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SOME ASPECTS OF THE ECOLOGY OF THE EASTERN CAPE ROCKY
SANDELIA BAINSII (PISCES: ANABANTIDAE) IN THE TYUME
RIVER, EASTERN CAPE, SOUTH AFRICA.

THESIS

Submitted in Fulfilment of the
Requirements for the Degree of

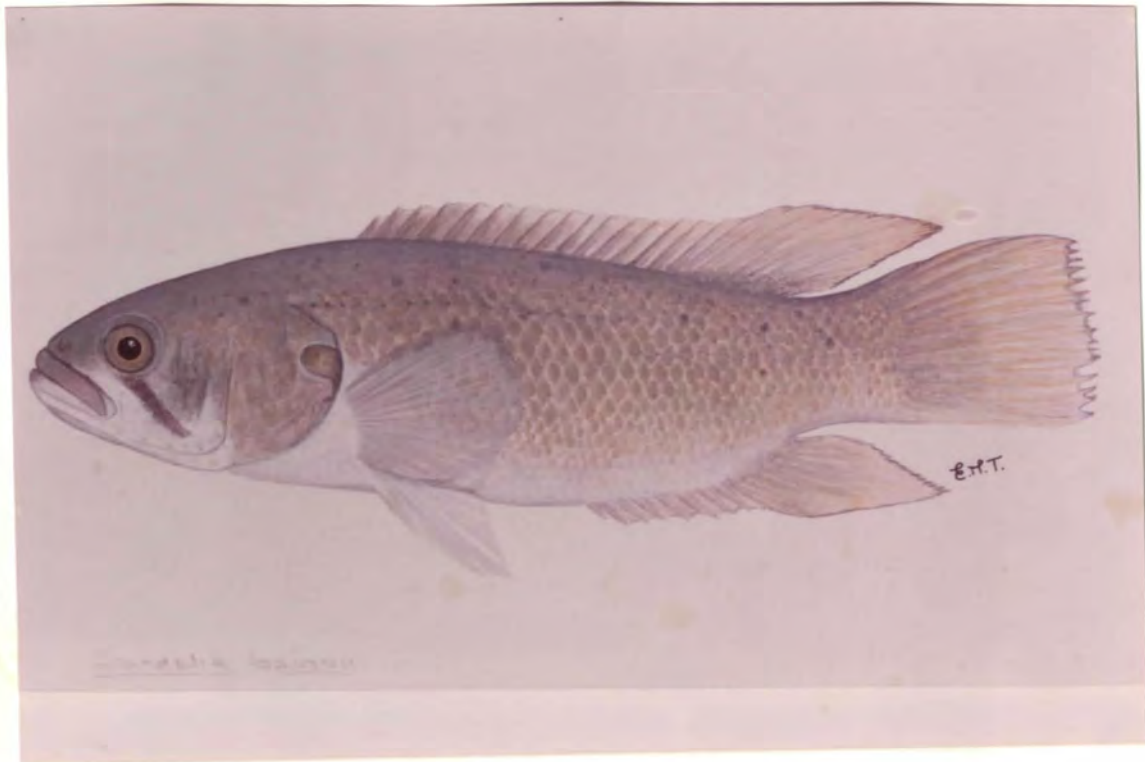
MASTER OF SCIENCE

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by

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FRONTISPIECE

The eastern Cape rocky, Sandelia bainsii, an endemic species to the eastern Cape of southern Africa.

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ABSTRACT

This is an account of some aspects of the ecology of the eastern Cape rocky, Sandelia bainsii Castelnau in the Tyume river in the eastern Cape.

Previous unpublished work carried out by the Zoology Department of the University of Fort Hare in the mid-seventies indicated that the species was rare in the Tyume river. Because of its uncertain conservation status, its restricted geographic distribution and the lack of information on its biology, demography, feeding and reproductive biology were studied. The species occurs in the upper, middle and lower reaches of the Tyume river and is common in rocky, shallow habitats in the middle reaches of the system. The most important threats to the survival of S. bainsii appear to be habitat alteration and alien species. The presence of these threats and the small size of the population suggest that the species may be vulnerable to local extinction. As the total range of the species extends to only a few rivers in the eastern Cape, the species might face extinction if these threats are faced throughout its range. A detailed study on the autecology of S. bainsii was therefore carried out in order to provide a basis for rational conservation and management of the remaining populations of the species.

