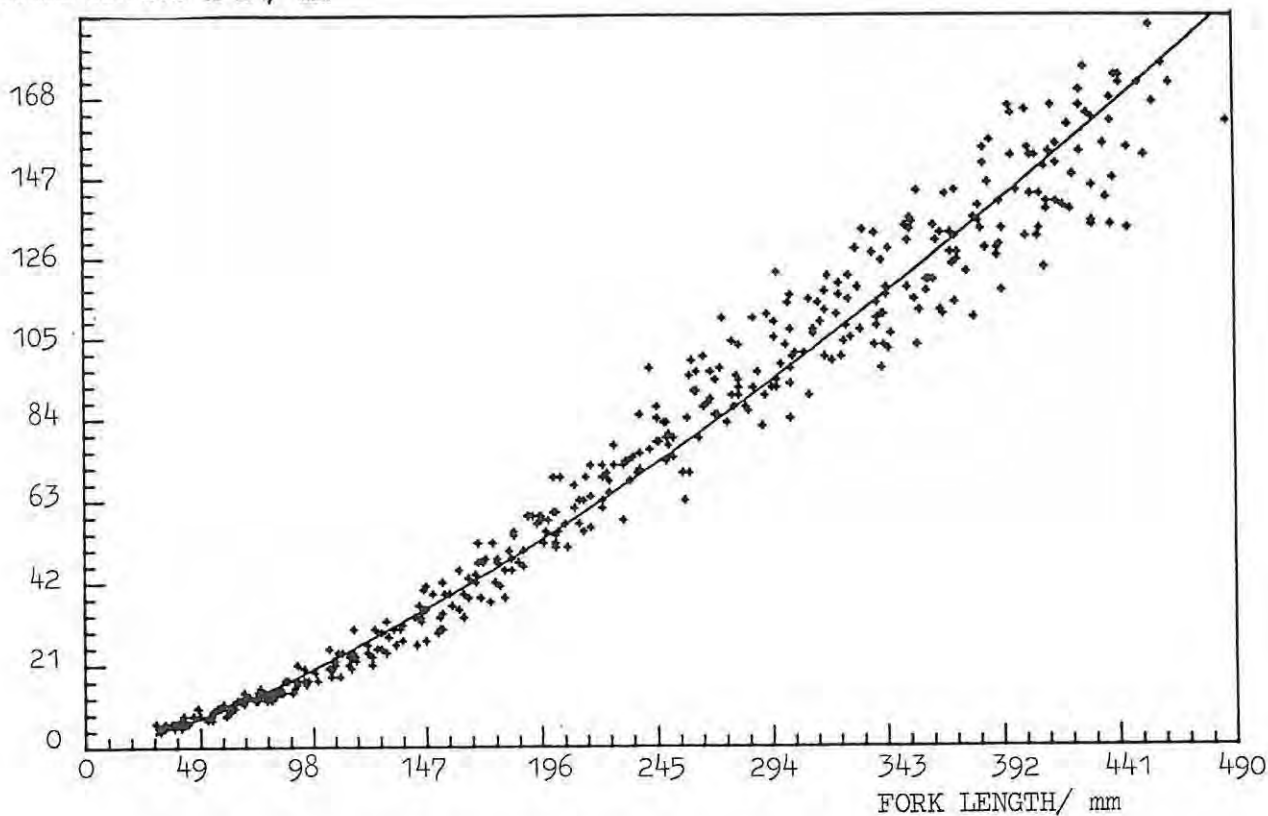
SCALE RADIUS $\times 24/ \text{mm}$ 

Figure 14. The relationship between anterior median scale radius and fork length of *Barbus holubi* in Lake le Roux.

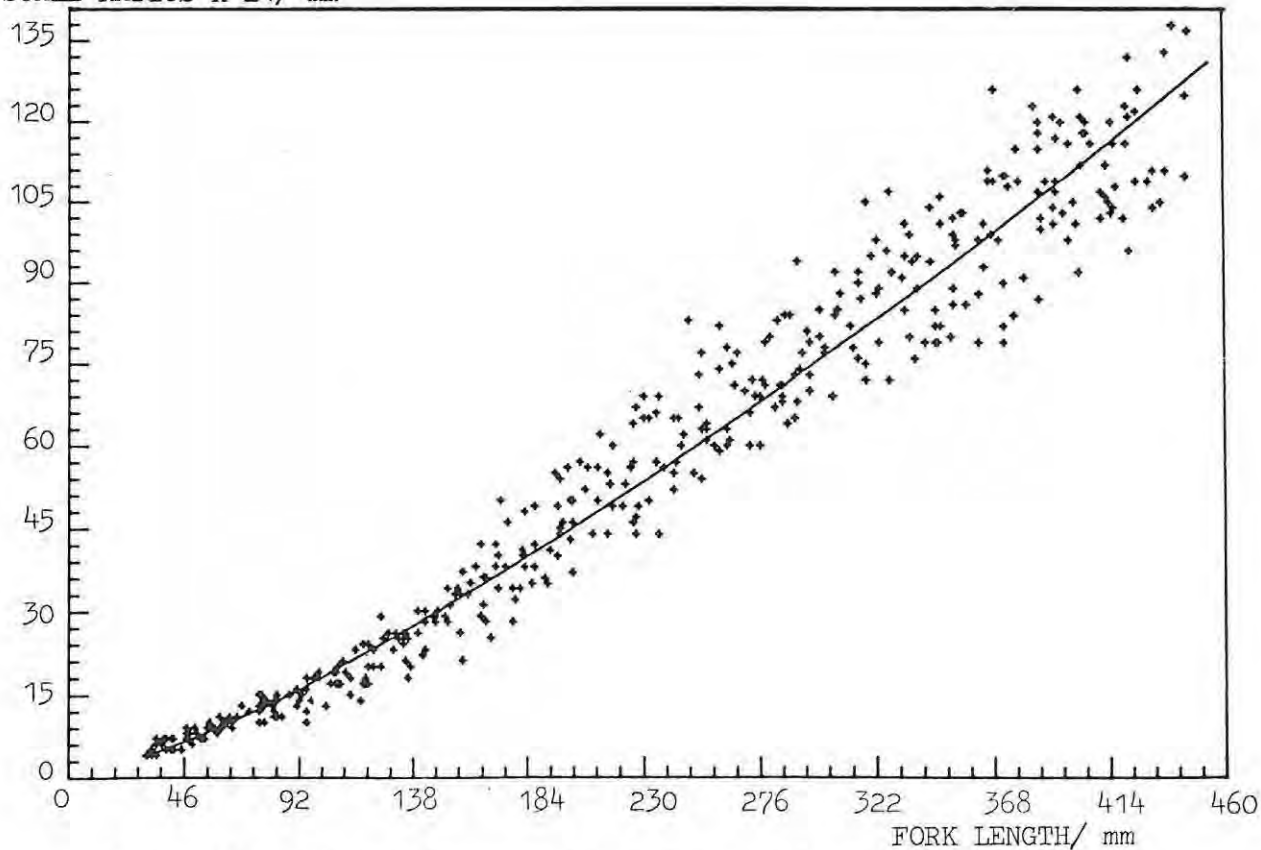
SCALE RADIUS $\times 24/ \text{mm}$ 

Figure 15. The relationship between anterior median scale radius and fork length of *Labeo capensis* in Lake le Roux.

From the body-scale relationships, lengths are backcalculated using the formula :

$$F_x = F_y \frac{S_x^{1/b}}{S_y^{1/b}}$$

where F = fish length
S = scale radius

and the subscripts x and y indicate time of capture and time of check formation respectively (Weatherley & Rogers, 1978).

All backcalculations of growth and analyses of growth data were done by the author using the ICL computer at Rhodes University and the Statistical Package for the Social Sciences (Nie et al., 1975).

F. CALCULATION OF YEAR CLASS STRENGTH

To calculate year class strength, the proportions of the catch, or the catch corrected for any bias of the sampling year, of a given year class is computed. There are two basic ways to do this. One is to superimpose length distributions of each year class on the full length frequency distribution. This is frequently done using probability paper ("Cassie curves") (Harding, 1949; Cassie, 1954). This method is also used to discern modes, but here it offers no advantage over the regular length-frequency distribution, upon which it is based (Macdonald & Pitcher, 1979). The separation of year classes in this way always assumes a normal or near-normal distribution and can be very time consuming. Several authors have contributed computer models to separate length-frequency mixtures, but these invariably require that the number of year classes in the mixture is known (McNew & Summerfelt, 1978; Macdonald & Pitcher, 1979).

The other main approach which was adopted in this study is to use an age-length key, first used by Fridriksson (1943). A subsample of the catch is aged and the proportion of fish of a certain age in a given length group is assumed to be the same in the sample as in the total catch. In using an age-length key, Ricker suggests that the following conditions must be met (1975, p. 206):

"In using an age-length key, one must remember that the fish used for age determination must be taken from the same stock, during the same seasons, and using the same selective properties as that used to take the length-frequency samples. Above all, an age-length key cannot be applied to length samples of any year except the one from which it was derived, unless the year classes represented always have the same initial abundance and are subjected to the same fishing experience - a condition seldom encountered".

The age samples can be collected from a random subsample - an approach recommended by Kimura (1977) or from a fixed subsample as recommended by FAO (1981). In this study, it was decided to use a fixed age subsample for the following two reasons :

- i. It was difficult to obtain a random sample from the CPA gillnet catches. The catches were worked by nets and the fish cut open.
- ii. A fixed sample ensured that relatively scarce age-groups were included.

During the CPA surveys one sample was taken from each one cm group from stations 1,3,5 and 6 and two from stations 2,4 and 7. No samples were taken during the July 1980 survey and inadequate samples were obtained in July 1981. Here samples from the following October surveys were used since no growth was observed between those surveys.

The systematic collection of samples for age and growth analysis were discontinued in late April 1982. The examination of scales and otoliths collected at station 2 in October 1982 showed that neither the large Barbus species nor L. capensis had grown since April. Therefore the ageing results from material collected in April 1982 were also applied to the catches from the October 1982 survey. Prior to calculating year class strength, catches were adjusted for gillnet selectivity.

The sampling between CPA surveys was too small to be of value in calculating relative year class abundance. Generally two or more samples were taken from each cm group for the growth study. Larger fish were scarce in these samples. Scales of B. holubi collected by CPA workers in October 1978 were interpreted and included when determining the growth of the 1977/1978 season. Since early checks are difficult to interpret when no guidance can be had from otoliths, no attempt was made to compute year class strength on the basis of those samples.

IV. THE ENVIRONMENT AND AGEING

In this chapter, temporal and spatial variations in the biotic and abiotic environment are described. This is followed by a section on ageing in which the validity and reliability of age determinations and backcalculation of lengths are assessed. In variable environments, the accuracy of these methods largely depends on the knowledge of environmental changes and how these may affect the fish populations.

The two sections of this chapter set the scene for the following chapter on population dynamics. The ageing is necessary for the estimation of population parameters, such as growth, mortality and year class strength and the environmental variability is important in explaining changes in these parameters.

A. ENVIRONMENTAL VARIABLES

Generally, reservoirs pass through a succession of changes before they stabilize or mature. Production is usually high initially after filling, but decreases after two to three years when a phase of "trophic depression" is entered. This stage lasts for a variable time whereafter production increases again before stabilizing (Lowe-McConnell, 1973). The species composition of fish and their prey is also likely to change in the face of new environments. Changes of this nature are long term, but superimposed upon these are seasonal changes.

In this section seasonal and longer term changes in important environmental variables in Lake le Roux are described. Changes in density and composition of the fish community will be treated later.

1. Temperature

Temperature varies seasonally, reaching 22° - 24°C in the surface waters of the pelagic zone in summer and decreasing to 12°C in winter (Fig. 16). It appears that changes in water temperatures are primarily influenced by changing air temperatures, with the release pattern not directly influencing the direction or rate of change. The upper and lower thermal extremes may however be restricted by initial

WATER LEVEL
(gauge depth m)

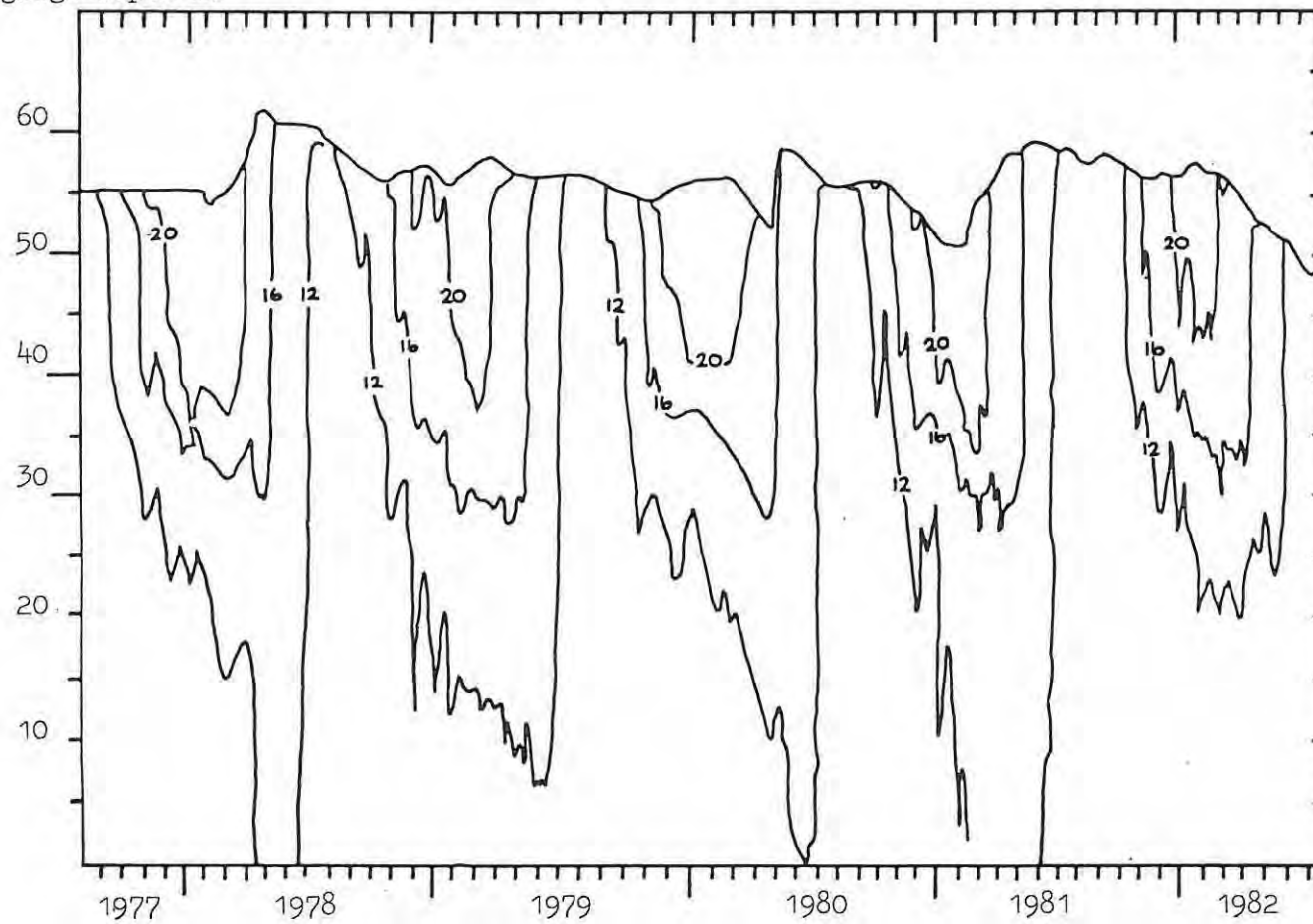


Figure 16. Temporal changes in temperature and lake levels at Station 1. (From Allanson, pers. comm.). The isotherms are in degrees Celsius.

temperatures of water released from Lake Verwoerd (Allanson, 1981).

From Fig. 16 it can be seen that water is typically coldest in July to August and warmest in November to April, showing a distinct seasonal pattern, although there are some inter-annual variations both in timing (Table 12) and depth penetration of particular isotherms (Fig. 16).

Water temperatures in sheltered shallows around the lake are more extreme than those found in the pelagic zone. After frosty winter nights a thin sheet of ice was found along the water's edge, while in summer temperatures between 35° and 40°C were frequently measured.

Table 12. Time intervals in which surface waters of Lake le Roux were at or above 20°C. (Based on data from Allanson, pers. comm.).

Season	Period
1977/1978	Early November - early April
1978/1979	Early December - late April
1979/1980	Mid November - early April
1980/1981	Early December - late March
1981/1982	Early December - mid March

2. Fluctuations in water level

Water level fluctuations and associated effects have important repercussions for the success of fish populations in reservoirs (Bhukaswan, 1980). Sometimes fluctuations are used as a management tool to interfere, either positively or negatively, with the reproduction of a species, as discussed in Chapter I. Water level fluctuations have a major effect on the reproductive success of the species under study in Lake le Roux.

The difference between high and low water mark in the lake is about 13 m (Fig. 16). At the lower limit the reservoir is only filled to about 50% of its capacity. Under natural conditions the river normally rises in early spring, but in the lake, water levels are generally receding at that time because of reduced releases from Lake Verwoerd. Usually, water levels in Lake le Roux rise sharply in late

summer. Thus flow in the river connecting the reservoirs does not exhibit the seasonal pattern of the pristine river (Fig. 17).

Tributaries to Lake le Roux and the Orange River between the two reservoirs drain a total catchment of 19 093 km² (Noble & Hemens, 1978). Flow in these tributaries is unpredictable and mainly consists of short-lived flash foods. The largest of the tributaries, Seekoei River (Stn. 6), drains approximately 25% of the local catchment. Flow records from a gauging station on the Seekoei River were examined for a two year period from July 1980 to June 1982. Flow was only observed between February and October 1981 (Fig. 18). Compared to the volumes discharged from Lake Verwoerd, the contribution of the tributary inflow is minor.

Changes in water levels in the lake, the inflowing Orange River and the tributaries, will be discussed further under the heading of reproduction (Chapter V, C).

3. Turbidity

Turbidity in Lake le Roux is primarily caused by suspended silt particles and greatly affects several fish population parameters, such as growth, mortality and dispersal. The system is light-limited and even a moderate increase in turbidity severely reduces primary production (Selkirk, 1982) and thus food supply. However, the most dramatic influence comes about because changes in turbidity can be sudden but not seasonal and thus changes are not anticipated by the fish populations.

Temporal changes in water clarity at Station 1 are shown in Fig. 19. It is noteworthy that changes in turbidity occur chiefly during the summer months, but are not cyclical, with markedly different conditions every year. For example, in the summer of 1977/1978, Secchi disc readings ranged from 0,6 m in November to 1,6 m in February after which there was a rapid decline to 0,3 m in April. In summer 1978/1979, readings were consistently around 0,2 m, but in spring 1979 they rose to 0,4 m and remained constant until spring 1980.

Apart from temporal changes, there are spatial variations as well (Fig. 20). In general, turbidity decreases down the lake, with

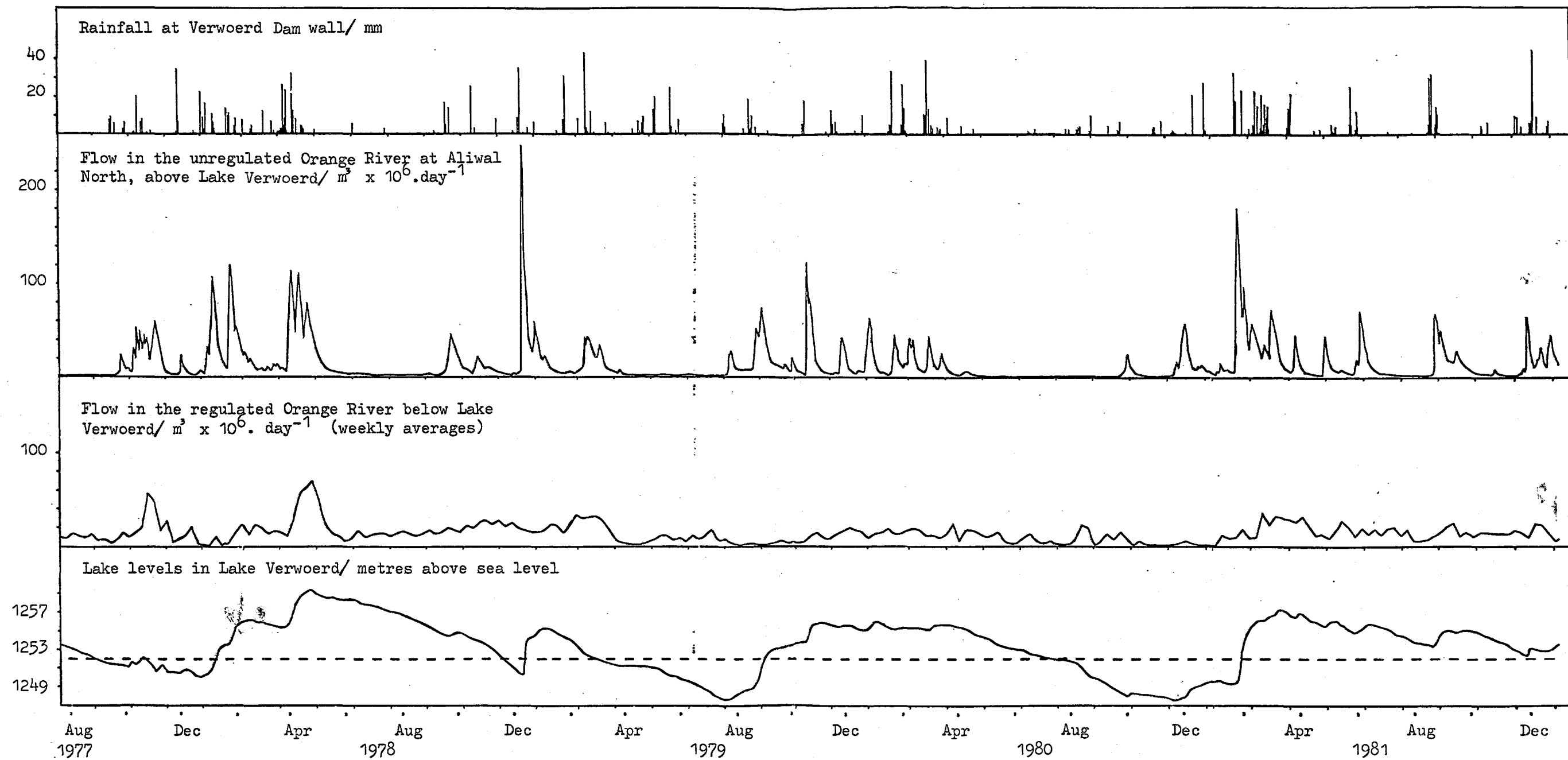


Figure 17. Daily variations in environmental variables in the Orange River system.
(Based on data supplied by the Department of Environment Affairs, Pretoria).

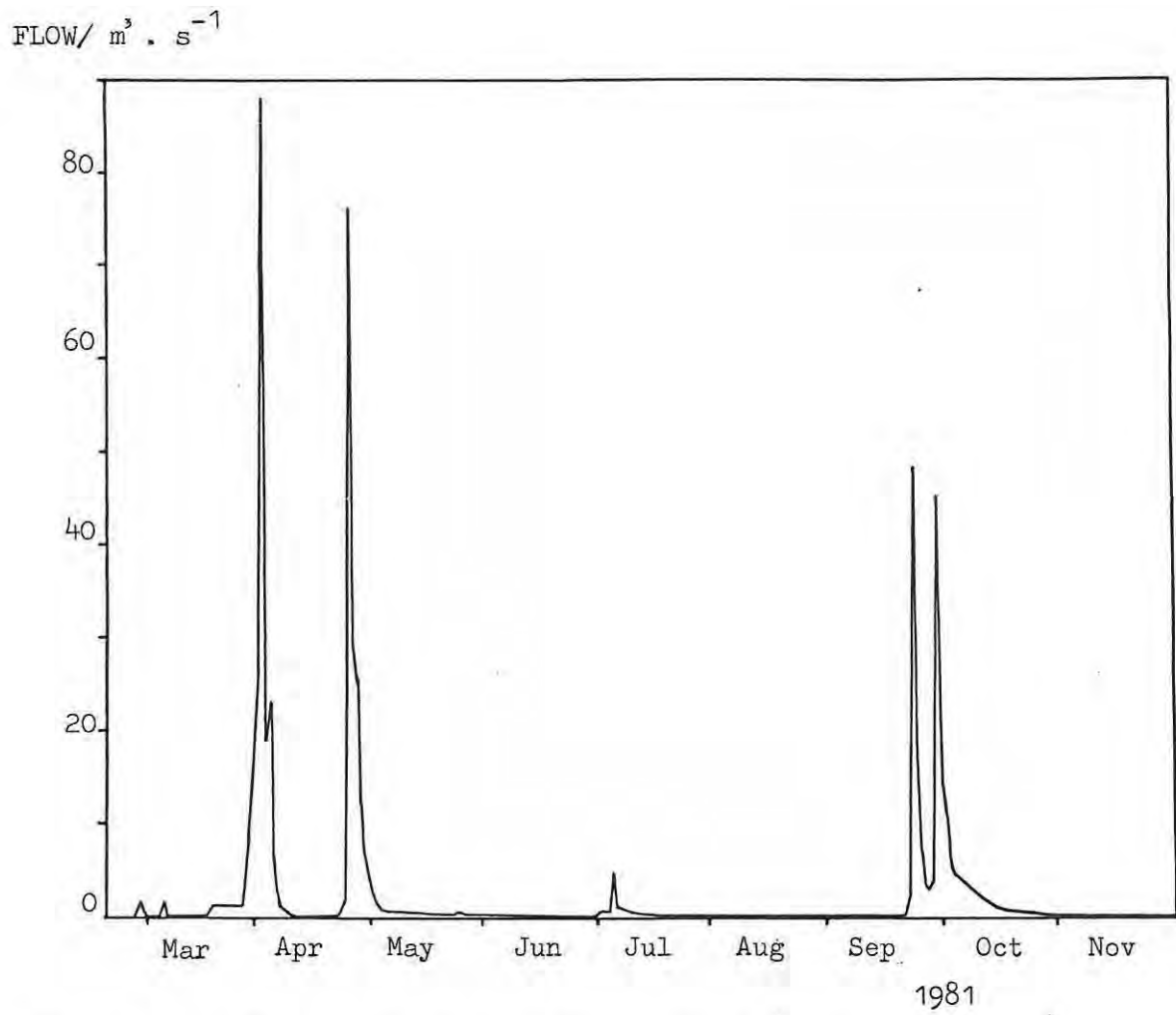


Figure 18. Flow in the Seekoei River, the largest tributary to Lake le Roux. (Based on data supplied by the Department of Environment Affairs, Pretoria).

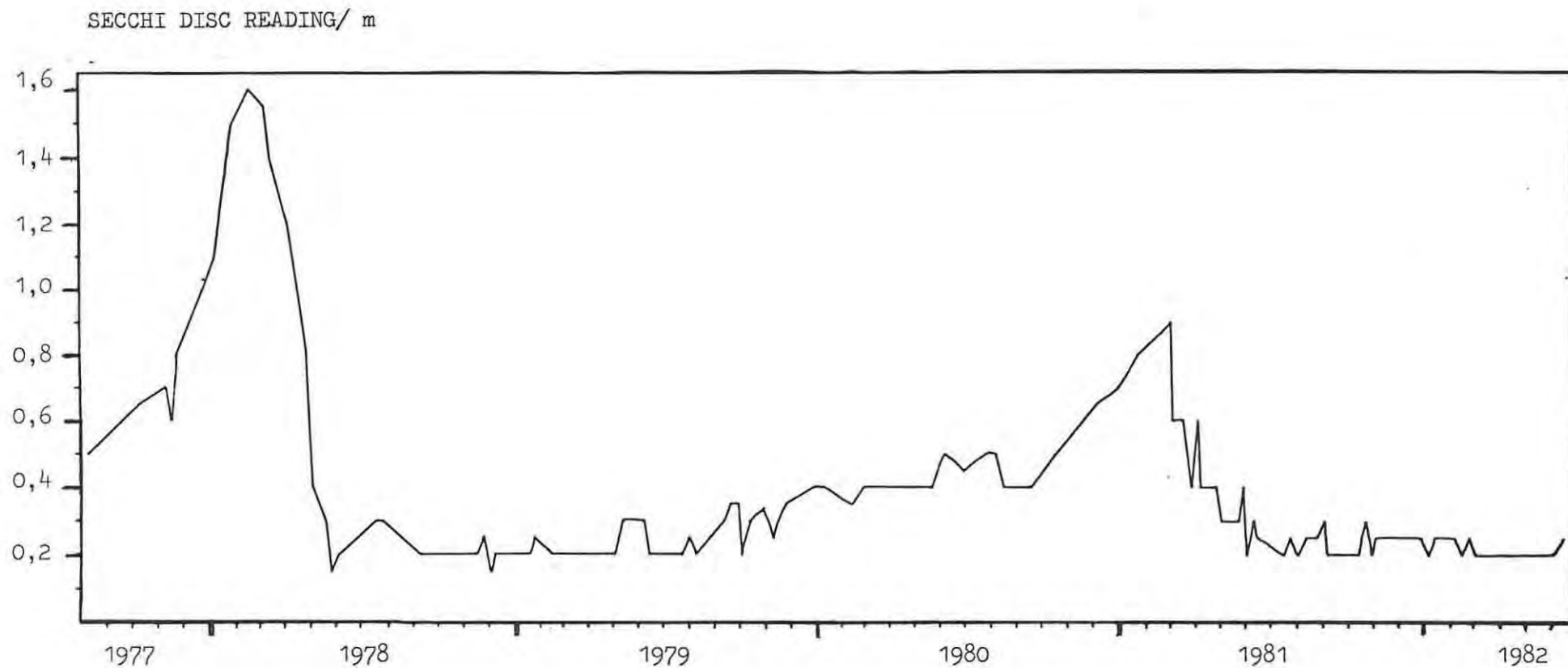


Figure 19. Temporal variations in turbidity at Station 1 in Lake le Roux.
(Based on data supplied by Allanson, pers. comm., and on personal observations).

SECCHI DISC READING/ m

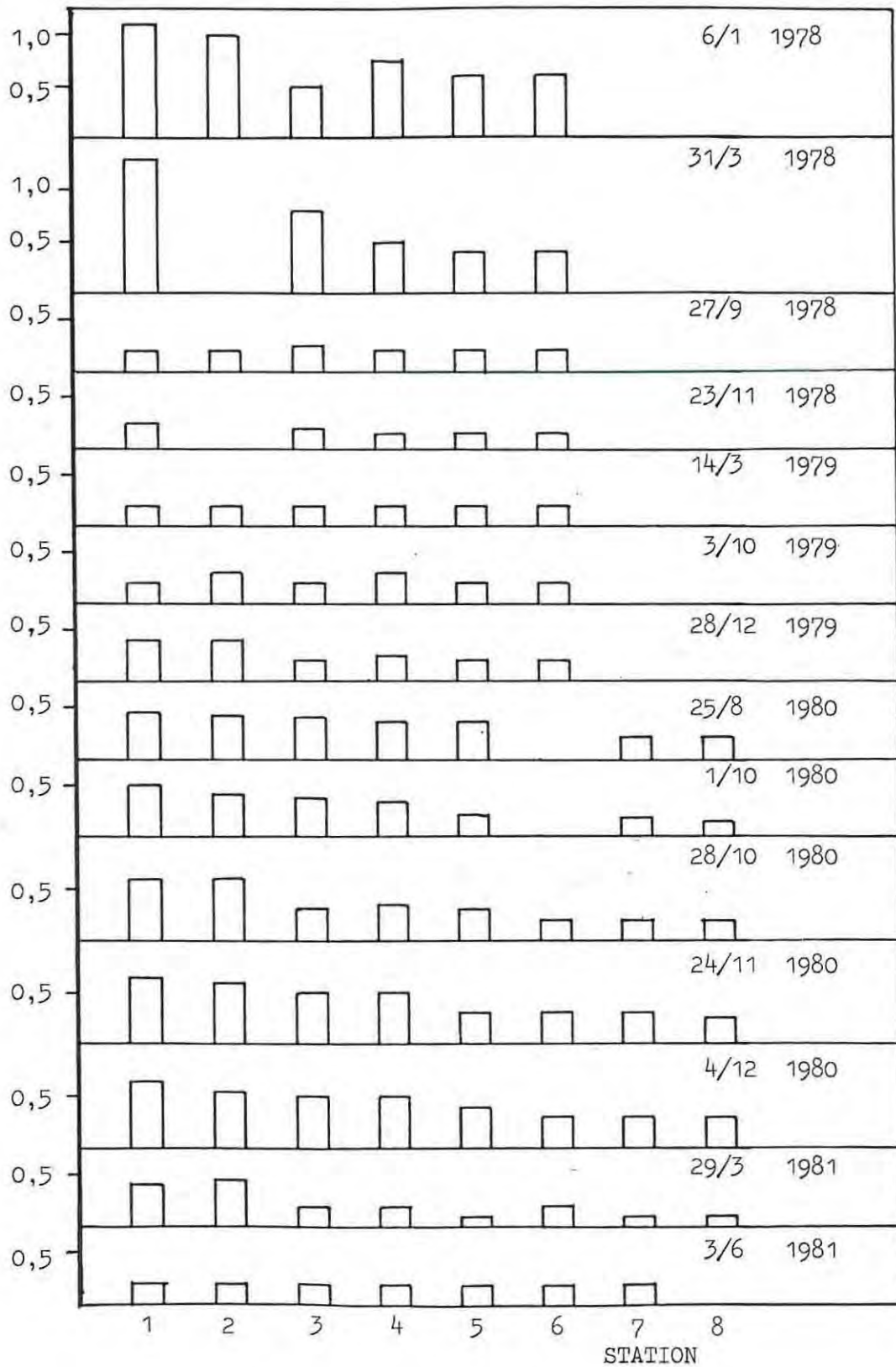


Figure 20. Spatial variations in turbidity in Lake le Roux.
(Based on data from Allanson, pers. comm., and on personal observations).

the gradient steepest during periods when changes are most marked, but reduced or disappearing inbetween. Thus there was a marked gradient in summer 1977/1978 and again in 1980/1981. In 1979/1980 the gradient was less marked and in 1978/1979 and 1981/1982 conditions were generally uniform throughout the lake.

Turbidity is of overriding importance for population size and structure as will be discussed in Chapter V. It becomes important to identify the main causes which govern the turbidity regime in Lake le Roux if the fish populations are to be well managed. Lake le Roux receives most of its water from Lake Verwoerd and local runoff only has a minor effect on overall hydrological conditions. Hence it is necessary to briefly consider processes in Lake Verwoerd.

The Orange River normally flows from September/October to April/May (Fig. 17), carrying heavily silt-laden water (Keulder, 1979). In winter the river is reduced to a trickle of clear water. During the first few years of Lake Verwoerd (early 1970's) the upper reaches were relatively clear in winter, but in summer the lake was clearest at the dam wall. Subsequently, due to silt deposition and the flat unprotected shoreline, the winter flow upon entering the lake became turbid through windmixing (Hamman, 1981). It follows that Lake Verwoerd is now clearest in spring to early summer near the dam wall before the seasonal floodwaters reach there.

Despite seasonal changes in turbidities in Lake Verwoerd, the hydrological processes which seem to exert the major influence on turbidity in Lake le Roux are water retention time in Lake Verwoerd and temperature of the water released into Lake le Roux. Stegmann (1974) found that the water just above the Verwoerd dam wall showed thermal stratification from early spring (October) and that a thermocline was well developed at 22 to 25 m by December. Temperatures in the epilimnion and hypolimnion were then 20°C and 12°C respectively. At times of thermal stratification, the temperature of the water released from Lake Verwoerd depends on lake level and which outlets are being used. Except for periods of minimum release for riparian owners, outlets other than through turbines are negligible. The turbine intake is at 1220,42 to 1227,73 m above sea level and cylindrical. Hence, if the water is passed through the turbines in early spring to summer, progressively more epilimnetic

water will be drawn off as the lake level drops below 1252 m.a.s.l., presuming an epilimnetic layer of 25 m. This level is marked on Fig. 17.

The sharp increases in turbidity during the late summers of 1978 and 1981 were associated with low spring water levels in Lake Verwoerd and consequently a short retention time and releases of epilimnetic water (Fig. 17). This water spread rapidly down Lake le Roux, and since it was relatively warm and buoyant it stayed on or near the surface where it would be susceptible to windmixing. This probably caused the sharp and sudden increase in turbidity in 1978 and 1981. (Fig. 19). In 1979/1980, when water clarity in Lake le Roux improved, retention time in Lake Verwoerd was relatively short due to low lake levels in late winter. The water released that spring and summer was, however, hypolimnetic (cold and dense) and probably entered Lake le Roux at some level below the surface and did not much affect water clarity in the upper strata.

The hydrological processes mentioned here and their influence on the turbidity regime of Lake le Roux are being studied by limnologists (Allanson et al., work in progress), and should be better understood once their analyses are complete.

4. Primary production and zooplankton

Standing stocks of phytoplankton (as chlorophyll) and both zooplankton abundance (as biomass) and species composition were studied by Hart (1981). There is a marked seasonal change in abundance (Fig. 21). Seasonal maxima in zooplankton biomass, particularly of herbivorous components, seem to be associated with water clarity (Hart, 1981; Fig. 22).

Zooplankton abundance generally increases upstream in the reservoir and probably reflects reduced predation by B. holubi in the more turbid environment (Hart, 1981). In the riverine part of Station 8, however, zooplankton biomass is generally less than 1% of that found elsewhere in the lake (Hart, pers. comm.) and probably not enough to support a pelagic population of B. holubi.

Ballpark estimates of total zooplankton production in Lake le Roux, based on mean annual biomass and generalized P/B values for

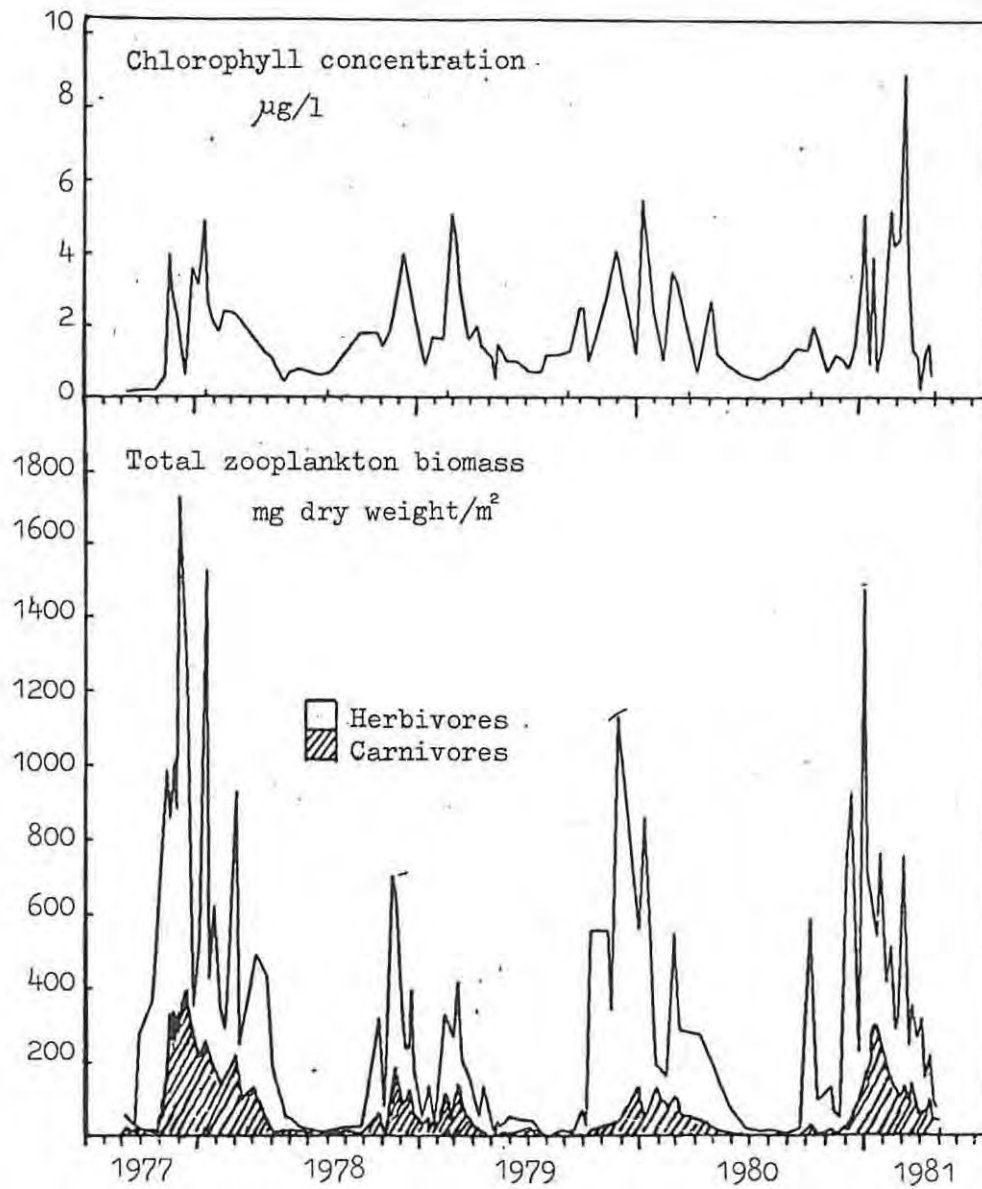


Figure 21. Seasonal variations in total zooplankton biomass (dry weight) and chlorophyll concentration at Station 1 in Lake le Roux. (From Hart, 1981).

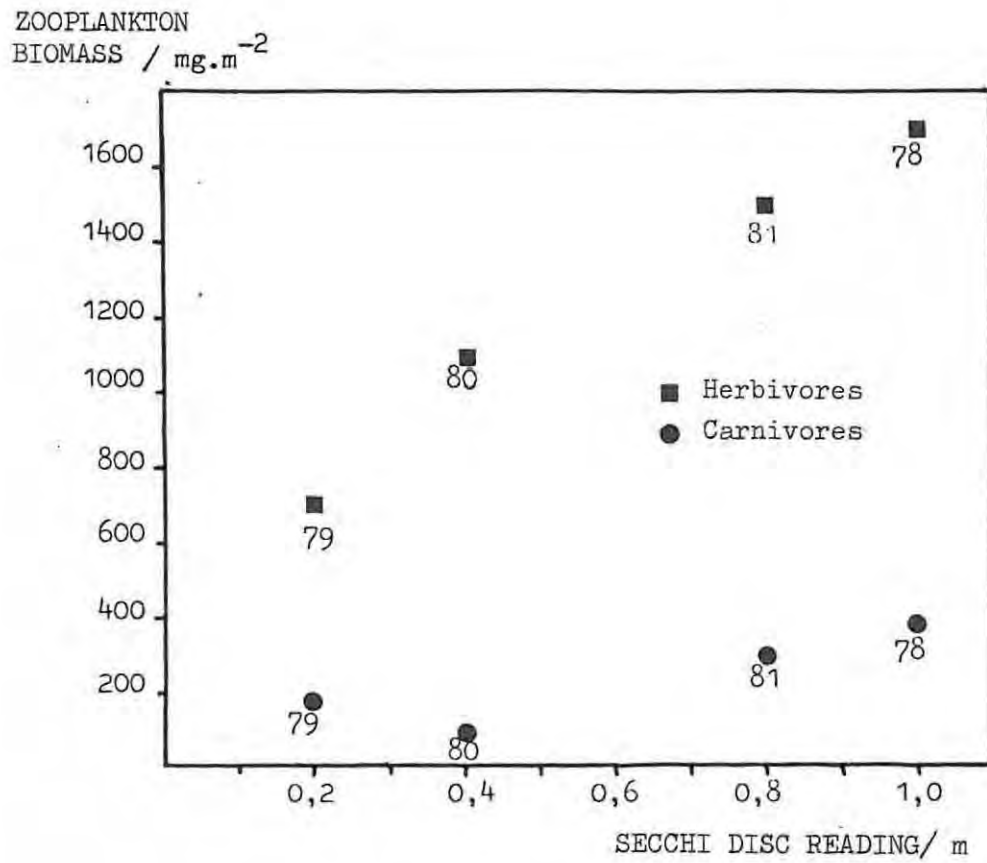


Figure 22. Maximum zooplankton biomass (dry weight) in a season plotted against Secchi disc readings in January. (Based on Fig. 19 and Fig. 21).

zooplankton communities found in the literature, are given in Table 13. The extent to which planktivorous fish can make use of this resource is undoubtedly influenced by the specific composition of the zooplankton community and turbidity levels which jointly influence the vulnerability of zooplankton to visual and tactile predators. But, judging from the annual variation in potential production of zooplankton, fisheries production can be expected to be highly variable between seasons.