The age structure and the growth rate of S. bainsii was determined using checks on scales and otoliths. Males grow faster and reach a larger size than females. The maximum length of S. bainsii is compared to that of other anabantids. The longevity of males is 5 years and that of females 3 years.

Food preferences were determined by three different methods and the indices of relative importance of food items calculated for different length groups and seasons. S. bainsii was found to be an euryphagous and opportunistic predator whose diet consists largely of insects. A considerable overlap was found between the diet of S. bainsii and that of the two alien species, Salmo gairdneri and Micropterus salmoides which indicates a possibility of competition for food.

Mark and recapture experiments showed that S. bairdii is a "sedentary" species which is unlikely to be seriously affected by man-made barriers to fish migration, such as weirs. The species reaches maturity during its second growing season (males 80-89mm and females 60-69mm) and the length at maturity is related to the modal length of males and females. A large proportion of the fish are thus mature at any given time. The fish spawn repeatedly during the summer breeding season, October to February resulting in near continuous recruitment. The possible adaptive value of this habit is discussed.

An attempt is made to evaluate the life history style of S. bairdii in terms of the theory of r- and K- selection and altricial and precocial life history styles.

CHAPTER 1

INTRODUCTION

The labyrinthine fishes of the suborder Anabantoidei (Order Perciformes) occur in Africa, India, the Malayan archipelago, the Philippines, China and Korea (Forselius 1957). The suborder Anabantoidei consists of four families, the Belontiidae, Helostomatidae, Osphronemidae and the Anabantidae. Of these, the Anabantidae is the most primitive (Liem 1963). The interrelationships of the anabantoid families, subfamilies and genera are shown in Figure 1.

The family Anabantidae consists of three genera, Anabas, Ctenopoma and Sandelia (Liem 1963). Owing to osteological similarities, Liem (1963) suggests that Anabas and Ctenopoma are closely related and are probably derived from a common ancestor, whereas Sandelia is derived directly from Ctenopoma.

The Anabantidae probably originated in tropical Asia. This hypothesis is supported by the great abundance and diversity of extant Anabantoidei in Asia (Darlington 1957). The ancestral anabantid form is believed to have differentiated by schistic evolution into the genus Anabas, known in Asia since the Pliocene and Pleistocene, and into the genus Ctenopoma in Africa following the invasion by this group of the continent during the upper Eocene (Liem 1963). The route used by the ancestral anabantids to Africa has not yet been determined.

The anabantids exhibit a disjunct distribution (Figure 2). The genus Anabas is confined to south east Asia. Ctenopoma is found in central and south central Africa and the two Sandelia species, Sandelia capensis and S. bainsii are found only in the southern tip of Africa. The present distribution pattern of the African anabantids indicates that Ctenopoma spread from North Africa into more southern regions. Liem (1963) is of the opinion that the expanding Ctenopoma populations could only cross the climate barrier between the tropics and more temperate regions, with great difficulty. The Ctenopoma population that was able to cross this barrier was isolated and differentiated from their ancestors. The isolated and disjunct distribution of the anabantids and some cyprinids can possibly explained by an alternative hypothesis

(Skelton 1980). The hypothesis is that the groups originated in Africa and their distribution is a result of a vicariance - continental drift event.

In support of the former hypothesis that Sandelia evolved from Ctenopoma, Liem (1963) presents evidence that shows a progressive change in certain osteological features in African anabantids in the series Ctenopoma muriei from central tropical Africa, Ctenopoma multispinis from south-central Africa and Sandelia from temperate South Africa.

There are several other progressive changes in anatomical and osteological features which can possibly be related to the geographic distribution of the anabantids. These include :

(i) The suprabranchial organ

Anabas testudineus and the Ctenopoma species have well-developed suprabranchial organs used for airbreathing in poorly oxygenated waters (Hora 1935, Liem 1963) whereas the Sandelia species, which are found in well-oxygenated waters, have vestigial organs (Barnard 1943). Cambray (1981) has suggested that the reduction of the suprabranchial organ in Sandelia was accompanied by an increase in the gill respiratory area. This example of cyclic evolution is similar to that observed in African Clariidae (Greenwood 1961).

(ii) The sub-operculum

A. testudineus and the Ctenopoma species are able to move overland using their sub-operculum as a lever (Munro 1955, Jackson 1961) whereas Sandelia is probably not able to do so. Jubb (1971) observed that the posterior and ventral borders of the sub-operculum are deeply serrated in A. testudineus, moderately serrated in Ctenopoma and smooth in Sandelia. The ability to walk overland is probably of adaptive value to A. testudineus and Ctenopoma which inhabit swamps that periodically become dry. This ability has been lost in Sandelia probably because there is no selective pressure favouring its retention in the near permanent river systems in which they are found.

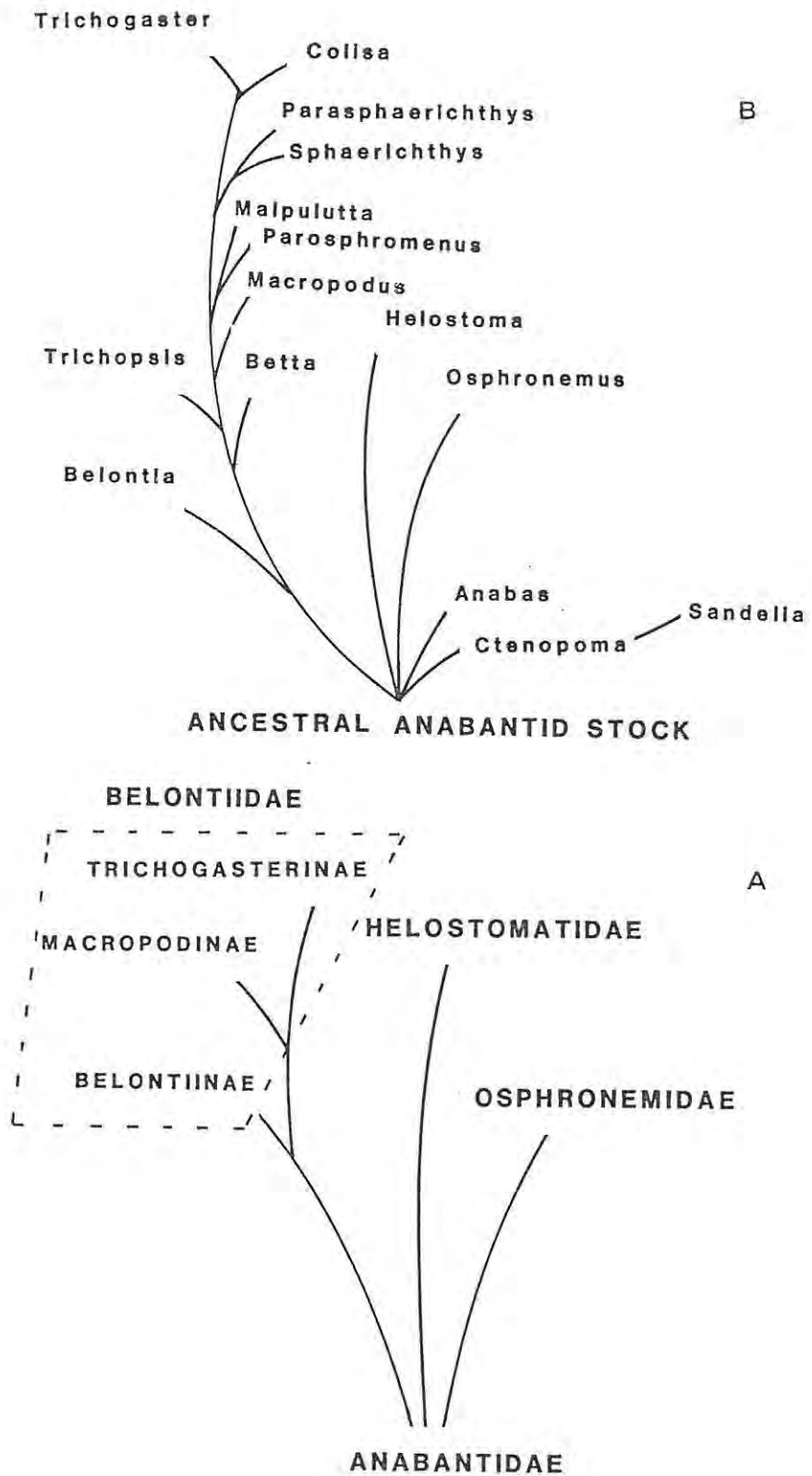


Figure 1. The interrelationship of the anabantoid families and subfamilies (A) and the interrelationship of the anabantoid genera (B) (After Liem 1963).