Table 13. Tentative estimates of seasonal zooplankton production in Lake le Roux (dry weight; from Hart, 1981).

Season	Estimate
1977/78	1 035 tons
1978/79	360 tons
1979/80	580 tons
1980/81	635 tons

B. AGEING

In most age and growth studies in temperate climates, two basic assumptions are made. Firstly it is assumed that growth checks are registered once a year on hard parts of the body, such as scales and otoliths. Secondly it is assumed that these checks form at the same time each year, when growth commences in spring. Thus the number of checks should indicate the age of the fish and distances between the checks could be taken as a measure of a year's growth. The latter assumption forms the basis for backcalculation of length to a previous age. However, in any ageing study, a critical examination of the two basic assumptions is necessary (De Bont, 1967; Ottaway & Simkiss, 1977).

In this section, time and frequency of check formation on scales and otoliths will be examined. Photographs of scales and otoliths are frequently used to illustrate points made in the text. In spite of much effort, these photographs are not as clear as the material when viewed under the microscope or on a microfiche reader. It was felt, however, that their inclusion still benefitted the presentation.

1. Time and frequency of check formation

Check formation was examined by calculating the growth corresponding to the measured increment shown on the scale beyond the last check. This method was chosen in preference to direct scale measurements since the relationship between scale radius and fish length is not proportional (Figs. 14 and 15). The data were then analysed by age groups (i.e. number of checks shown on the scale and otolith) since it is well known that growth is largely size dependent. Indeed the validity of age and growth studies is often inferred from how well a von Bertalanffy growth curve fits the data, using the method of Walford (1946) (e.g. Hellowell, 1974; Linfield, 1974; Bruton & Allanson, 1980; Hecht, 1980). However, this may be a dubious practice unless inter-annual variations in environmental variables is small, since it assumes that the fish populations are in a steady state (Weatherley, 1972).

a. *Barbus holubi*

Growth, calculated from marginal increments of scales from *B. holubi*, is presented as a time sequence of histograms in Figs. 23 and 24. Time of check formation occurs when the modal length of the histograms shifts from right to left over a period of time. The 1977/1978 year class had formed an annulus by late November 1979, but had a more protracted period of annulus formation in October 1980 to January 1981 (Fig. 23). In contrast, the younger fish of 1978/1979 and 1979/1980 year classes had mostly formed their annulus in October 1980 (Fig. 24) and in November their modal increment was 10 mm larger than that of the older fish (Fig. 23).

The samples collected in winter 1981 showed that about 20% of the two younger year classes had formed a check since the March sampling, before cessation of growth that season (Fig. 24). Most of these checks could not be distinguished from true annuli (Fig. 25). Checks were also formed on the scales of some larger (older) fish, but could be distinguished from true annuli in that no "cutting over" of circuli was observed laterally on the scales as is common at this size.

Frequency

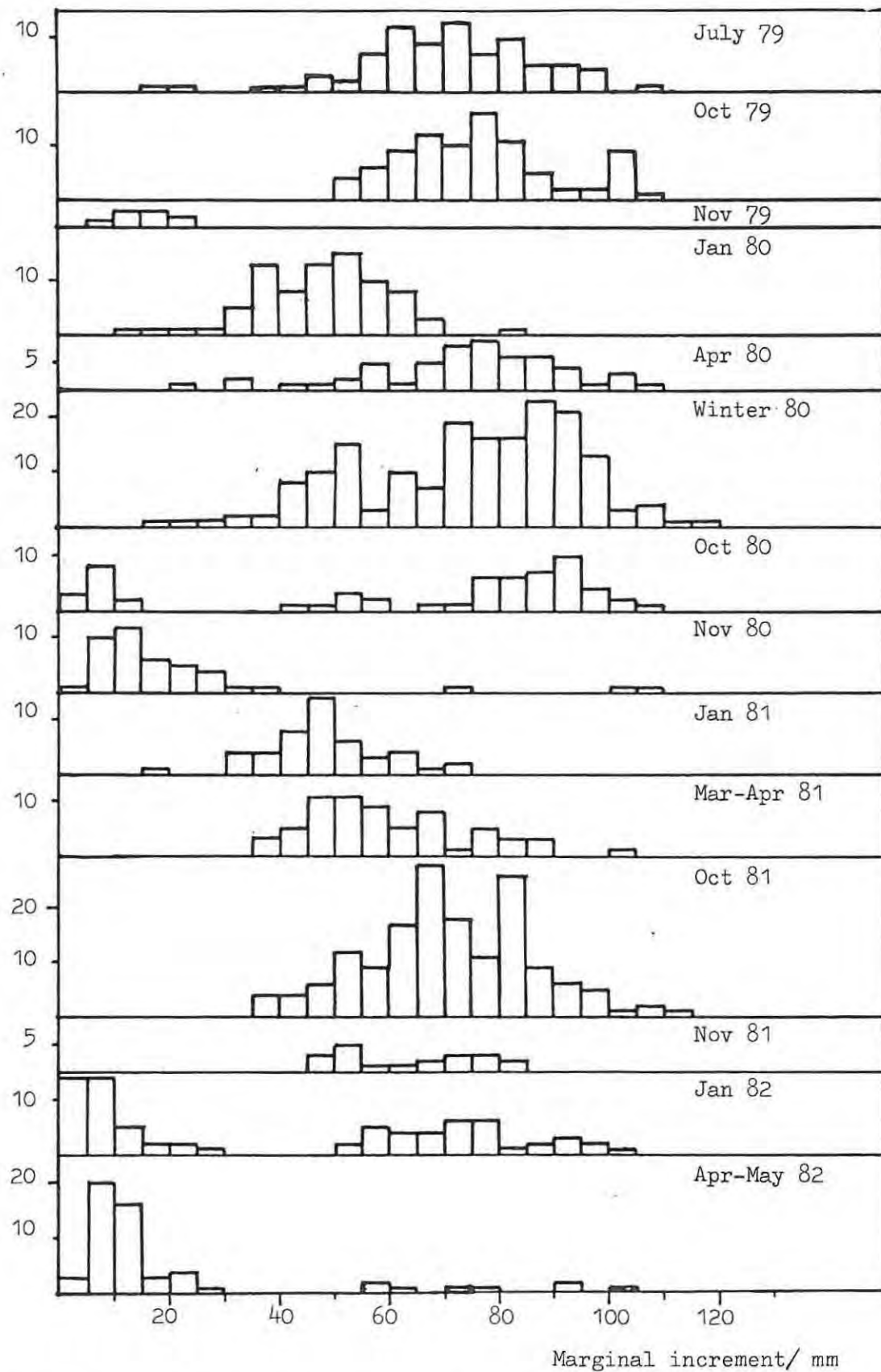


Figure 23.

Backcalculated growth from last check formation on scales of *Barbus holubi*, 1977/78 year class. A check is formed when the mode of the length frequency distribution moves from right to left with time.

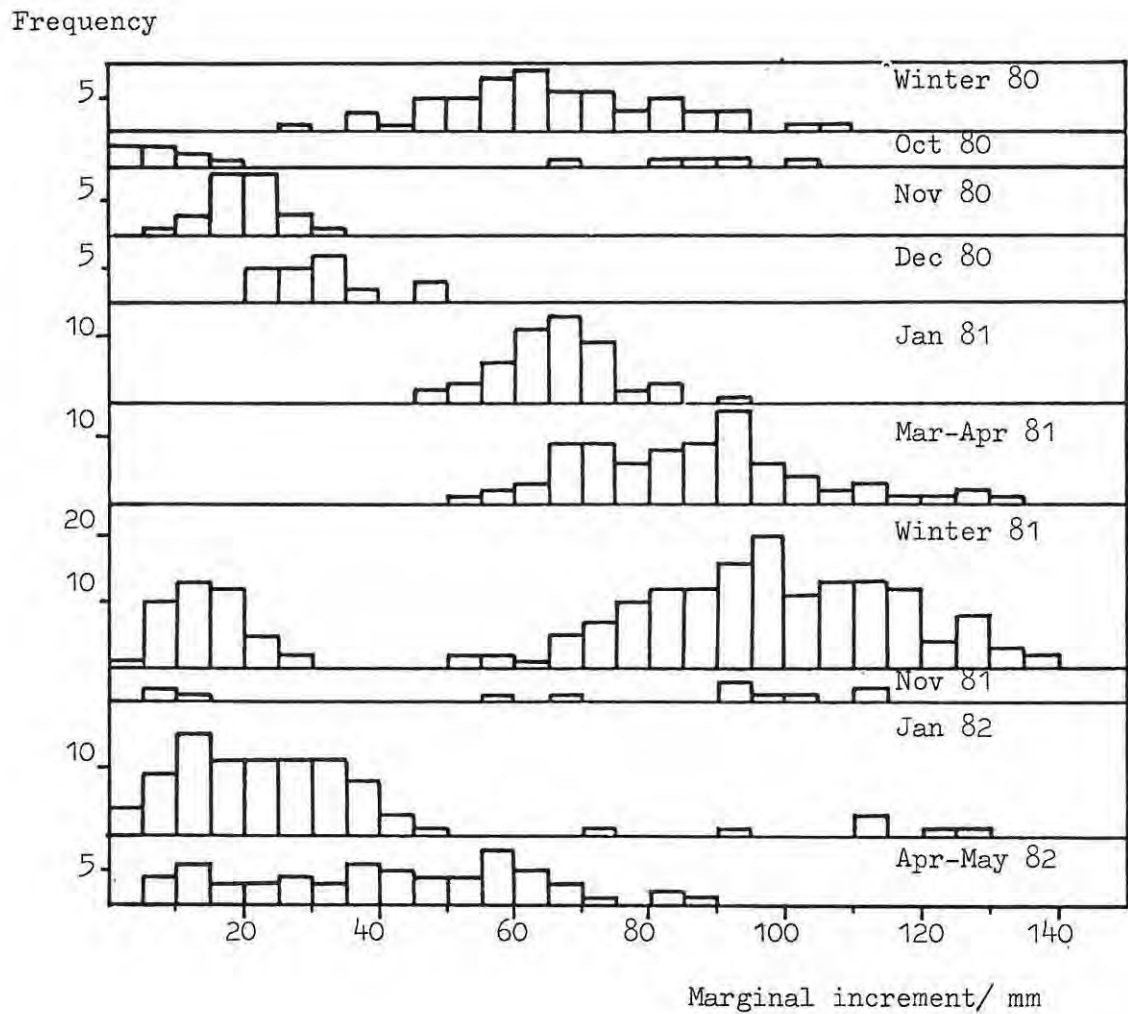


Figure 24. Backcalculated growth from last check formation on scales of *Barbus holubi*, 1978/79 and 1979/80 year classes. A check is formed when the mode of the length frequency distribution moves from right to left with time.

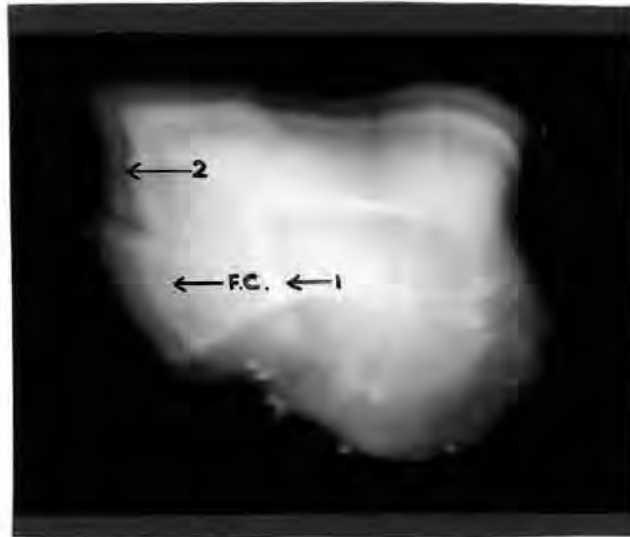


Figure 25. Otolith and a scale from E. holubi caught 13/1 1982 at station 4, 177 mm FL. Age 2+. Both scale and otolith show a false check formed in April 1981.

Otoliths showed the same pattern as the scales and were generally easier to interpret. In larger fish the interruption in growth in late summer 1980/1981 was not registered on the otolith, but the formation of a false check was increasingly common in smaller fish. Thus in the 1980/1981 year class, known from length-frequency distributions, 31% ($n = 175$) of those examined had false checks on their otoliths (Fig. 26). False checks could not be detected on scales of the youngest fish.

The formation of checks on scales and otoliths in April 1981 can be attributed to a sharp and sudden increase in turbidity in March (Fig. 19). The two Barbus species feed on zooplankton in the pelagic zone, selecting their prey visually (Eccles, 1980). The much reduced field of vision, caused by the increase in turbidity, may temporarily have caused a cessation in feeding. High water temperatures still maintained a high metabolic rate, causing a growth check. The physiological condition of individual fish determines their reaction to environmental conditions and may cause checks to be formed on some or all fish of a year class (De Bont, 1967). In Lake le Roux the smaller fish appear to be more sensitive to changes in the environment. This is further borne out by seasonal changes in relative condition (Chapter V, A).

In 1977/1978 there was similarly a sharp increase in turbidity in late summer (Fig. 19). The results related above led to a revision of the ageing of fish which had been spawned prior to that time. It was concluded that about 30% of the 1977/1978 year class had a false check on their otoliths (Fig. 27) and had erroneously been assigned to the 1976/1977 year class. This had given the impression that growth in 1977/1978 had been highly irregular and particularly poor for a large percentage of small fish. No evidence of a similar occurrence was found during the 1978/1979 and 1979/1980 growing seasons.

A majority of the 1978/1979 and 1979/1980 year classes formed annuli in spring and summer of 1981/1982 (Fig. 24). Of the 1977/1978 year class, 15% ($n = 55$) did not show plus growth on the scales by April/May 1982 and a further 42% showed less than 10 mm of plus growth (Fig. 23). Considering that scales may resorb (Fig. 28) it can become difficult to age these fish in later years, unless their

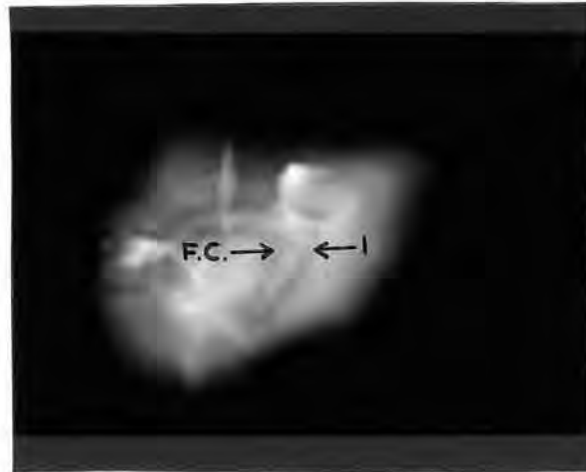


Figure 26. Otolith from B. holubi, 93 mm, caught at station 7, 11/3 1982. Age 1+. The centre check is a false check formed in April 1981.

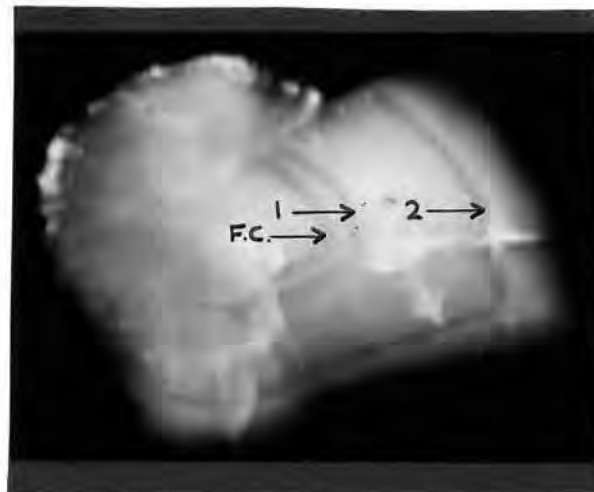


Figure 27. Otolith from B. holubi, 215 mm, caught at station 4, 30/3 1980. Age 2+. The centre check is taken to be a false check formed in March-April 1978.

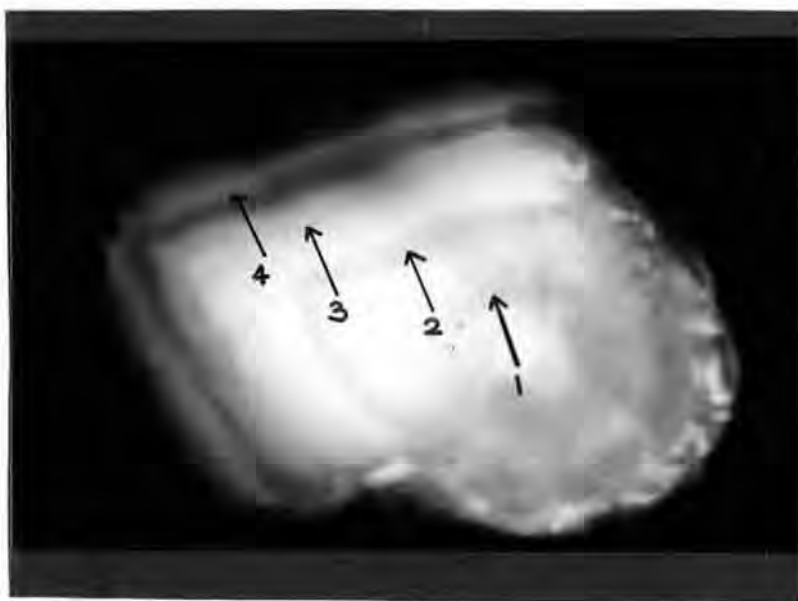
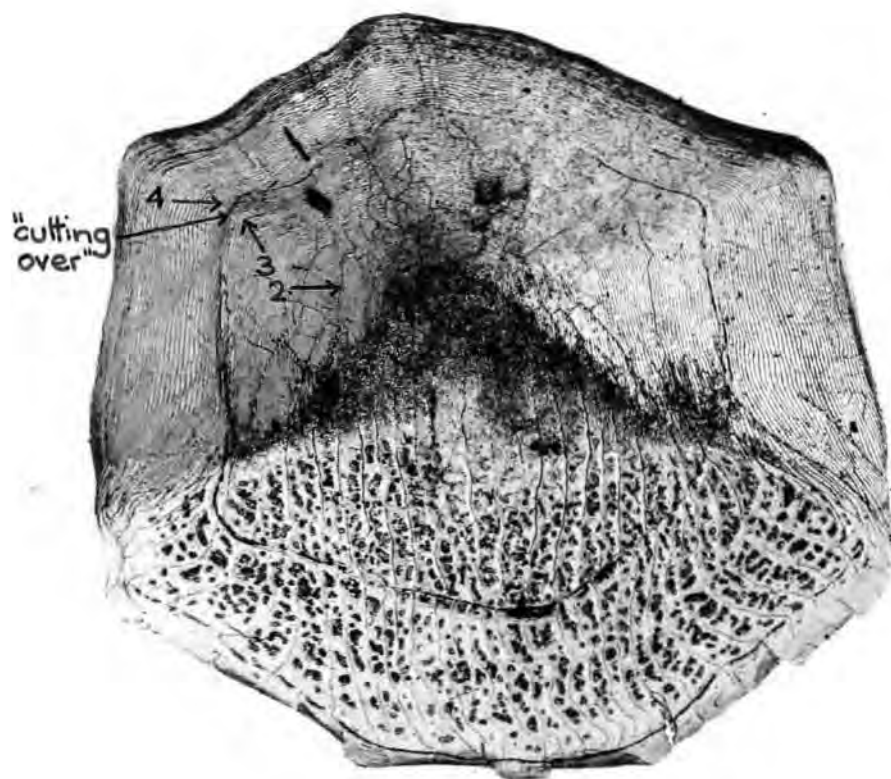


Figure 28. Scale and otolith from *B. holubi*, 262 mm caught 25/7 1980, station 2. Age 4+. The entire season's growth has resorbed laterally on the scale. The first check is unclear on the scale.

growth history is kept in mind. Otoliths tend to be more reliable than scales for identifying years of poor growth, although when there are several successive years of poor growth ageing becomes difficult (Fig. 29). In summer 1981/1982 it was often difficult to distinguish between false checks and annuli, especially early in the season. The risk of error was reduced as the season progressed in that the smaller fish which are most susceptible to false check formation, are also the fish which first resume growth.

b. Barbus kimberleyensis

The results for B. kimberleyensis are similar to those for B. holubi, although growth is resumed earlier in spring in B. holubi (compare October and November 1980 in Figs. 23 and 24, and 30 and 31). Time of annulus formation is generally earlier and less protracted in fish of smaller size. False checks were formed in late summer of 1981 in 25% (n = 48) of the 1978/1979 and 1979/1980 year classes (Fig. 30) and in 10% (n = 112) of the 1976/1977 and 1977/1978 year classes (Fig. 31). The occurrence of false checks was related to size. This result can be explained by the smaller size reached by B. kimberleyensis than B. holubi in the first few years of life in Lake le Roux (Chapter V, B).

A majority of the 1978/1979 and 1979/1980 year classes showed plus growth in 1981/1982, but older fish commonly showed no plus growth on their scales. Of the 1976/1977 and 1977/1978 year classes, 35% (n = 37) failed to register plus growth (Fig. 31). Older B. kimberleyensis had a distinctive short period of growth in 1975/1976 clearly visible on the otoliths (Fig. 32), which was used as a "marker" to determine the age of these fish. In April 1982, six out of twelve fish in this group did show some plus growth on their scales.

c. Labeo capensis

While the majority of B. holubi caught and examined in this study were spawned in 1977/1978 and later, older L. capensis dominated in the L. capensis catches throughout the period of study. The results have been presented according to age, separating pre- and post-impoundment year classes (Figs. 33 to 35). Time of annulus formation

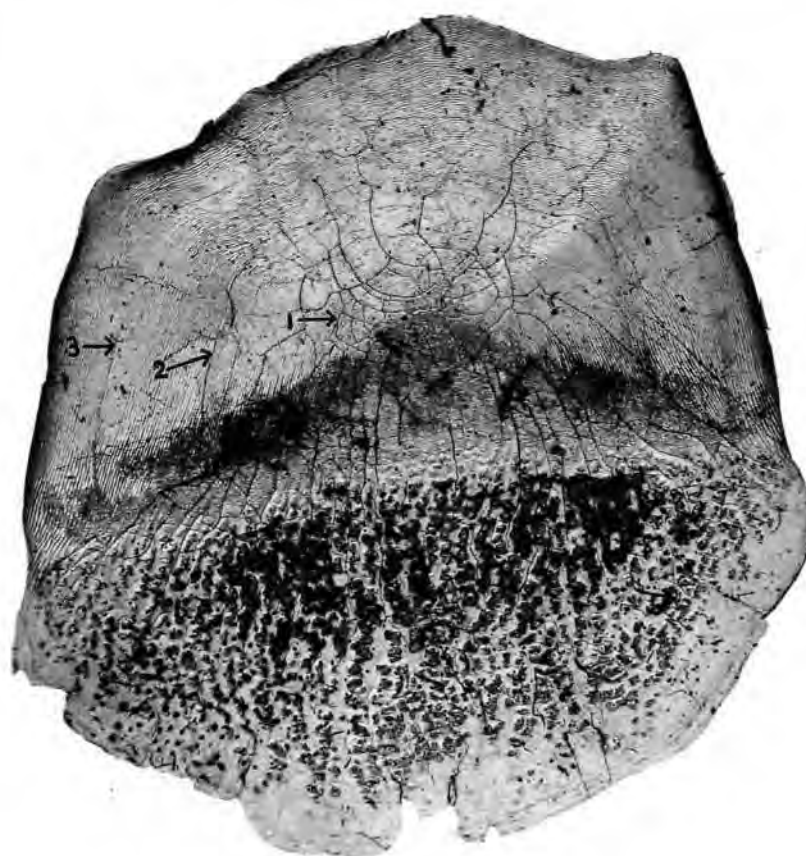
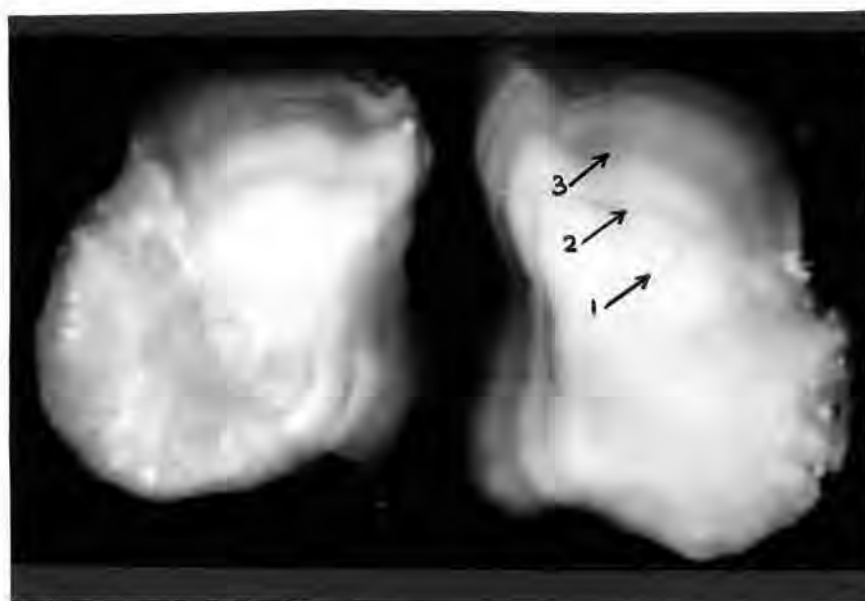


Figure 29. Otoliths and scale taken from *B. holubi*, 344 mm female caught in Lake Verwoerd 20/11 1981. The left otolith has been ground, revealing two additional checks. The first two and last 4-5 checks on the otolith cannot be identified from the scale. Corresponding checks on the scale and otolith are marked. Based on the scale, the fish would probably have been assigned an age of 4+, but an age of 8 or 9+ is obtained from the otolith reading.

Frequency

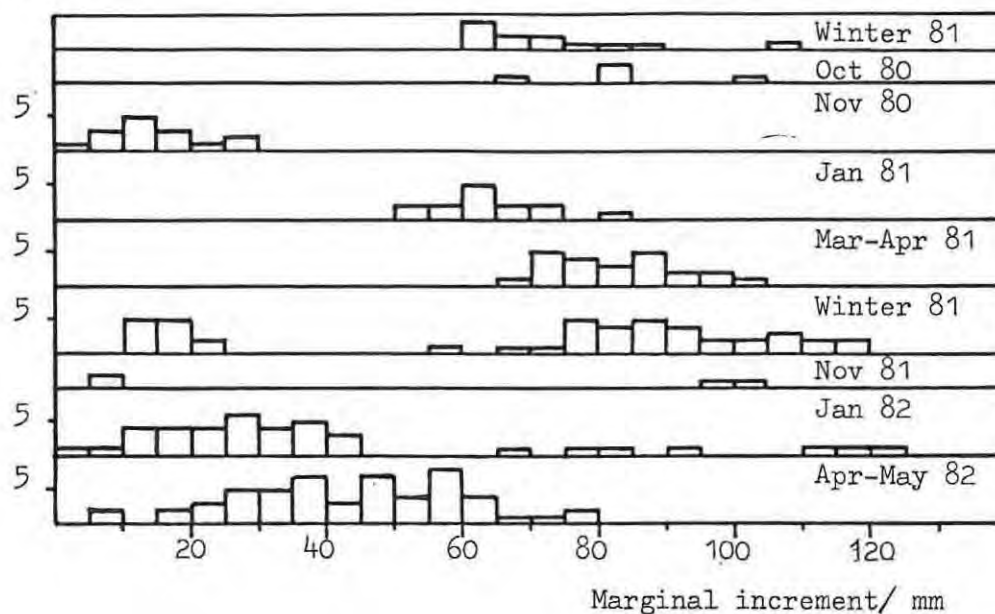


Figure 30. Backcalculated growth from last check formation on scales of *Barbus kimberleyensis*, 1978/79 and 1979/80 year classes. A check is formed when the mode of the length frequency distribution moves from right to left with time.

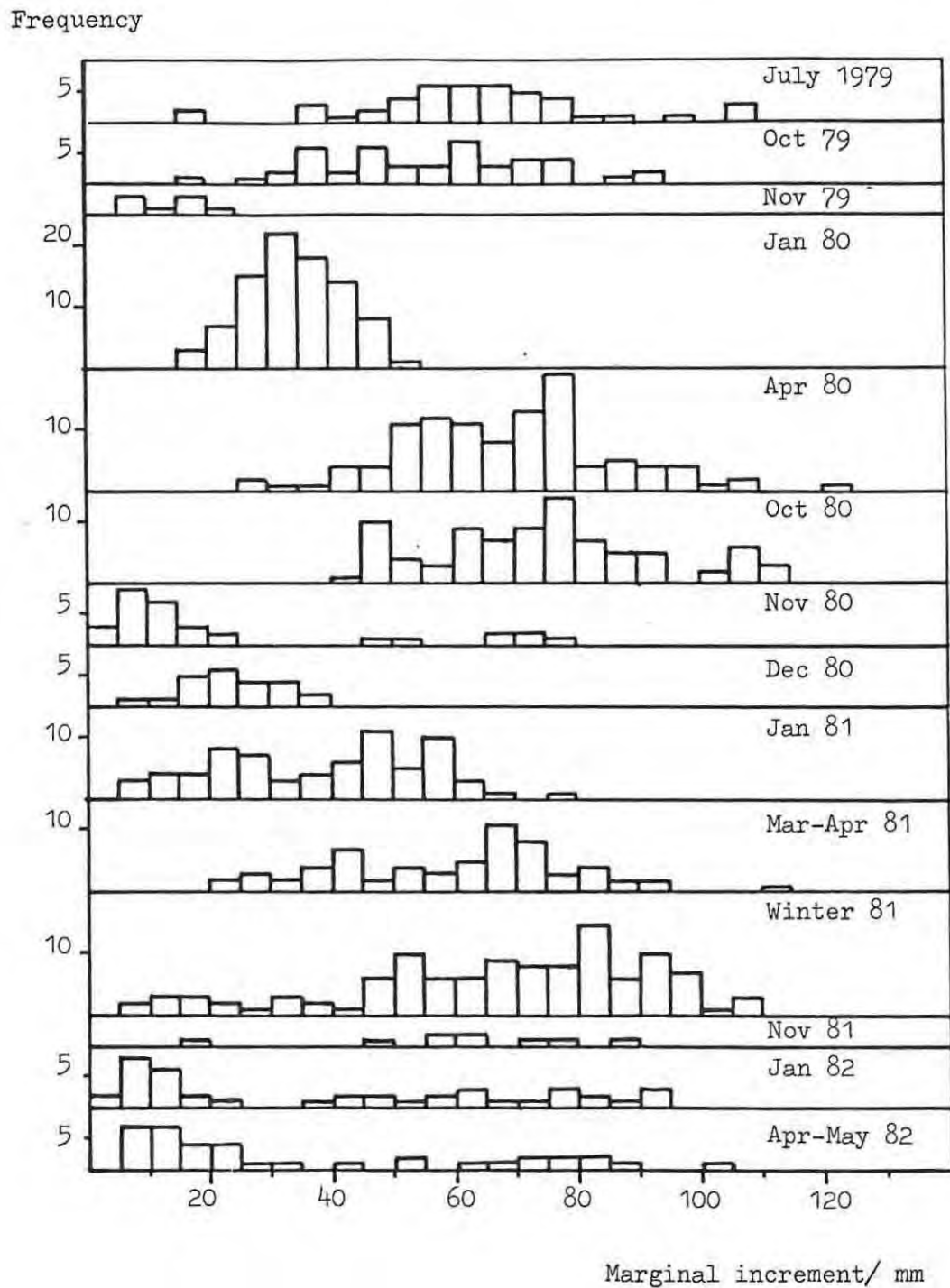


Figure 31. Backcalculated growth from last check formation on scales of *Barbus kimberleyensis*, 1976/77 and 1977/78 year classes. A check is formed when the mode of the length frequency distribution moves from right to left with time.

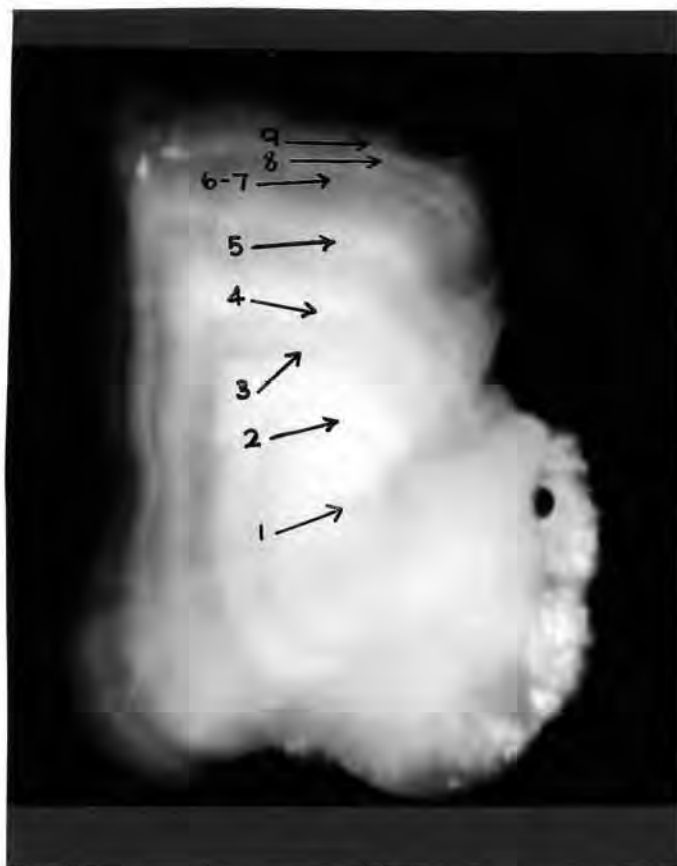


Figure 32. Otolith from B. kimberleyensis, 458 mm FL male, caught 17/1 1982, station 5. Age 9 (no plus growth in season of capture). A characteristic short growth band between the 3rd and 4th check, corresponding to the 1975/76 season, can be seen.

Frequency

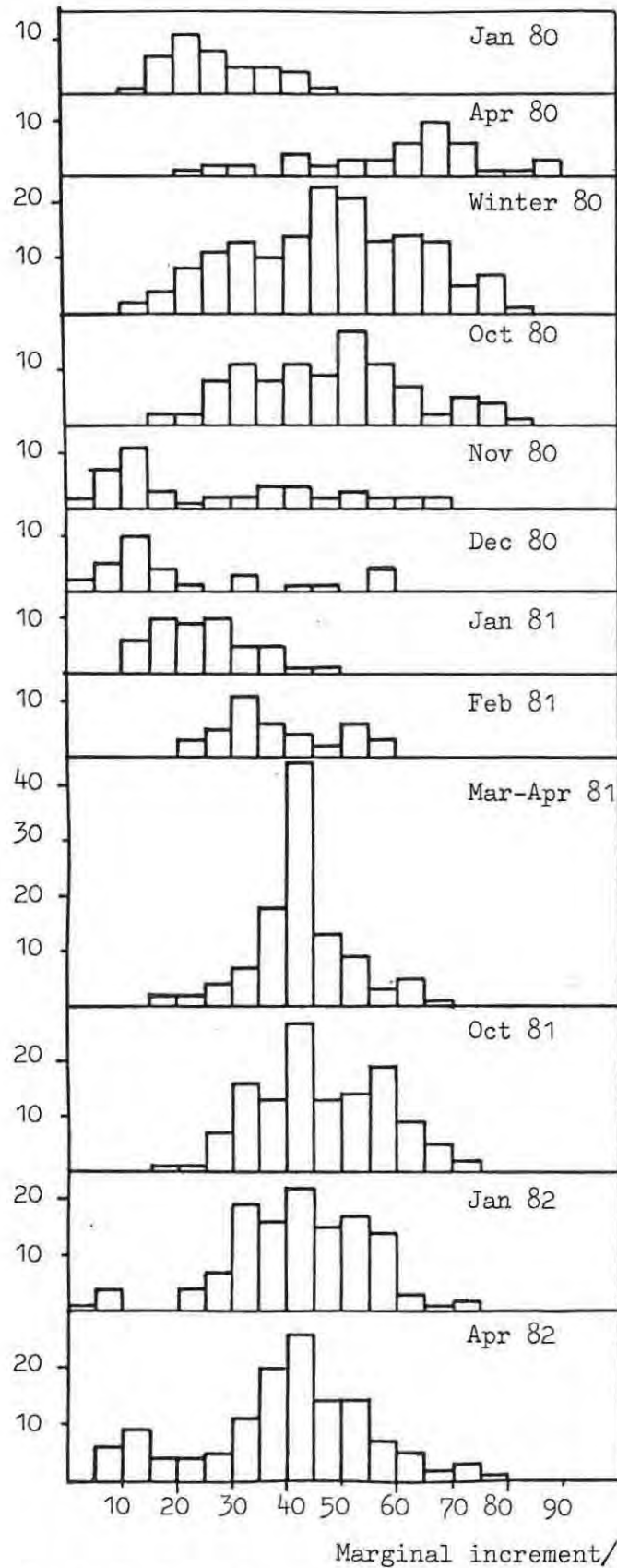


Figure 33. Backcalculated growth from last check formation on scales of *Labeo capensis*, 1976/77 and 1977/78 year classes. A check is formed when the mode of the length frequency distribution moves from right to left with time.

Frequency

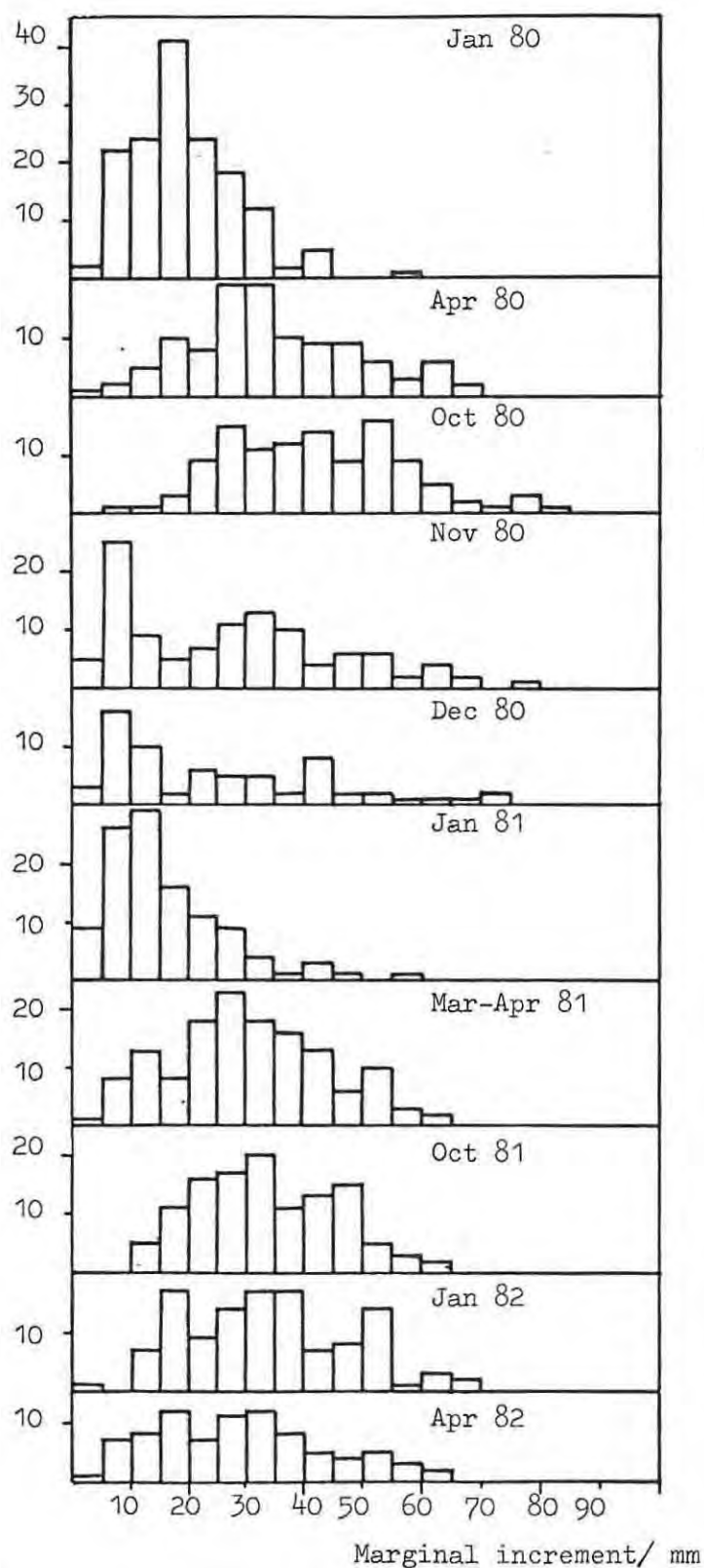


Figure 34.

Backcalculated growth from last check formation on scales of *Labeo capensis*, 1973/74, 1974/75 and 1975/76 year classes. A check is formed when the mode of the length frequency distribution moves from right to left with time.

in 1980/1981 occurred over a long period (November to January) especially in the older fish (Fig. 33). In 1981/1982 no plus growth (annulus formation) was observed for the majority of the population. Even in the smallest fish (Fig. 35) seven out of eighteen did not show any plus growth.

Growth in L. capensis often appears to be slow. In such cases, growth can only be inferred from otolith readings (Fig. 36). Age determination of L. capensis was aided by the generally poor growth in the 1978/1979 season. This showed up clearly on the otolith but was often difficult to determine on the scales. The season of poor growth then served as a "marker" in the same way as the 1975/1976 season's growth for B. kimberleyensis. Examples are shown in Figs. 37 and 38.

Unlike the two Barbus, false checks did not form in this species in late summer 1981. L. capensis is a herbivore-detritivore which feeds off the bottom and does not rely on sight to do so. Production in Lake le Roux is primarily limited by light penetration (Selkirk, 1982). Thus, while increased turbidity may have limited the food supply of L. capensis, the effect was not as immediate as in the case of the two Barbus species.

2. Comparisons between observed and backcalculated lengths

The ageing of large cyprinids in Lake le Roux is complicated by irregular growth among seasons and the occasional formation of false checks. It is thus important to test the conclusions reached in other ways. One of the criteria applied to evaluate the accuracy of ageing by scales is to compare backcalculated lengths to observed lengths of fish at a known age (Maraldo & MacCrimmon, 1979). The usefulness of this comparison depends, however, largely on how constant conditions remain through time. In this study, large amounts of data were generated using backcalculations. There are potentially three main problems associated with using such data (Bagenal & Tesch, 1978) :

- i. Only survivors are sampled. Differential growth-related mortality may cause average growth rates based on back-calculated data to differ from actual average growth rates.

Frequency

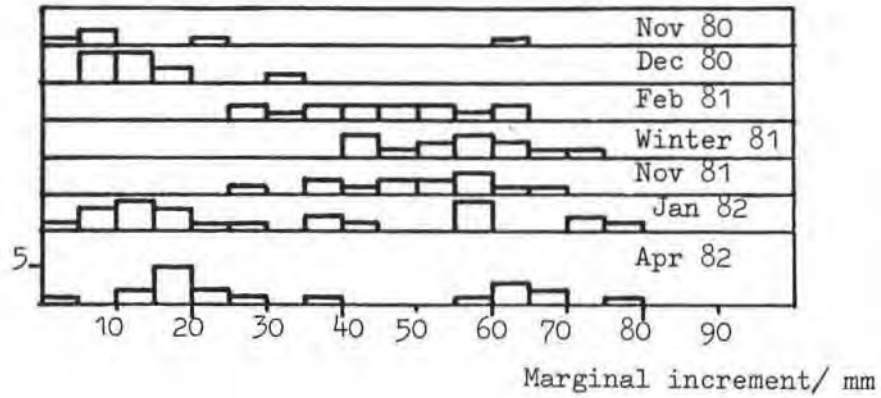


Figure 35.

Backcalculated growth from last check formation on scales of *Labeo capensis*, 1978/79 and 1979/80 year classes. A check is formed when the mode of the length frequency distribution moves from right to left with time.