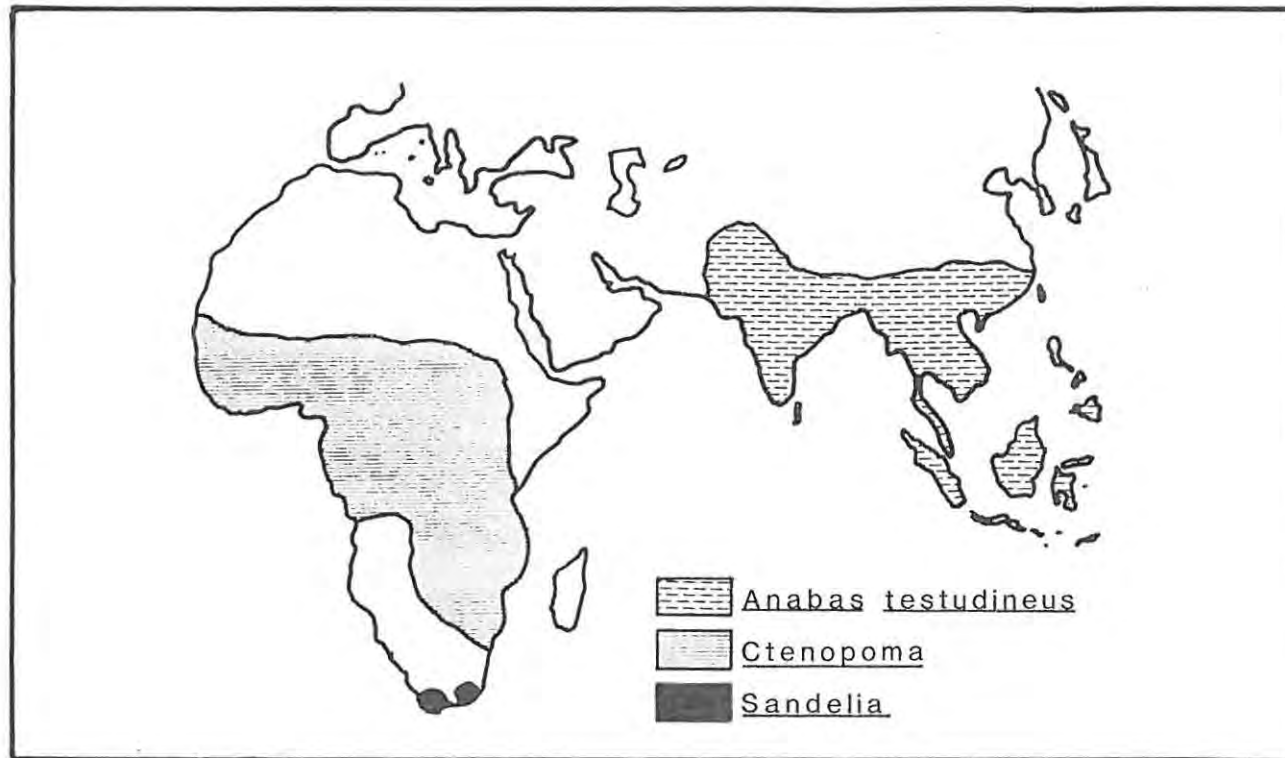


Figure 2. The approximate distribution of the Asiatic species *Anabas testudineus* and its African relatives belonging to the genera *Ctenopoma* and *Sandelia* (after Forselius 1957).

(iii) The swimbladder

The anabantids have swimbladders with posterior prolongations that extend to the caudal peduncle (Liem 1963). In contrast to its tropical and south tropical relatives, Anabas and Ctenopoma, Sandelia has a swimbladder with very long anterior prolongations as well. The long anterior prolongations in Sandelia might indicate a compensation for loss of buoyancy caused by the regressed suprabranchial cavity (Cambray 1981).

(iv) Occurrence and position of contact organs

Contact organs are found in the African Anabantidae which do not show parental care (eg Ctenopoma argentoventer, C. muriei, C. oxyrhynchus, C. kingsleyae and C. multispinis) whereas those that show parental care (eg Ctenopoma ansorgei, C. damasi, C. nanum and C. fasciolatum) do not have them (Peters 1976, Cambray 1980). The occurrence, number and position of the contact organs appears to be related to the geographic distribution of the species. The more equatorial and northerly species like C. kingsleyae and C. muriei have both an anterior and a posterior contact organ (Peters 1976). The south tropical C. multispinis and the more southerly S. bainsii have only the anterior organ whereas the most southerly S. capensis lacks contact organs completely (Cambray 1980).

(v) Scale type

The scales also show a progressive change from Anabas in Asia to Sandelia in South Africa. Anabas has only ctenoid scales (Liem 1963), C. multispinis from south tropical Africa has predominantly ctenoid scales, S. bainsii from the eastern Cape both ctenoid and cycloid scales and S. capensis found in the eastern and western Cape predominantly cycloid scales (Cambray 1980). The significance of the progressive change from a situation in which ctenoid scales predominate in tropical Anabantidae to a situation in which cycloid scales predominate in temperate Anabantidae has not yet been determined. Willey and Collette (1970) believe that cycloid and ctenoid scales are fundamentally similar. The ctenii on ctenoid

scales may have evolved to act as contact organs. There may have been a strong selection pressure towards ctenoid scale formation in order to keep spawning pairs in close contact during spawning so as to ensure fertilization in fast-flowing water, as contact organs are found only in freshwater and inshore marine species (Willey & Collette 1970). The opposite seems to have occurred in the Anabantidae. For example, Ctenopoma which is generally found in slow-flowing and stagnant waters (Jackson 1961, Jubb 1967, Bell-cross 1976) has more ctenoid scales than the Sandelia species which are found in relatively fast-flowing water. It is therefore unlikely that ctenoid scales in the Anabantidae evolved only to keep mating pairs together in fast-flowing water.

On the basis of the above zoogeographic and morphological data, it is hypothesized that the present geographic distribution of S. bainsii has resulted in this species adopting a life history style which is different from that of its relatives. Following the ideas of Dobzhansky (1950), it is further hypothesized that the subtemperate Sandelia spp. have been selected more towards the r- side of the r- and K- continuum of MacArthur & Wilson (1967), relative to their tropical and subtropical relatives. Some of the other biological studies that have been undertaken on anabantids, and which have provided comparative material with this study, include those of Chanchal et al (1978) and Singh & Samuel (1981) on A. testudineus, Albaret (1982) on C. kingsleyae, Richter (1977) on C. ansorgei, Berns & Peters (1969) on C. muriei and C. damasi, Benl & Foerch (1978) and Bruton (1979a) on C. multispinis and Siegfried (1963) on S. capensis. No detailed study of the biology and ecology of S. bainsii has been undertaken previously.

The genus Sandelia, whose type specimen came from Kowie river near Grahamstown (Jubb 1971), was named by Count Castelnau in 1861 after Chief Sandile (1820-1878), Chief of the Rarabe branch of the Xhosa (Harrison 1952). The species name is in honour of Andrew Geddes Bains, a pioneer of South African geology.

S. bainsii is endemic to the eastern Cape where it has a limited distribution (Figure 3). The common name of the species, eastern Cape rocky, is derived from its distribution and habitat preference (Harrison

1952). It is confined to the area from the Nahoon river in the east to the Kowie river in the west. It has been reported from the upper reaches and major tributaries of the Keiskamma, the Buffalo, the Koonap and Kat rivers of the Fish river system and the Bloukrans tributary of the Kowie (Harrison 1952, Jubb 1965).

According to unconfirmed reports, the eastern Cape rocky was abundant in the Tyume river during the 1950s. Surveys undertaken by the Zoology Department of the University of Fort Hare in 1975, 1976 and 1977, however, showed that the species is relatively rare in this river. These findings have given rise to fears that the species may be endangered. Skelton (1977 p.3) defines an endangered species as "one that is in danger of extinction and that its survival is unlikely if the causal factors continue operating. Included in this category are species whose numbers have been reduced to a critical level or whose habitats have been so drastically reduced or changed that they are deemed to be in immediate danger of extinction".