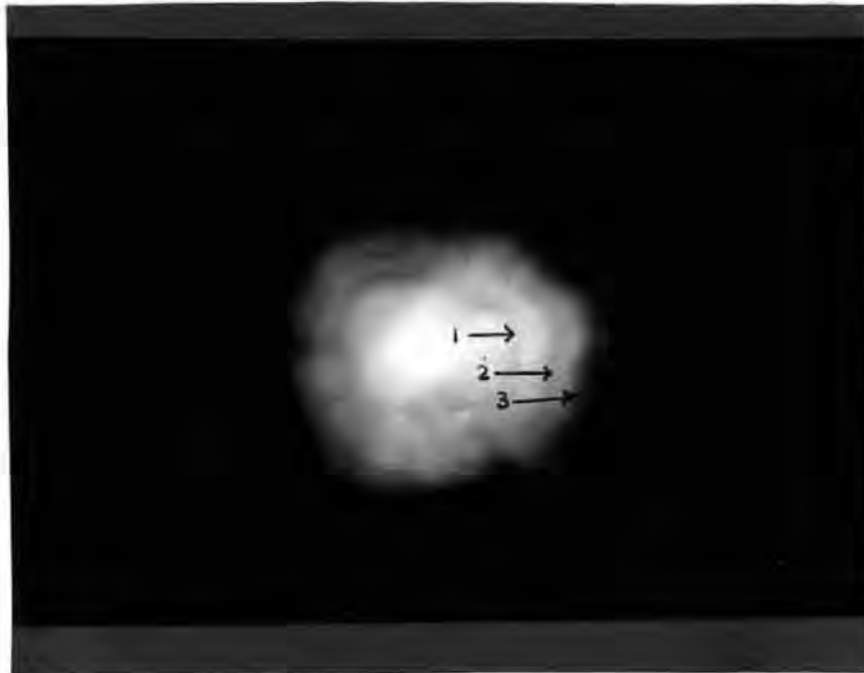


Figure 36. Otolith from *L. capensis*, 98 mm FL, caught 22/11 1980, station 8. Age 3+. The plus growth is only just visible on the edge.

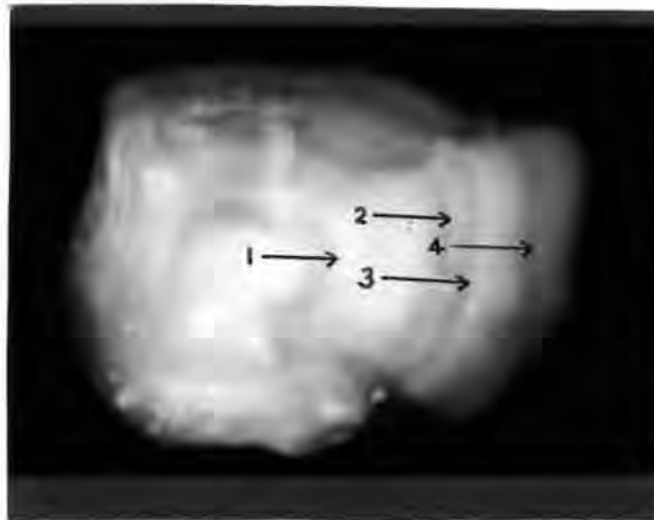


Figure 37. Scale and otolith from L. capensis, 222 mm FL, caught 26/3 1981, station 1. Age 4+, showing typically poor growth in the 1978/79 season.

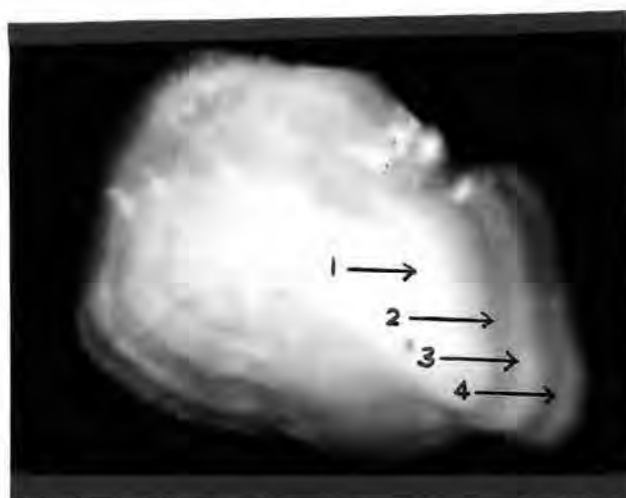


Figure 38. Scale and otolith from L. capensis, 225 mm FL, caught 21/4 1982, station 1. Age 5. Typical poor growth in 1978/1979 season and no plus growth during the 1981/1982 season can be seen.

- ii. Body-scale relationship used for backcalculations may be inaccurate. This can introduce a systematic bias into the results.
- iii. Sampling of ageing material is not random. This can be caused by gear selectivity, and in Lake le Roux, by local differences in growth rate.

All three types of errors have been observed in previous studies, often giving rise to "Lee's phenomenon" of backcalculated lengths at a given age becoming smaller when scales from older fish are used (Ricker, 1975; Bagenal & Tesch, 1978).

To validate the results of backcalculation, backcalculated lengths and observed lengths of the same year classes were compared. These comparisons will now be discussed.

a. Barbus holubi

The results for different year classes are presented in Figs. 39 and 40. Growth generally tapers off in April and there is good agreement between observed lengths in winter and subsequent backcalculated lengths. There is a characteristic reduction in backcalculated lengths to the second annulus from the beginning of the third growing season. This is because cohorts do not become fully recruited into the gillnets until early in their third growing season. Other variations in the results may be due to variations in the sampling gear (Table 9). Relatively greater numbers of large fish were sampled during CPA gillnetting surveys than at other times.

b. Barbus kimberleyensis

This species shows a higher degree of variability than B. holubi (Figs. 41 and 42). There is a reduction in backcalculated lengths to the third annulus from the beginning of the fourth growing season. This reflects the smaller size at age in B. kimberleyensis than B. holubi in Lake le Roux (compare backcalculated lengths at age for the same year class, e.g. 1977/1978 year classes, Figs. 39 and 42).

c. Labeo capensis

It is commonly observed that ageing becomes less accurate with older fish (Carlander, 1974). However, the relatively constant

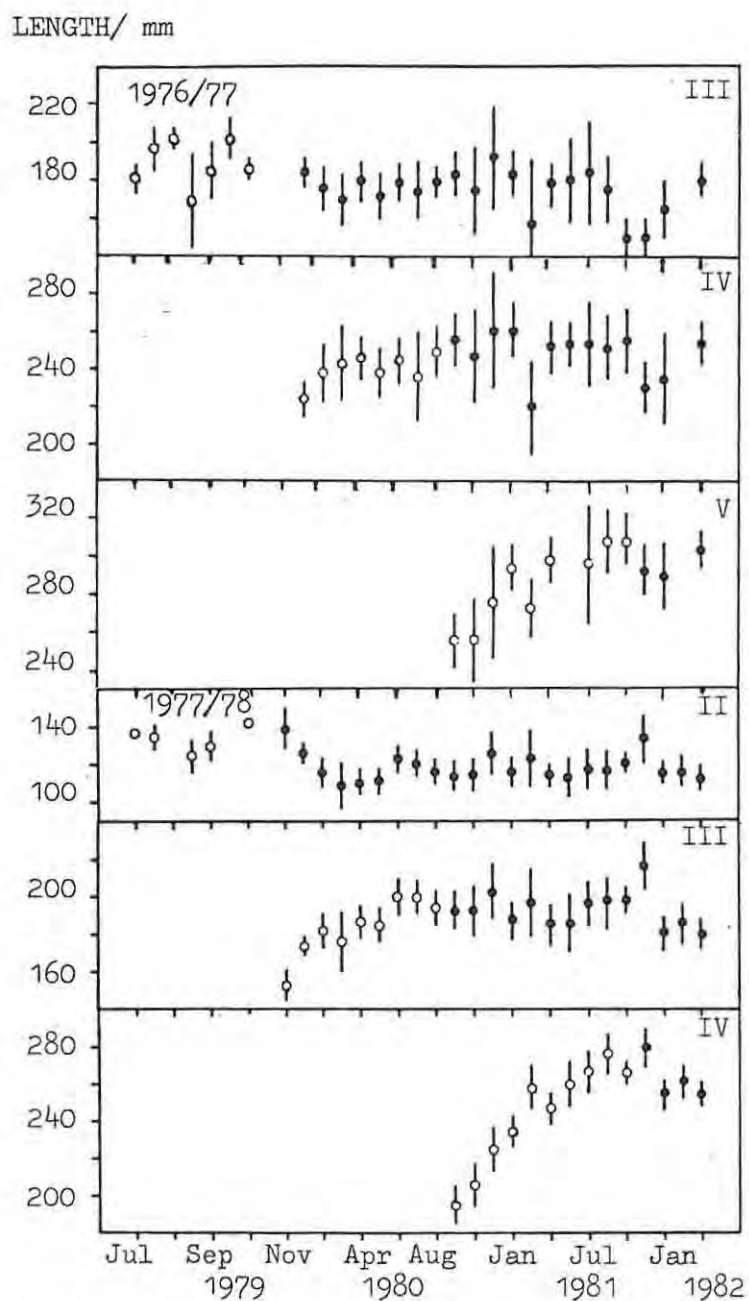


Figure 39. Backcalculated lengths to different annuli (●) compared to observed lengths (○) of *Barbus holubi*, 1976/77 and 1977/78 year classes. The mean length and a 95% confidence interval are given. Note that the time scale is sequential but not regular.

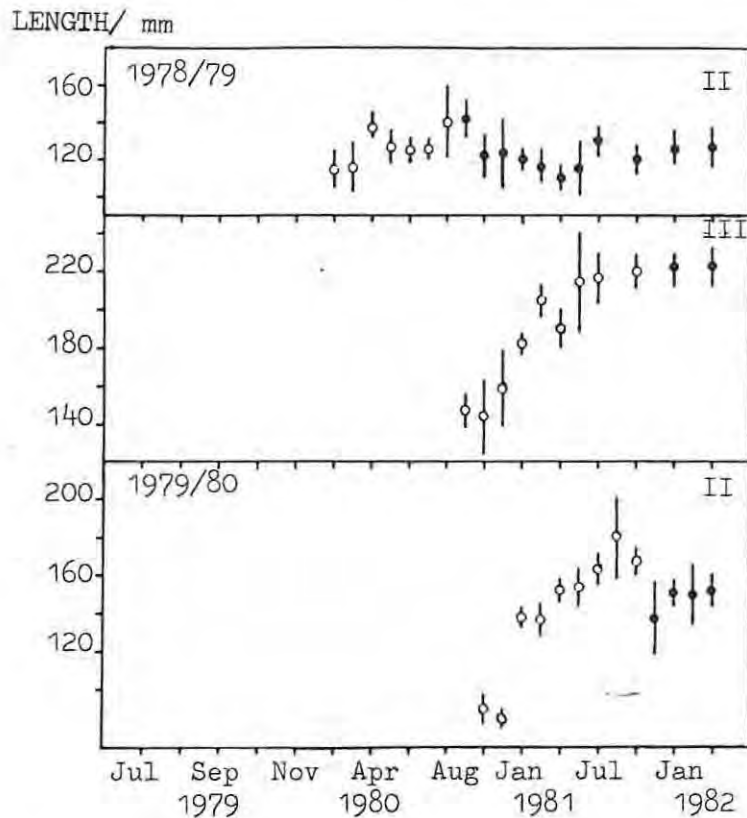


Figure 40. Backcalculated lengths to different annuli (●) compared to observed lengths (○) of *Barbus holubi*, 1978/79 and 1979/80 year classes. The mean length and a 95% confidence interval are given. Note that the time scale is sequential but not regular.

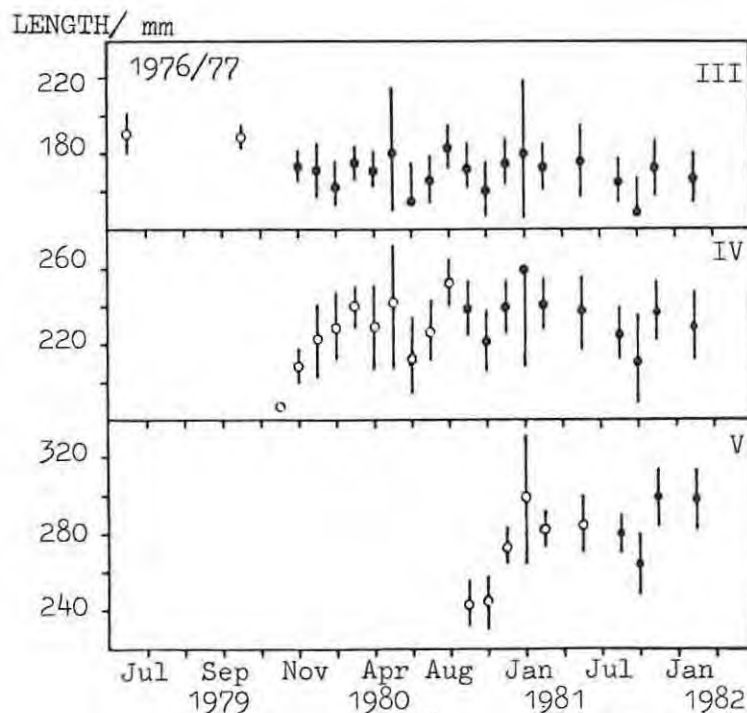


Figure 41. Backcalculated lengths to different annuli (●) compared to observed lengths (○) of *Barbus kimberleyensis*, 1976/77 year class. The mean length and a 95% confidence interval are given. Note that the time scale is sequential but not regular.

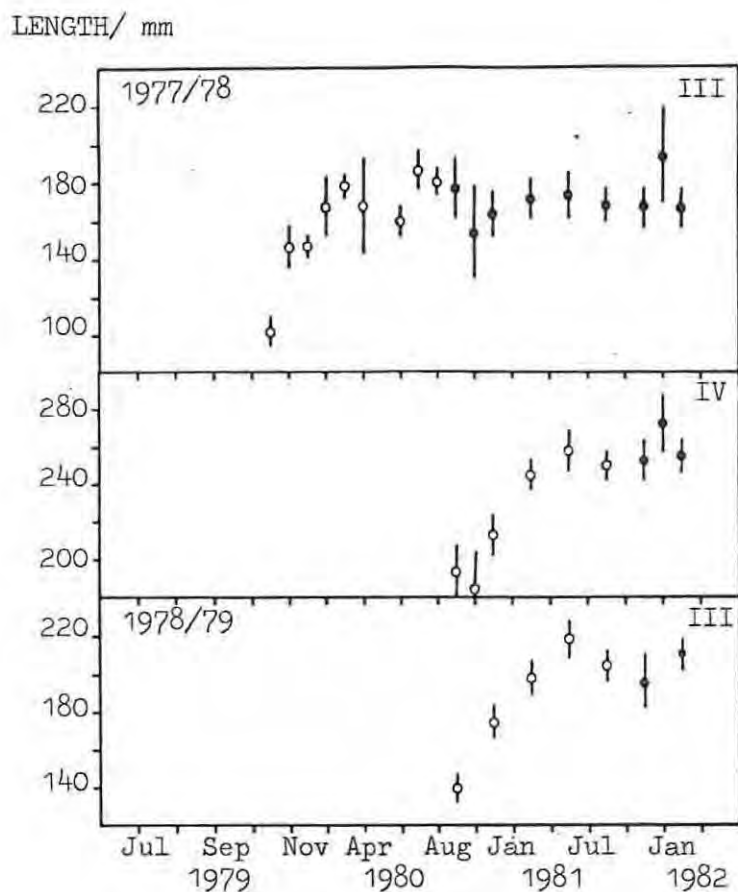


Figure 42. Backcalculated lengths to different annuli (ϕ) compared to observed lengths (ϕ) of *Barbus kimberleyensis*, 1977/78 and 1978/79 year classes. The mean length and 95% confidence interval are given. Note that the time scale is sequential but not regular.

results for the 1973/1974 year class (Fig. 43) indicate a consistency in the ageing procedure. Comparison of backcalculated and observed lengths for the younger year classes (Figs. 44 to 46), show a high degree of variability. In the 1977/1978 year class, (Fig. 46) a gradual decline in backcalculated lengths at the third annulus may indicate that recruitment was incomplete prior to the fourth summer. However, much of the variation in the 1977/1978, 1976/1977 and 1975/1976 year classes (Figs. 44 to 46) may reflect variable growth rate and pattern of dispersal of this species in the lake (see Chapter V). Thus variations in sampling have a greater effect on results for L. capensis than for the Barbus.

3. Conclusions and discussions

As a rule, an annulus is formed when growth is resumed in spring or early summer, though interpretation is complicated by the following four main factors :

- i. The first annulus is often difficult to interpret from scales or may even be missing.
- ii. False checks may be formed during sudden in-season environmental changes, but do not affect the entire population uniformly.
- iii. Time of annulus formation may be protracted over several months. The older (larger) the fish, the later in the season growth is resumed.
- iv. Growth is highly variable among seasons. In extreme cases no incremental growth may be registered on the scales.

It is concluded that a study of age and growth, using scales and otoliths, of the large cyprinids in Lake le Roux can only be successful if :

- i. Sampling is done frequently throughout the year and
- ii. the history of environmental changes in the lake is well known and borne in mind when scales and otoliths are interpreted.

Marked fish have often been used successfully to evaluate ageing results, but tags may affect growth and results must be interpreted with care (Bagenal & Tesch, 1978). Practical difficulties, discussed in Section A, prevented the use of marked fish in this study.

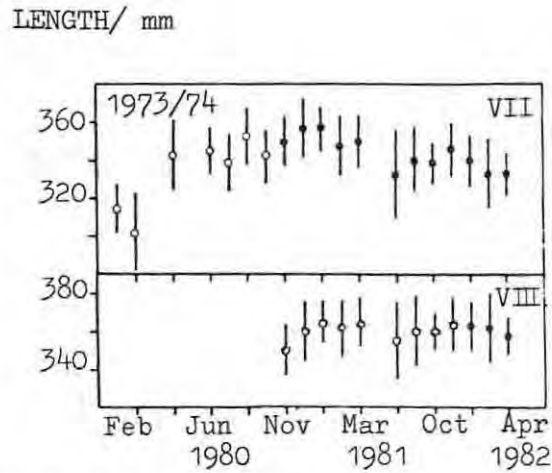


Figure 43. Backcalculated lengths to different annuli ($\blacklozenge$) compared to observed lengths ($\circ$) of *Labeo capensis*, 1973/74 year class. The mean length and a 95% confidence interval are given. Note that the time scale is sequential but not regular.

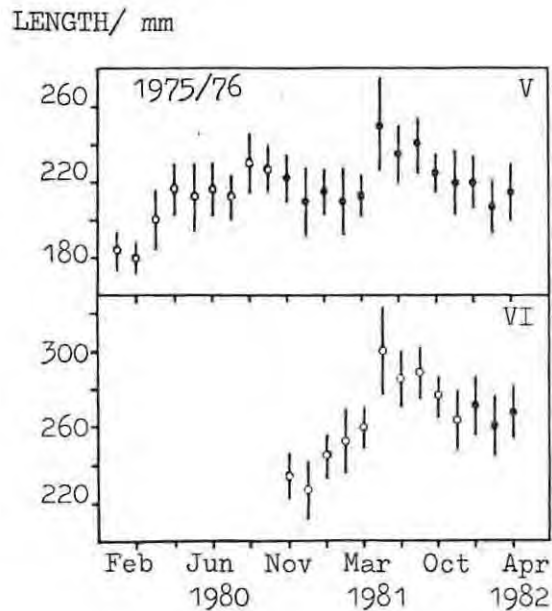


Figure 44. Backcalculated lengths to different annuli ($\blacklozenge$) compared to observed lengths ($\circ$) of *Labeo capensis*, 1975/76 year class. The mean length and a 95% confidence interval are given. Note that the time scale is sequential but not regular.

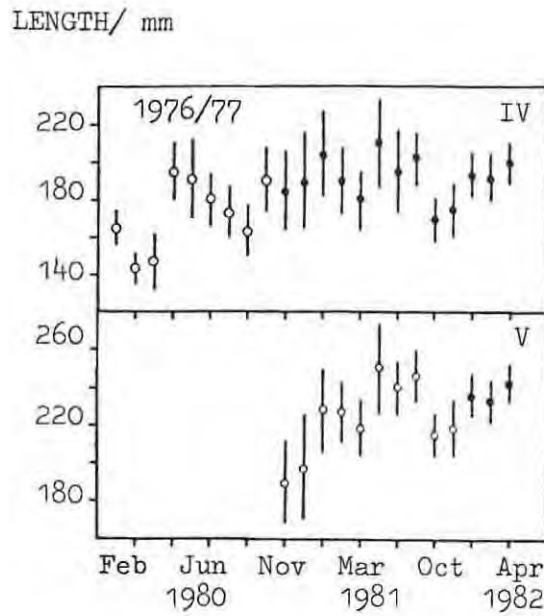


Figure 45. Backcalculated lengths to different annuli ($\bullet$) compared to observed lengths ($\circ$) of *Labeo capensis*, 1976/77 year class. The mean length and a 95% confidence interval are given. Note that the time scale is sequential but not regular.

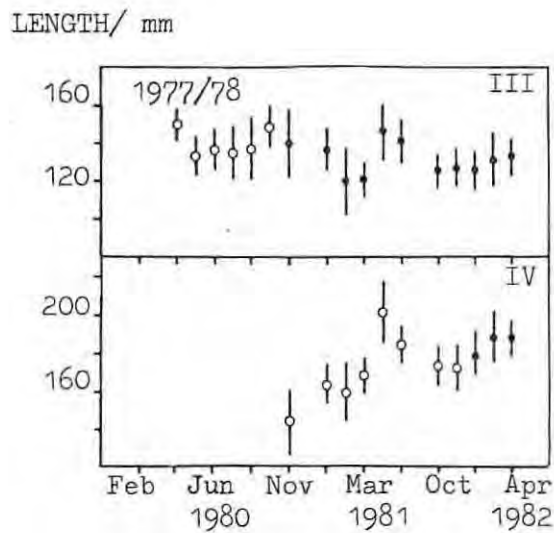


Figure 46. Backcalculated lengths to different annuli ($\bullet$) compared to observed lengths ($\circ$) of *Labeo capensis*, 1977/78 year class. The mean length and a 95% confidence interval are given. Note that the time scale is sequential but not regular.

It appears that in previous age and growth studies in South Africa, periodicity of check formation on scales and otoliths (Bruton & Allanson, 1974; Hecht, 1979; 1980) and spines (Bruton & Allanson, 1980) has only been investigated in subtropical regions. None of the above authors found that checks were formed regularly once each year. Studies in more temperate regions usually assume that checks are formed annually, usually during the cold season. However, as seen in the present study, such assumptions may not always be warranted, especially if only scales are used. Several factors, other than temperature, have been shown to cause check formation in temperate climates. These include handling, injury, water level fluctuations and variation in food supply (Ottaway & Simkiss, 1977; Weatherley & Rogers, 1978). Little or no growth in scales of old (large) fish often causes age to be underestimated by the scale method, and is commonly observed in temperate climates (e.g. Alvord, 1954; Regier, 1962; Buchholz & Carlander, 1963; Beamish, 1973; Jonsson, 1976; Maraldo & MacCrimmon, 1979; Mills & Beamish, 1980). Ageing using otoliths is generally better in these cases (e.g. Jonsson, 1976; Maraldo & MacCrimmon, 1979; Mills & Beamish, 1980) although the reverse situation has also been observed (Messieh & Tibbo, 1970). All methods of age determination are not equally suited for different populations and more than one method should be used in each study.

V. GROWTH, MORTALITY AND REPRODUCTION

The reaction of a fish population to exploitation is largely governed by those parameters which define population size and structure, i.e. growth, mortality and reproduction. There are two basic ways in which these are estimated (Pitcher & Hart, 1982) :

- i. If the environment is stable and variation in reproductive success is small, growth and mortality can be estimated by comparing size at age and the relative abundance of successive cohorts at a given point in time.
- ii. If the environment is variable, large fluctuations in population parameters may occur. It is then necessary to follow the fate of individual cohorts through time. Factors influencing population parameters can then be identified and their relationships established to guide management decisions.

Due to the large environmental fluctuations in Lake le Roux (Chapter IV, A), and the relative lack of previous studies on these aspects in South African reservoirs, the second approach was adopted in this study.

Length-weight relationships are necessary for the estimation of population biomass from length measurements, and changes in relative condition also provide supporting evidence when temporal changes in the populations are interpreted. These will be described prior to examining growth, mortality and reproduction.

A. RELATIVE CONDITION

Condition factor is a measure of weight relative to length and is often used to monitor the general well-being of a population (Bagenal & Tesch, 1978). Ivlev (in Weatherley, 1972) showed that interspecific differences in relative condition increased when fish were starved. It can thus be useful to measure not only the mean but also the range in condition within a population at any given time.

Different ways to compute and interpret condition factor are discussed by Le Cren (1951), Weatherley (1972), Ricker (1975), Bagenal & Tesch (1978) and Bruton (1979). The one chosen in this study is :

$$C = \frac{\text{observed weight}}{\text{expected weight}} = \text{relative condition factor}$$

where expected weight is calculated from an overall length-weight relationship. This method has the advantage that the condition of different size fish can be compared even if growth is allometric. Thus size composition of the sample does not affect the value of C, provided that the length-weight relationship does not change with size, sex or age. Length-weight relationships therefore need to be established.

1. Length-weight relationships

The relationship between length (L) and weight (W) can usually be described by the formula

$$W = a L^b$$

where a and b are constants (Le Cren, 1951; Bagenal & Tesch, 1978). If the exponent b equals three then growth is isometric, i.e., if the density of the fish remains constant, so will the shape of its body (Ricker, 1975). If b does not equal three, body form will change with size and growth is said to be allometric.

The length-weight relationships were calculated based on data collected in November 1979 to October 1980 for the Barbus species and from January to October 1980 for L. capensis. The results are given in Table 14. The relationships for all species are similar for both sexes and when unsexed fish are included. The two Barbus species have near isometric growth ($b \sim 3$). L. capensis has allometric growth ($b > 3$), becoming relatively heavier with increasing length. The relationships fit the data well and there is no need to divide the data according to size, sex or age.

In this study, length-weight relationships were calculated primarily to monitor changes in relative condition with time, but also for the conversion of length measurements to mass (Section B).

2. Temporal changes in relative condition

The selective properties of fishing gear may influence the relative condition of the catch (Le Cren, 1951; Kipling, 1957).

Table 14. Length-weight relationships of some large cyprinids in Lake le Roux.

Species	Sex	Relationship	n	Significance	r ²	Sampling time
<u>B. holubi</u>	Males	$W = 1,24 \times 10^{-5} L^{3,010}$	621	$p < 0,00001$	0,99	November 1979 to October 1980
	Females	$W = 1,08 \times 10^{-5} L^{3,037}$	856	$p < 0,00001$	0,99	
	All	$W = 1,06 \times 10^{-5} L^{3,039}$	1749	$p < 0,00001$	0,99	
<u>B. kimberleyensis</u>	Males	$W = 0,74 \times 10^{-5} L^{3,091}$	265	$p < 0,00001$	0,99	November 1979 to October 1980
	Females	$W = 0,62 \times 10^{-5} L^{3,125}$	261	$p < 0,00001$	0,99	
	All	$W = 0,71 \times 10^{-5} L^{3,099}$	664	$p < 0,00001$	0,99	
<u>L. capensis</u>	Males	$W = 0,28 \times 10^{-5} L^{3,298}$	951	$p < 0,00001$	0,98	January 1980 to to October 1980
	Females	$W = 0,28 \times 10^{-5} L^{3,297}$	1217	$p < 0,00001$	0,99	
	All	$W = 0,38 \times 10^{-5} L^{3,241}$	3170	$p < 0,00001$	0,98	

Therefore, the relative condition factor was only calculated for the samples taken during the CPA gillnetting surveys. Since these samples were collected in the same way each time, they should be comparable. Possible variations in relative condition with size were examined by plotting individual deviations from expected weight against length for each season (i.e. summer and winter) (Fig. 47). In winter 1981 and summer 1981/1982 changes with size of condition of B. holubi were abrupt between 220 and 240 mm (Fig. 47). The condition of B. holubi was therefore examined in two groups, those less than 230 mm and those larger than 230 mm (Fig. 48). In general, the relative condition of B. holubi reaches a peak in summer (January), with a seasonal trend showing more in the smaller fish. In October 1981, condition of B. holubi < 230 mm was poor and variable, but this size group had recovered by January 1982. Fish $\geq$ 230 mm showed high individual variation in condition in October 1981 and January 1982 (Fig. 49) as indicated by the large standard deviation (Fig. 48). By April, relative condition was again more uniform.

The relative condition of Barbus kimberleyensis was, for comparative purposes, calculated separately for the same size groups as B. holubi (Fig. 50) although no trends were seen with size. No seasonal trends can be seen (Fig. 50) and this may in part be the result of variations in size composition of the sample for different sample dates. Catches were usually so low that the samples reflected the size distribution of the catch.

Analysis of individual deviations from expected weight for L. capensis showed a trend with size in winter 1981 which became more pronounced the following summer (Fig. 47). On this basis, samples were divided into three size groups for the analysis of relative condition; $\leq$ 180 mm, 181 - 310 mm and $>$ 310 mm. The smallest group shows similar seasonal trends to B. holubi, with relative condition peaking in summer (Fig. 51). In the larger groups this trend is not observed and generally the condition of L. capensis declined from October 1980 until the end of the study period (Fig. 51). Although small and large L. capensis were in better condition in late summer 1982 than medium-sized fish, all size groups examined were in relatively poor condition.

PERCENTAGE DEVIATION
FROM EXPECTED WEIGHT

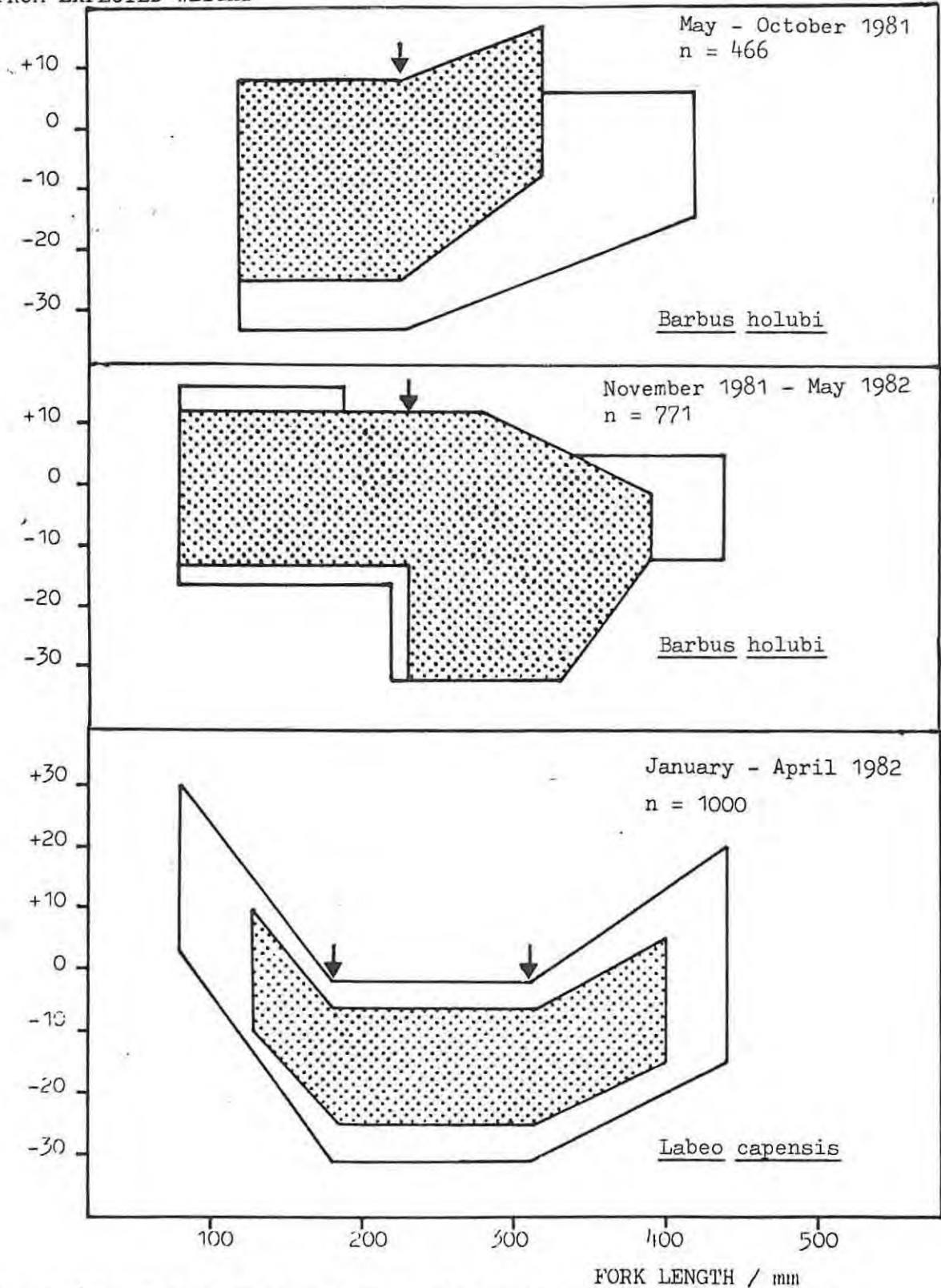


Figure 47. Deviation with length of observed weight from expected weight. 90% of the observations fall within the dotted area and a further 5% in the undotted areas. Changes in the general trend of the deviations are indicated with arrows and lead to the length sub-divisions in Figs. 48, 50 and 51. Positive deviations indicate that fish are in a relatively good condition.

RELATIVE CONDITION FACTOR

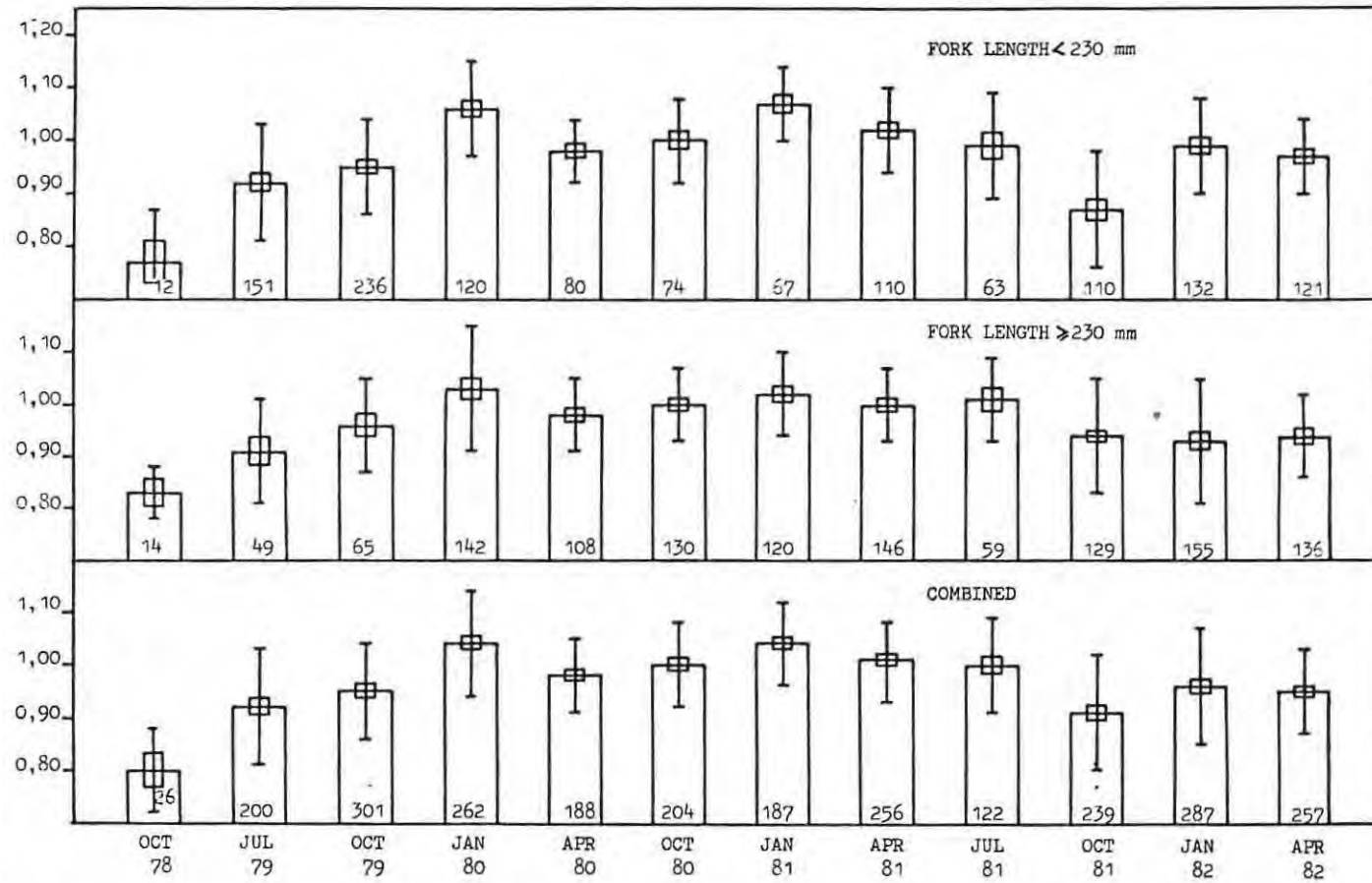


Figure 48. Relative condition of *Barbus holubi* caught during CPA gillnetting surveys in Lake le Roux. The bar shows one standard deviation, and the rectangle a 95% confidence interval. The number of observations is given at the base of the histogram.



Figure 49. Barbus holubi caught at station 5, 16/1 1982, illustrating variation in relative condition. Fish A is 297 mm FL, 346 g, $C = 1,00$ and Fish B is 276 mm FL, 160 g, $C = 0,58$.

RELATIVE CONDITION FACTOR

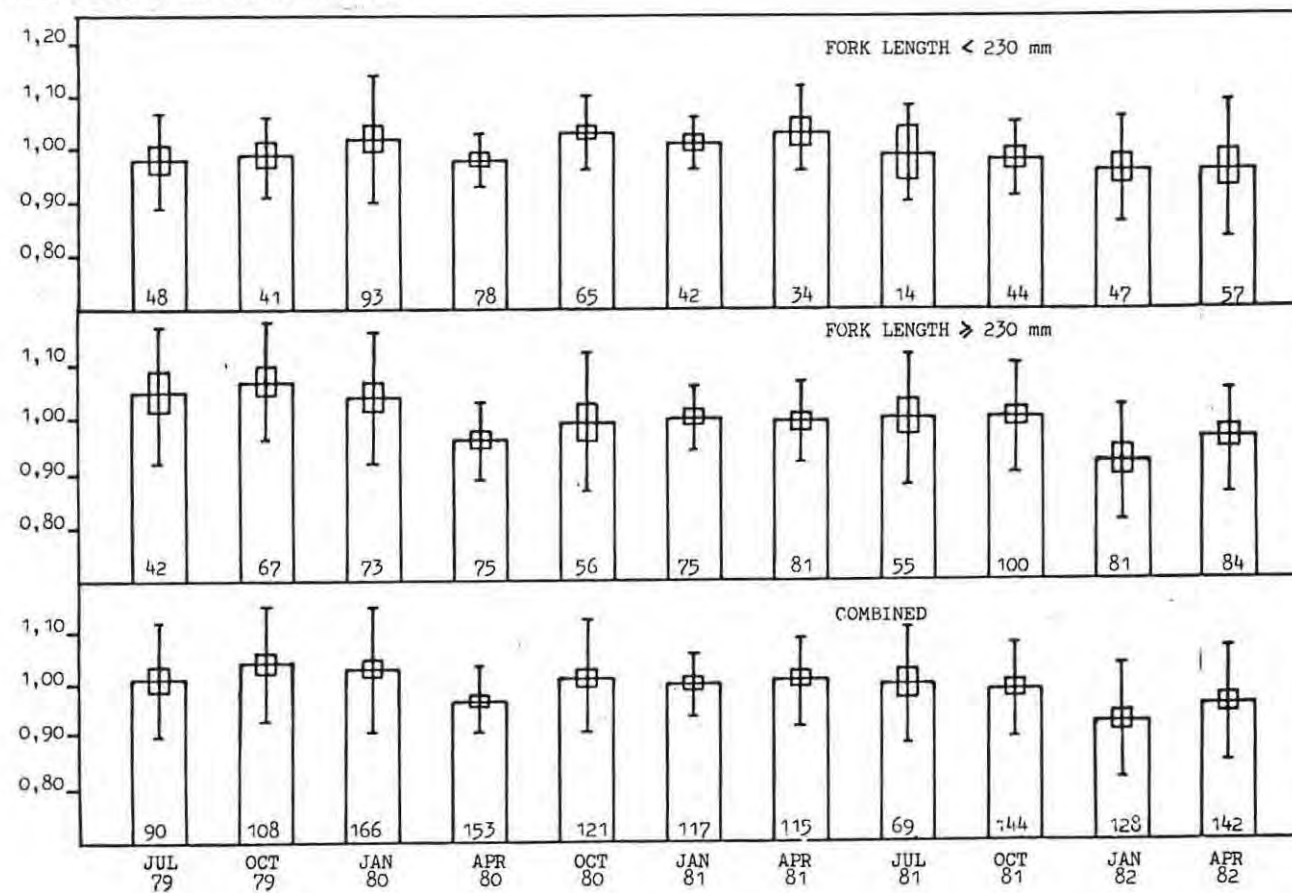


Figure 50. Relative condition of *Barbus kimberleyensis* caught during CPA gillnetting surveys in Lake le Roux. The bar shows one standard deviation and the rectangle a 95% confidence interval. The number of observations is given at the base of the histogram.

RELATIVE CONDITION FACTOR

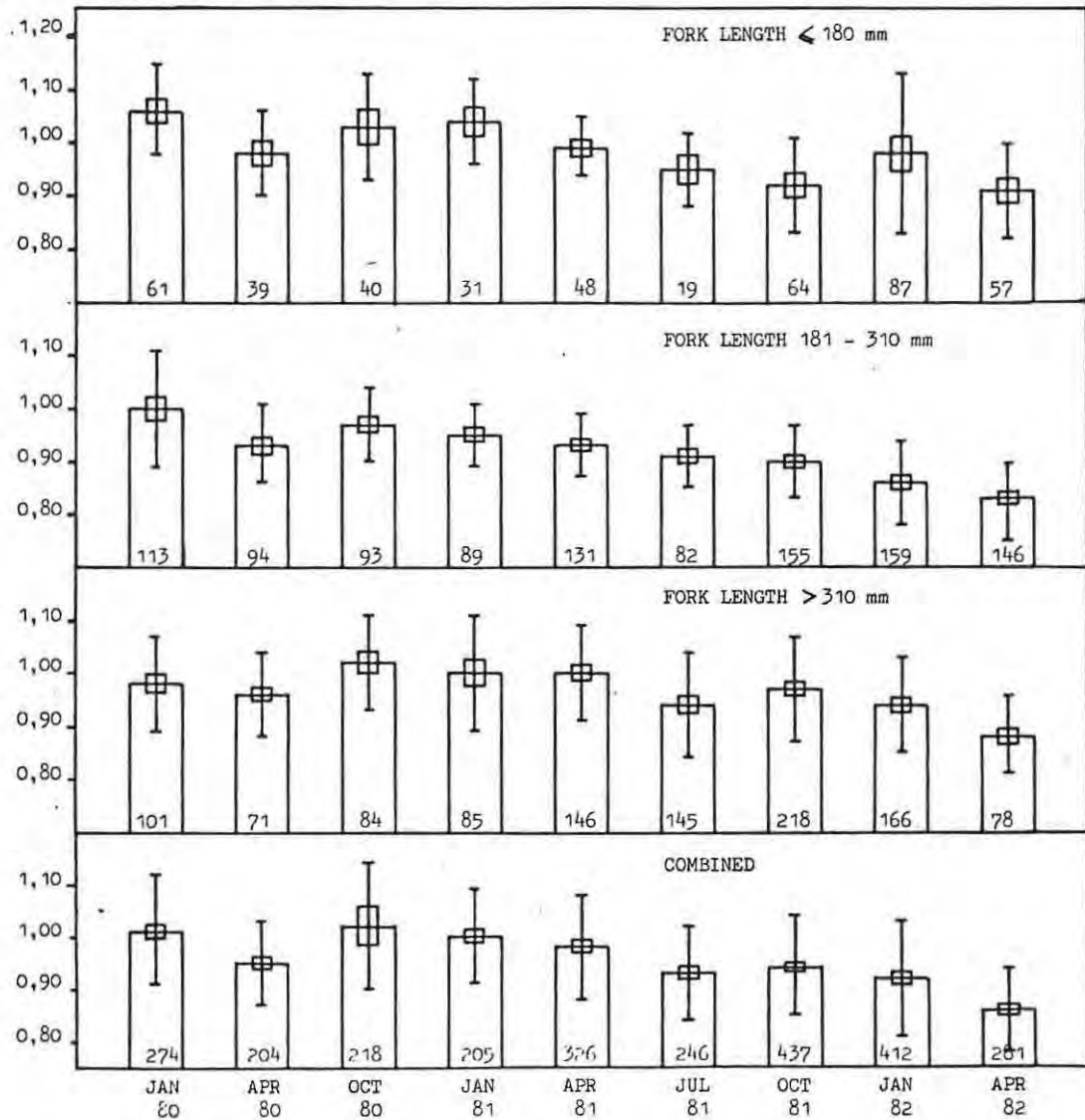


Figure 51. Relative condition of *Labeo capensis* caught during CPA gillnetting surveys in Lake le Roux. The bar shows one standard deviation and the rectangle a 95% confidence interval. The number of observations is given at the base of the histogram.

3. Discussion

Several authors have examined length-weight relationships for B. holubi (Mulder, 1973a; Koch, 1975; Hamman, 1981), B. kimberleyensis (Mulder, 1973a; Bloemhof, 1974; Hamman, 1981) and L. capensis (Mulder, 1973b; Bloemhof, 1974; Baird & Fourie, 1978; Hamman, 1981). In all cases the exponent b does not deviate markedly from three, as was found in this study.

Length-weight relationships in other species may be affected by the selectivity of the fishing gear (Kipling, 1957), size at sexual maturity (Weatherley, 1972) and feeding periodicity (Bruton, 1979). Thus the size composition of the sample and the time of year when samples were taken can affect the relationship. In this study, the relationship for the two Barbus species is based mainly on young, immature fish. However, old individuals of this species can become very deep-bodied and heavy (Chapter II, F). Mulder (1973a) found that B. holubi in the Vaal River became relatively deep-bodied when they exceeded 20 cm in length. The sample used to determine the relationship for L. capensis included many sexually mature fish, in which gonads can make up 20% of total weight. However, as L. capensis grow larger they often accumulate large quantities of intestinal fat as well, which has also been observed by Baird & Fourie (1978). The relationship probably accurately reflects a relative increase in "plumpness" with size.

Seasonal differences in relative condition of B. holubi and L. capensis have also been reported from other water bodies. In Lake Boskop the condition of B. holubi was lowest in winter (Koch, 1975). In Lake Verwoerd, Hamman (1981) found no seasonal differences in the condition of B. holubi, but there was a decline from 1972 to 1976. In this study, only males > 260 mm and females > 310 mm were included. Smaller fish have been shown in the present study to exhibit greater seasonal differences than larger fish and this may account for the absence of seasonal trends in Hamman's (1981) data.

Relative condition of L. capensis was found to be generally higher in summer than at other times of the year in Lake Hardap (Bloemhof, 1974), Lake Boskop (Koch, 1975) and in Lake Verwoerd (Hamman, 1981). In the Caledon River, seasonal differences in

condition were minimal (Baird & Fourie, 1978).

In the present study, B. holubi were in particularly poor condition in October 1978 and October 1981. In both cases, this was preceded by a sharp rise in turbidity during the latter half of the previous summer (Fig. 19). Increasing turbidity can be expected to interfere negatively with the feeding of B. holubi since this species feeds on zooplankton, selecting its prey visually (Eccles, 1980). The negative effects of turbidity are most apparent in spring when the temperature of the water is rising. The small fish adjusted to the new conditions by January, but many of the larger fish were still in poor condition at that time as seen by the large standard deviation (Fig. 48).

The decline in condition of the larger L. capensis had started before the lake became turbid. This may be the result of increasing population density which was then further aggravated by the rise in turbidity (Section B).

B. GROWTH

1. Introduction and rationale

Growth can be studied as changes in individual size or as changes in the size of a population. Growth of individuals and populations is closely linked. Individual growth is usually inversely related to population density (Backiel & Le Cren, 1967), and since fecundity is positively related to size, individual growth increases the reproductive potential of a population (Weatherley, 1972). Generally then, growth of a population is usefully analysed in terms of individual growth.

Fish typically have a wide intraspecific range of growth rates, which reflect different conditions in the environment (Weatherley & Rogers, 1978). Variations in growth rates are usually larger in freshwater than in marine populations, because of larger inter-seasonal variations in freshwater habitats (Weatherley, 1972). Large variations in growth among individuals within a season are also observed, especially when food becomes limiting (Nikolskii, 1969). Similarly, individual growth rate is highly variable in the pond

culture of many species (Purdom, 1974), particularly if there is competition for food (Purdom, 1979). However, it is difficult to differentiate between the effects of space and the effects of food availability (Weatherley, 1972).

Within fresh waters, a distinction can be made between the response to limitations in space or food of fish populations in lotic habitats and lentic habitats. In perennial rivers, territorial behaviour acts to regulate density through reducing population numbers when space or food becomes limiting. In seasonally flowing rivers, biomass also is regulated through reduction in numbers since predation pressure may be extremely high, particularly during the dry season (Jackson, 1961^b; Lowe-McConnell, 1967). In lakes, adult fish tend to respond to limitations in food supply by a reduction in individual growth rate, rather than a reduction in population numbers (Le Cren, 1965). This is the basis for the inverse relationship between density and growth rate in fish populations (Backiel & Le Cren, 1967). Thus the growth rate of individuals in lake populations may improve when subjected to heavy fishing pressure (Healey, 1980), or when there is a marked reduction in population density, due to catastrophic natural events, such as a heavy parasitic infestation (Burrough & Kennedy, 1979).

The mode of population regulation in lakes is particularly important to reservoir fisheries management. During and shortly after filling, reservoirs are usually relatively fertile with rapidly expanding fish populations. The fish population explosion coincides, however, with reduced productivity of the water and unless measures are taken to reduce population numbers at this stage, the food supply may become limited and the fish stunted (Fowler, 1978). Thus a progressive decrease in individual growth rate and a shift in size structure of the population towards smaller fish has frequently been observed and has led to drastic population reduction measures, as reviewed by Thompson (1955), Parsons (1958), Shields (1958) and Jenkins (1970).

Fish production in lakes and ponds depends on density and is highest at some intermediate density (Backiel & Le Cren, 1967; Hofstede, 1974). Thus the estimation of growth should be central to the proper management of fish populations.

In this section, growth will be considered in terms of length. Changes in length are indicative of long term changes, whereas weight changes may occur in the short term (Welcomme, 1979). Changes in weight in relation to length were discussed in Section A. Growth as measured in seasonal length increments will be analysed according to age, sex, locality and size.

2. Spatial differences in growth rates in Lake le Roux

As outlined in the introduction to this section, it is important to continuously monitor seasonal growth of the fish populations. However, it is imperative that before such a study is undertaken, the homogeneity of each species should be established. It is especially important for management purposes to know whether the species exploited forms one population or consists of discrete stocks (MacLean & Evans, 1981). If stocks are spatially separated, one can expect to find differences in population parameters, although this does not necessarily imply reproductive isolation (Casselman et al., 1981).

Patterns of changes in length frequency distribution with locality (Section C) suggest that L. capensis has a tendency to form local populations. Parker & Larkin (1959) argued that size rather than age is the most important factor in determining the growth response of fish to environmental conditions. For example, the ability of fish to obtain and digest food changed with size rather than age. Valid comparisons of growth rates can thus best be made by comparing growth of the same size groups in different years, at different times of the year or from different environments. In Lake le Roux, growth rates for all the species studied become slower further from the dam wall. Longitudinal differences in growth rate showed the same trend in all seasons, but the 1979/1980 season was the earliest from which information on all three species was available.

Analysis of growth rates by locality and season can be used to assess the mobility (mixing) of a species in the lake. This was done in the following manner. Individual growth in the 1979/1980 season was summarized according to the size of individuals at the beginning of the season. This was done separately for stations 2, 4 and 7

at which most sampling has been performed. Growth rate was calculated separately for samples obtained in winter 1980, summer 1980/1981, winter 1981 and summer 1981/1982. The increments of the 1979/1980 season were then compared for each sampling period by size group and locality. For example, Table 15 shows that B. holubi which were 50 - 99 mm in winter 1979 showed increments of 81, 66 and 58 mm at stations 2, 4 and 7 respectively as calculated from samples taken at these stations in winter 1980. Increments for the same size group in the 1979/1980 season, calculated from samples taken in subsequent seasons show that the differences with locality observed in the winter of 1980, disappear with time. The reduction in increment at station 2, and the increase at station 7 cannot be explained by differential mortality and is almost certainly the result of mixing.

a. Barbus holubi

The results from the samples taken in winter 1980 show a significant difference in length increments between stations 2 and 7 for all length groups (Table 15). There is an increase in both absolute and relative difference with size. In the 50 - 99 mm group, there is a general reduction in increments calculated from the data collected in summer 1980/1981, from the winter 1980 results. This is caused by recruitment, with some of the slower growers of that size group not fully recruited into the sampling gear by winter 1980. The observed differences in winter 1980 disappear during the following one or two seasons, indicating that B. holubi move freely within the lake and do not form local populations. Mixing is slower in the smallest size group than the larger ones.

b. Barbus kimberleyensis

Growth increments of size groups at different stations in 1979/1980 as calculated from samples taken in subsequent seasons are shown in Table 16. The pattern observed is similar to that of B. holubi. There is an increase in relative difference of increments with size group between localities in winter 1980. Differences in growth rate with locality disappear with time and the rate of mixing is faster in the larger size groups than in the smallest one.

Table 15. Length increments of different size groups of B. holubi in summer 1979/80, by locality and season.

Length group	Station	Growth in 79/80 (mm $\pm$ 95% confidence interval) as calculated from samples collected in			
		winter 80	summer 80/81	winter 81	summer 81/82
50 - 99 mm	2	81(5,8)	68(5,8)	68(5,2)	65(12,1)
	4	66(5,4)	57(7,1)	75(10,0)	68(6,5)
	7	58(5,7)	52(6,3)	60(9,0)	66(15,2)
100 - 149 mm	2	87(3,7)	83(4,5)	76(7,2)	85(6,9)
	4	79(4,9)	80(7,1)	83(5,1)	82(5,0)
	7	63(5,9)	76(5,8)	74(5,0)	75(5,6)
150 - 199 mm	2	77(4,2)	79(6,6)	78(6,9)	78(7,8)
	4	65(7,0)	73(8,3)	76(9,8)	76(6,6)
	7	50(6,7)	68(9,1)	74(8,9)	76(9,1)
200 - 249 mm	2	70(7,1)	76(7,5)	74(11,4)	81(8,3)
	4	63(7,0)	58(13,0)	65(15,0)	66(12,3)
	7	40(17,0)	59(11,3)	69(24,0)	67(38,2)

Table 16. Length increments of different size groups of B. kimberleyensis in summer 1979/1980, by locality and season.

Length group	Station	Growth in 79/80 (mm $\pm$ 95% confidence interval) as calculated from samples collected in			
		winter 80	summer 80/81	winter 81	summer 81/82
50 - 99 mm	2	99(9,2)	71(8,0)	64(8,0)	68(11,3)
	4	81(12,7)	71(8,5)	64(4,6)	65(14,7)
	7	63(8,7)	57(4,7)	62(13,3)	64(11,0)
100 - 149 mm	2	86(19,6)	76(9,0)	70(13,9)	59(6,3)
	4	74(10,8)	72(18,1)	63(9,2)	59(11,3)
	7	57(6,9)	59(6,8)	57(26,1)	62(10,3)
150 - 199 mm	2	81(6,0)	68(7,2)	60(9,4)	74(22,6)
	4	65(8,0)	69(6,4)	63(9,2)	67(9,2)
	7	50(8,0)	59(6,1)	51(8,0)	76(24,7)

c. Labeo capensis

The pattern of observed differences in the 1979/1980 length increments with size group and locality for L. capensis are presented in Table 17. The temporal change in observed differences of the smallest size group follows the same pattern as in the Barbus species. Differences are maintained for longer in the 100 - 149 mm group than in the same group of Barbus, but growth rates between localities in the 150 - 199 mm group were not significant. Significant differences between increments at stations 2 and 7 in the 200 - 299 mm groups were maintained throughout the period of study. In the two largest groups observed initial differences disappear with time.

The reasons for the disappearance of observed differences in the smallest and largest size groups are probably not the same. The smaller fish dispersed in the lake following a sharp increase in turbidity in 1981 (Section C). The largest size groups may experience a differential mortality rate. Results presented in the following subsection indicate that fast-growing L. capensis males have a higher mortality rate than slower growers.

3. Growth of individual year classes

Initial differences in growth rate have been found in all the species studied. The two Barbus species are highly mobile and form homogenous populations. Labeo capensis is less mobile, but although exploitation might cause local depletion, such areas would eventually be "seeded" from other parts of the lake (Section C). Each species can thus be considered to form one stock and it is valid to combine all observations when temporal patterns in growth are examined.

When backcalculated lengths were compared to observed lengths (Chapter IV, B, Figs. 39 to 46) no trend could be observed with time that could not be ascribed to recruitment. Therefore, to increase the number of observations, all observed lengths at age in winter and backcalculated lengths have been combined when the growth of year classes was studied. The results are presented in detail in Appendix 1, and are presented in graphical form in this subsection.

Table 17. Length increments of different size groups of L. capensis in summer 1979/1980, by locality and season.

Length	Station	Growth in 79/80 (mm 95% confidence interval) as calculated from samples collected in			
		winter 80	summer 80/81	winter 81	summer 81/82
50 - 99 mm	2	62(5,0)	54(7,8)	56(8,6)	45(6,7)
	4	51(4,8)	46(5,7)	44(5,7)	43(4,3)
	7	33(5,2)	29(5,1)	44(6,4)	42(5,2)
100 - 149 mm	2	57(5,5)	51(5,6)	58(6,1)	48(5,2)
	4	40(3,8)	47(4,9)	49(5,7)	49(4,0)
	7	36(4,5)	38(5,7)	45(9,2)	45(5,5)
150 - 199 mm	2	56(4,0)	57(4,3)	56(6,0)	57(4,8)
	4	43(4,7)	51(5,8)	53(6,4)	45(4,7)
	7	48(12,2)	35(7,2)	43(8,8)	48(6,3)
200 - 249 mm	2	53(3,5)	51(4,9)	54(4,9)	54(4,1)
	4	42(4,0)	45(4,8)	58(5,8)	50(5,5)
	7	34(7,8)	36(5,8)	45(7,6)	37(8,2)
250 - 299 mm	2	40(4,5)	45(5,5)	51(5,7)	45(5,5)
	4	39(6,1)	37(4,9)	34(9,8)	33(10,6)
	7	21(9,07)	25(5,7)	31(6,4)	24(7,2)
300 - 349 mm	2	33(2,7)	38(4,0)	31(5,8)	28(4,7)
	4	27(3,0)	34(3,6)	32(4,5)	34(5,7)
	7	18(2,8)	27(4,3)	28(5,0)	25(4,3)
350 - 399 mm	7	26(4,1)	33(4,4)	27(8,0)	29(7,6)
	4	22(5,5)	27(7,6)	17(2,0)	28(9,1)
	7	17(2,8)	21(5,7)	19(4,2)	31(4,5)

a. Barbus holubi

Lengths at age for each year class are presented separately for males (Fig. 52) and females (Fig. 53). Growth rates of the two sexes are similar initially, but females grow faster than males from the age of five to seven years, depending on year class. Length at the end of the first summer is fairly constant for all year classes, except for the 1980/1981 year class. The observed similarity may in part be due to the method used. The first annulus is difficult to identify or may be absent on the scales of fish which are less than 50 mm in length at the end of their first growing season. The apparent larger size at age 1 for the 1980/1981 year class is probably caused by gear selectivity. At the end of the sampling programme, only the faster growers of this year class were recruited into the gillnets. In previous years, backcalculated data for slower growers was included.

At age 2, post-impoundment year classes are significantly larger than pre-impoundment year classes (Appendix 1, Tables 1 and 2), indicating improved growing conditions for 1+ fish in the lake. There are large inter-seasonal variations in growth, which increase with the age (size) of the fish. This variation in growth will be analysed further in the following subsection.

b. Barbus kimberleyensis

B. kimberleyensis reach a larger size than B. holubi in Lake le Roux. The growth rates of males (Fig. 54) and females (Fig. 55) are similar, but, as seen from the relatively abundant 1972/1973 year class (Appendix 1, Tables 3 and 4), females grow faster than males late in life. The contrast at age two between pre- and post-impoundment year classes is not as sharp as that observed for B. holubi. Size at age two is smaller for B. kimberleyensis than for B. holubi, but the difference is less at age three and disappears by age four.

c. Labeo capensis

Size at age is similar for males and females of the 1975/1976 year class and younger, but in older fish, females tend to be larger than males even at age 3 and sometimes at age 2 (Figs. 56 and 57, Appendix 1, Tables 5 and 6). These results indicate that differences

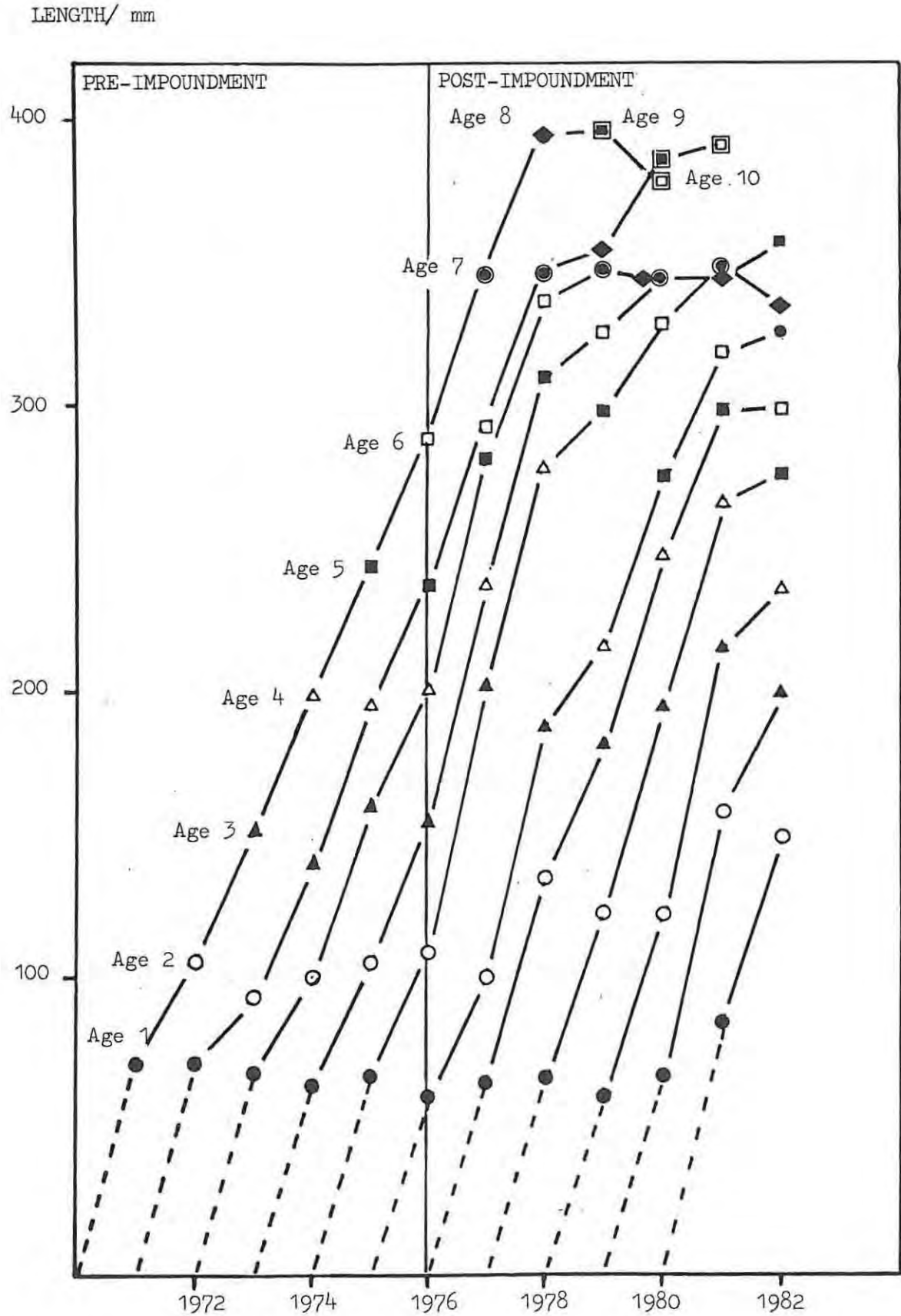


Figure 52. Length at age of male *B. holubi* in Lake le Roux, based on backcalculated and observed lengths. Year classes are connected by solid lines. All fish of the same age are denoted by the same symbol.

LENGTH/ mm

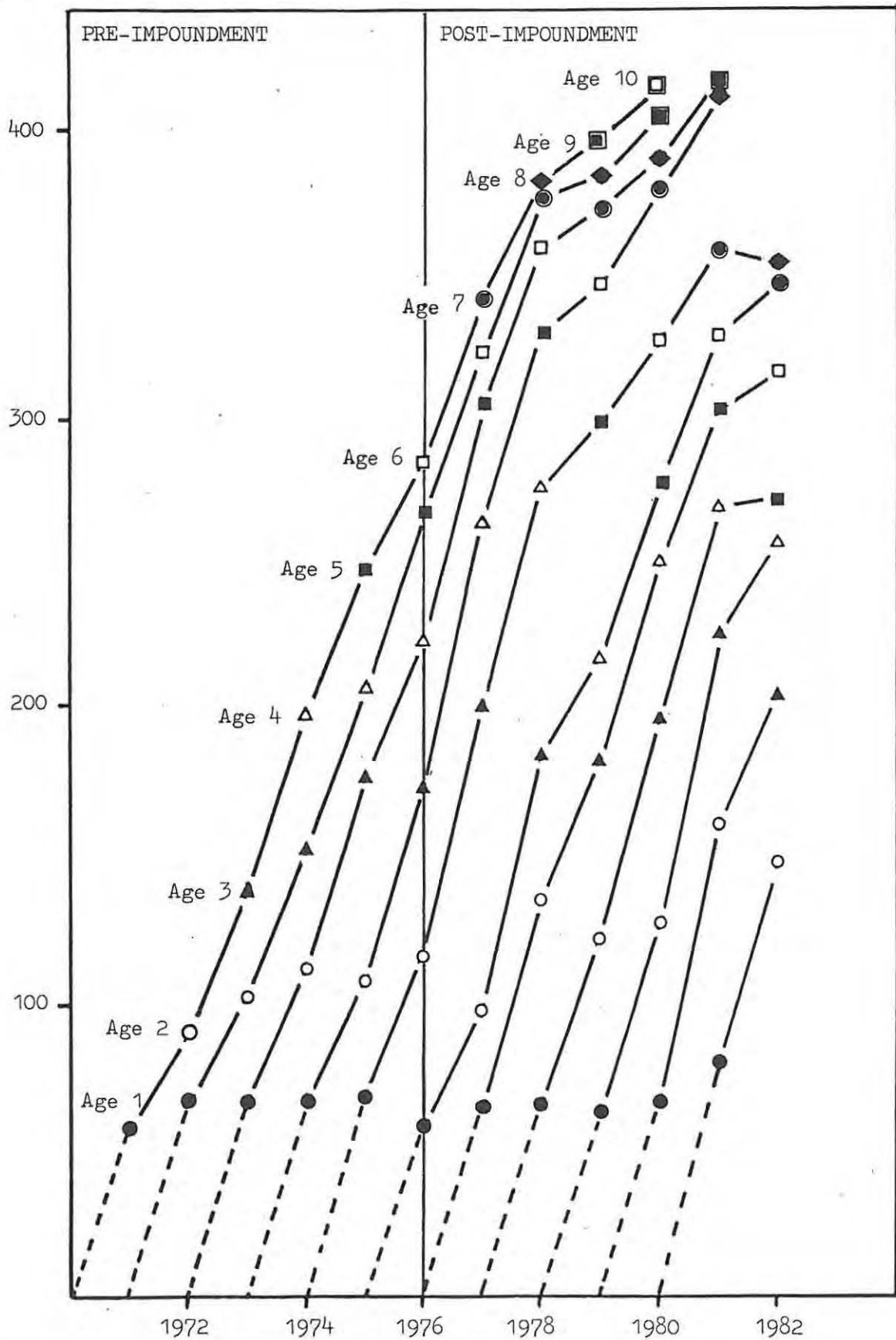


Figure 53. Length at age of female *B. holubi* in Lake le Roux, based on backcalculated and observed lengths. Year classes are connected by solid lines. All fish of the same age are denoted by the same symbol.

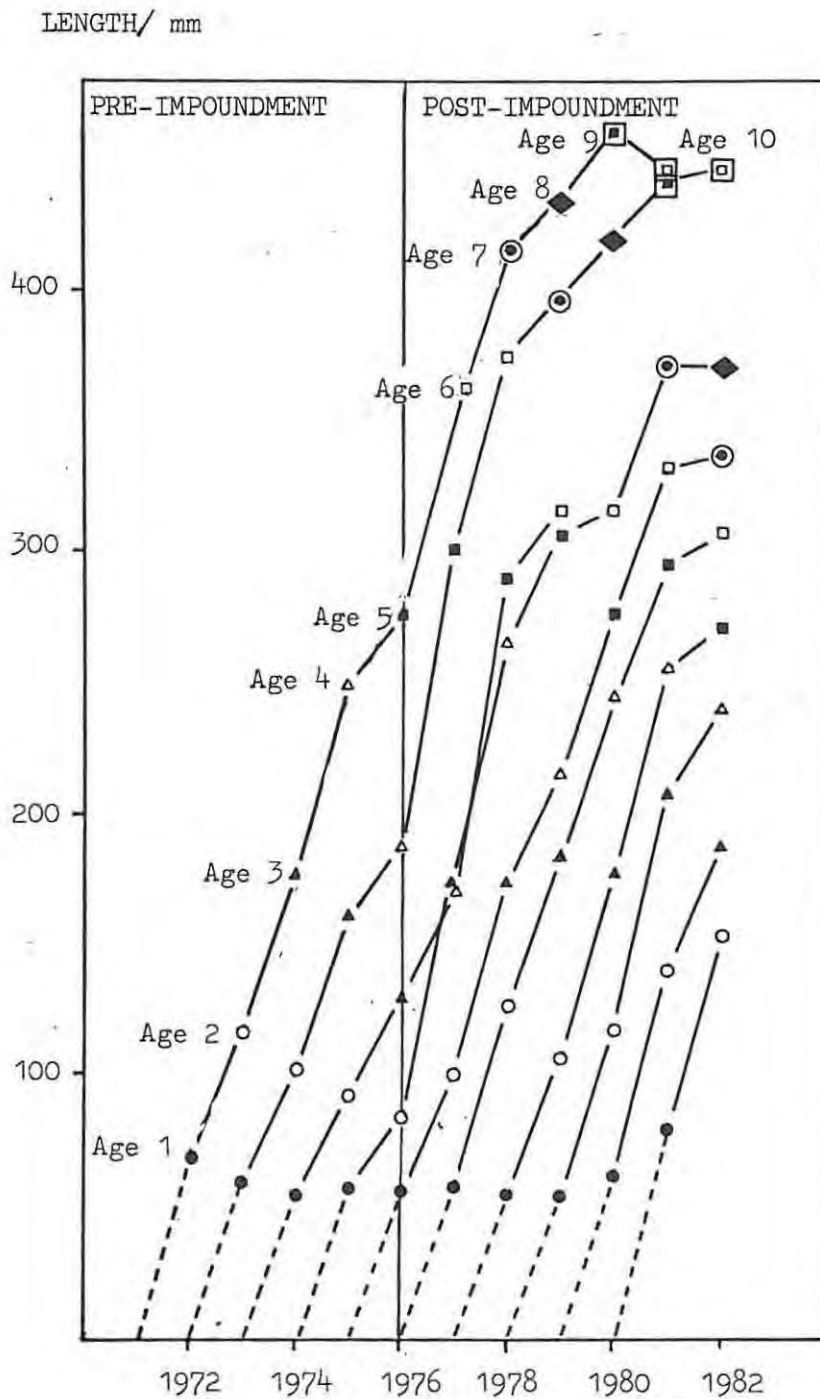


Figure 54. Length at age of male *B. kimberleyensis* in Lake le Roux, based on backcalculated and observed lengths. Year classes are connected by solid lines. All fish of the same age are denoted by the same symbol.

LENGTH/ mm

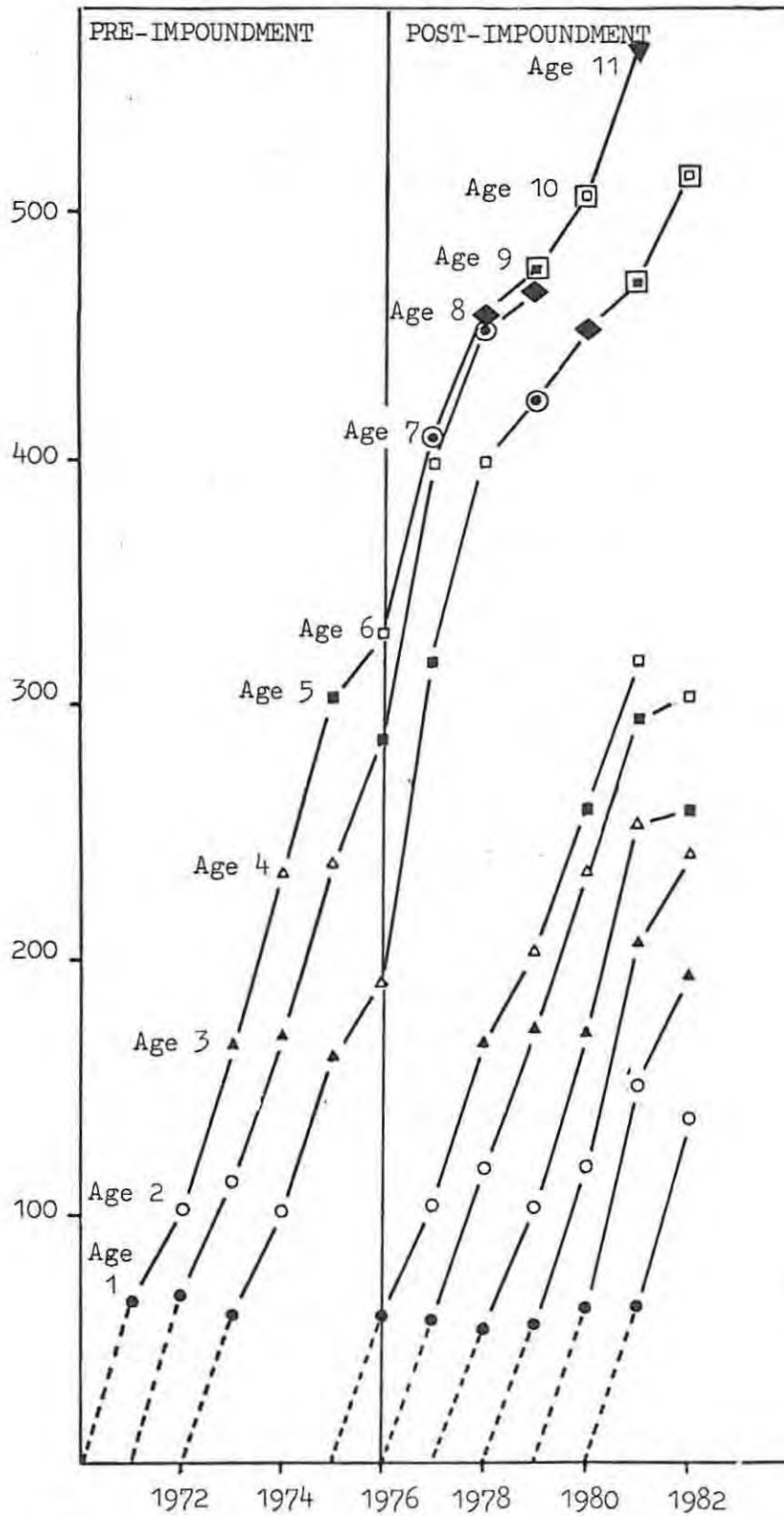


Figure 55. Length at age of female *B. kimberleyensis* in Lake le Roux, based on backcalculated and observed lengths. Year classes are connected by solid lines. All fish of the same age are denoted by the same symbol.

LENGTH/ mm

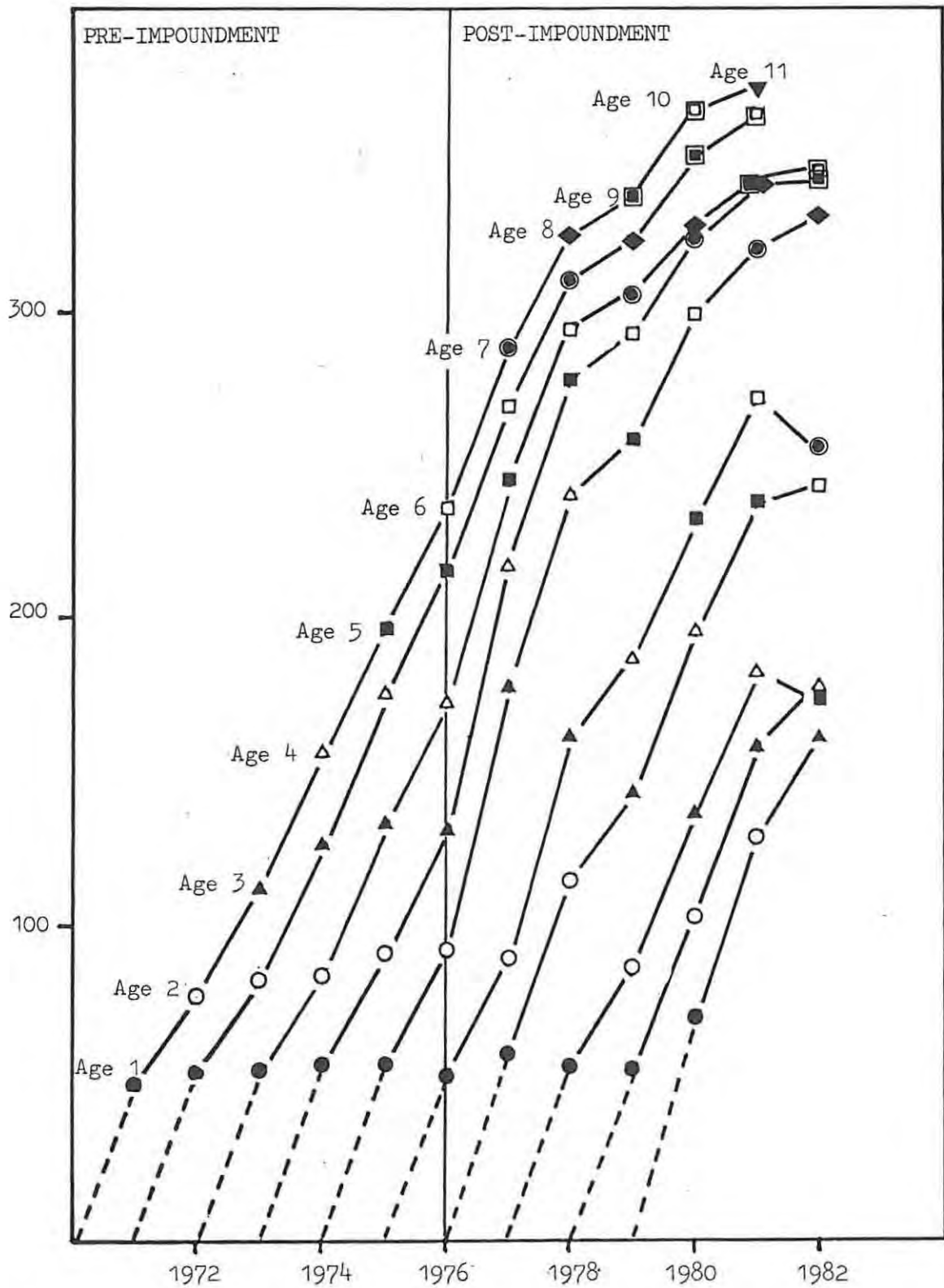


Figure 56. Length at age of male *L. capensis* in Lake le Roux, based on backcalculated and observed lengths. Year classes are connected by solid lines. All fish of the same age are denoted by the same symbol.

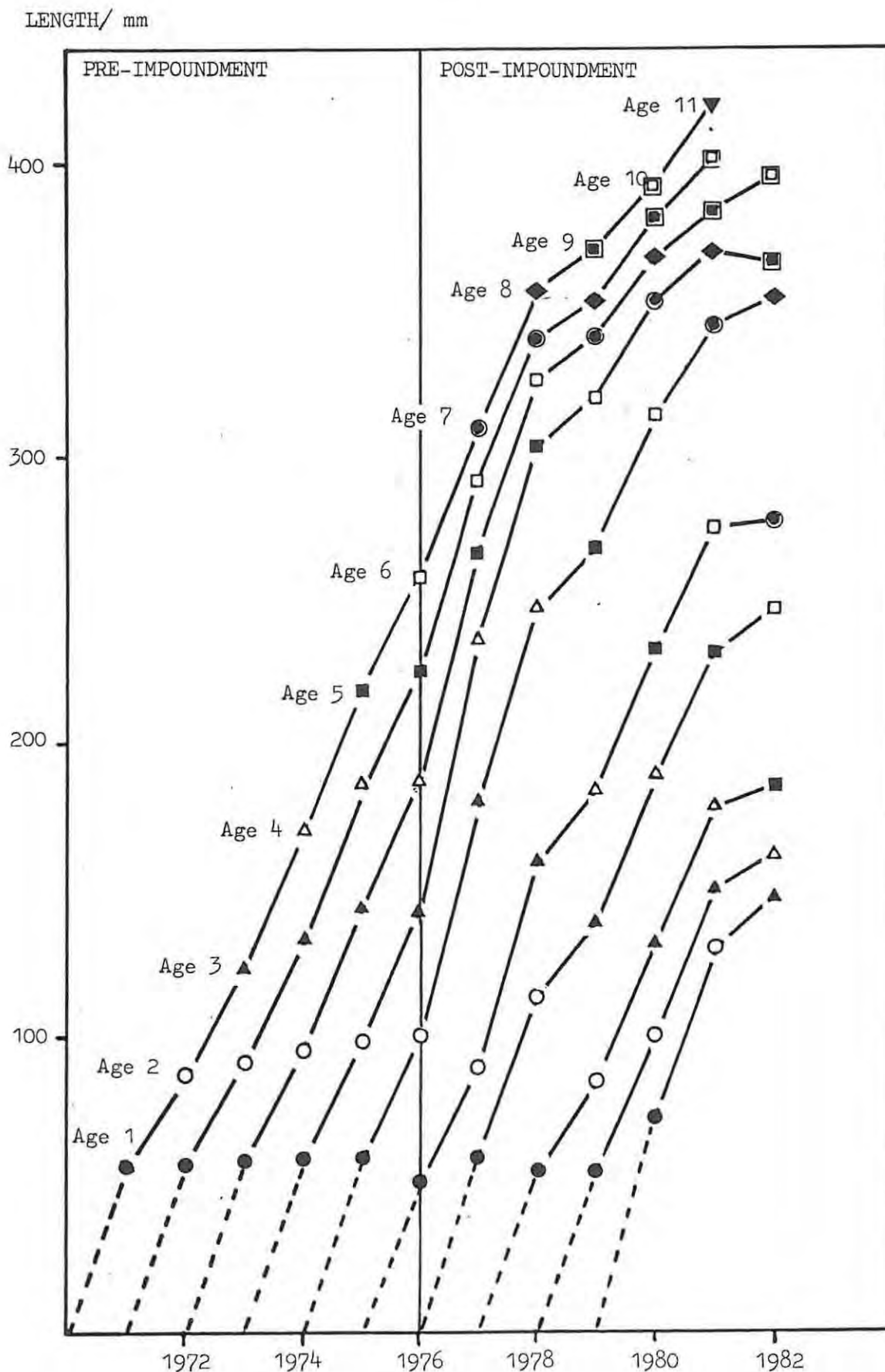


Figure 57. Length at age of female *L. capensis* in Lake le Roux, based on backcalculated and observed lengths. Year classes are connected by solid lines. All fish of the same age are denoted by the same symbol.

in observed lengths-at-age between males and females are due to differential mortality between fast and slow growing males, and do not necessarily reflect sex-related differences in growth rate. Males mature at a smaller size than females (Section C) and faster growing individuals mature at a younger age than slower growers.

Alm (1959) found for many species that spawning did not cause increased mortality. In Lake le Roux, spawning of L. capensis does not necessarily weaken individuals enough to induce increased mortality. Spent L. capensis were often caught and invariably found to be in good condition. However, spawning occurs in temporary habitats in newly inundated shallow marginal areas. Thus breeding populations are susceptible to stranding and their vulnerability to predation is increased during spawning. In the Orange River, downstream from Lake le Roux, farmers have reported that in spring and summer adult L. capensis were occasionally found stranded in small residual pools when flow in the river had suddenly been reduced.

The good growing conditions which were created in the lake during the first two years of impoundment apparently could only be utilized to the full by fish in their third growing season or older. This has caused the relatively large gap between the growth lines of the 1974/1975 year class and the 1975/1976 year class. The latter year class, and younger cohorts, show a particularly poor growth rate as compared to the two Barbus species.

4. Inter-seasonal variations in growth rate

Figs. 52 to 57 show that there have been considerable inter-seasonal variations in growth since the lake was formed in October 1976. It is however difficult to quantitatively compare seasonal growth rates from these figures. In this subsection, inter-seasonal variations in growth will be assessed using two different methods. The first method, described by Kempe (1962), considers relative growth of year classes among seasons. The second method, developed in this study, is based on absolute length increments of size groups, from which growth curves are constructed.

a. Description and discussion of methods

In the method presented by Kempe (1962), a "standard of growth" is calculated as the average increment of each age group over a series of years. For example, the standard of growth of age 2 Barbus holubi in Lake le Roux is 71 mm, the average increment of age 2 fish in the six seasons since the lake was formed (Table 18). Increments for each year class in individual years are then expressed as a percentage of the standard, giving relative growth. In the original method (Kempe, 1962), weighted averages were taken, but in the present study arithmetic averages were used. There are two reasons for this :

- i. The calculations of growth of year classes in the present study are largely based on backcalculated values and sample size does not necessarily reflect the relative abundance of year classes in any given year.
- ii. The main interest here is to examine variations in individual growth, whereas Kempe's (1962) original method is more appropriate when population growth is analysed.

In calculating length increments, both sexes have been combined and only growth for the third season onwards has been considered. This is because the first annulus on many scales could not always be read. An estimate of the first season's growth would therefore be positively biased and negatively biased for the second season's growth. Also, time of spawning varies among seasons and, if an accurate assessment of the first season's growth was possible, it might not accurately reflect growing conditions in the lake. This method offers a quick way to compare seasonal growth rates within a lake.

The second method is laborious, but is less susceptible to sampling bias than the first method. Growth is usually more dependent on length than on age (Parker & Larkin, 1959), and data analysed according to length are not affected by non-random sampling of the population, except possibly for the smallest size groups. This method does not require a "standard" and comparisons can be made between water bodies. In populations where annuli are difficult to interpret near the centre of the scale, growth curves can be constructed from the last few years' increments. There is no

need to know the absolute age of the fish.

In constructing growth curves for each season, it was assumed that length at the end of the first season was always 60 mm. This value was chosen based on Figs. 52 to 57. Variations in growth usually increase with size (age) (Deelder, 1951; Kempe, 1962). Fixing the size at the beginning of the second season should not introduce a marked bias. The increment in the second season is taken as the average increment of the 50, 60, and 70 mm size groups. This increment added to 60 mm gave the hypothetical size at the beginning of the third growing season. Growth in the third season was calculated from three length groups around the value obtained for size at the beginning of the season. This procedure was then repeated for the whole size range for which data were available. For example, the growth curve for male *B. holubi* during the 1980/1981 season (Fig. 58) was calculated as follows:

- i. Length at end of first season: 60 mm.
- ii. Average increment of 50, 60 and 70 mm length groups in 1980/1981: 88 mm.
- iii. Length at end of second season: $60 + 88 = 148$ mm.
- iv. Growth during third season was the average increment of 130, 140 and 150 mm size groups: 94 mm.
- v. Length at end of third season is thus: $148 + 94 = 242$ mm.

This procedure is then continued until no more data are available.

Growth curves were usually calculated separately for males and females. The von Bertalanffy growth model was fitted to the data, as described by Everhart *et al.* (1975). The model describes a sigmoid curve approaching an asymptotic length. The curve is given by the relationship

$$l_t = L_{\infty} (1 - e^{-K(t-t_0)})$$

where l_t is length at time t ($t = 1, 2, 3 \dots$),

L_{∞} is the asymptotic length,

e is the base for natural logarithms,

K is a "coefficient of growth" which describes how fast L_{∞} is approached,

and t_0 is the time at which length equals 0.