The IUCN World Conservation Strategy (1978) lists six major factors threatening vertebrate species in general. Skelton (1983) considers two of these as major threats to freshwater fishes in southern Africa viz. habitat alteration or degradation and the effects of introduced species. As regards habitat degradation Gaigher *et al* (1980) identified three major factors threatening fish species in the Cape viz. : (a) farming and related forms of land use, (b) mining, industrial development and human settlement and (c) the construction of dams and weirs. These three factors may all affect S. bainsii in the Tyume river. Moreover, three alien predatory species, the largemouth and smallmouth bass (Micropterus salmoides and M. dolomieu) and rainbow trout (Salmo gairdneri) were introduced into the Tyume river early this century. Endemic species with a limited distribution such as Barbus trevelyani, Oreodaimon quathlambae and Barbus treurensis have already been severely affected by predatory aliens (Bruton & Merron 1985). Harrison (1952) gives conclusive evidence that Micropterus species led to the extinction of Sandelia capensis in Paarde Vlei near Somerset West in the western Cape. The extinction of S. capensis in that system was exacerbated by the inability of this species to increase its numbers rapidly (Harrison 1952). Recent sampling in the Tyume river (March 1985) has shown that a

translocated indigenous predator Clarias gariepinus has also established itself in the Tyume river.

In view of these potential threats the primary objectives of this study were to investigate the demography, feeding and reproductive biology of the species in the Tyume river as a possible means to develop a conservation strategy. Moreover, the data obtained from these biological studies could also possibly be used to test the hypothesis that the life history style of this species is different from that of its relatives due to its geographic distribution.