The correlation coefficient (r^2) for a Walford regression of length at

age $t + 1$ against length at age t varied from 0,98 to 1,00. A good fit for the Walford regression shows that the data are well described by the von Bertalanffy model (Everhart et al., 1975). This confirms that, given a constant environment, growth is dependent on length, as was suggested earlier in this section.

b. Barbus holubi

The relative growth rate of different year classes of B. holubi in Lake le Roux is shown in Table 18. Relative growth varies among seasons, the variation increasing with age. However, the extent of growth in different years is similar for all age groups. Exceptions to this are age 4 in 1980/1981 and 1979/1980 and age 2 in 1980/1981. The latter is possibly due to differential mortality with fast growing fish of the 1974/1975 year class (age 2 in 1976/1977) being shorter lived than the slower growers.

The growth curves constructed on the basis of seasonal increments of size groups are shown in Fig. 58, and the von Bertalanffy growth equations are given in Table 19. Females reach a larger ultimate size than males and their coefficient of growth (K) is generally lower than that of males. This is supported by the observation that females predominate among older fish (Appendix 1, Tables 1 & 2).

Growth was best in the 1976/1977 season when the lake filled (Table 18). During subsequent seasons, relative growth rates of B. holubi are closely related to turbidity (Fig. 59). However, as seen in Fig. 58, the growth rates of fish smaller than 260 - 280 mm were faster in 1980/1981 than in 1979/1980. The trend is reversed in fish larger than 280 mm which grew slower in 1980/1981 than the previous season. This is probably an effect of density. In October 1980, density of B. holubi was more than three times higher than in October 1979 (Fig. 60).

Similarly, the differences in both relative growth rates (Table 18) and growth curves (Fig. 58) between the 1978/1979 and 1981/1982 seasons in which the water was equally turbid can partially be explained by density effects. There was a large-scale mortality before and during both seasons as indicated by the decline in biomass in Fig. 60. However, in 1978 the effect was more severe (the relative condition factor in October 1978 was 0,80 as opposed to 0,91 in October 1981,

Table 18. Average annual increments of B. holubi in Lake le Roux, expressed as increments in fork length, in mm, and as percentage of average growth over all seasons.

Growth of <u>B. holubi</u> at age							
Season		2	3	4	5	6	Average percentage of standard
1981/1982	mm	42	38	7	6	10	
	%	59	59	15	17	33	37
1980/1981	mm	94	73	52	47	26	
	%	132	114	108	134	87	115
1979/1980	mm	72	67	61	29	26	
	%	101	105	127	82	87	101
1978/1979	mm	46	31	20	16	15	
	%	65	48	42	46	50	50
1977/1978	mm	86	79	59	48	49	
	%	121	123	123	137	163	133
1976/1977	mm	87	98	89	62	57	
	%	123	153	185	177	190	166
Mean increment "standard"	mm	71	64	48	35	30	

Table 19. Values for the constants in the von Bertalanffy growth equation as fitted to length increments of Barbus holubi in different seasons in Lake le Roux.

Season	Sex	L_{∞}	K	t_0
1977/1978	males	603	0,19	0,52
	females	710	0,16	0,47
1978/1979	males	403	0,20	0,61
	females	435	0,16	0,15
1979/1980	males	529	0,19	0,31
	females	535	0,18	0,21
1980/1981	males	435	0,31	0,50
	females	476	0,26	0,37
1981/1982	males	261	0,34	0,25
	females	260	0,37	0,30

LENGTH/ mm

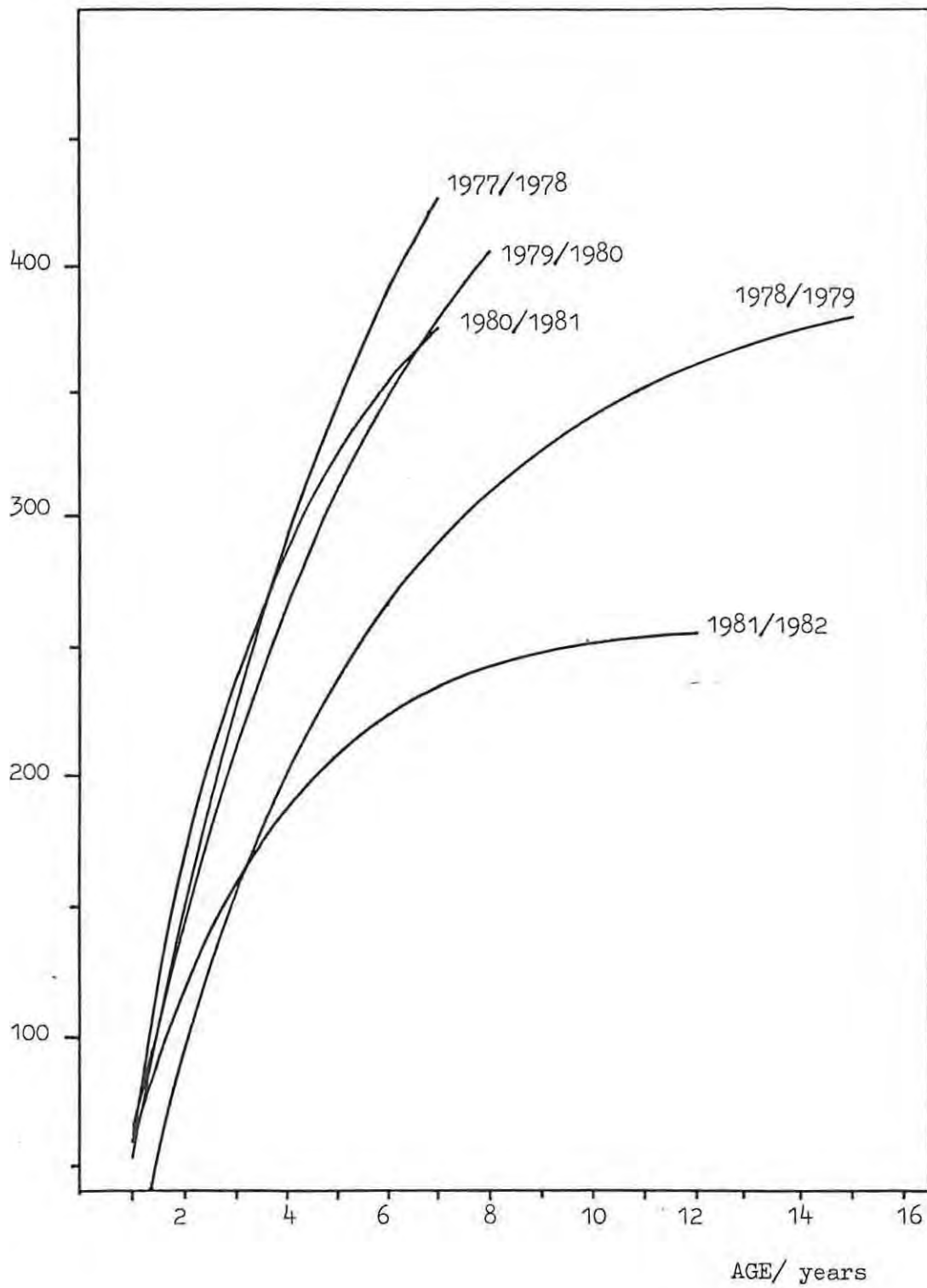


Figure 58. Constructed growth curves for male *B. holubi* in Lake le Roux during different seasons, fitted to the von Bertalanffy growth model.

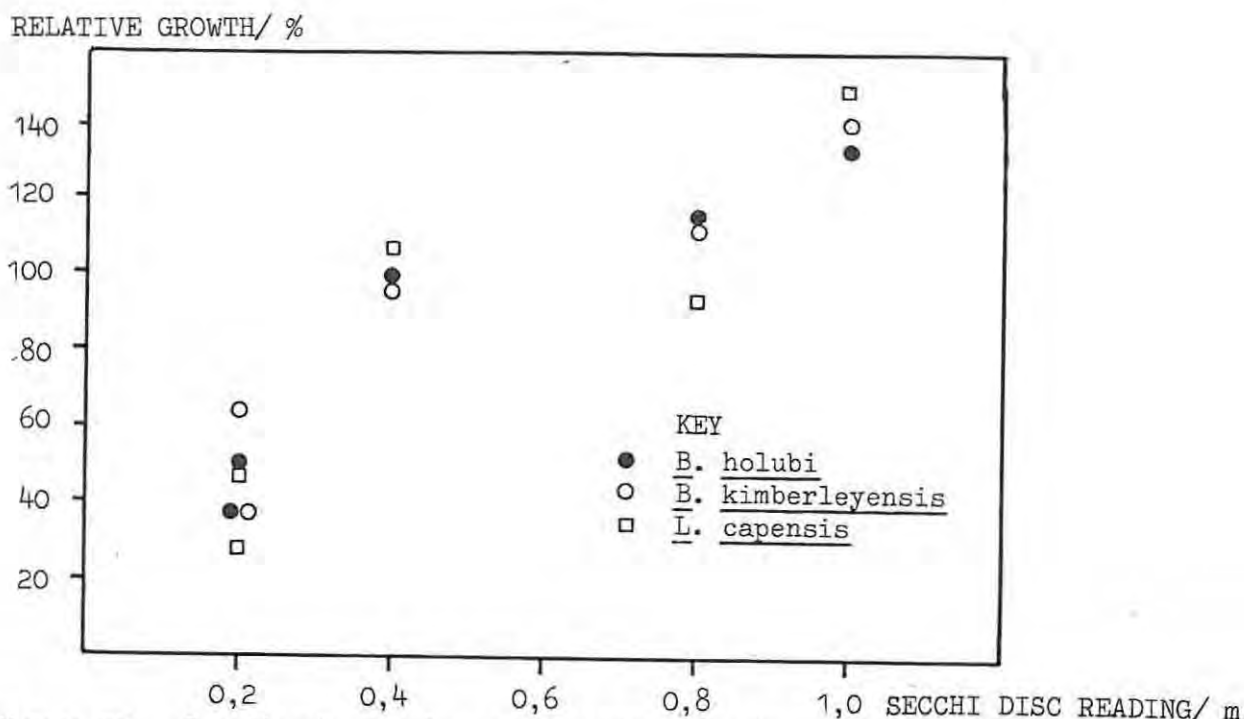


Figure 59. Growth of some large cyprinids in Lake le Roux from 1977 to 1982, in relation to water clarity at Station 1 in January. A season's growth is expressed as a percentage of average length increments in 1976 to 1982.

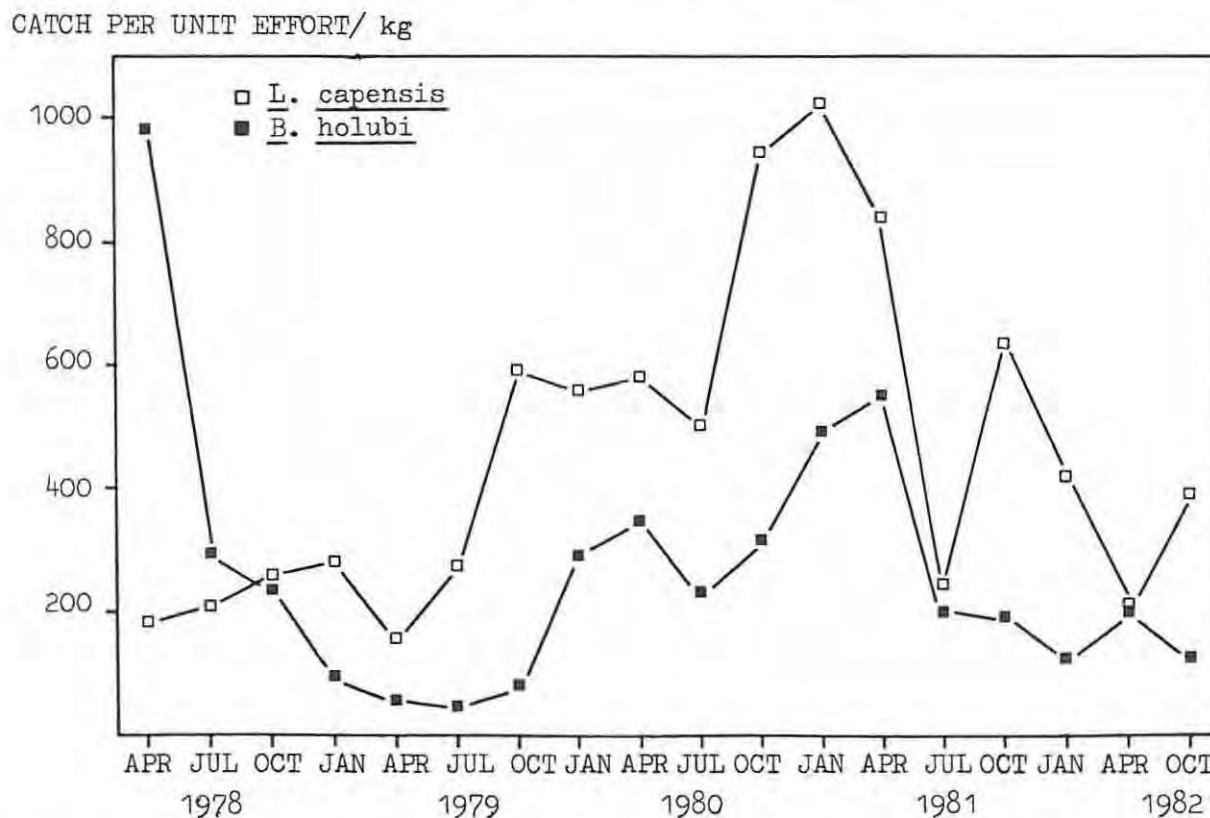


Figure 60. Temporal changes in catch per unit effort of Barbus holubi and Labeo capensis in Lake le Roux. Catches were adjusted for gillnet selectivity (Figure 14) and then converted to biomass using length-weight relationships (Table 14) and relative condition (Figure 48 and 51). When relative condition was not known, it was taken to be 1,00.

Fig. 48), probably due to the higher initial abundance of fish in 1978. Thus, while a large portion of the fish in 1981/1982 lingered on for most of the season, density was adjusted sooner in 1978/1979 to below the carrying capacity of the environment and growth was resumed. The growing period in 1978/1979 may also have been longer than in 1981/1982. Temperatures during the 1978/1979 seasons were generally warmer and surface waters in the pelagic zone remained above 20°C for about six weeks longer than in 1981/1982 (Table 12).

The effect of turbidity may be two-fold. Hart (1981) found that zooplankton production is negatively related to turbidity and reduced field of vision further limits the use B. holubi can make of this resource. This may explain why larger fish show a greater density-dependent decline in growth rates than the smaller individuals.

c. Barbus kimberleyensis

The relative growth rate of B. kimberleyensis is presented in Table 20. The trend with age and season is the same as observed for B. holubi (Table 18, Figs. 58 and 61. This is to be expected since during the first years of their lives, these species have similar feeding habits. Later B. kimberleyensis turn to piscivory and this is reflected in the large L_{∞} values in the von Bertalanffy growth equations for this species (Table 21). The growth curve for 1981/1982 is based on the growth of individuals which were less than 270 mm. The result is misleading in that nine specimens larger than 400 mm caught in April 1982 showed an average increment of 7 mm. However, if conditions in the lake were to remain as they were in 1981/1982 (Fig. 61), it would be several years before B. kimberleyensis turned to piscivory. Such a situation does not favour the building up of substantial numbers of large specimens of this prized sport fish.

d. Labeo capensis

L. capensis growth is characterized by equal reduction in relative growth rates for all age groups when conditions are poor e.g. 1978/1979 and 1981/1982 seasons (Table 22). Relative growth is similar for all year classes in each year, whereas in the Barbus species it was much less variable for the younger fish. However, when combined, the pattern is like that observed for the Barbus, except in the 1979/1980

Table 20. Average annual increments of B. kimberleyensis in Lake le Roux, expressed as increments in fork length, in mm, and as percentage of average growth over all seasons.

Season		Growth of <u>B. kimberleyensis</u> at age				Average percentage of standard
		2	3	4	5	
1981/1982	mm	45	32	12	12	39
	%	65	53	18	22	
1980/1981	mm	90	81	54	55	112
	%	130	135	83	102	
1979/1980	mm	69	61	60	*	98
	%	100	102	92		
1978/1979	mm	56	39	38	30	65
	%	81	65	58	56	
1977/1978	mm	69	88	109	78	140
	%	100	147	168	144	
1976/1977	mm	88	60	119	97	148
	%	128	100	183	180	
Mean increment "standard"		mm	69	60	65	54

* insufficient data available

Table 21. Values for the constants in the von Bertalanffy growth equation as fitted to length increments of Barbus kimberleyensis in different seasons in Lake le Roux.

Season	Sex	L_{∞}	K	t_0
1977/1978	combined	1073	0,09	0,48
1978/1979	males	553	0,13	0,03
	females	639	0,11	0,10
1979/1980	males	556	0,16	0,20
	females	630	0,14	0,20
1980/1981	males	512	0,22	0,39
	females	574	0,18	0,38
1981/1982	combined	288	0,40	0,43

LENGTH/ mm

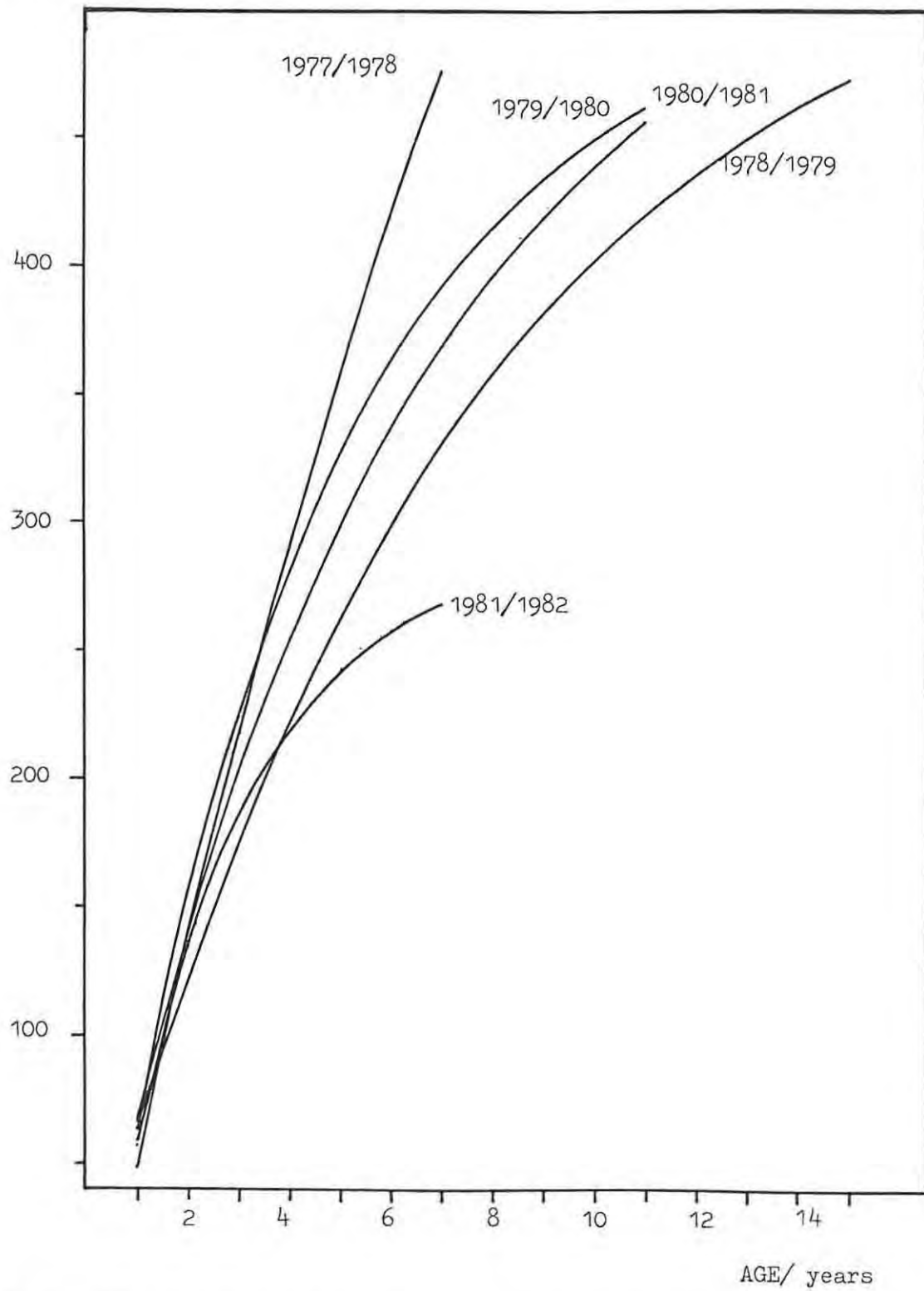


Figure 61. Constructed growth curves for male *B. kimberleyensis* in Lake le Roux during different seasons, fitted to the von Bertalanffy growth model.

Table 22. Average annual increments of L. capensis in Lake le Roux, expressed as increments in fork length, in mm, and as percentage of average growth over all seasons.

		Growth of <u>L. capensis</u> at age						Average percentage of standard
Season		2	3	4	5	6	7	
1981/1982	mm	18	13	1	11	*	11	
	%	37	27	2	29		46	28
1980/1981	mm	52	46	42	41	27	16	
	%	106	94	102	108	79	67	93
1979/1980	mm	47	52	49	43	34	26	
	%	96	106	120	113	100	108	107
1978/1979	mm	26	25	19	16	14	13	
	%	53	51	46	42	41	54	48
1977/1978	mm	70	66	60	56	46	47	
	%	143	135	146	147	135	196	150
1976/1977	mm	82	92	78	64	50	34	
	%	167	188	190	168	147	142	167
Mean increment "standard"		mm	49	49	41	38	34	24

* insufficient data available

Table 23. Values for the constants in the von Bertalanffy growth equation as fitted to length increments of Labeo capensis in different seasons in Lake le Roux.

Season	Sex	L_{∞}	K	t_0
1977/1978	males	506	0,19	0,39
	females	609	0,16	0,43
1978/1979	males	533	0,07	0,11
	females	742	0,04	0,92
1979/1980	males	593	0,11	0,07
	females	688	0,09	0,12
1980/1981	males	490	0,15	0,13
	females	557	0,13	0,08

and 1980/1981 seasons (Fig. 59). Relative growth of L. capensis was better during the former season whereas B. holubi grew on average better during the latter season.

The relative growth of L. capensis in 1981/1982 is high (Table 22). Only 13% (n = 283) of the L. capensis caught in April 1982 showed any growth in this season. Taken over the whole sample, average growth in 1981/1982 was 2 mm. Thus the growth in this season is not accurately reflected in the data of length-at-age. There is a large size range for each year class in this species, and the discrepancy in the results can be explained by insufficient sample sizes obtained in April 1982. Alternatively, differential mortality of smaller fish dying at a faster rate than larger fish could also explain the results, but there are no other indications of this occurrence.

The growth curves reflect a similar relative change in growth in all length groups. Ultimate length (L_{∞}) values (Table 23) are relatively constant, but the time it takes to reach the ultimate size varies greatly between seasons (Fig. 62). Females reach a larger ultimate size than males (Table 23). No growth curve could be constructed for the 1981/1982 season, since average increments in that season were too small to make the exercise meaningful.

The growth rates of L. capensis are apparently related to turbidity (Fig. 59) but the relationship is not as close as for the Barbus. The decrease in growth rates from 1979/1980 to 1980/1981, in spite of reduced turbidity, is probably due to the high density of L. capensis at the beginning of the 1980/1981 season (Fig. 60). Similarly, relative condition of L. capensis declined from October 1980 until the end of the study (Fig. 51).

5. Summary and discussion

In all the species, females attain a larger size than males. In the two Barbus species this is due to sex related differential growth rates. In L. capensis the observed differences were probably due to differential mortality with faster growing males experiencing higher mortality rates than slow growers.

B. holubi grows faster than B. kimberleyensis for the first two years, but by age 4 the two species are of a similar size, whereafter

LENGTH/ mm

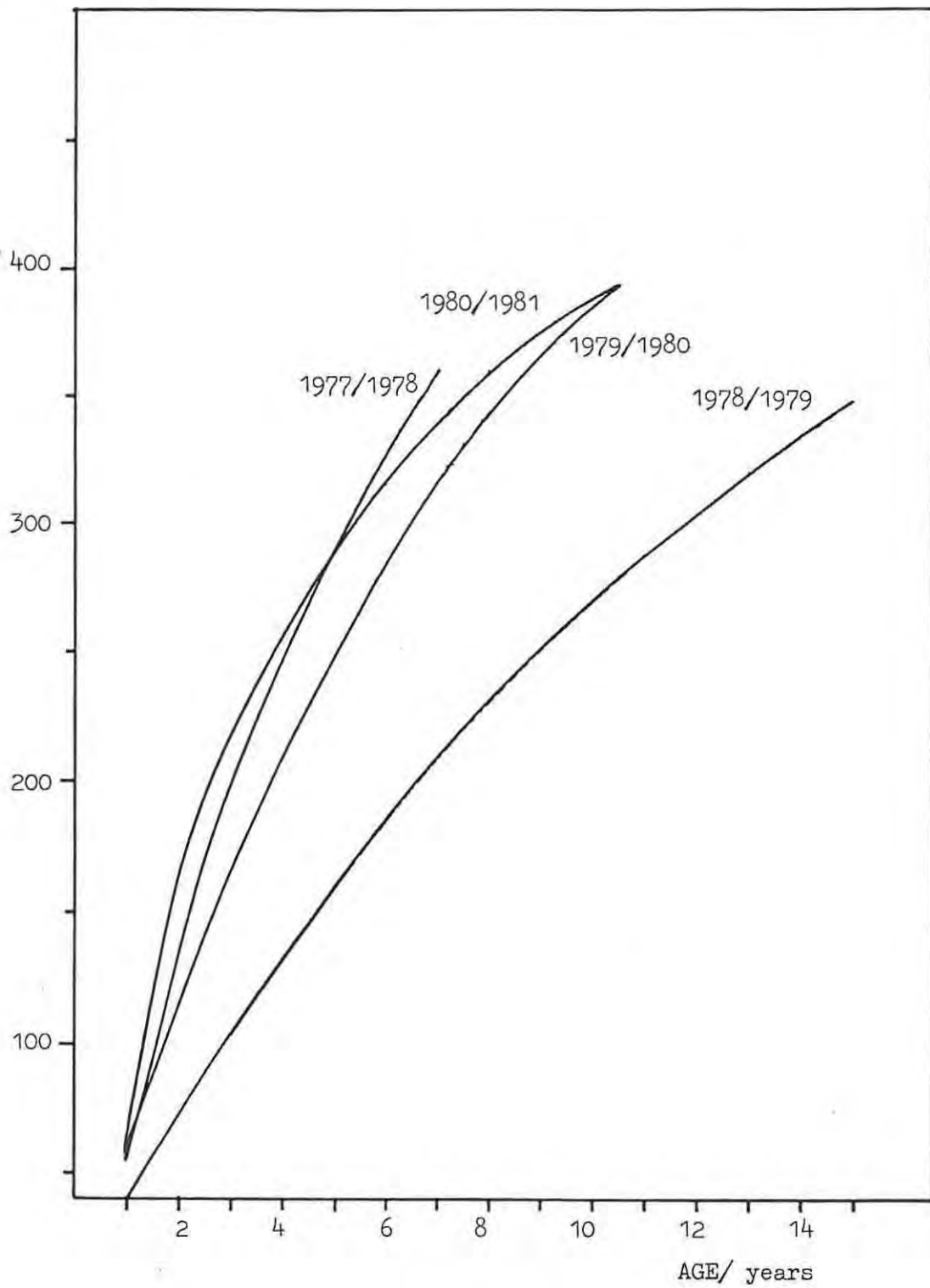


Figure 62. Constructed growth curves for male *L. capensis* in Lake le Roux during different seasons, fitted to the von Bertalanffy growth model.

B. kimberleyensis is larger. L. capensis generally grow at a slower rate than either of the Barbus species.

Growth in all species is reduced with increased distance from the dam wall (Tables 15 to 17). The disappearance of observed growth differences for a given season with time shows that the Barbus species mix uniformly in the lake. L. capensis, particularly the smaller size groups, mix when living conditions become adverse and reproductively isolated units are not maintained.

There are large inter-seasonal differences in growth rates, which are closely related to turbidity and population density. Both these factors operate to reduce available food resources per individual. Absolute seasonal length increments are inversely related to length of the fish. In the two Barbus species inter-seasonal variation in growth increases with size and L_{∞} , calculated from the growth in each season, varies. In L. capensis relative differences in growth rates between seasons are similar for all size groups. L_{∞} is thus relatively constant in spite of varying growth rates.

As expected, both the Barbus species and L. capensis reacted to changing conditions by adjusting individual growth rate. However, the sudden deterioration in environmental conditions in 1978 and 1981 (increased turbidity) also caused high mortalities in B. holubi on both occasions and L. capensis in 1981. Thus the expected slow deterioration in growing conditions was interrupted.

Growth in fish generally follows a sigmoid curve directed towards an asymptotic length, determined by environmental conditions (Warren, 1971). A reduction in growth rates is usually accompanied by a reduction in L_{∞} . Beverton & Holt (1957) concluded that while W_{∞} (L_{∞}) was affected negatively by adverse growing conditions, K (the rate at which L_{∞} is approached) was a species specific constant. The results of the present study are at variance with Beverton & Holt's (1957) conclusion. Although L_{∞} closely reflects growth rates of the two Barbus species, K also varies considerably between season. In L. capensis, changes in growth rates are mainly reflected in changes in K , while L_{∞} is relatively constant.

Sainsbury (1980) showed that, because of individual variation in growth, values of K and L_{∞} represent a distribution around a mean but are not a fixed property of a population. Pitcher & Hart (1982),

in discussing the von Bertalanffy growth equation, question the biological interpretation of constants in the model, but conclude that it is a convenient way to describe growth. Similar views were expressed by Warren (1971). However, the von Bertalanffy model describes well the growth of the cyprinids in this study and highlights a major difference in growth response between the Barbus species and L. capensis. The significance of variable asymptotic lengths in the Barbus species and a relatively constant L_{∞} in L. capensis will be discussed in more detail later.

C. REPRODUCTION, RECRUITMENT AND MORTALITY

The prediction of future yields is an important part of fisheries management. If a fishery depends only on a few species whose abundance fluctuates markedly in response to non-cyclic environmental variations (as is the case in Lake le Roux, Fig. 60), the monitoring of year class strength prior to recruitment becomes an important facet of management (Regier, 1977). When long-term data are available, models can be developed to predict yields in relation to environmental changes.

Growth has been discussed in the previous section, and other aspects influencing the recruitment process will be considered here. Reproduction is discussed in terms of time and locality of spawning, and recruitment in terms of year class strength and mortality. Catch per unit effort (CPUE) is used extensively in interpreting year class strength, reproduction and mortality. However, CPUE can be influenced by such factors as water temperatures, wave action and turbidity. If these act uniformly in the population, relative abundance is still a valid measurement of year class strength. If, however, patterns of distribution change, CPUE may not be a good measure of temporal changes in abundance of different cohorts (Jester, 1977). It is necessary then to first describe the distribution of subadult and adult fish, i.e. fish recruited into the CPA gillnets (generally ≥ 130 mm).

1. Distribution of subadult and adult fish in Lake le Roux

Catches in the CPA gillnets accurately reflect the location of modes in the size distribution of the populations (Chapter III, B). Therefore it is valid to compare length-frequency distribution of catch through time and between localities. The catch of B. holubi, B. kimberleyensis and L. capensis during the quarterly CPA gillnet surveys is presented as length-frequency histograms (Figs. 63 to 65). Catches of B. holubi and L. capensis at stations 1 & 2, and at stations 4 & 5 consistently showed similar patterns, so these have been combined and the average catch plotted. For the last two sampling dates, after the number of gillnet sites had been reduced from 28 to 20, the catch has been adjusted to represent the catch as four settings per station in order to make it comparable to previous sampling dates. Catches of B. kimberleyensis were too low for subdivision into stations.

a. Barbus holubi

The length-frequency distribution of B. holubi generally showed distinct modes (Fig. 63). The mode of the smallest fish is usually highest at the upper station (particularly station 7) in January or April. As the mode moves, it becomes best represented at the lower station, reflecting the same trend in distribution as larger fish. General declines in catches with distance from the dam wall are associated with an increase in turbidity (Fig. 20).

A mode at 240 mm in April 1980 was relatively small and indistinct. This represented a weak year class which by January 1981 separated the mode of new recruits at 130 - 140 mm and older fish. Relative year class strength will be discussed in the following sub-section.

It may be concluded that new year classes are first recruited in the upper parts of the lake, but within a year an unbiased catch anywhere in the lake should give a good indication of B. holubi's relative ^{year class} strength.

b. B. kimberleyensis

B. kimberleyensis larger than 350 mm are relatively well

NUMBER

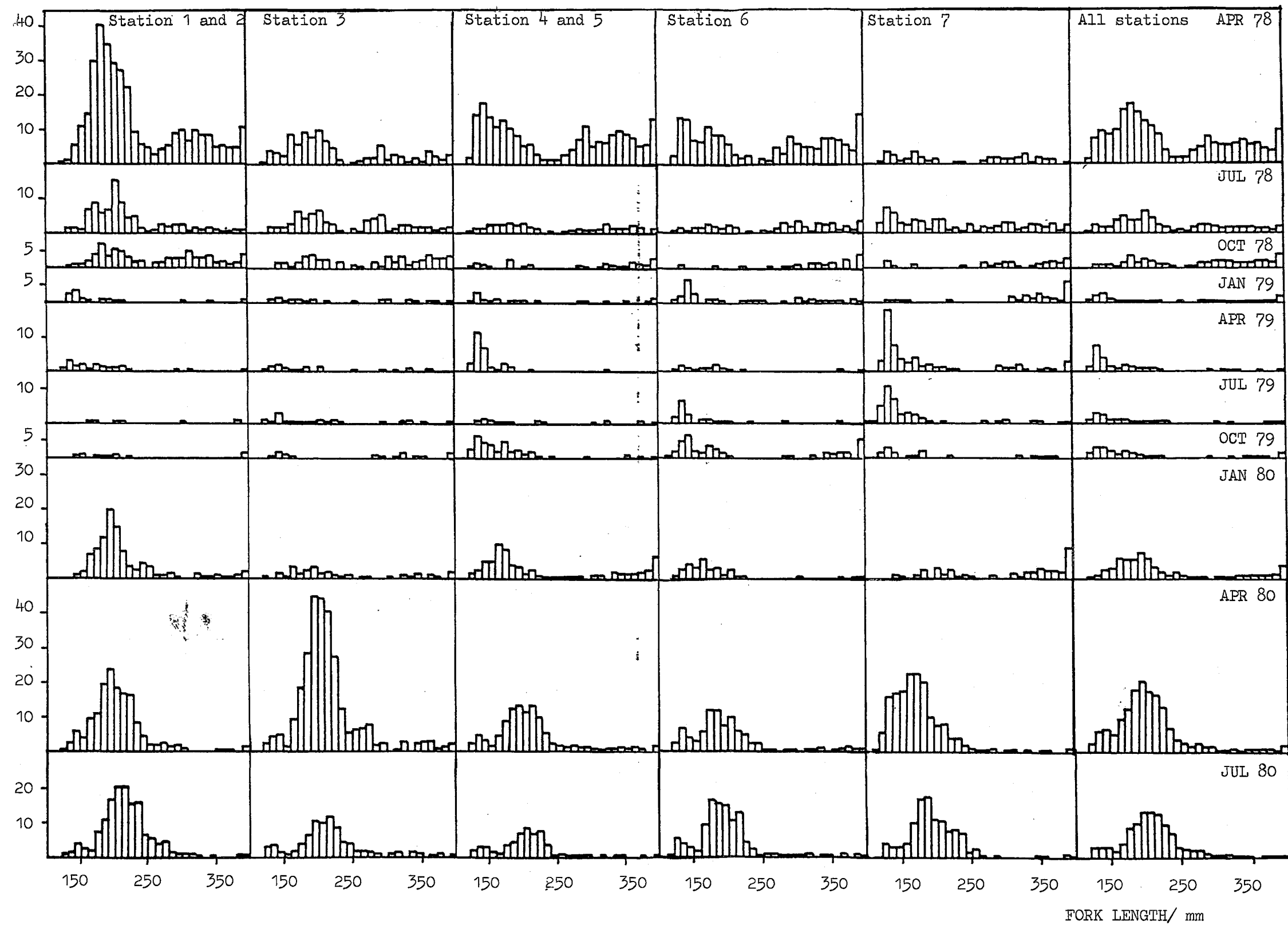


Figure 63. Length frequency distribution by station of *Barbus holubi*, caught during CPA gillnetting surveys on Lake le Roux. The numbers graphed represent the catch in four settings. All fish 390 mm and larger are combined.

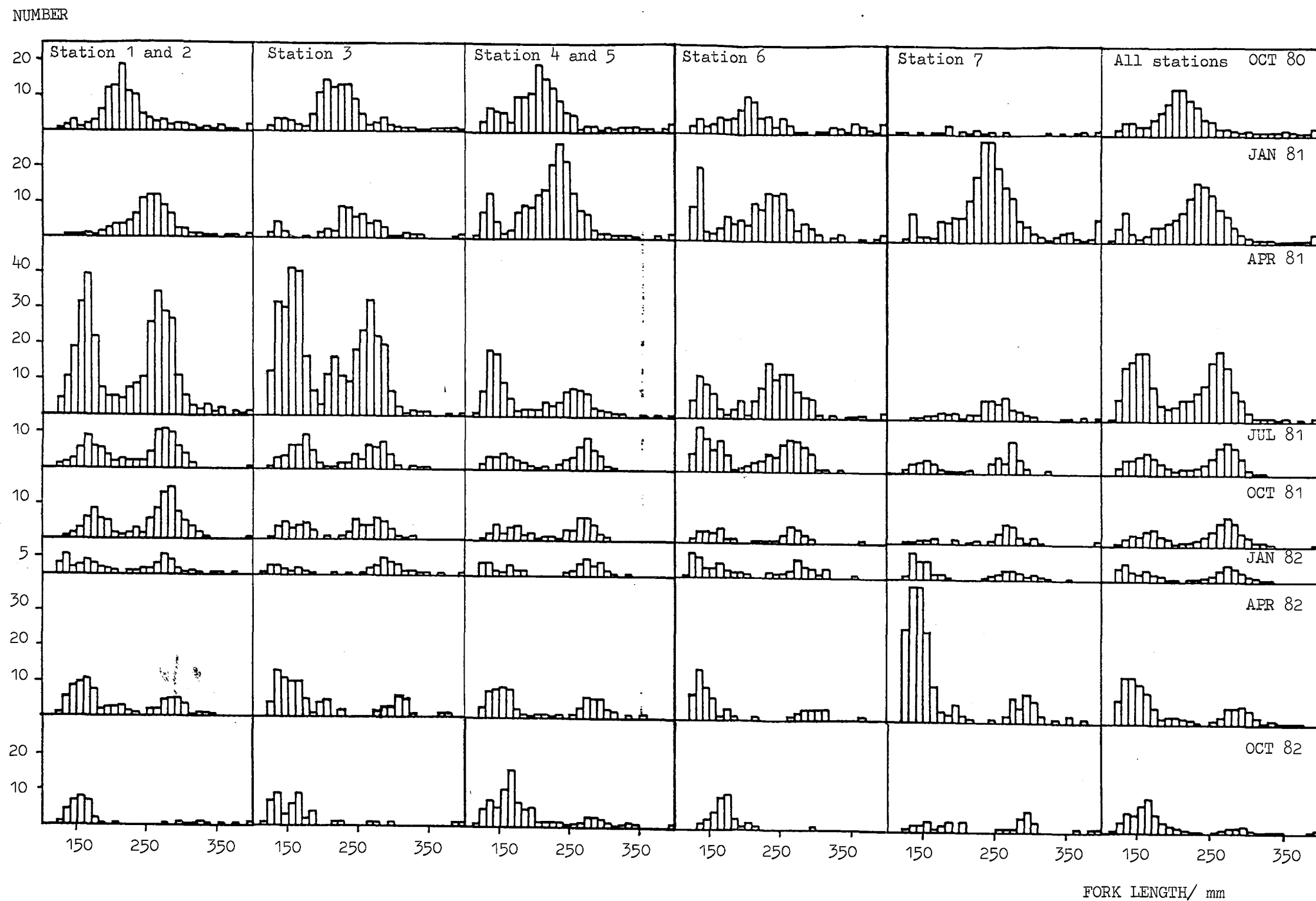


Figure 63 continued. Length frequency distribution by station of Barbus holubi.

represented in the catches (Fig. 64). In contrast to B. holubi, modes in fish smaller than 300 mm are indistinct and the catches fluctuate less.

c. Labeo capensis

Catches of L. capensis in April 1978 showed a bimodal distribution at all stations, although the smaller mode was only poorly represented at stations 1 to 3 (Fig. 65). The two modes are probably caused by the good growth of the 1974/1975 year class and older fish during the first year of impoundment (Section B, Figs. 56 and 57).

Fish in the smaller mode (1975/1976 year class and younger) were well represented at stations 1 to 3 by January 1979 (Fig. 65). Growth in that season was poor (Table 22) which indicates that these fish had immigrated to the area. With time, small fish are recruited at all stations. In the 1980/1981 season, recruitment at stations 1 to 3 failed, and fish 120 - 200 mm were poorly represented in the catches in April 1981. In April 1981, small fish disappeared from station 7, and subsequently, small fish (≥ 200 mm) entered the catches in the lower station while catches were reduced further up the lake. Growth in 1981/1982 was very poor (Section B) and can be ruled out as the cause of recruitment of fish ≤ 200 mm at the lower stations in January 1982, and again immigration is the most plausible explanation. This is in agreement with results on growth differences within the lake presented earlier in this chapter (Table 17), which indicated movement of fish ≤ 200 mm in winter 1981 and summer 1981/1982.

It is evident then, that changes in CPUE of L. capensis in Lake le Roux, especially of fish smaller than 200 mm, may reflect dispersal within the lake, as well as changes in gear efficiency and in numerical abundance. The reasons for and effects of movement of small L. capensis in 1978/1979 and in 1981/1982 will be discussed further in the following sub-section.

2. Mortality and relative year class strength

The reproductive potential of fish is reduced by factors which limit spawning and subsequent survival during various stages of their

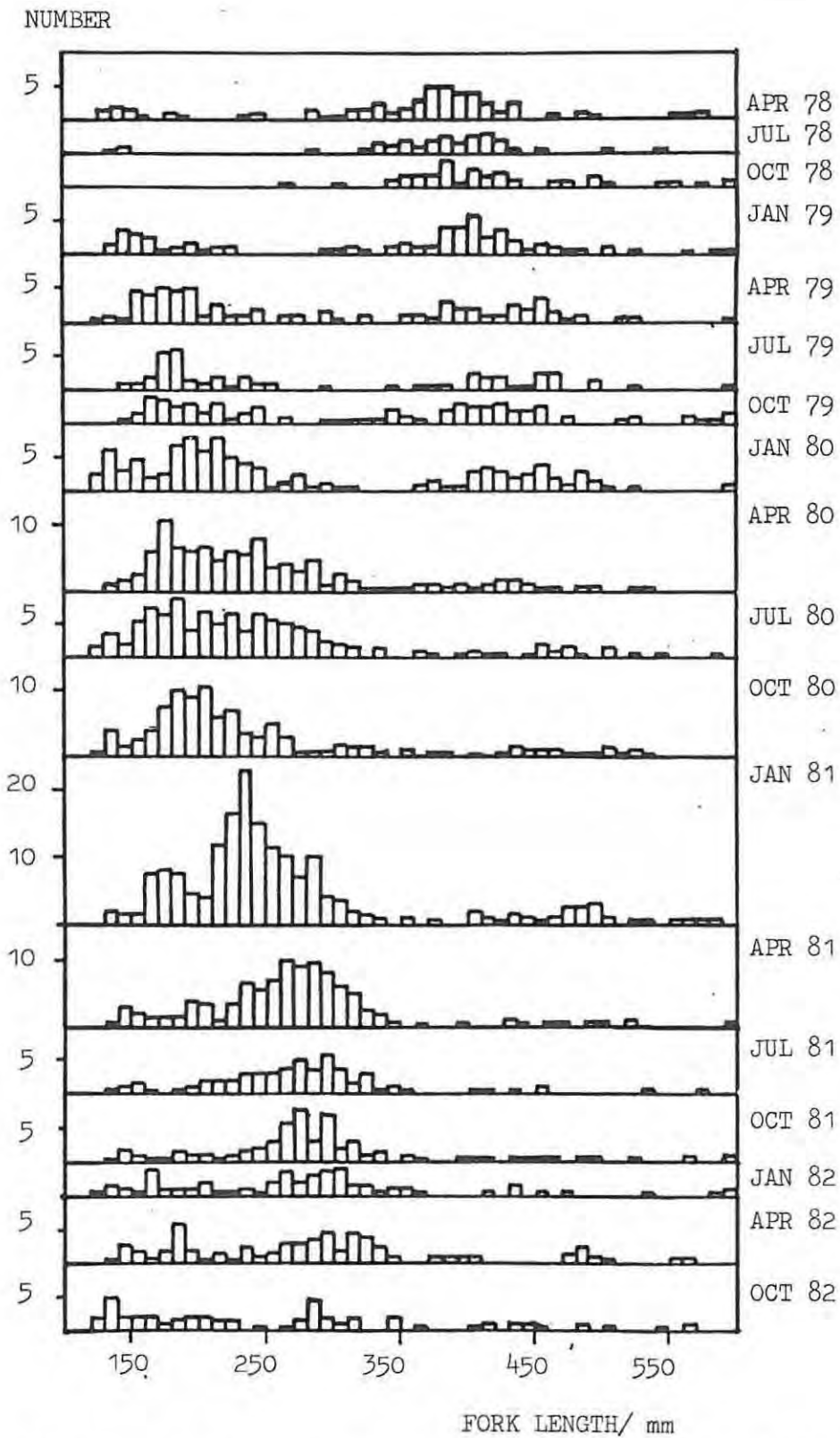


Figure 64. Length frequency distribution of *Barbus kimberleyensis* caught during CPA gillnetting surveys on Lake le Roux. The numbers graphed represent catches from 28 settings. All fish 590 mm and larger are combined.

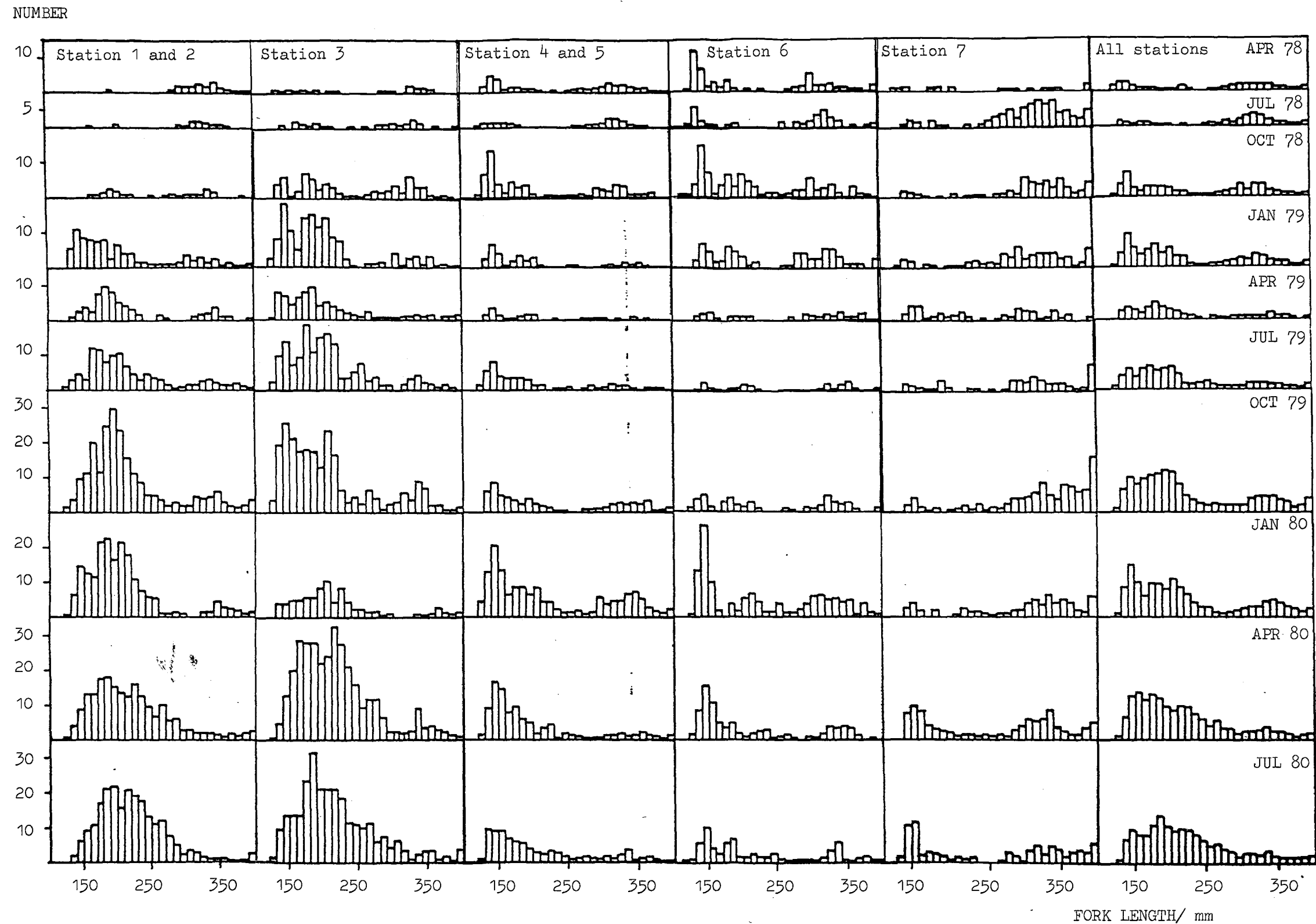


Figure 65. Length frequency distribution by station of *Labeo capensis*, caught during CPA gillnetting surveys on Lake le Roux. The numbers graphed represent the catch in four settings. All fish 400 mm and larger are combined.

NUMBER

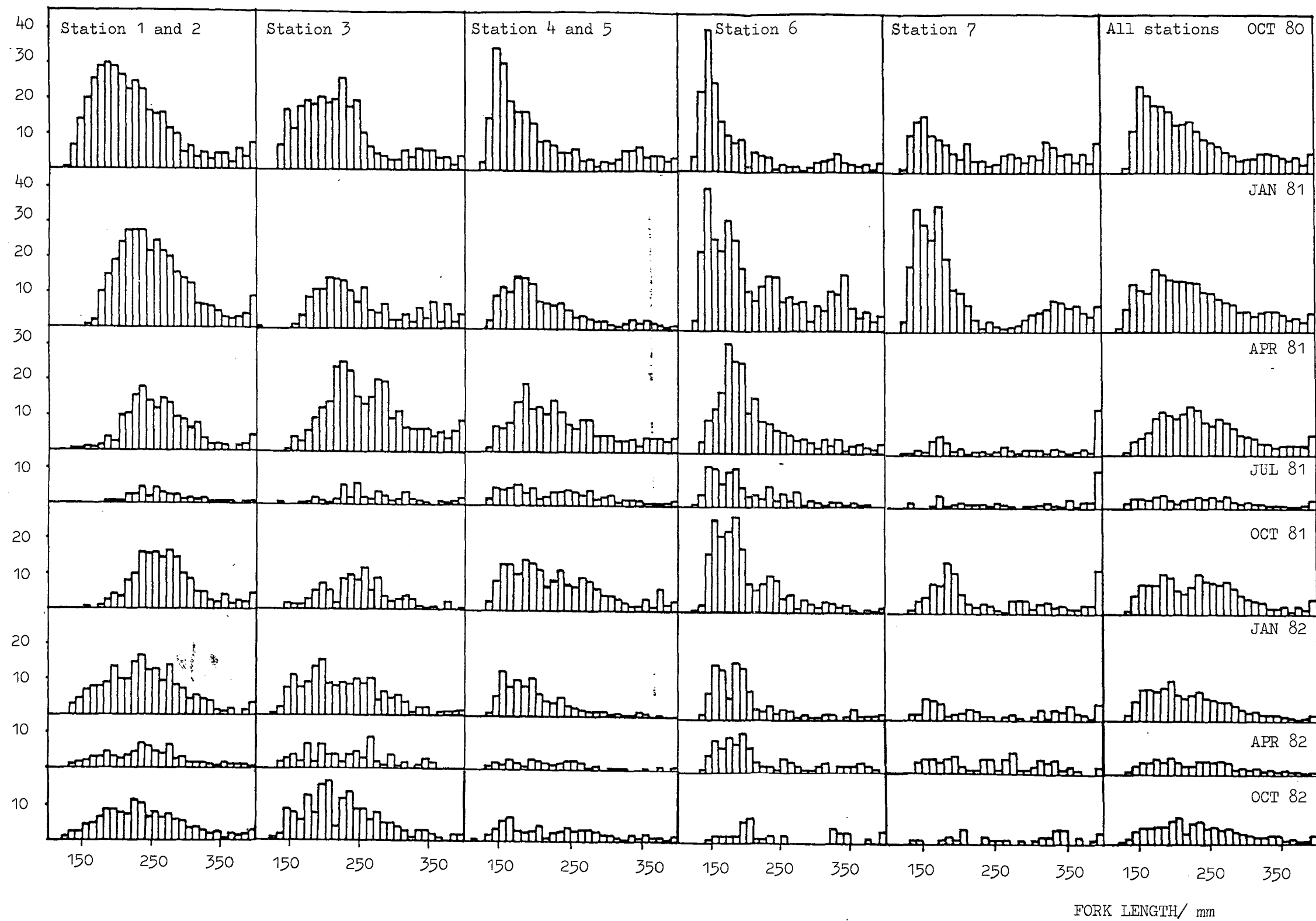


Figure 65 continued. Length frequency distribution by station of *Labeo capensis*.

life history. If the factors which limit reproduction and recruitment do not operate uniformly between seasons, it becomes imperative that they be identified and that their relationships are understood.

In this sub-section, year class strength will be assessed on the basis of CPUE of newly recruited year classes into the CPA gillnets. Subsequent changes in CPUE of individual year classes are presented and discussed. Reproduction will be dealt with in the following sub-section.

a. Barbus holubi

Changes in CPUE of individual year classes show a considerable temporal variation (Fig. 66, Table 24). These variations are due to changes in catchability and to changes in abundance (result of mortality and recruitment), and their effects are difficult to separate. New year classes are recruited into the catches during their second year, but results from backcalculation of lengths at age indicate that the slowest growers are only recruited early in their third year (Chapter IV, B).

Ageing, based on scales collected in October 1978, showed that the first mode in the catches in April 1978 (Fig. 63) was chiefly made up of the 1976/1977 year class, but that the upper range and the dip in the frequency distribution, reflects a relatively weak 1975/1976 year class. The changes in CPUE of these two modes from 1978 are presented in Fig. 67.

There was a sharp decrease in CPUE after 1978 (Fig. 67) and again after April 1981 (Figs. 66 and 67). In both cases this followed a sharp increase in turbidity (Fig. 19). B. holubi feeds visually in the open water (Eccles, 1980), and a reduced field of vision will also reduce the speed at which it effectively can search for prey. Larger fish may also turn to a benthic mode of life and then be less vulnerable to capture in floating nets. A decline in the effectiveness of the gillnets towards B. holubi undoubtedly accounts for some of the decrease in CPUE.

The increase in CPUE until January 1980 (Fig. 67) probably reflects improved clarity of the water. The further large increase in CPUE in April 1980 of the 1975/1976 and younger year classes

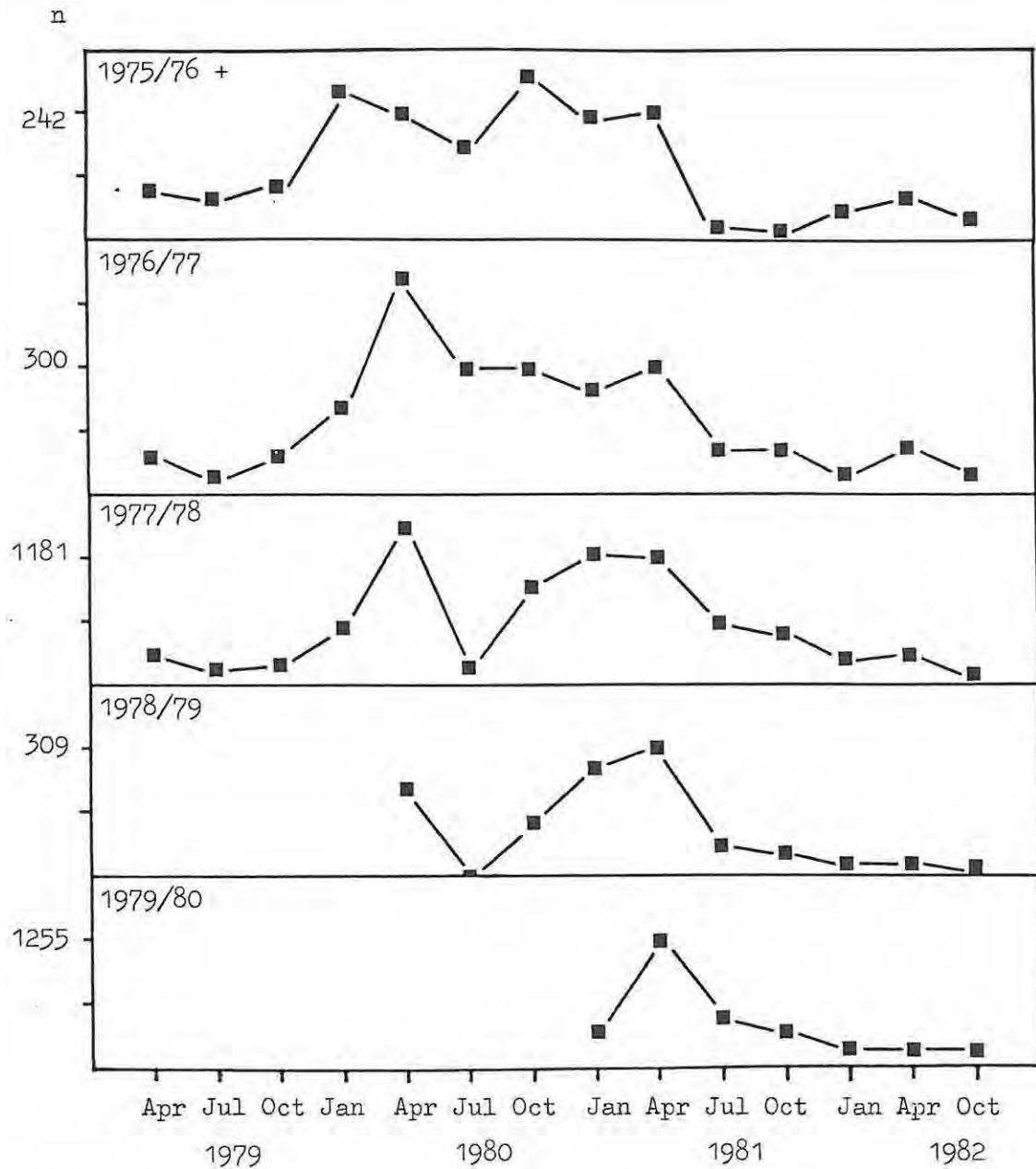


Figure 66. Temporal changes in catch of different year classes of *Barbus holubi* in Lake le Roux. Catches have been adjusted for gillnet selectivity and reduced effort in April and October 1982. The scales have been adjusted to represent catches as a portion of catches in April 1981.

Table 24. Calculated catch per unit effort of different year classes of B. holubi during CPA surveys. The original catch was adjusted for gillnet selectivity and the catches in April and October 1982 have been corrected for reduced effort to make the data comparable.

Time	Year class catch per unit effort						
	80/81	79/80	78/79	77/78	76/77	75/76	74/75+
Apr. 79				273	86	19	84
Jul. 79				113	41	15	73
Oct. 79				187	83	12	99
Jan. 80				508	203	27	281
Apr. 80			212	1449	513	77	234
Jul. 80			134	996	273	85	174
Oct. 80			126	895	297	117	318
Jan. 81		364	259	1207	246	106	232
Apr. 81		1255	308	1181	300	161	242
Jul. 81		458	64	549	103	6	10
Oct. 81		321	51	472	105	9	20
Jan. 82	227	164	26	242	46	39	56
Apr. 82	935	164	25	263	108	46	79
Oct. 82	554	165	15	92	44	26	47

PERCENTAGE

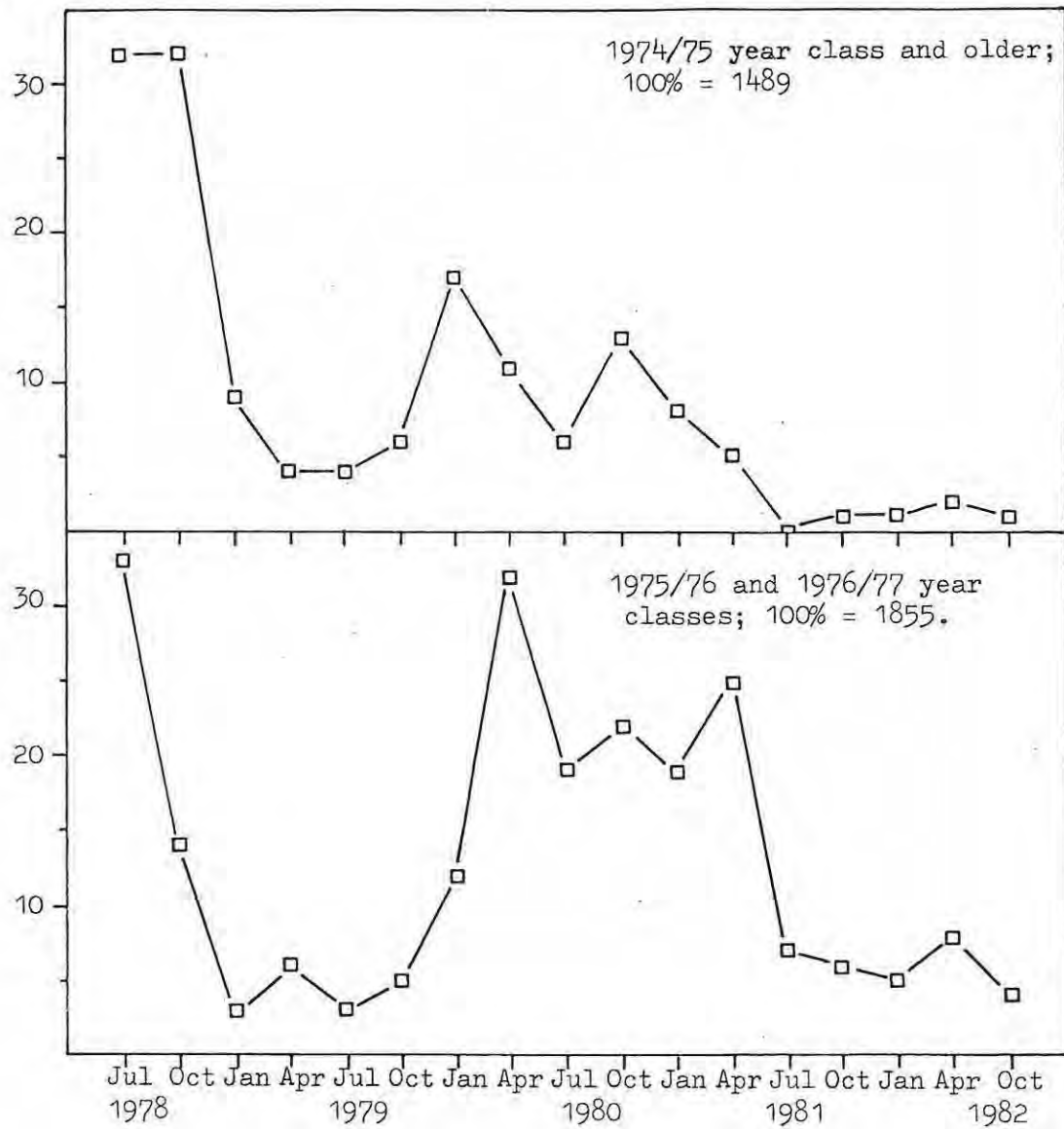


Figure 67. Catch of B. holubi spawned in 1976/77 and earlier in Lake le Roux during gillnetting surveys as a percentage of the catch in April 1978. Catches have been adjusted for gillnet selectivity and reduced effort in April and October 1982.

(Table 24, Fig. 66) is probably the result of changed twine thickness of gillnets (Table 8, Chapter IV, A). The 1975/1976 and 1976/1977 year classes at that time were caught mainly in the 57 and 73 mm meshes. The twine thickness of the larger meshes did not change, which may explain why a similar increase in CPUE was not observed in the older fish (Fig. 66).

Changes in the effectiveness of the gear make it difficult to estimate mortality and relative year class strength. The reduction of catches from April 1978 was permanent, although catches in subsequent surveys varies (Fig. 67). Taking into account the change of nets in April 1980, it can be assumed that the increase in turbidity in late summer 1978 caused 80 to 90% mortality in year classes 1976/1977 and older. The decline in catches was less sharp following the second increase in turbidity in late summer 1981. A year later, catches were between 10 and 30% of the April 1981 catch (Fig. 66) as compared to about 5% for the corresponding period in 1978/1979 (Fig. 67). Low relative condition in October 1978 (Fig. 48) further supports the contention that there was a substantially greater decline in the population in 1978/1979 than in 1981/1982. This is probably due to the higher density of B. holubi in April 1978 than in April 1981 (Fig. 60), as well as the greater changes in turbidity in April 1978 (Fig. 19).

Young-of-the-year probably do not suffer the mortality of the older cohorts at times when turbidity increases sharply. The 1977/1978 year class was entering the catches in January 1979 (Fig. 63) when catches of older fish were at their lowest. Similarly the 1980/1981 year class was beginning to be recruited in January 1982 (Fig. 66). Relatively small variations in growth during the second year of life (Fig. 52) further indicate that this age group is not as affected by an increase in turbidity as older fish.

The 1977/1978 year class dominated in the catches for three years (Table 24) but catches of the 1978/1979 year class numerically only made up between 10 and 26% of the 1977/1978 year class. The catch of the 1979/1980 year class was 4.6 times higher in April 1981 than the catch of the 1977/1978 year class in April 1979. However the catches of the two were similar in April 1981 (Table 24). The 1979/1980 year class was probably weaker than the 1977/1978 year

class had been. The difference in the April catches of age 1 fish almost certainly is the result of different gillnets and clearer water in 1981.

The 1980/1981 year class was caught with more efficient nets at the end of its second season than the 1977/1978 year class, but water clarity was similar on both occasions. Although other factors than water clarity and twine thickness of nets may influence the catchability of B. holubi, it is likely that the 1980/1981 year class is at least as strong as the 1977/1978 year class.

In conclusion, the B. holubi 1977/1978 and 1980/1981 year classes appear to be strong, the 1978/1979 year class weak and the 1979/1980 year class moderately strong. The causes for these differences will be examined in the sub-section on reproduction.

b. Barbus kimberleyensis

Catch per unit effort of individual year classes of B. kimberleyensis is presented in Fig. 68 and Table 25. New year classes are mainly recruited into the gillnets during their third growing season. There are considerable temporal variations in CPUE which to some extent undoubtedly reflect the small numbers.

The reduction in catch seen in B. holubi after April 1981 is only observed in the 1977/1978 year class of B. kimberleyensis (Fig. 68). Older year classes do not show a particular temporal trend. This may be an expression of good survival, but could also be a result of the increased catchability of larger predatory fish.

The 1977/1978 year class appears to be the strongest of the post-impoundment year classes but the relative strength of other cohorts is difficult to assess because of small numbers and late recruitment.

c. Labeo capensis

Catch per unit effort of individual year classes of L. capensis is presented in Fig. 69 and Table 26. Temporal variations in catch are similar for all year classes and indicate that generally, the same factors influence the catchability of all size groups. There are exceptions to the general pattern which will now be examined.

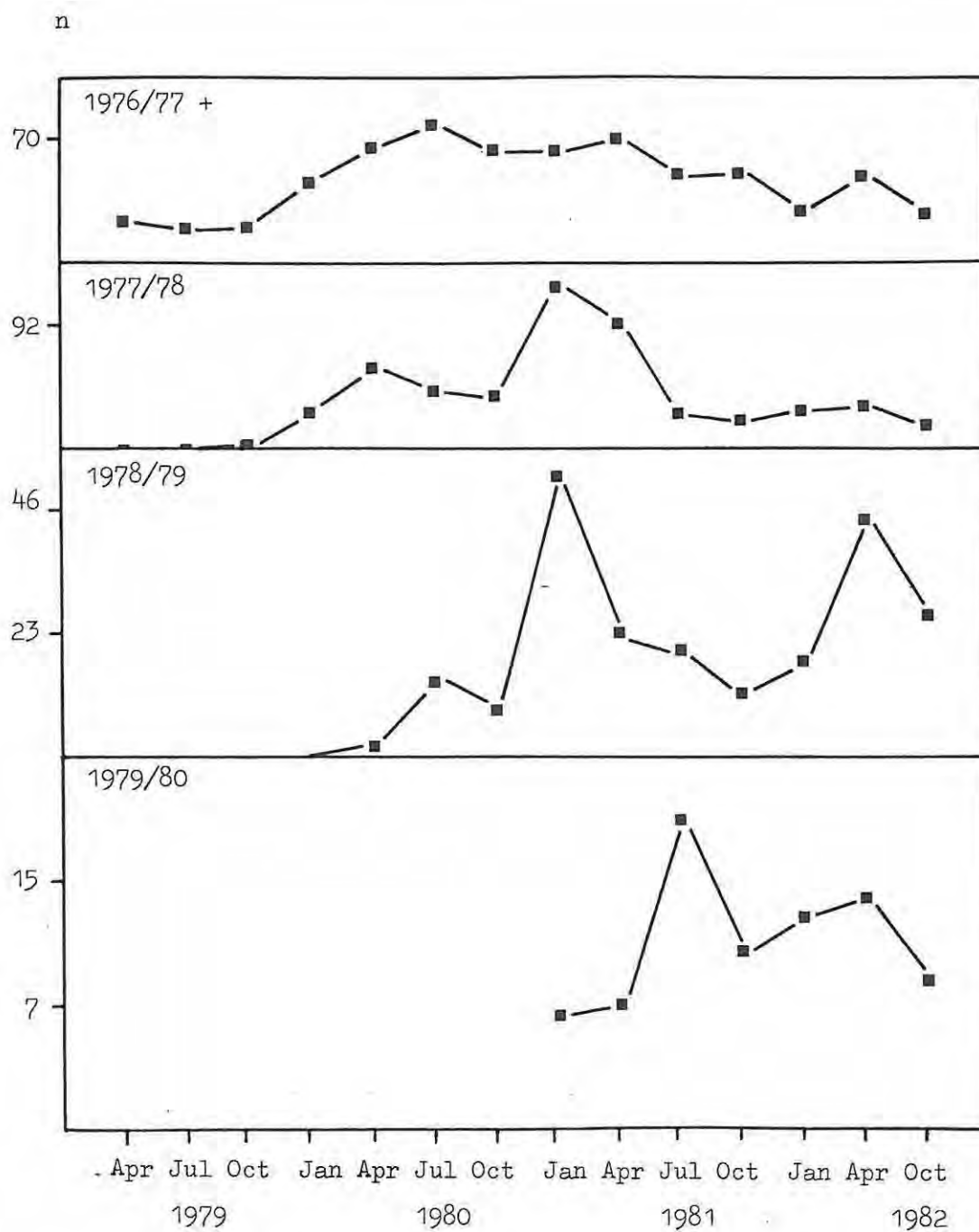


Figure 68. Temporal changes in catch of different year classes of *Barbus kimberleyensis* in Lake le Roux. Catches have been adjusted for gillnet selectivity and reduced effort April and October 1982. The scales have been adjusted to present catches as a portion of catches in April 1981.

Table 25. Calculated catch per unit effort of different year classes of B. kimberleyensis during CPA surveys. The original catch was adjusted for gillnet selectivity and the catches in April and October 1982 have been corrected for reduced effort to make the data comparable.

Time	Year class catch per unit effort					
	80/81	79/80	78/79	77/78	76/77	75/76 & older
Apr. 79				1	23	118
Jul. 79				1	19	111
Oct. 79				3	19	101
Jan. 80				28	46	190
Apr. 80			2	60	66	134
Jul. 80			14	42	78	51
Oct. 80			9	33	64	55
Jan. 81		7	53	121	64	72
Apr. 81		8	23	92	70	66
Jul. 81		19	20	26	51	18
Oct. 81		11	12	20	51	28
Jan. 82	5	13	18	28	28	33
Apr. 82	6	14	45	31	49	60
Oct. 82	21	9	27	16	28	35

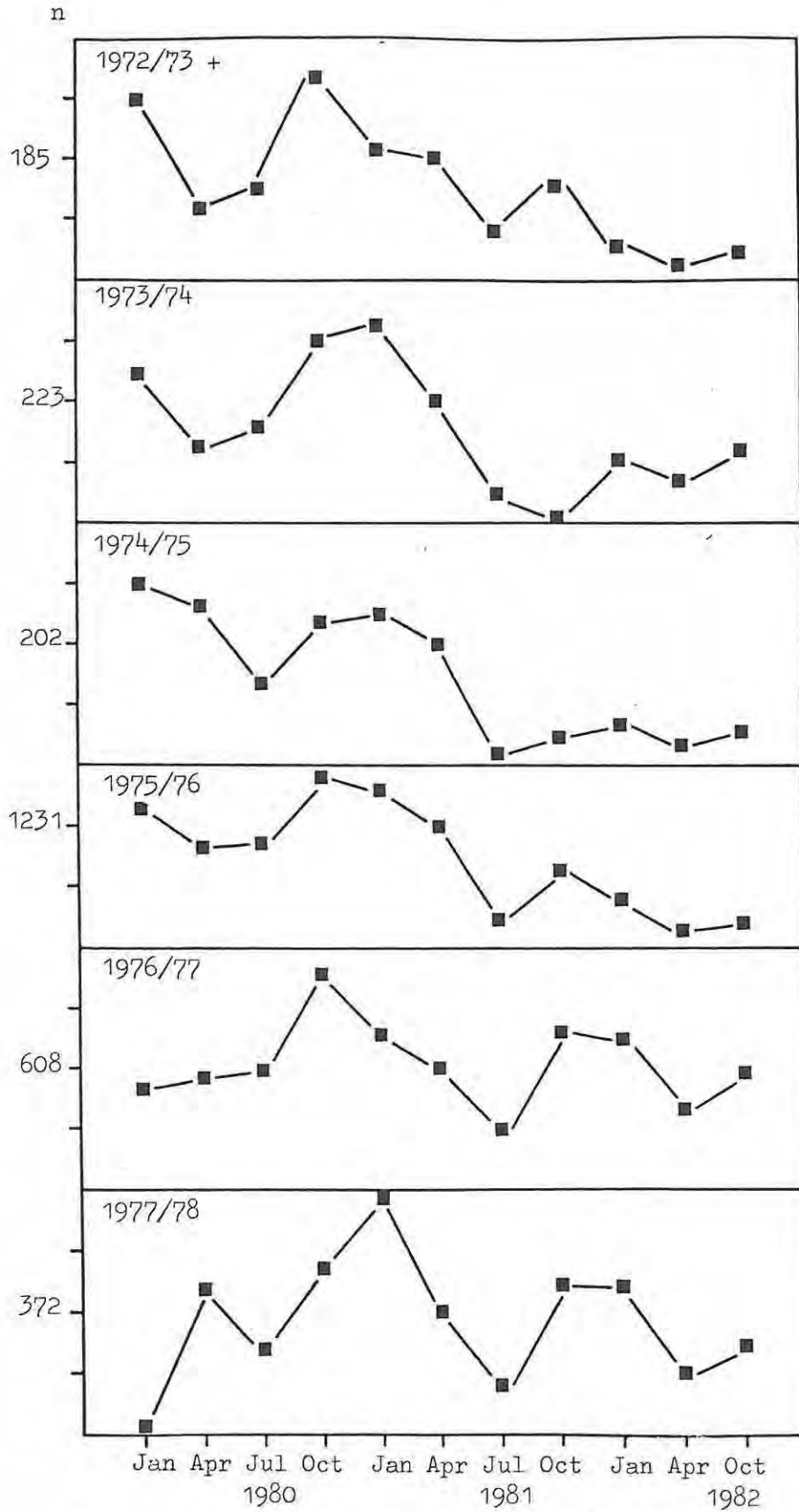


Figure 69. Temporal changes in catch of different year classes of *Labeo capensis* in Lake le Roux. Catches have been adjusted for gillnet selectivity and reduced effort in April and October 1982. The scales have been adjusted to represent catches as a portion of catches in April 1981.

Table 26. Calculated catch per unit effort of different year classes of L. capensis during CPA surveys. The original catch was adjusted for gillnet selectivity and the catches in April and October 1982 have been corrected for reduced effort to make the data comparable.

Time	Year class catch per unit effort							
	79/80	78/79	77/78	76/77	75/76	74/75	73/74	72/73 & older
Jan. 80			24	546	1394	298	271	273
Apr. 80			440	612	993	267	140	110
Jul. 80			261	666	1045	138	174	139
Oct. 80			508	1191	1735	240	337	309
Jan. 81	19		722	843	1603	254	361	198
Apr. 81	18	38	372	608	1231	202	223	185
Jul. 81	13	32	147	320	261	19	52	68
Oct. 81	29	73	456	869	775	47	8	141
Jan. 82	49	28	443	826	492	68	116	51
Apr. 82	54	28	187	433	179	33	76	24
Oct. 82	71	35	266	635	262	53	131	41

Changes in CPUE of L. capensis from April 1978 to October 1979 are examined separately for the two main modes in length frequency distribution in the catch (Fig. 65) and presented in Fig. 70. Following an increase in turbidity in 1978, there was about a four fold increase in CPUE of the smaller fish, while catches of larger fish remained fairly constant. This reflects changes in distribution within the lake. Instead of only being caught at the upper stations of the lake, the smaller fish become vulnerable to capture throughout the lake following dispersal in 1978/1979.

The increase in CPUE of the 1977/1978 year class from January to April 1980 probably mainly reflects recruitment, although reduction in twine thickness of the smaller nets would also influence the catches. This influence is lessened in older year classes, but a slight increase in CPUE in the 1976/1977 year class and a reduction in CPUE which becomes more pronounced in older fish (Fig. 69) points to the increased efficiency of the smaller meshes.

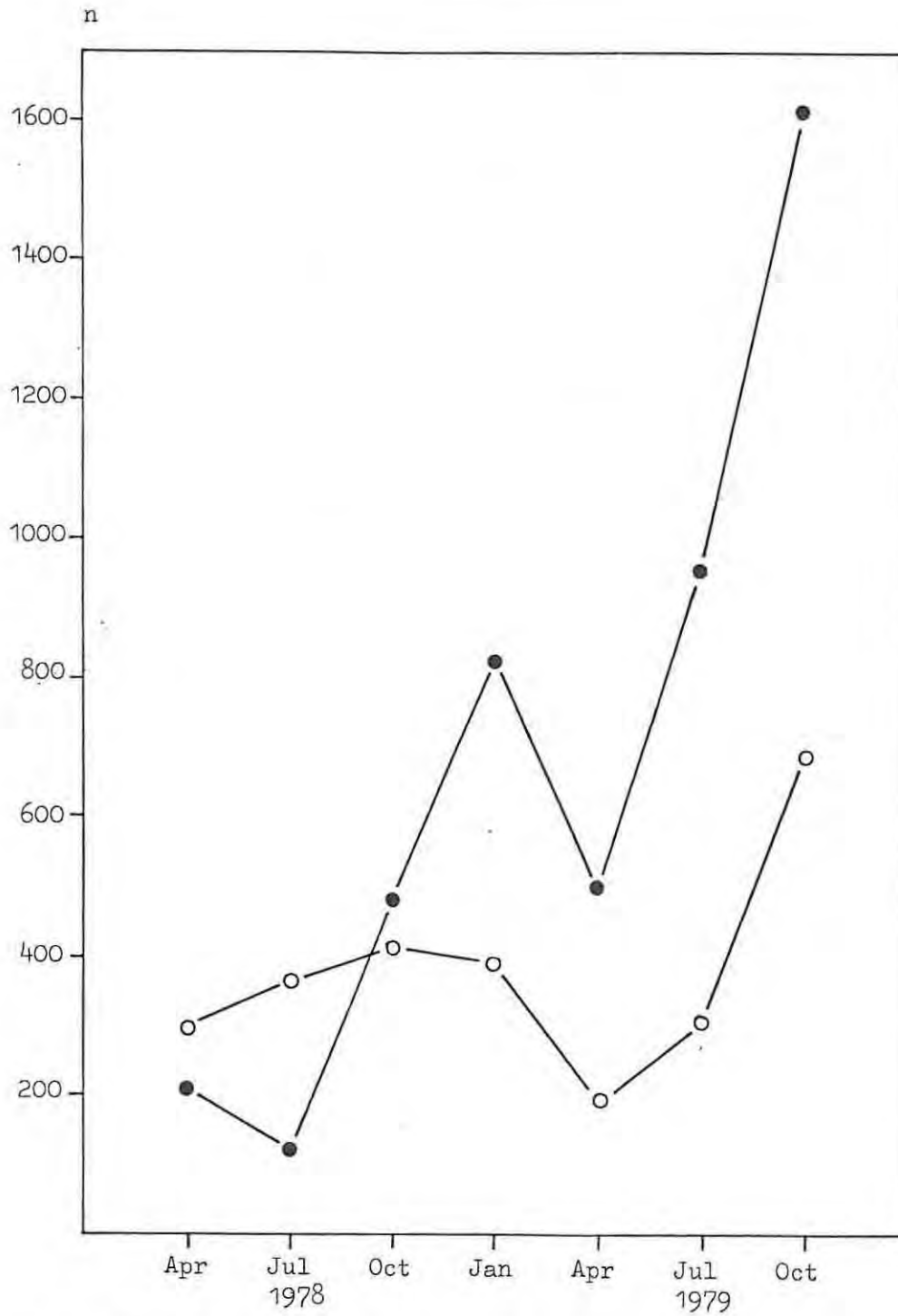


Figure 70. Changes in catch at 28 sites (adjusted for selectivity) of the two main size groups of Labeo capensis in Lake le Roux. The smaller fish (●) include fish < 240 mm in 1978, < 250 mm in January 1979 and < 260 mm for the remainder of 1979.

Catches generally decrease in April and July, but rise sharply in October and remain high in January (Figs. 69 and 70). This probably reflects an increase in feeding and breeding activity in spring and summer. However there is an overall trend of decrease in catches from January 1981 until the end of the study. This decrease is relatively less in the post-impoundment year classes than in older fish, because of the dispersal of L. capensis ≤ 200 mm from the upper stations down the lake after April 1981.

Increases in turbidity in 1978 and 1981 in both cases caused the dispersal of L. capensis smaller than 200 mm. In 1978, the lower stations of the lake, which include the largest basin, were underpopulated by L. capensis. Growth was relatively poor in the 1978/1979 season, but dispersal into previously vacant areas allowed for some growth and generally good survival. In 1981, however, the whole lake was densely populated by L. capensis. When resources were further limited by the increase in turbidity, the fish did not grow in length (Section B) and there was a large reduction in relative condition (Fig. 51). It is likely that the reduction in CPUE in 1981/1982 represents an acceleration in mortality rate, which up until then appeared to be very low.

Because of the discontinuous pattern in distribution, it is problematic to assess relative year class strengths. Of post-impoundment year classes, the 1976/1977 year class was strong, probably about twice the strength of the 1977/1978 year class (Table 26). The following two year classes were both very weak. The late recruitment of year classes into the CPA gillnets prevent any information on the strength of the 1980/1981 and 1981/1982 year classes.

3. Reproduction

The increase in CPUE of small fish (subadults) may initially reflect distributional tendencies in B. holubi and at times largely reflect dispersal in L. capensis. Ultimately though recruitment depends on reproduction. It has been argued that reproductive adaptations, more than any other stages of life history, determine

the success (measured as distribution and abundance) of a species of fish (Balon, 1975; 1978).

In this sub-section, reproductive adaptations are studied with particular reference to how they are affected by the lake environment.

a. Barbus holubi and Barbus kimberleyensis

The two large Barbus species in the lake cannot be distinguished in the field until they reach a size of about 80 mm. Catches of subadult and adult B. kimberleyensis only form a minor percentage of the total catch, but caution must be exercised when inferences are made from juvenile samples.

Juvenile Barbus appeared first in the riverine section of the lake (station 8), where evidence of two distinct spawnings was found (Fig. 71). Time of spawning was variable, although the time when evidence of each spawning was found was influenced by the sampling time and frequency.

Table 27. Time of juvenile surveys when evidence of first and second spawning of large Barbus was found at station 8
(Extracted from Figs. 72 and 73)

Season	Date when evidence of spawning was found	
	<u>First</u>	<u>Second</u>
1977/1978	1/2 1978	1/2 1978
1978/1979	26/3 1979	26/3 1979
1979/1980	17/12 1979	29/2 1980
1980/1981	26/11 1980	9/1 1981
1981/1982	12/12 1981	13/1 1982

To examine whether multiple spawning could explain the two spawnings, ova diameter of 22 B. holubi females was measured. The distribution was typically unimodal and skewed to the right (Fig. 74). In two of the samples however, ova diameter distribution was clearly bimodal (Fig. 74). Both these samples were taken after the spawning

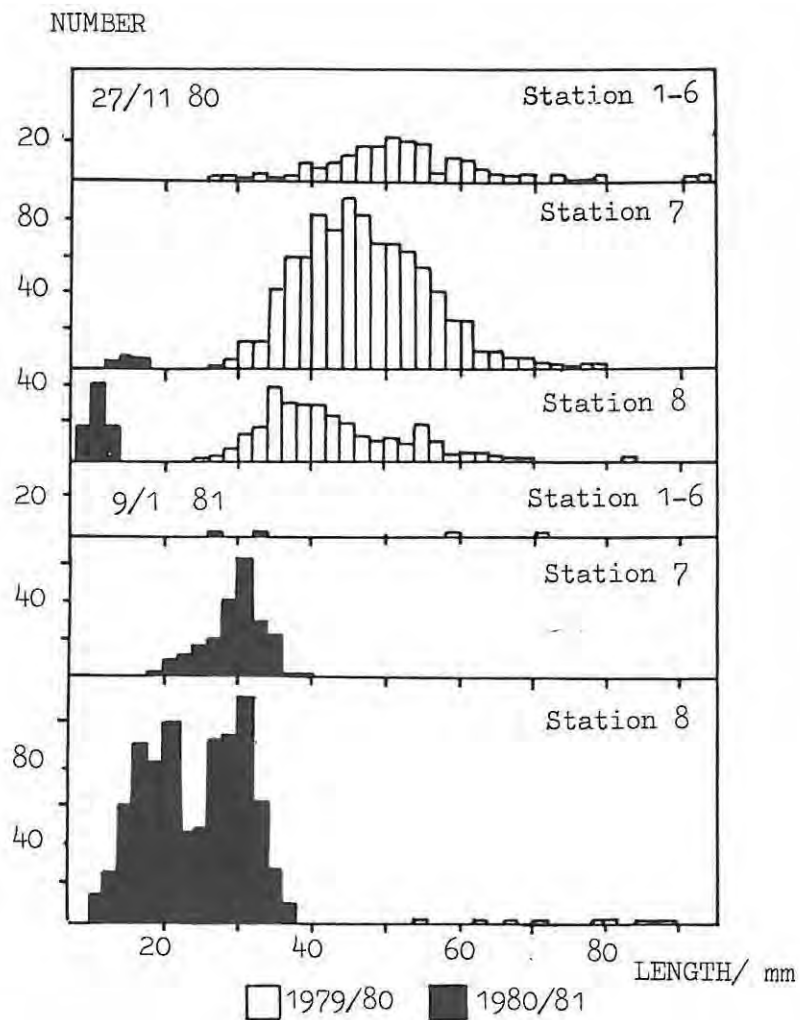


Figure 71. Length frequency distribution of juvenile large Barbus species caught in beach seines in different parts of Lake le Roux. First evidence of two spawnings was found in the riverine section (station 8).

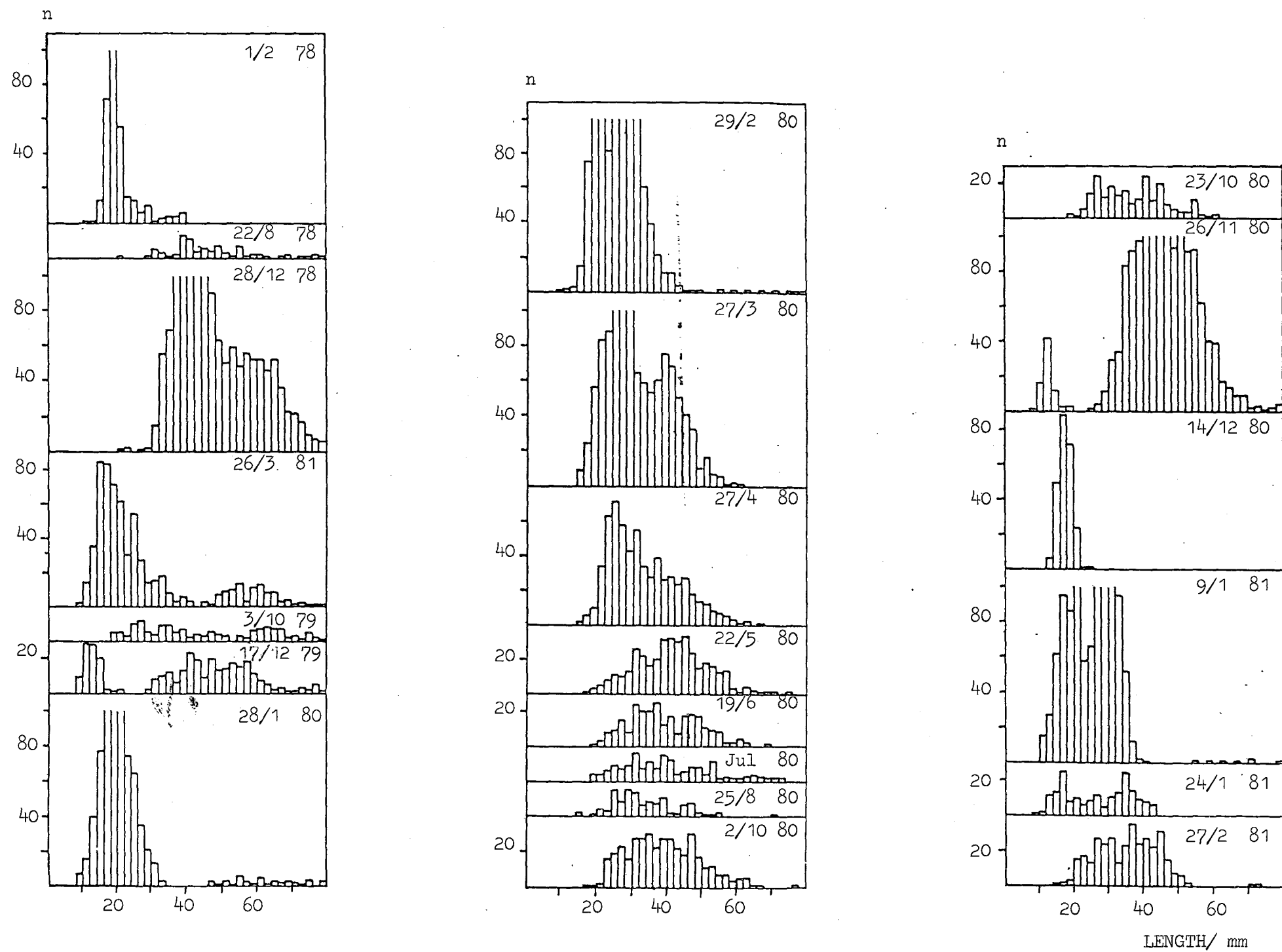


Figure 72. Length frequency distribution of juvenile large *Barbus* species caught in the marginal areas of Lake le Roux.

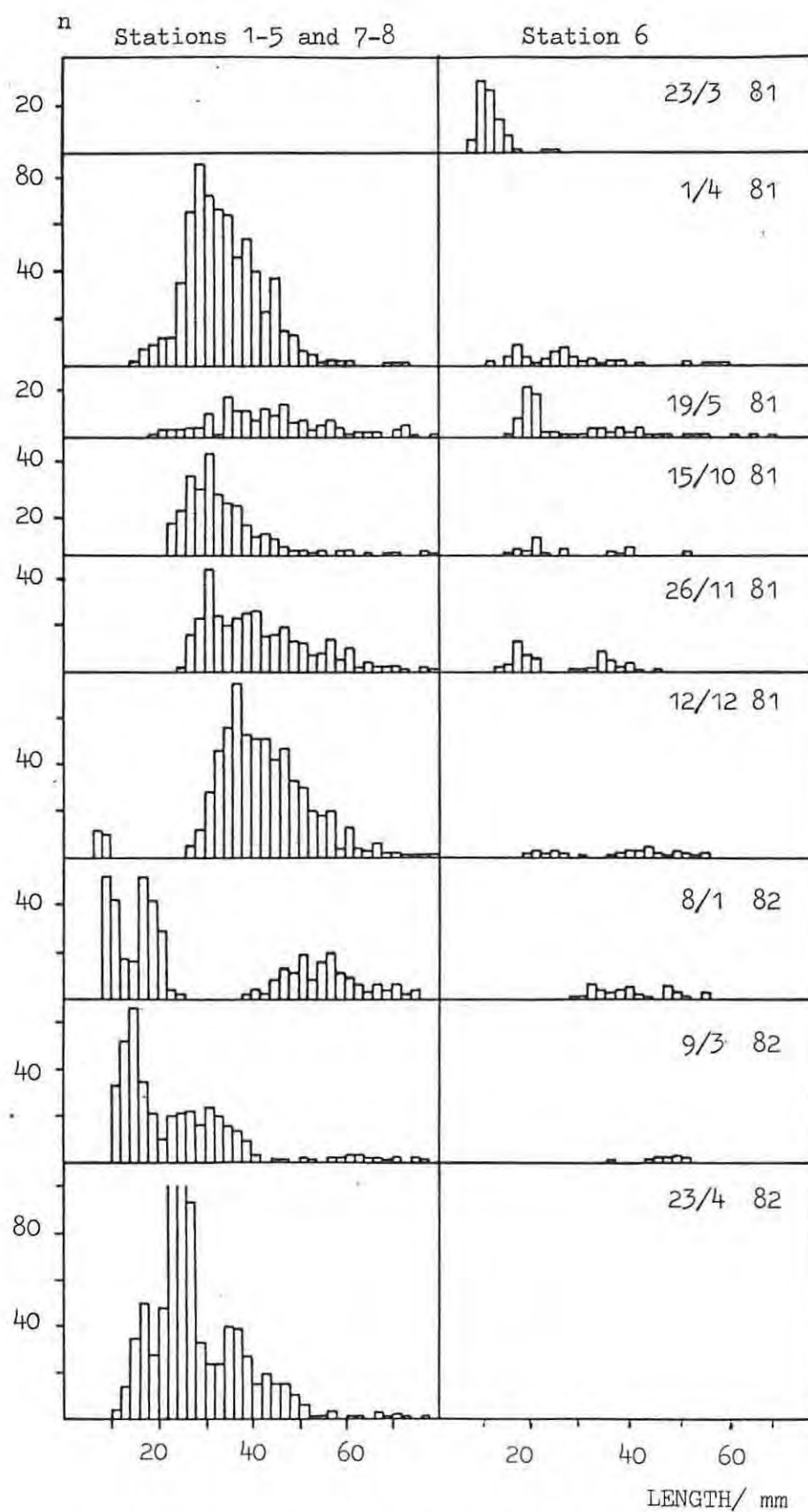


Figure 73. Length frequency distribution of juvenile large *Barbus* species caught in the marginal areas of Lake le Roux.

season and it could be that the lower mode was due to resorption.

Ova diameter was related to GSI. Ripe females had a GSI of three to eleven, and usually between four and seven (Fig. 75). Insufficient samples were obtained to relate changes in GSI or ova diameter to time of spawning.

Males mature at a smaller size (younger age) than females and were thus more common in the catches. The GSI of 30 males in ripe, running condition (milt was extruded by light pressure on the belly) caught in December and January was on average 2,4 (range 0,7 - 4,2). The small gonads and relative scarcity of mature fish made it meaningless to weigh gonads in the field.

Measurements of ova diameter indicate that each fish only spawns once during a season. The two spawnings of large Barbus may represent spawning of the two species. Mulder (1973a) concluded that large Barbus in the Vaal River spawned once in a season and that B. kimberleyensis spawn later in the season than B. holubi. There is some circumstantial evidence which indicates that the first spawning is by B. holubi and the second by B. kimberleyensis in Lake le Roux. The size obtained by the latter at the end of the first and second growing season is significantly smaller than that of B. holubi (Appendix 1, Tables 1 to 4). B. kimberleyensis appears to be adapted to higher water temperatures than B. holubi, since in spring 1980 growth commenced earlier in B. holubi than in B. kimberleyensis (Chapter IV, B). Also B. holubi is found at higher altitudes than B. kimberleyensis (Jubb, 1970).

Evidence of spawnings in the Seekoei River (station 6) was found in late summer 1981 and evidence of the next season's spawning was recorded on 28/11 1981 (Fig. 73). Both these spawnings coincided with a flooding of the river (Fig. 18), and probably resulted from a resident population.

Time of first spawning since 1979/1980 was inferred from the time of capture of small juveniles in the riverine section, using information on incubation time and size in early life from le Roux (1968) and Mulder & Franke (1973). A 10 mm larva is approximately 10 days old at water temperatures of 19°- 21°C. Spawning times prior to 1979/1980 were inferred from growth rates of juveniles in subsequent years. It was assumed that the characteristics of water

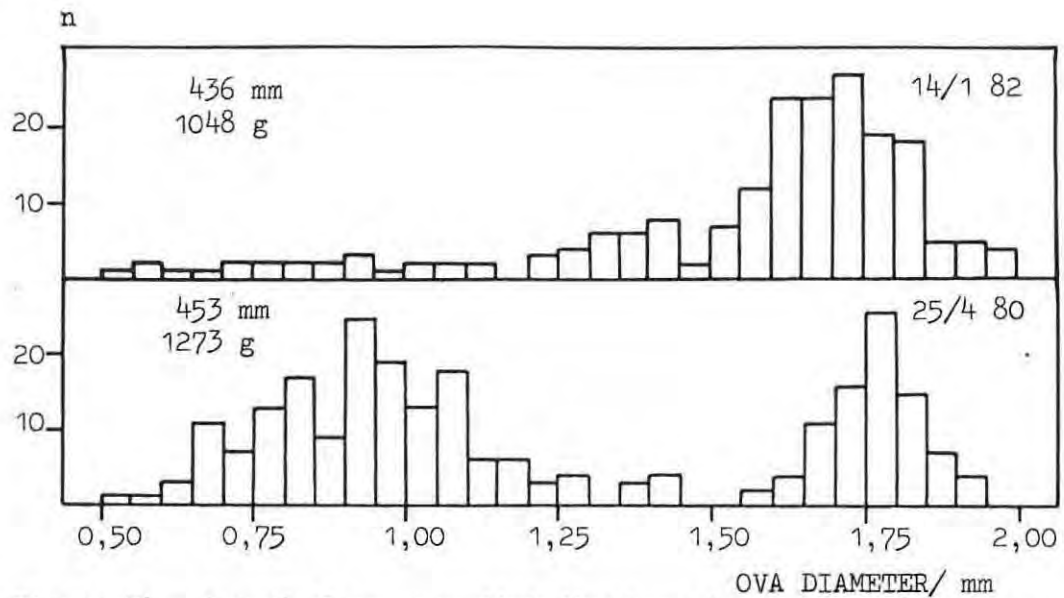


Figure 74. Length frequency distribution of ova diameter in two *Barbus holubi* from Lake le Roux. A skewed unimodal distribution (above) was typically found, but a bimodal distribution (below) was also encountered.

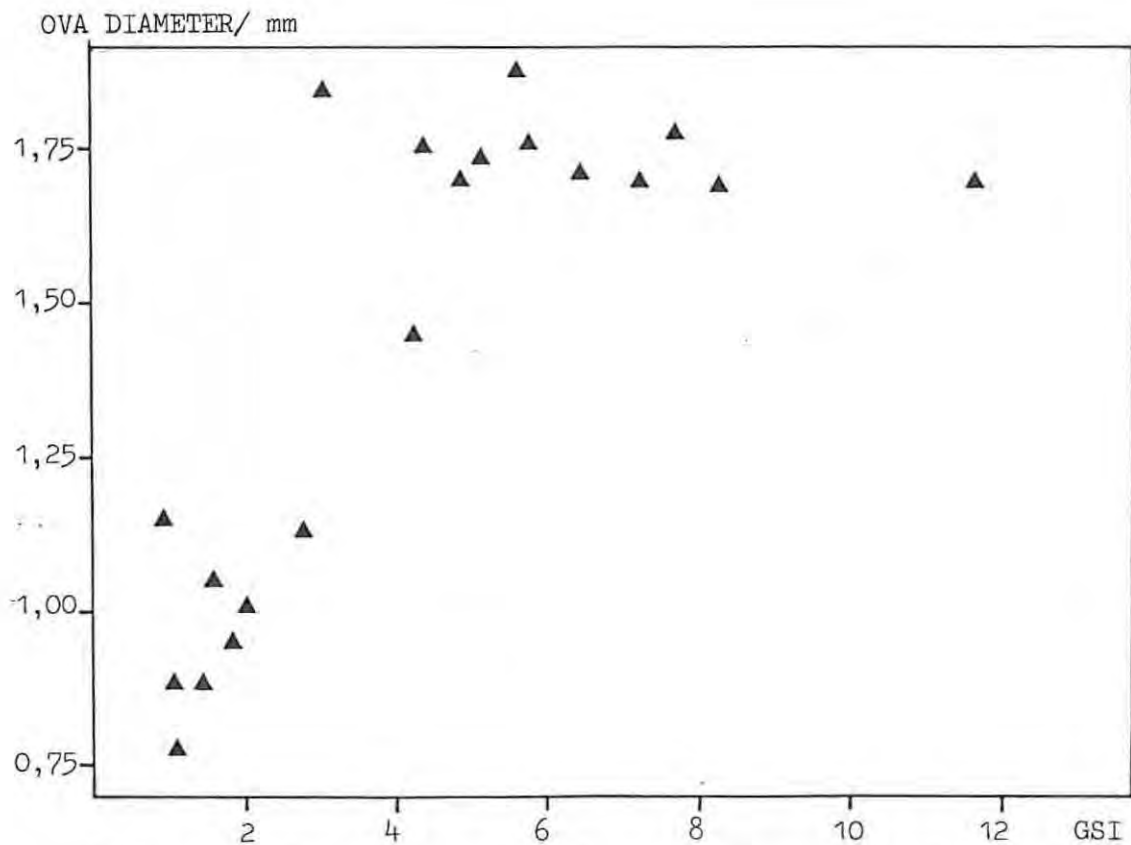


Figure 75. Average ova size of maturing and mature *Barbus holubi* in Lake le Roux, in relation to the percentage which gonad weight constituted of total weight (GSI).

released from Lake Verwoerd have an over-riding influence on growth. Thus it was assumed that initial growth in 1977/1978 was similar to that in 1980/1981 (relatively clear, epilimnetic water), and in 1978/1979 conditions were similar to those in 1981/1982 (turbid, hypolimnetic water).

Information on estimated spawning time, pattern of water release from Lake Verwoerd, initial growth rate and of relative year class strength of B. holubi is given in Table 28. Time of spawning depends on hydrological management. Temperatures are warmer when epilimnetic water is released (when Lake Verwoerd is low, Fig. 17), or when the rate of release of hypolimnetic water is slow. The conditions which determine time of spawning also affect initial growth rates. When spawning is late, initial growth rates are slower than when spawning is earlier (Table 28).

Table 28. Estimated year class strength and time of spawning of Barbus holubi in successive seasons in Lake le Roux. Characteristics of water released from Lake Verwoerd before and during time of spawning (from Fig. 17) and initial growth rates (from Figs. 72 and 73) are included.

Season	Time of spawning	Characteristics of water released from Lake Verwoerd	Initial growth rate	Year class
1977/1978	Late Oct. - early Nov.	10-50 x 10 ⁶ m ³ /day epilimnetic		strong
1978/1979	Early-mid Dec.	15-20 x 10 ⁶ m ³ /day hypolimnetic		weak
1979/1980	Mid-late Nov.	5-20 x 10 ⁶ m ³ /day hypolimnetic	0,33 mm/day	medium
1980/1981	Late Oct.-early Nov.	5-10 x 10 ⁶ m ³ /day epilimnetic	0,43 mm/day	strong
1981/1982	Late Nov. - early Dec.	10-15 x 10 ⁶ m ³ /day hypolimnetic	0,25 mm/day	?

There is a clear relationship between time of spawning and relative strength of the resulting cohort. In view of the late time of spawning and poor initial growth, it is likely that the 1981/1982 year class will be a poor one.

b. Labeo capensis

Unlike the two Barbus, L. capensis appears to spawn throughout the lake. In the juvenile survey on 1/2 1978, thousands of L. capensis 30 - 50 mm were caught at station 7 and they were common down to station 4 (Cambray, pers. comm.). From then until the end of 1980, no small L. capensis juveniles were caught below station 7.

In December 1979 a few small L. capensis were caught at station 8, indicating that spawning had occurred during the season (Fig. 76). In late January 1980, there were two modes, and these modes remained relatively stationary throughout the summer, indicating slow growth. Similarly at station 7, a mode found in January 1980 remained practically unchanged until late October.

In January 1981, new modes were found at all stations, except 3 and 6 (Fig. 77). Comparing the movement of the modes at stations 1 to 5 to those at stations 7 and 8, it is evident that growth was poor in the upper reaches of the lake.

On 27/2 1981 evidence of a spawning at station 6 was found. This spawning must have occurred before the flood in the Seekoei River (Fig. 18), but on 1/4 1981, the smallest mode might have resulted from a spawning when the river flooded. A new mode on 26/11 1981 (Fig. 77) indicates that spawning occurred during the spring flood (Fig. 18).

In 1981/1982, juvenile distribution indicated that L. capensis had spawned throughout the lake (except at station 3) (Fig. 77). It is however evident that spawning activities are not always synchronized throughout the lake. This shows the importance of local conditions for spawning of L. capensis.

Ripe males and females were found throughout the lake. It was difficult to differentiate between resorbing and maturing gonads of males. Female gonads however started ripening in April when eggs were clearly visible in some of the individuals captured. Not all fish mature at the same time and there was a great variation in GSI (Fig. 78). Ova diameter of L. capensis invariably showed a near normal distribution with one distinct mode, and spent females were found to have shed all their eggs. The large variation in GSI (Fig. 78) reflects in part a variability in times of maturity within a season. The relationship between GSI and ova diameters indicates

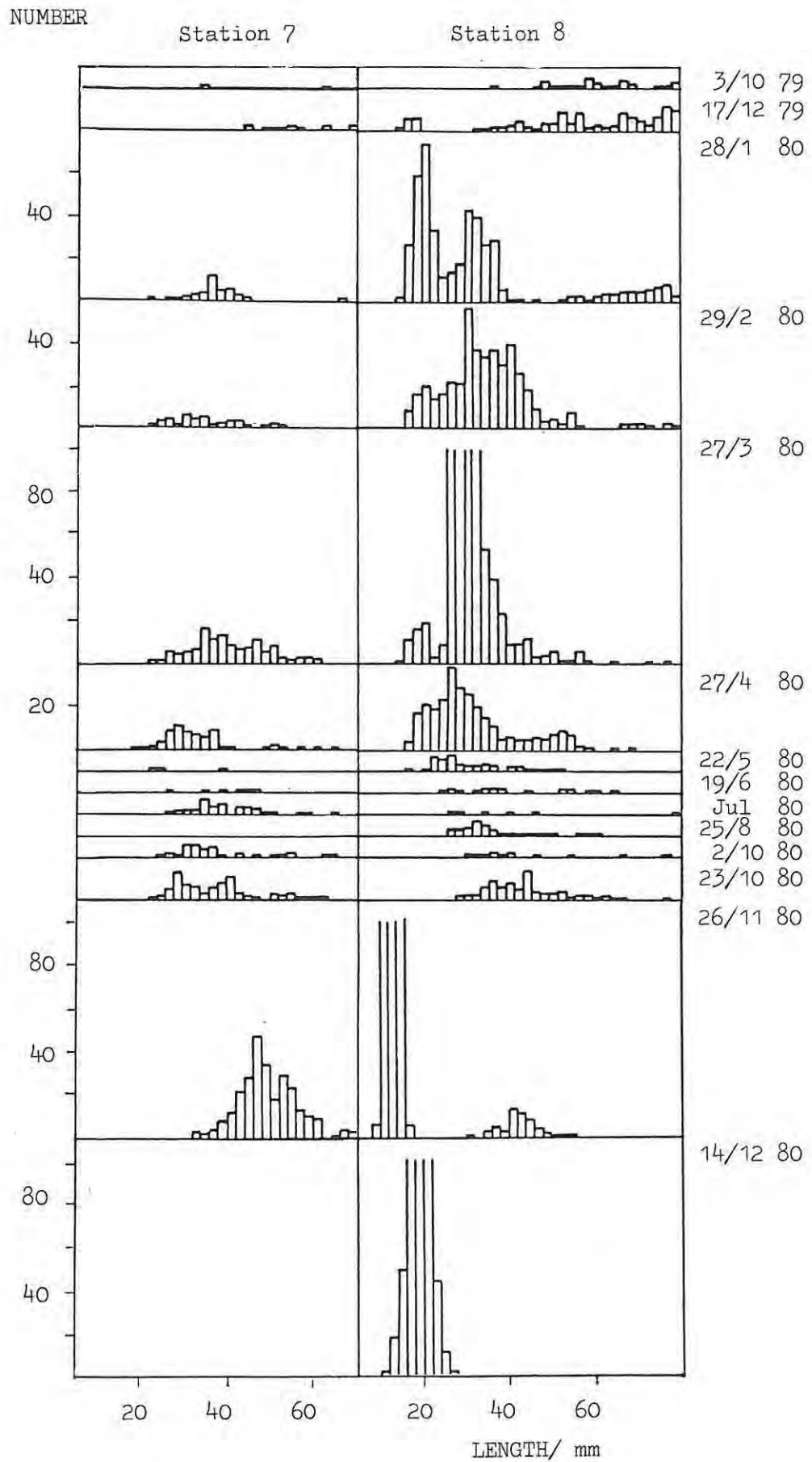


Figure 76. Length frequency distribution of juvenile Labeo capensis in Lake le Roux, caught in the marginal areas of stations 7 and 8.

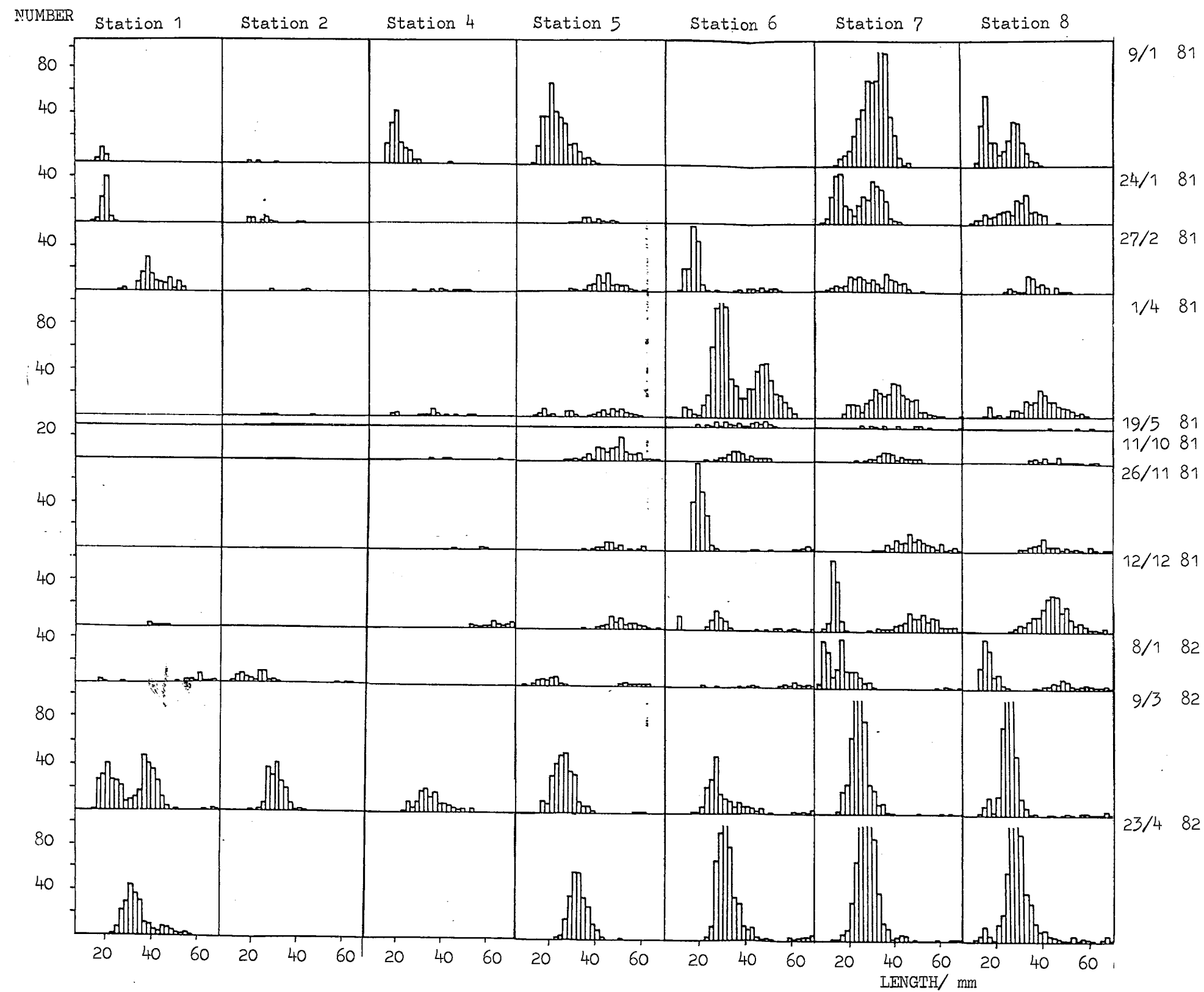


Figure 77. Length frequency distribution of juvenile *Labeo capensis* in Lake le Roux, caught in the marginal areas at different stations.

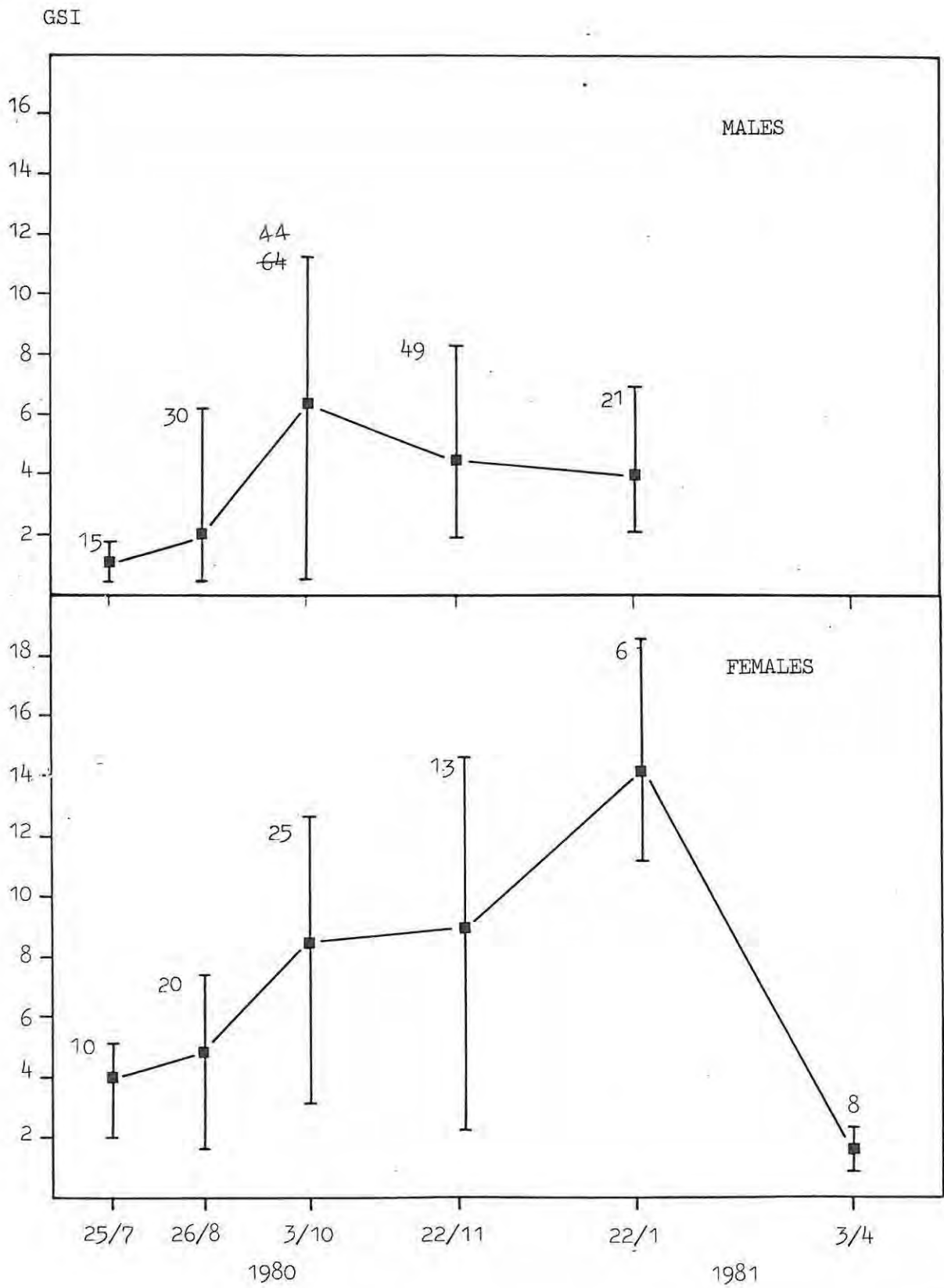


Figure 78. Temporal changes in percentage which gonad weight constitutes of total weight (GSI) of *Labeo capensis* in Lake le Roux. The mean, n and range are given.

that L. capensis are generally ready to spawn when GSI exceeds seven (Fig. 79).

The drop in GSI of males from October may be due to some spent fish being included in the data. Also ripe males often lost considerable amounts of milt while in the nets and while being handled. This may account for the drop in GSI when GSI of the females is still rising (Fig. 78).

The relative year class strength of L. capensis is different from that of B. holubi and a different explanation is required. The strong 1976/1977 year class was associated with the filling of the lake. During the 1977/1978 season, when a moderately strong year class was formed, lake levels rose by six to seven metres from January 1978 until the dam overflowed in April 1978 (Fig. 16). During the rise in lake level some ground was flooded for the first time. During the following two seasons, when very weak year classes were formed, lake levels remained fairly constant (Fig. 16).

Lake levels rose sharply by almost 10 m from January to April 1981. Different times of spawning in various parts of the lake in 1980/1981 (Fig. 76 and 77) show that it is unlikely that rising water levels triggered spawning. However, rising water levels may contribute to increased survival of young-of-the-year.

4. Size at sexual maturity

Although reproductive success and year class strength in Lake le Roux are probably more related to environmental fluctuations than to the size of the spawning stock, the monitoring of size at sexual maturity may be useful in guiding management decisions. Alm (1959) showed that growth rate directly influenced size at sexual maturity in several freshwater fish species and Iles (1974) showed that size at sexual maturity in herring (Clupea harengus) was directly affected by growth rate. The onset of sexual maturity did not slow down growth rate, but a reduced growth rate triggered the onset of sexual maturity.

In this study, the size at sexual maturity is taken to be the size when 40% of the population is in a breeding condition in October and January. Here all males classified as having gonads of stage 3

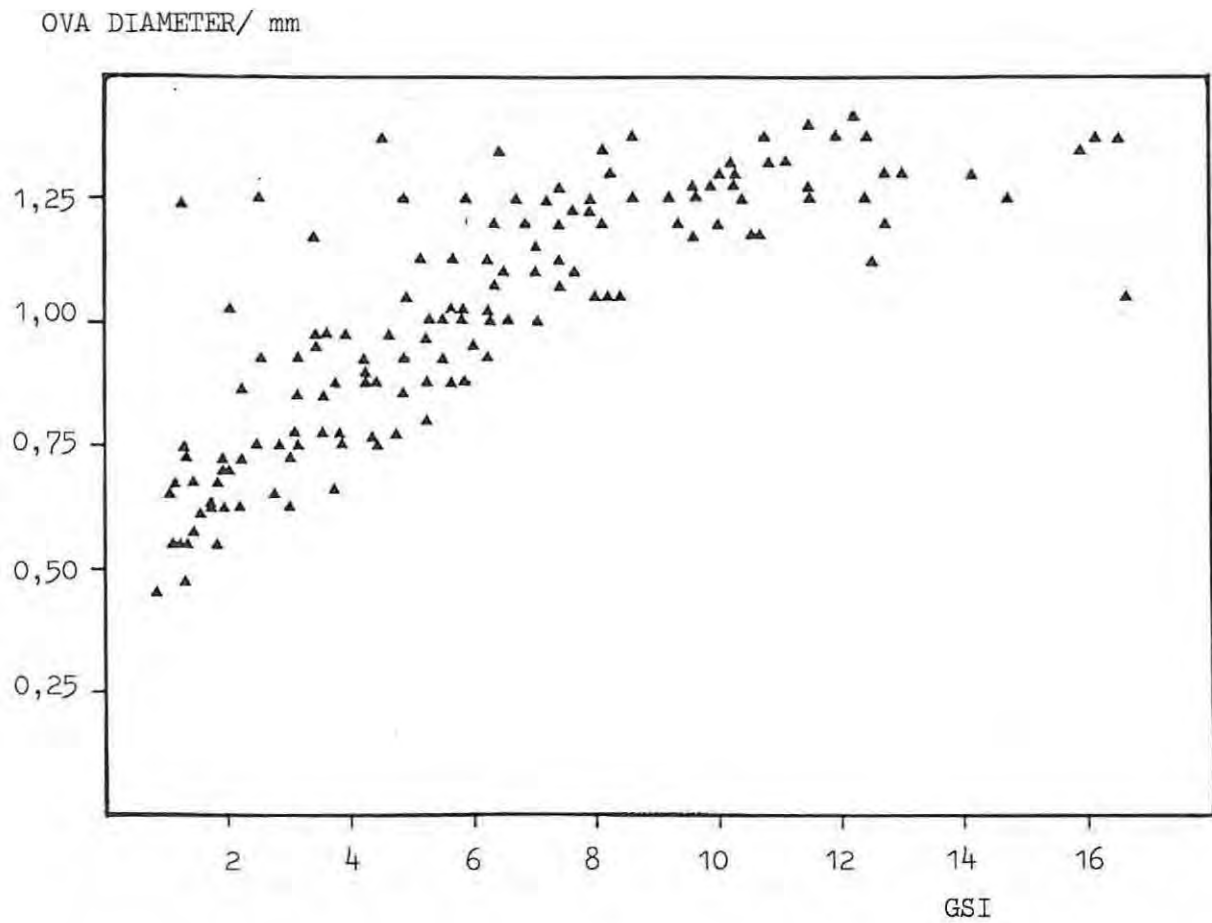


Figure 79. Average ova size of maturing and mature Labeo capensis in Lake le Roux in relation to the percentage which gonad weight constitutes of total weight (GSI).

(Nikolskii, 1963) or more were included. The size of their gonads was clearly larger than that of a 'resting' male. Females were considered to belong to the season's reproductive stock if their eggs were visible to the naked eye (maturity stage 2 and more). Only B. holubi and L. capensis will be considered, since data on B. kimberleyensis were too scarce. Data collected in Lake Verwoerd in December 1980 and 1981 are included for comparative purposes.

a. Barbus holubi

Size at sexual maturity in male B. holubi during different seasons in Lake le Roux and Lake Verwoerd is given in Table 29. There are considerable inter-seasonal variations in both lakes.

Table 29. Size at 40% maturity of B. holubi in Lake le Roux and Lake Verwoerd during different seasons.

Date	length/cm	percentage mature	n
<u>Lake le Roux</u>			
October 1978	41 - 42	38	8
January 1979	-	-	-
October 1979	31 - 32	50	4
January 1980	31 - 32	44	9
October 1980	33 - 34	64	11
January 1981	33 - 34	77	13
October 1981	-	-	-
January 1982	29 - 30	38	26
October 1982	29 - 30	28	68
	31 - 32	33	12
<u>Lake Verwoerd</u>			
December 1980	27 - 28	44	45
December 1981	23 - 24	53	62

The gonads of the large cyprinids in Lake le Roux develop during the winter months. The general reduction in condition at that time (Fig. 48) and lack of growth in length (Chapter IV, B) show that the reserves of one season are used for gonadal production in the following season. It has often been observed in teleosts that feeding and reproductive cycles do not, or only partially coincide, and that they are linked through a cycle of storage (Wootton, 1979).

In the Barbus species, L_{∞} calculated from length increments in each season (Table 19) reflect well the growing conditions of the large fish in the population, from which the following season's spawning stock will be drawn. Therefore, size at sexual maturity was plotted against L_{∞} of the previous season (Fig. 80). In December 1980 scales and otoliths of 318 B. holubi were collected in Lake Verwoerd and 347 samples were collected in December 1981. Since the early history of environmental conditions in the lake is not known in detail to the author, only the increment of the 1979/1980 and 1980/1981 seasons was calculated and used for the construction of a growth curve (Section B). These observations are included in Fig. 80.

There is a positive relationship between L_{∞} and size at sexual maturity. From Fig. 80, the size at sexual maturity in October 1982 would be expected to be at about 200 mm, but at 290-300 mm only 28% of the males were found to be mature (Table 29). In 1981/1982, growth of the smaller (younger) fish was relatively better than that of the larger fish (Table 18), some of which showed no length increment in that season (Chapter IV, B). Probably, the maintenance cost of a large fish in a resource limited environment did not allow for energy to be allocated to reproduction (Purdom, 1979). Similarly, the larger than expected size at 40% maturity following the 1978/1979 season (Fig. 80) may be caused by adverse conditions in the lake as indicated by poor relative condition in October 1978 (Fig. 48).

b. Labeo capensis

Size at sexual maturity in L. capensis in Lake le Roux is relatively constant but larger than size at sexual maturity in Lake Verwoerd (Table 30). Ageing of L. capensis from Lake Verwoerd was

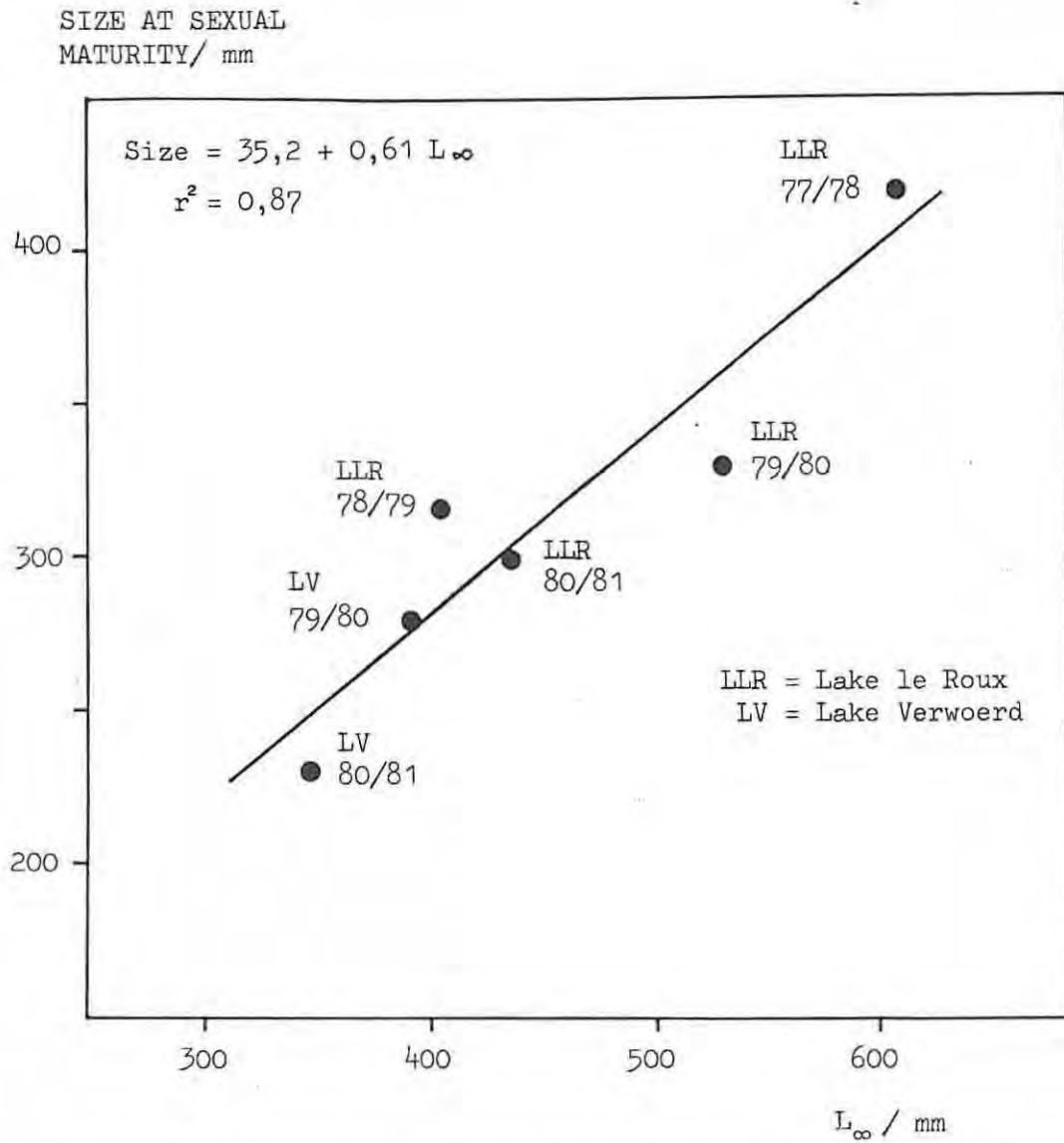


Figure 80. Size at 40% sexual maturity in male Barbus holubi in relation to the previous season's growth. The appropriate growing season has been marked on the graph. (Based on Tables 19 and 29).

attempted, but found to be difficult. It appeared that their growth rate was very slow over several years. In view of the results from Lake le Roux, it was decided that estimates of age would be unreliable, especially in the larger fish. It seemed though that growth in Lake Verwoerd had been slower, but less variable, than growth in Lake le Roux for some years.

Within Lake le Roux, no relationship was found between size at sexual maturity and L_{∞} calculated from the previous season's growth.

Table 30. Size at 40% maturity of L. capensis in Lake le Roux and Lake Verwoerd during different seasons.

Time	Males			Females		
	length/cm	percentage mature	n	length/cm	percentage mature	n
<u>Lake le Roux</u>						
October 1978	35-36	75	8	39-40	100	5
January 1979	33-34	44	11	39-40	58	12
October 1979	31-32	50	62	37-38	71	34
January 1980	33-34	40	50		indeterminate	
October 1980	33-34	40	68	39-40	53	45
January 1981	31-33	44	87		indeterminate	
October 1981	35-36	40	20	39-40	57	28
January 1982	33-34	45	29	37-38	56	16
October 1982	33-34	43	21	37-38	61	18
<u>Lake Verwoerd</u>						
December 1980	29-30	39	28	35-36	55	58
December 1981	27-28	58	24	35-36	50	54

5. Summary and discussion

a. Time and frequency of spawning

In common with most large Barbus species, B. holubi has been reported to spawn in gravel beds following a migration during the first floods in spring. The observed spawnings in the Seekoei River show that B. holubi is ready to spawn in early spring, but can also spawn in late summer if the floods are delayed.

The yellowfish populations in Lake le Roux spawn in the inflowing water in or above the riverine section of the lake. B. holubi spawn earlier in the season than B. kimberleyensis. Each species spawns once during a season, but there are inter-seasonal variations in time of spawning, related to water temperatures. Photoperiod and temperature are important factors regulating gonadal development in cyprinids (de Vlaming, 1972), and it is likely that the temperature of water released from Lake Verwoerd largely controls the rate of gonadal development in the two Barbus species.

Unlike the two Barbus species, spawning of L. capensis was not confined to the Orange River, but occurred throughout the lake. Time of spawning at station 8 was apparently not markedly influenced by temperatures of released water from Lake Verwoerd, nor was it necessarily triggered by rising lake levels. It seems that local conditions are important for the successful breeding of this species, and judging from the literature (Chapter II), local flooding is probably of major importance. There could be more than one spawning during a season in a given locality. This was probably related to high individual variation in gonadal development (Fig. 78) since each female only spawned once in a season.

b. Year class strength

Barbus holubi shows a pattern of year class strength variation which is closely linked to time of spawning. The later the spawning, the weaker the year class. L. capensis produced two relatively strong year classes when the lake was filling, but subsequent cohorts have been poor. These variations in observed year class strength will now be examined in more detail.

In the literature, year class strength is usually either related

to size of parental stock (Ricker, 1954; Beverton & Holt, 1957), the condition of parental stock (Nikolskii, 1962; 1969) or the influence of the biotic and abiotic environment on eggs and juveniles.

B. holubi forms a uniform population in Lake le Roux, but it is difficult to estimate the size of the spawning stock, which varies with size at sexual maturity. Catches of ripe females were low in all years and did not give a reliable estimate of the spawning stock. In a variable environment, size of the spawning stock can be expected to exert less influence than environmental conditions on year class strength (Regier, 1977).

Good growth and condition of a parent stock sometimes improve the quality of eggs laid the following year, enhancing prospects for juvenile survival (Nikolskii, 1962; 1969). In B. holubi such a mechanism may be operating. The strong year class in 1977/1978 followed a season of very good growth, and similarly the 1980/1981 year class was preceded by a season in which, particularly, the larger fish grew well (Fig. 58). The weak 1978/1979 year class was produced by a population in a relatively poor condition (Fig. 48). It is plausible that the quality of the eggs laid reflects the nutritional status of the population, but further research is needed to investigate a possible relationship.

Barbus kimberleyensis does not show the same distinctive reduction in year class strength from 1977/1978 to 1978/1979 as B. holubi (Table 25). This could possibly be explained by the better condition of the parental stock. Increased turbidity did not appear to have the same negative effects on large B. kimberleyensis as B. holubi (Section B).

Labeo capensis do not form one homogenous breeding population in the lake. The irregular breeding around the lake suggests that the influence of the parent stock is minor when compared to that of the environment.

Water temperatures may influence reproductive success. A sharp drop in temperature during the incubation period can cause large mortalities of embryos of fish adapted to spawn during rising temperatures (Hassler, 1970; Walburg, 1972). Strong year classes have often been related to warmer than average water temperatures in early life (Kempe, 1962; Hassler, 1970; Koonce et al., 1977; Goldspink, 1978;

Il'ina & Gordeev, 1981), and it has been suggested that this effect may be due to improved growth when the water is warmer (Kempe, 1962; Goldspink, 1978; Il'ina & Gordeev, 1981). The inference is that natural mortality is inversely related to size (Ware, 1975). Similarly, Pitcher & Hart (1982) concluded in their review of year-class strength that food supply (growing conditions) was the single most important factor affecting year class strength.

In B. holubi it was shown that year class strength could be related to water temperatures (Table 28). When these are at their lowest (large releases of hypolimnetic water from Lake Verwoerd), the range of temperatures experienced is also the largest. There are high daily variations in flow, and the greater the average rate of release, the larger the fluctuations in water flow and temperatures. Thus in B. holubi, year class strength may be related to the influence of water temperatures on embryonic survival and initial rate of growth.

In L. capensis, variable temperatures and rates of water released from Lake Verwoerd may influence reproduction at station 8. L. capensis spawn in flooded river banks and apart from the effect which a change in temperature may have on survival, changes in water level may be particularly important for this species.

Rising water levels usually favour the formation of strong year classes (Boon Swee & McCrimmon, 1966; Hassler, 1970; Walburg, 1972), and particularly strong year classes may be formed when well-vegetated new ground is inundated, particularly for the first time (Bhukaswan, 1980; Il'ina & Gordeev, 1981).

In other African reservoirs, strong year classes of Labeo species have often been observed to form during the initial filling phase, but subsequent year classes have been poor (Chapter II). In Lake le Roux the same pattern is evident. L. capensis spawn among newly inundated vegetation at times of flood and the juveniles are probably well equipped to exploit such habitats. Water level fluctuations appear to have less influence on the year class strength of B. holubi.

Predation and competition may in some cases be important in determining year class strength. Strong year classes may suppress the abundance of subsequent cohorts through predation (Ricker, 1950; Alm, 1952). Forney (1971) demonstrated that predation of juveniles

may accentuate differences in initial abundance.

It is possible that predation plays an important role in year class abundance of B. holubi in Lake le Roux, since successive year classes usually share the marginal habitat for some time (Figs. 72 and 73). In L. capensis intra-specific competition may play a role, but the relatively good growth rates of juveniles at stations 1 and 2 in 1980/1981 and 1981/1982 (Fig. 77) where CPUE of L. capensis was the highest (Fig. 65), indicates that conditions suitable for spawning and the survival of eggs and larvae are of major importance in determining year class strength.

Spawning time may be a good predictor of year class strength in B. holubi but other concurrent changes in the population may equally affect year class strength and further research is called for. Spawning time of L. capensis is probably determined by local floods which are highly irregular. Subsequent survival may be affected by water level fluctuations in the lake. However the shoreline has during the past been eroded by water-level fluctuations and increased lake levels are unlikely to provide conditions as conducive to survival as they were during the first two years after impoundment.

c. Mortality and dispersal

Barbus holubi form a mobile, uniform population in the lake, whose distribution appears to be determined by foraging conditions in the pelagic zone. When turbidity increases, B. holubi may be forced to turn to a benthic mode of living (Eccles, 1980). However, littoral areas, and hence benthic resources are scarce. The lake is turbid and deep with steeply sloping sides and epilithic algae contributes less than 0,1% to the carbon budget (Allanson, 1982). The increase in turbidity leads to a "scramble competition". Such competition is expressed in a lower individual ration and may lead to large scale mortality which more than compensates for the reduction in food supply (Pitcher & Hart, 1982).

Practically the whole B. holubi population is dependent on zooplankton, i.e. exploits the same resource. Therefore, the smaller the fish, the lower the zooplankton concentrations they require (at constant turbidity) for maintenance and growth. This is reflected in a decrease in inter-seasonal variations in growth in younger fish (Table 18).

and the earlier resumption of growth of younger fish in 1981/1982 (Figs. 23 and 24). Changes in relative condition reflect the same trend, with smaller fish recovering earlier than larger ones (Fig. 48).

L. capensis are more stationary than B. holubi and this leads to uneven exploitation of resources in the lake. This was particularly evident prior to 1978/1979 when L. capensis <240 mm were relatively scarce at stations 1 to 3 (Fig. 65). When the turbidity in the lake increased in 1978, L. capensis dispersed, and because of relatively large underexploited areas, the population did not decline. In 1981/1982, however, dense populations of L. capensis throughout the lake meant that redistribution of individuals within the lake may not have provided the means to adequately feed the whole population. Accelerated mortality (Fig. 70) and reduction in relative condition (Fig. 51) took place, but changes in abundance were less dramatic than in B. holubi.

d. Size at sexual maturity and reproductive effort

Barbus holubi has a variable size at sexual maturity which is directly related to conditions in the previous season. When growing conditions deteriorate, size at sexual maturity is rapidly adjusted and the fish mature at a smaller size in the following season (Fig. 80). Labeo capensis in Lake le Roux have a fixed size at sexual maturity. However, L. capensis matures at a larger size in Lake le Roux than in Lake Verwoerd. In the Caledon River, size at sexual maturity is still smaller (Baird, 1976).

It is a common observation that length at maturity is generally positively related to the asymptotic length reached by a species (Holt, 1962; Cushing, 1981), and within a family the length at maturity tends to be a fixed proportion of L_{∞} (Beverton, in Cushing, 1981). When asymptotic size varies among populations of the same species, or changes with time for a population, it is reasonable to expect size at sexual maturity to change as well.

Alm (1959) found that size at sexual maturity was directly dependent on growth rate, but his analysis was complicated in that he compared size at an age but not relative growth rate of different populations. This may explain why he found that fish which grew rapidly in early life often mature at a smaller size than fish

which grew at a moderate rate. The relative decrease in rate of growth with size might have been a better criterion for the comparison of size at sexual maturity. Parker & Larkin (1959) found that size is a better measure of the potential growth of a fish in a given environment than is age. Their reasoning was that the opportunity to exploit and the ability to digest food resources change with size rather than age. Many examples of this can be found in the literature and if the change in the range of resources available at a given size is sudden enough, a new growth stanza is entered for which the asymptotic length is larger than the previous stanza (Warren, 1971).

The reduction of growth rate and smaller size at sexual maturity is commonly known as stunting or dwarfing. An alternate explanation to the one outlined above, i.e. that it is a function of nutritional limitation, was put forward by Fryer & Iles (1969) and further developed by Iles (1973). Their argument was that the maturing of 'Tilapia' at a small size reflects an adaptation to variable environmental conditions and high rates of mortality. However, it can equally be argued that the examples of stunting in 'Tilapia' given by Iles (1973) reflect a resource limitation (food or space). Cichlids are prolific breeders and tend to overcrowd the habitat and stunt (Odulege, 1982). This is further supported by an observation by Holden (1969) who found that the L_{∞} of Oreochromis niloticus increases with increasing yields in different populations. The reduction in yield is possibly associated with overpopulation.

The reduction in size at sexual maturity with decreased growth in B. holubi can be seen as an adaptation to a limitation in food availability. L. capensis in Lake le Roux does not appear to show the same response. However size at sexual maturity in Lake Verwoerd is smaller than in Lake le Roux, and growth rates in Lake Verwoerd appear on average to be slower than in Lake le Roux. The smaller size at sexual maturity in the Caledon River (Baird, 1976) could also reflect poorer average growing conditions in the river than the large reservoirs. It is, therefore, probable that in the long term size at sexual maturity in L. capensis is reduced in response to deteriorating growing conditions, although in the short term it is relatively constant.

VI. CONCLUSIONS AND RECOMMENDATIONS

The management of fish populations becomes more species-directed as knowledge of particular populations increase. Thus in the early stages of a freshwater fishery, resources are often assessed on the basis of general models which predict yield. The most popular of these 'first generation' models, Ryder's morphoedaphic index, and several other models, are reviewed by Ryder (1978) and Bhukaswan (1980).

When more is known about the fish populations, management may be aided by theories of life history (Adams, 1980), comparative studies in biology (Holt, 1962) and knowledge of the complexity and environmental influence on the populations (Regier, 1977). Ultimately, management of fish resources for different purposes is best guided through an understanding of the adaptiveness of a population to its environment. Nikolskii stated this clearly (1962, p.277):

"A knowledge of the forms of adaptive response of populations to changes in the conditions of life, and, particularly, to changes in food supply, is as necessary for a rational organization of a fishery, as is a knowledge of the changes in living conditions of the population. It is impossible to build up a rational fishery industry, based only on studies of the changes in living conditions, without trying to understand the adaptive response of the population. The fishing industry should be planned in such a way that it becomes a component of the environment of the species exploited, i.e. the rate of the industry's influence should not exceed the range of the adaptations of a species."

In this chapter the life history strategies of B. holubi, B. kimberleyensis and L. capensis in relation to environmental fluctuations in Lake le Roux are discussed and compared. Influences on life history are drawn from the present study and a review of the literature (Chapter II). On this basis, management alternatives are briefly examined and recommendations for future research are made.

A. LIFE HISTORIES AND THE ENVIRONMENT

1. Barbus holubi

In its natural habitat, B. holubi spawns over gravel beds in rivers, following a spawning migration during the first floods in

spring or summer. This appears to be a general trend in all large Barbus species (Chapter II). B. holubi in Lake le Roux spawn in the regulated Orange River and the time of spawning is dependent on water temperatures in spring.

Time of spawning is related to the survival of eggs and/or larvae and a weak year class may result from a late spawning. The eggs are, however, relatively large and after an incubation period of a few days, the larvae hide in the gravel and live off the yolk sac for some time. They are, therefore, not dependent on immediate external feeding. The juveniles live in shallow marginal areas, but at 50 mm they begin to move away from the shore and disperse throughout the lake.

B. holubi is an opportunistic feeder. In early life zoobenthos and zooplankton is eaten, but later plant matter may dominate in the diet. This transition towards herbivory is reflected in an increase in the gut length: fish length ratio with size. In Lake le Roux B. holubi exploits the zooplankton community, visually selecting individual prey. Turbidity and zooplankton density may therefore determine the upper size limit of B. holubi which can sustain a living in the pelagic zone.

Individual growth rates vary between seasons with inter-seasonal variations increasing with age (size). Resources other than the zooplankton are restricted and sharp increases in turbidity may therefore cause large scale mortalities. A schematic diagram of the principal factors governing the density and size structure of the B. holubi population in Lake le Roux is presented in Fig. 81.

Reproductive effort is moderate, but when growing conditions deteriorate, size at sexual maturity is reduced. In Lake le Roux an increase in turbidity occurs when the retention time in Lake Verwoerd is short, i.e. when the water level in Lake Verwoerd is low in spring and silt-laden floodwaters enter the lake. However, when Lake Verwoerd is low, water released into the Orange River between the two lakes is epilimnetic and relatively warm. This causes an early spawning of B. holubi and a rapid initial growth, resulting in a strong cohort. The size structure of the population thus rapidly adjusts to changes in environmental conditions. It appears that man-made manipulations of the hydrological regime are an important factor in determining the population structure of B. holubi.

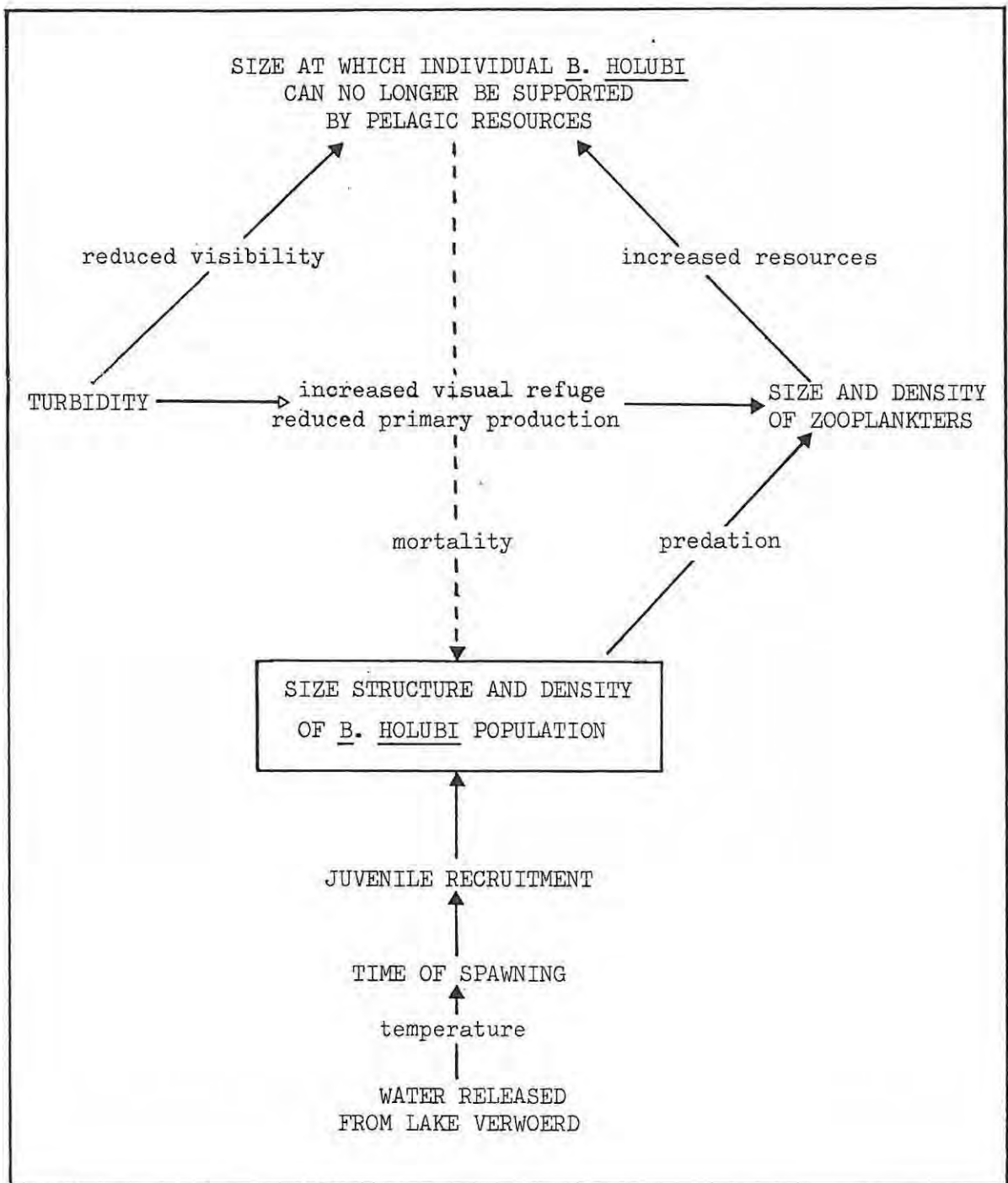


Figure 81. Major factors affecting size and structure of the B. holubi population in Lake le Roux.

From this study, it appears that B. holubi is adapted to a relatively stable environment. This is reflected in the synchronized spawning, moderate reproductive effort, relatively large egg sizes and rapid adjustment in size at sexual maturity to growing conditions, i.e. it reacts to change as if the change is permanent. B. holubi is, however, well equipped to adjust to the fluctuating environment in Lake le Roux because of relatively secure breeding and early survival and quick dispersal.

2. Barbus kimberleyensis

Two important differences separate the life histories of B. holubi and B. kimberleyensis. Firstly, B. kimberleyensis appears to be adapted to relatively warmer temperatures than B. holubi. This is reflected in later resumption of growth and later spawning for B. kimberleyensis, probably causing the consistently weak, although variable, year classes. At times when B. holubi suffers high mortalities, B. kimberleyensis is much less affected, possibly because feeding activity is normally resumed later in spring/early summer, by which time there has already been a considerable reduction in the B. holubi population. Thus "scramble competitions" may to some extent be avoided.

A second major difference between the two large Barbus species is that B. kimberleyensis becomes increasingly piscivorous with size. In Lake le Roux this results in a considerably larger ultimate size reached by B. kimberleyensis. However, because of the late spawning of B. kimberleyensis it is unlikely that this population will ever become a major component of the fish community.

3. Labeo capensis

As is common in other Labeo species, L. capensis spawns over newly flooded ground at times of flood, but longitudinal spawning migrations are apparently not required. There is a large intra-seasonal individual variation in gonadal development and spawning can occur around the lake, but breeding is erratic due to the limited, undependable and localized nature of rainfall in the area. L. capensis can spawn once, or more often, in the riverine section every season, but survival

may be reduced because of the short duration of floods. Similarly, flash floods in tributaries may be of short duration. However, the eggs are non-adhesive and neutrally buoyant, and stranding may thus be avoided.

The eggs are small (about $1/3$ the size of B. holubi eggs), have a short incubation period and the newly hatched larvae swim up into the water column, possibly to avoid stranding. Due to the small size of the larvae, external feeding is required after a short time. Newly inundated vegetation may provide optimal conditions for early feeding and survival, as indicated by the strong year classes which formed when the lake filled. In subsequent years, spawning in the riverine section or due to local flooding did not coincide with rising water levels, which may be the main determinant of year class strength.

In the pristine Orange River, flow is seasonal, but the height and duration of peak floods are variable (Fig. 17). The variation in gonadal development ensures that different members of the population spawn at different peaks in flow, but survival may depend on the duration of high flow. The variable rates of gonadal maturation can therefore be seen as a lack of advantage associated with a particular time of spawning. The chances of juvenile survival are not necessarily related to time of spawning.

Dispersal in the lake is slow which may reflect the reliance on currents for transport in early life. Lack of pre-spawning migrations may further reduce the necessity for active dispersal of the juveniles.

Knowledge of the feeding of L. capensis in early life is lacking, but presumably they are carnivorous before turning herbivorous. Labeo species are specialist feeders and L. capensis appears to rely on autochthonous material as a source of food. Thus when turbidity increased in 1981, L. capensis reacted by a reduction in relative condition and increased mortalities. Food shortages also triggered the dispersal of fish smaller than 200 mm. A major source of organic carbon ($\pm 80\%$) comes from allochthonous sources (Allanson, 1982), but the marked reaction of L. capensis to increases in turbidity indicates that they cannot make extensive use of this source. A schematic diagram of the main factors affecting distribution and density of L. capensis is presented in Fig. 82.

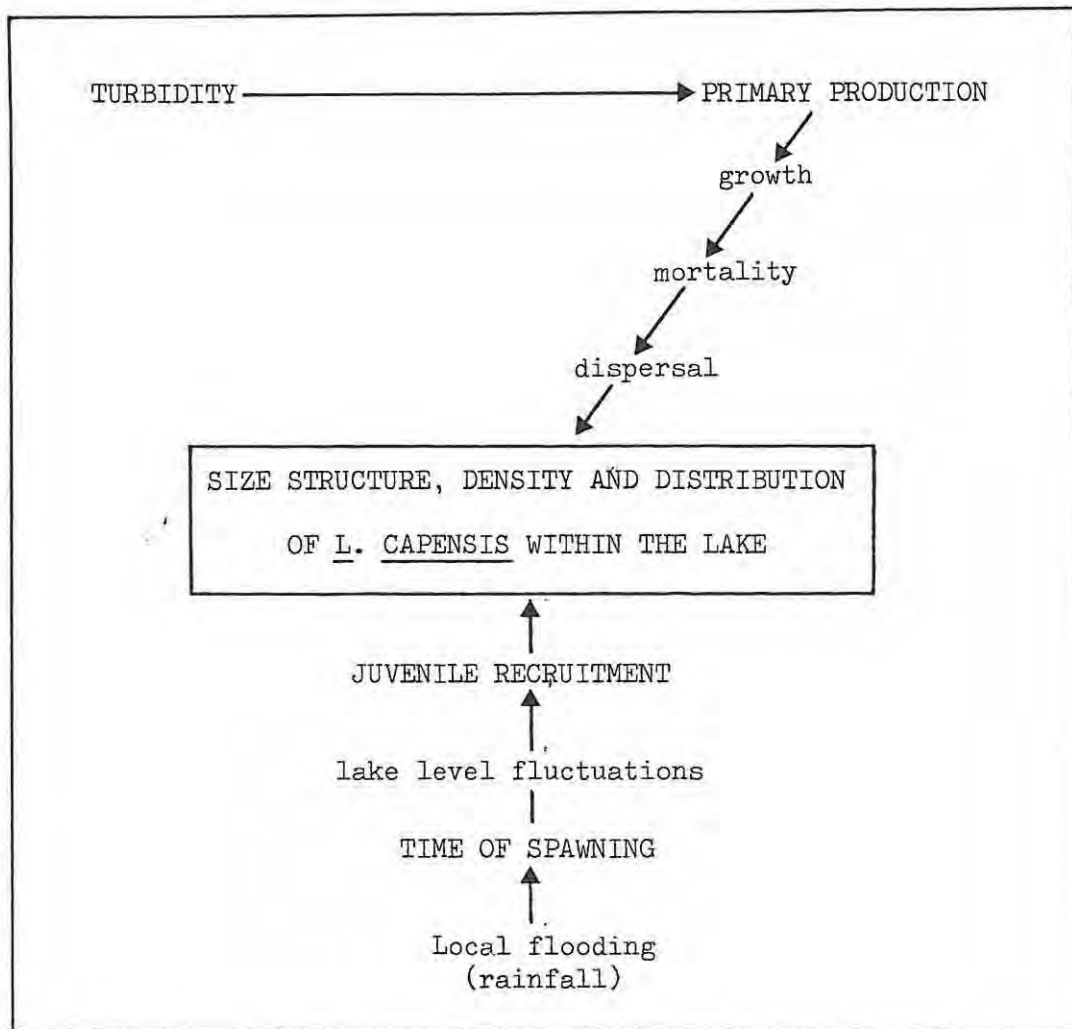


Figure 82. Major factors affecting size structure, density and distribution of L. capensis within Lake le Roux.

Growth rates are variable and related to density and turbidity. When growing conditions are poor, subadults and adults appear to be equally affected, unlike B. holubi. Reproductive effort is relatively high, about twice that of B. holubi, and changes in growing conditions do not bring about an immediate change in size at sexual maturity. Deteriorating growing conditions may, however, result in reduced size at sexual maturity in the long term.

Results of the present study indicate that L. capensis is adapted to a relatively variable environment. This is reflected in the variable time of spawning within a population, high reproductive effort, relatively small egg size and slow changes in size at sexual maturity in response to changes in growing conditions, i.e. it reacts to change as if change is a normal feature of the environment. L. capensis is, however, poorly equipped to adjust to the lake environment. The risk of reproductive failure is increased since reproduction relies on local floods and chances of rising water levels accompanying floods are also reduced, negatively affecting the survival of larvae and juveniles. Dispersal of larvae and juveniles in the lake is poor leading to an uneven distribution of the population in relation to available resources.

B. MANAGEMENT CONSIDERATIONS

Decisions on exploitation of a fish resource are influenced by an array of socio-economic considerations (Rothschild, 1973). The present study has been confined to a biological investigation of three species in the lake, and has not considered the benefits or losses society might accrue from different types of exploitation. Lake le Roux is in a relatively sparsely populated area, remote from large population centres, and no official policy on exploitation of the fish population is available. Therefore, the management considerations presented here are of a general nature. The consequences of the two main aspects of exploitation, i.e., the intensity and size composition of the catch, are considered.

1. Barbus holubi

Barbus holubi is a popular angling fish in South Africa (Groenewald,

1951; le Roux, 1968) but because of the remoteness of Lake le Roux from urban areas, angling pressure is light and fishing mortality negligible. The population of B. holubi shows a considerable temporal variation in abundance (Fig. 60) and size composition (Fig. 63), both of which are closely related to turbidity and density.

In 1978/1979 the index of population density was reduced from 1000 to 50, and in 1981/1982 there was a second major reduction from about 550 to 200 (Fig. 60). These reductions were brought about by increases in turbidity which reached the same level in 1979 and 1982 (Fig. 19). However population density in 1982 was about four times higher than in 1979 (Fig. 60). This shows the effect of 'scramble competition' (Pitcher & Hart, 1982), which leads to a mortality in excess of the reduction in carrying capacity. The excess mortality is positively related to initial abundance. This suggests that exploitation of B. holubi could have a stabilizing effect on the population. In order to attain maximum yields the largest size groups in the pelagic zone should be exploited. If there is a desire to retain larger individuals for recreational fisheries, an upper size limit of fish caught in commercial or artisinal operations might be imposed. This could be achieved by regulating mesh size of nets used in fishing operations.

Year class strength of B. holubi is variable and can be weak depending on hydrological management (Table 28). If fishing pressure is light, variations in year class strength will only have a moderate effect on total catches, while changes in turbidity and likely to have an overriding effect on population changes. However, if the population is being exploited heavily, a fishery might be more affected by variations in year class strength than by variation in production due to changes in turbidity.

B. holubi forms a highly mobile population (Chapter V, B). Thus fishing in one area of the lake will probably not lead to local depletions. Catches are usually highest where the water is the clearest, i.e., near the dam wall (Figs. 20 and 63). In spite of this mobility there are enough areas inaccessible to fishing to ensure adequate spawning stocks, even if a fishery was relatively intensive.

The major population parameters of B. holubi such as growth, recruitment and mortality are sensitive to environmental fluctuations which are largely the result of hydrological management (Chapter IV, A).

If the hydrological management cannot be adjusted to meet the needs of a future fishery, predictions of changes in environmental conditions will be indispensable for the planning and optimal use of such a fishery. Predictions should be based on an understanding of hydrological principles and estimated water-use practices.

2. Barbus kimberleyensis

This species is not abundant in the lake and is unlikely to play an important role in a commercial or artisanal fishery. However, it is a prized angling fish (Mulder, 1973a; Gaigher, 1976). B. kimberleyensis is long-lived (Mulder, 1973a; Chapter V, B) and it might be useful to impose an upper mesh size limit to protect large individuals, which then would contribute to the excitement of angling. It would be impossible selectively to fish for small B. holubi or B. kimberleyensis because of the similar habits of these two species.

3. Labeo capensis

Labeo capensis is not readily caught with hook and line and is not a potential angling species. In Lake le Roux this species does not show as large a fluctuation in CPUE as B. holubi (Fig. 60). Light or moderate fishing effort might have reduced natural mortality in 1981/1982 (Fig. 69) and left the survivors in a relatively better condition (Fig. 51). Although this species is relatively sedentary, there was a considerable movement of fish smaller than 200 mm associated with increases in turbidity (Chapter V, C). If the population of L. capensis at stations 1 and 2 had been reduced prior to the increase in turbidity in 1981/1982, a situation similar to the one in 1978/1979 might have arisen. When turbidity increased sharply in 1978, a redistribution of L. capensis into relatively vacant areas at stations 1 to 3 accounted for a considerable increase in CPUE of this species (Fig. 70) and survival appeared to have been good.

A major problem associated with the exploitation of Labeo capensis is the reproductive uncertainty of this species, which in the lake is greater than in the pristine river. Murphy (1967, 1968) showed that when reproductive success is variable, a heavy fishery which reduces

the number of year classes in the breeding population, may cause a collapse of the population in a relatively short time. Multiple spawning and numerous breeding year classes allow for a population to maintain a high abundance even if reproductive success is poor in consecutive years. It appears that Labeo species in general may be similarly adapted to variable reproductive success, and examples of the collapse of large populations may be found.

Labeo altivelis supported an intensive fishery for several years in Lake Mweru and during spectacular spawning migration (known as "Kapata" which means explosion) up the Luapula River during floods early in the year (Matagne, 1950; De Kimpe, 1964). Length frequency distribution indicated that the population had a simple age structure, with fish larger than 140 mm falling into two distinct modes (Matagne, 1950). In 1949 the usual summer floods failed and spawning of L. altivelis did not appear to have been successful (Matagne, 1950). In 1950, floods were again poor and spawning activity was limited (De Bont & Maes, 1956). Fishing pressure was not reduced and yields remained high until 1951 when catches dropped sharply and the following year catches of L. altivelis were insignificant. The catches remained low even into the sixties (De Kimpe, 1964).

River fisheries for Labeo victorinus during spawning runs up flooded tributaries to Lake Victoria were at one time of great economic importance locally (Cadwalladr, 1965a). As in the Luapula - Mweru system, catches remained at a high and relatively constant level for several years. In 1955 and 1956 catches decreased sharply and in subsequent years catches remained a small fraction of previous levels (Cadwalladr, 1965a). The simultaneous decline of catches in two rivers suggests that broad climatic factors might have influenced the reduction.

The relatively high fecundity and small egg size of Labeo species (Chapter II, C) indicates that they are adapted to variable reproductive success. Most Labeo species appear to require lateral migrations on to a flooded river bank to spawn (Chapter II, B), and reproductive success may be determined by the height and duration of floods. Rainfall in South Africa is relatively scarce and shows high inter-annual variations, especially in the interior (Dyer, 1981). These variations appear to be superimposed upon cycles of approximately 10 years of relatively dry and wet climates (Dyer, 1978). There is a

good possibility of a run of either wet or dry years.

An intensive fishery on Labeo species would lead to a reduction of repeat spawners and a simple age structure of the population. Increased exploitations (reduced density) is also likely to lead to an increase in growth rate (Backiel & Le Cren, 1967), which is usually accompanied by a narrower size range for each year class (Nikolskii, 1969). In view of the rainfall pattern in South Africa and the effect of exploitation on population structure, care must be taken if Labeo populations are to be exploited. A high yield can only be sustained for as long as reproductive success remains good, but may decline rapidly, particularly when reproduction fails in successive years. Once reduced, it may take the population a long time to recover (Murphy, 1968).

In Lake le Roux, reproductive success is likely to be more variable than in the pristine river. Spawning has to depend on erratic local rainfall and survival is probably chiefly influenced by water level fluctuations in the lake. Therefore a large scale fishery on L. capensis should not be contemplated, although catches could be relatively good in the short term.

4. Conclusion

B. holubi in Lake le Roux appears to have the potential to sustain a fishery on a continuous basis, particularly if hydrological management can be adapted to avoid exceptionally weak year classes. The intensity of the fishing should be guided by predictions of changes in the turbidity regime of the lake. If a recreational fishery becomes a primary objective, large scale removal (netting) of small fish, or hydrological management aimed at reducing spawning success would be necessary to increase the numbers of larger fish (Fig. 81). A commercial fishery should, therefore, not be seen as a threat but rather as a benefit to recreational fisheries, since it could be used to promote good angling.

L. capensis is not an angling species and does not have the potential continually to sustain a large fishery. This species does not react as quickly to environmental changes as B. holubi and has a relatively fixed size at sexual maturity. Therefore, it might be best

exploited on an "accumulated stock" basis, i.e. the population would be exploited intensively for relatively short periods of time but left to recover for long periods in between.

In the event of a commercial fishery being established, the best procedure might be to mainly exploit L. capensis at times when catches of B. holubi are low. This could be achieved to some extent by setting floating gillnets well off shore when the aim is to catch B. holubi, while setting in shallower water or near the shore would yield a relatively larger catch of L. capensis.

Catches are generally highest near the dam wall. If a fishery was concentrated at stations 1 and 2, these would be "seeded" from other areas, although L. capensis would only disperse when conditions deteriorated. If an even supply of catches was desired, a fishery which could switch from B. holubi to L. capensis would be essential. In a commercial situation, a rotational fishery, based on several impoundments (there are four reservoirs in the Orange - Vaal River system larger than 100 km²), might be the most efficient. In that case a monitoring programme could be established to decide when each reservoir is to be exploited to see to the interest of commercial and recreational fisheries alike.

C. RECOMMENDATIONS FOR FURTHER RESEARCH

One of the main shortcomings of the present study is the lack of knowledge on absolute population numbers and therefore potential yield. Without information on potential yield it is difficult to plan the use of a resource. An intensive experimental fishery should be undertaken in a limited area, e.g. the bay at station 4 (Fig. 8), in order to estimate population density and the meaning of CPUE.

Little is known about the marketability of indigenous large cyprinids and a marketing survey, including variously processed fish is urgently required. If undertaken, it could be done in conjunction with an experimental fishery as suggested above.

Ageing is an important facet of population studies. The lack of validation of ageing methods in studies on other South African cyprinids reduces their value. The environmental variability is high and it is essential that future studies take into account environmental influences

on growth and check formation.

Although the present study can be considered to be long-term in relation to most other studies on the fish faunas of South African reservoirs, it is short in relation to the growth rate of the fish and to the range of environmental fluctuations in the impoundment and river. It is therefore recommended that a monitoring programme is continued so that the relationships between the life history strategies of the fishes and the environmental fluctuations in the impoundment can be clarified.

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APPENDIX

APPENDIX IAppendix tables 1 to 6.

Average lengths (from backcalculated lengths and observed lengths in winter) at the end of successive growing seasons in Lake le Roux. Age refers to the number of annuli at the end of the 1981/1982 growing season. For example, age 2 refers to a fish at the end of its third growing season. The number of observations are given above the average lengths and are included when there is a change in the number of observations from the previous year. A 95% confidence interval is included in brackets.

Appendix table 1. Average length at age of male B. holubi.

Age	LENGTH/ mm											
	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982
1											69 84(4)	32 149(7)
2										171 66(2)	130 158(5)	19 198(8)
3									118 59(2)	113 122(4)	57 215(7)	14 235(11)
4								519 66(1)	532 122(2)	325 194(4)	155 265(4)	28 276(8)
5							197 64(2)	209 135(4)	181(4)	97 247(6)	36 297(6)	10 298(13)
6						61 60(2)	85 100(6)	186(7)	215(7)	57 275(10)	22 318(7)	7 324(12)
7					55 67(4)	65 109(6)	201(11)	277(10)	298(9)	30 328(11)	8 347(20)	2 333(70)
8				36 64(4)	56 105(7)	154(10)	237(12)	309(9)	325(9)	28 344(12)	4 344(18)	1 357
9			9 68(9)	15 100(15)	159(21)	200(25)	281(26)	336(19)	347(16)	7 344(24)	-	-
10		3 71(17)	5 93(28)	139(25)	194(37)	236(32)	292(26)	346(11)	354(10)	2 385(3)	1 391	-
11	3 71(14)	105(25)	151(40)	198(48)	244(35)	288(64)	345(40)	394(42)	396(37)	1 379	-	-
12	2 87(23)	116(29)	144(39)	173(22)	208(8)	230(15)	286(15)	329(17)	350(28)	372(17)	1 406	
13	1 100	156	204	238	280	313	354	400	422	450		

Appendix table 2. Average length at age of female B. holubi.

Age	LENGTH/ mm											
	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982
1											57 80(4)	29 149(5)
2										192 67(2)	140 160(4)	27 203(6)
3									115 64(2)	106 127(4)	35 224(9)	2 255(1)
4								619 66(1)	643 122(2)	425 195(3)	177 269(4)	26 272(10)
5							281 66(1)	297 135(4)		168 249(6)	47 304(10)	10 317(15)
6						70 58(2)	107 98(5)			71 277(9)	18 330(14)	4 348(16)
7					39 69(4)	51 116(8)		198(13)		28 327(16)	8 360(20)	3 355(42)
8				56 68(3)	80 107(6)		172(9)	263(12)	331(10)	39 378(12)	5 412(28)	-
9			47 67(3)	59 112(6)	175(9)	221(13)	306(13)	360(10)	374(10)	36 390(11)	4 415(12)	2 416(60)
10		16 67(6)	27 103(10)	31 151(13)	205(16)	267(16)	324(13)	377(15)	384(16)	15 404(16)	415(22)	
11	1 58	5 91(8)		133(27)	197(17)	246(15)	285(18)	343(6)	383(17)	2 415(2)		
12	1 74		111	155	181	199	221	288	333	1 376		
13	1 140		208	256	279	329	345	398	430			

Appendix table 3. Average length at age of male B. kimberleyensis.

Age	LENGTH/ mm											
	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982
1											6 79(5)	5 152(3)
2										41 61(4)	40 139(7)	22 187(6)
3									65 54(2)	65 116(4)	43 207(7)	11 239(9)
4								112 54(2)	128 105(3)	102 176(5)	58 255(7)	15 270(11)
5							264 57(1)	280 125(4)	183(4)	140 244(6)	48 294(8)	11 306(18)
6						19 55(4)	31 99(13)	173(17)	214(17)	13 276(22)	5 331(25)	3 336(2)
7					3 57(16)	10 83(16)	173(34)	265(43)	305(39)	4 315(52)	1 370	370
8				3 54(9)	5 91(30)	128(30)	170(76)	239(70)	315(66)			
9			76 59(2)	95 101(4)	96 160(6)	187(6)	300(8)	374(7)	396(6)	43 420(10)	26 443(11)	9 446(20)
10		6 69(10)	10 115(21)	176(20)	248(20)	276(20)	361(21)	416(15)	434(13)	2 460(53)	1 446	
11		2 73(25)	3 103(32)	168(36)	241(58)	283(47)	360(38)	417(40)	431(44)			
12	4 92(20)	147(25)	194(43)	248(34)	315(33)	340(32)	420(26)	448(21)	463(20)			
14	1 180	255	314	350	424	443	512	573	588	622		

Appendix table 4. Average length at age of female B. kimberleyensis.

Age	LENGTH/ mm											
	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982
1											2 63(3)	2 138(7)
2										29 63(4)	28 151(8)	14 193(9)
3									37 56(3)	36 119(6)	28 206(9)	5 241(23)
4								127 54(1)	137 103(3)	99 171(5)	45 253(6)	5 257(17)
5							233 57(1)	257 118(3)	173(4)	144 234(7)	51 293(9)	6 302(23)
6						14 59(7)	20 104(13)	167(19)	203(18)	8 259(30)	4 317(44)	
7					2 48(26)	89(59)	169(93)	231(125)	260(129)	1 241	284	
8				3 69(9)	143(33)	183(50)	273(15)	368(32)	403(44)	1 431	442	
9			48 59(2)	76 101(4)	161(5)	190(5)	316(7)	399(8)	424(8)	31 453(13)	13 472(24)	3 515(43)
10		4 68(9)	7 113(33)	170(42)	237(48)	285(37)	398(46)	452(40)	468(42)	1 375		
11	5 65(6)	13 102(9)	166(12)	233(17)	302(24)	328(25)	409(23)	459(24)	477(21)	6 507(33)	1 567	
12	2 89(22)	127(4)	180(56)	245(49)	313(51)	338(52)	406(79)	435(65)	451(59)	1 496		
15	1 230	291	335	415	467	496	571	601	615			

Appendix table 5. Average length at age of male L. capensis.

Age	LENGTH/ mm											
	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982
1												
2										18 71(4)	14 129(7)	1 161
3									14 55(4)	103(8)	13 158(14)	2 177(11)
4								118 56(2)	87(3)	110 137(43)	77 182(7)	17 175(12)
5							317 60(2)	329 115(4)	143(5)	290 195(6)	187 238(7)	37 243(17)
6						399 52(1)	429 90(2)	161(4)	186(4)	360 233(5)	134 272(7)	17 257(21)
7					125 56(2)	130 92(4)	177(7)	240(8)	259(8)	90 299(9)	24 321(19)	6 332(12)
8				138 56(2)	162 91(3)	130(5)	217(5)	278(5)	293(5)	134 325(5)	58 342(7)	13 345(18)
9			57 54(3)	65 84(5)	133(8)	172(10)	246(9)	294(7)	306(8)	44 328(9)	14 342(13)	2 346(18)
10		31 53(5)	35 83(6)	126(10)	175(12)	216(14)	269(11)	311(10)	324(9)	29 352(10)	366(11)	
11	10 50(6)	12 78(10)	13 112(18)	156(30)	196(29)	236(30)	289(21)	326(17)	338(16)	11 367(12)	1 374	
12	4 76(18)	105(31)	148(37)	202(61)	244(58)	287(59)	319(42)	346(30)	356(27)	3 375(23)		
13	4 99(25)	142(47)	183(31)	239(49)	269(51)	299(41)	322(34)	351(29)	360(31)	375(32)	1 378	

Appendix table 6. Average length at age of female L. capensis.

Age	LENGTH/ mm											
	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982
1											1 82	
2										23 72(3)	23 130(6)	12 147(8)
3									16 55(5)	100(8)	14 150(12)	4 161(19)
4								142 55(2)	148 85(3)	139 131(4)	105 178(6)	22 184(12)
5							371 59(2)	113(4)	138(4)	337 189(5)	224 231(7)	53 247(14)
6						456 51(1)	497 89(2)	159(4)	183(4)	388 233(5)	162 275(7)	25 278(20)
7					133 59(3)	141 100(6)	180(9)	247(10)	268(10)	90 314(13)	26 345(19)	6 355(34)
8				284 59(1)	303 98(3)	142(4)	236(4)	302(4)	320(4)	245 354(4)	102 370(6)	18 367(10)
9			113 58(2)	123 95(5)	126 143(7)	186(8)	266(7)	326(6)	341(6)	100 368(6)	40 384(9)	6 396(19)
10		85 57(2)	98 91(4)	132(6)	185(7)	225(8)	291(7)	340(6)	353(6)	72 381(7)	27 402(10)	
11	24 56(5)	31 87(9)	32 122(11)	169(15)	218(16)	258(16)	310(14)	357(12)	370(11)	23 393(12)	4 420(24)	
12	18 83(7)	133(12)	184(20)	238(21)	283(20)	321(17)	356(13)	384(11)	395(10)	15 416(9)	2 430(39)	
13	6 129(35)	157(43)	203(53)	249(58)	291(52)	313(49)	348(34)	387(22)	399(18)		2 439(42)	
16	1 285	310	330	350	377	396	414	436	447			

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Table 10. Linear relationships between anterior median scale radius (x 24) mm and fork length* (mm) of B. holubi in Lake le Roux.

Time	Relationship	r^2	n	p
Jan 1981	SR = 0,44 FL - 29	0,95	168	<0,00001
July 1981	SR = 0,45 FL - 33	0,94	109	<0,00001
Oct 1981	SR = 0,46 FL - 33	0,94	218	<0,00001

* Length range 120 - 430 mm.

Table 11. Relationship between fork length (mm) and anterior median scale radius (mm x 24) for some cyprinids in Lake le Roux.

Species	Relationship	r^2	n	p
<u>B. kimberleyensis</u>	SR = 0,044 FL ^{1,314}	0,97	457	<0,00001
<u>B. holubi</u>	SR = 0,031 FL ^{1,412}	0,98	421	<0,00001
<u>L. capensis</u>	SR = 0,041 FL ^{1,318}	0,97	411	<0,00001

PAGE 199 Gaigher, I.G., K.C.D. Hamman and S.C. Thorne. 1980b. Possible adaptive significance of sex ratio and sexual differences in size at maturity in the Orange River labeo, Labeo capensis. Journal of the Limnological Society of Southern Africa 6: 35-38.

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