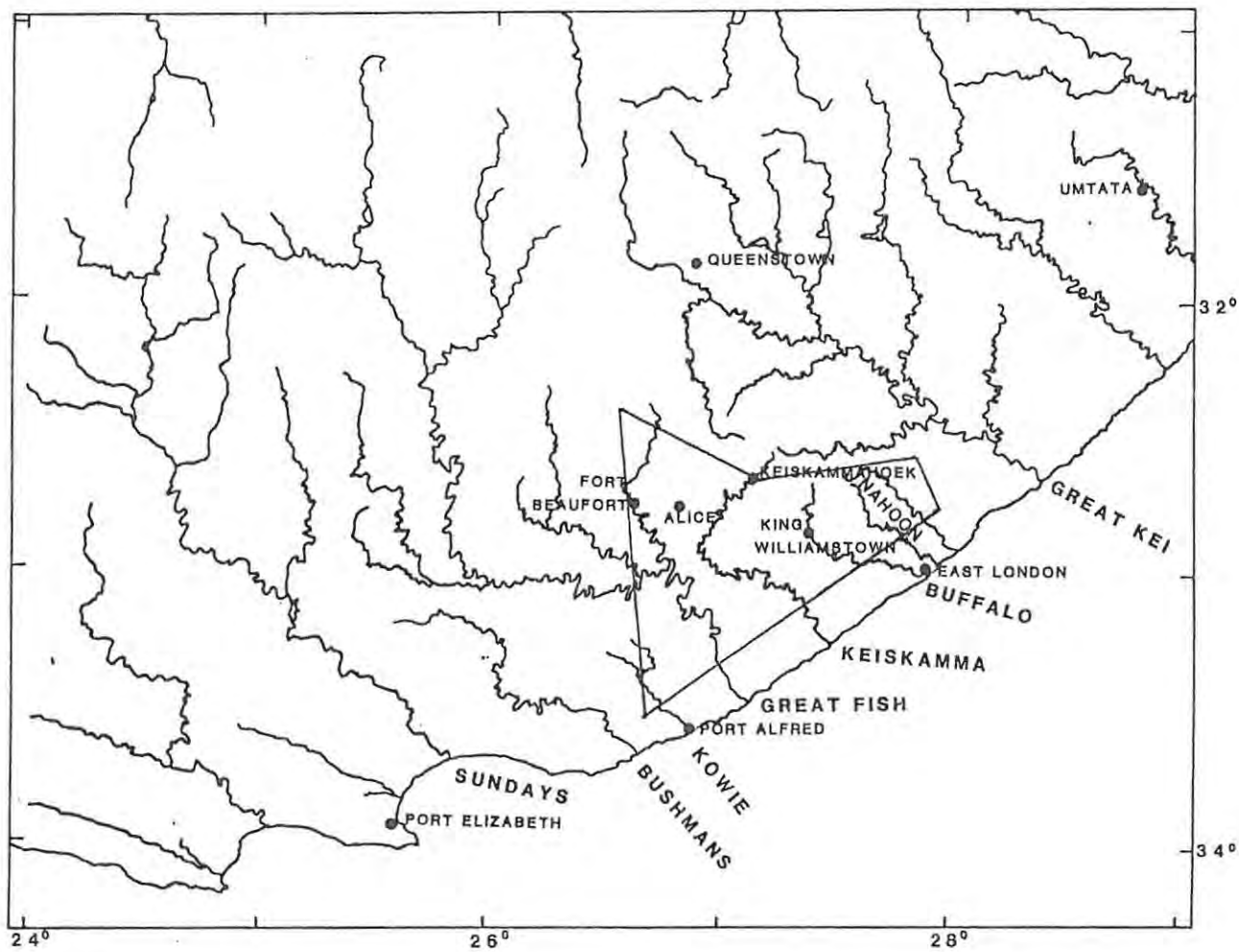


Figure 3. The distribution of *S. bairdii* in the eastern Cape.

CHAPTER 2

THE STUDY AREA

The Tyume river is the main tributary of the Keiskamma river system. In order to give an overall picture of the study area, environmental features of both the Keiskamma and Tyume river systems are described. The Tyume was chosen as the main study area as it is central in the known distributional range of S. bainsii. The type locality, the Kowie river, is at the western limit of the species distribution.

Although the Tyume is one of the major tributaries of the Keiskamma river system it was deemed necessary to undertake a survey of the whole system in order to obtain an overview of the distribution and abundance of the species.

2.1 The Keiskamma river system

2.1.1 Topography and climate

The Keiskamma river arises as several small streams in the Winterberg mountain range at an altitude of approximately 1500 meters above sea level (m ASL)(Figure 4). The confluence of these streams is near Keiskammahoek ($32^{\circ}41'S : 27^{\circ}09'E$) at an altitude of approximately 740 m ASL. The Keiskamma has several annual tributaries along its course and the size of the river increases with decreasing altitude. The tributaries drain severely eroded land and as a result the river bed changes from a sandy or rocky substratum in the upper reaches, to silt-laden in the lower reaches. Several weirs have been erected along the course of the river. Moreover, the Sandile dam has recently (1982) been completed at the confluence of the Wolf and Keiskamma rivers. The dam is approximately 40 meters high and will effectively halt any fish migration as no fish ladders were incorporated.

The mean annual air temperature in the upper reaches of the Keiskamma river is $11^{\circ}C$ (at the Winterberg mountains) and $18^{\circ}C$ in the lower reaches (above the ebb and flow section of the river) (Hill et al 1977). The coldest months are May, June and July. The mean monthly variations

in the minimum and maximum temperatures are shown in Table 1. The rainfall season extends from October to March. The mean annual rainfall is 1200 mm in the upper reaches and 500 mm in the lower reaches. The average monthly variation in the minimum and maximum rainfall is also shown in shown in Table 1. The mean monthly run-off is high during the period from October to April. The changes in the mean monthly run-off are also shown in Table 1 and the climatic data are summarized in Figure 5.

2.1.2 Vegetation and soil erosion

Prior to settled agriculture, the vegetation in the area was utilized by a wide variety of wild ungulate species. During that time the catchment area was largely grassland with woody vegetation confined to river valleys at lower altitudes and to the southern aspects of the foothills of mountains at high altitudes (Trollope & Coetzee 1978).

The advent of settled agriculture saw the wild ungulate species replaced by cattle, sheep, goats and equines. This was accompanied by overstocking and overgrazing which resulted in the grassland areas being considerably reduced in size. In the higher rainfall areas along the foothills of mountains the grasslands persisted but were reduced to a continuously short, cropped sward with reduced plant cover. In lower rainfall areas the grasslands were replaced by Karroo and arid macchia vegetation which has poor plant cover and which leads to widespread soil erosion (Trollope & Coetzee 1978).

The erosion status of the Keiskamma river basin is described by Hill et al (1977). The Keiskamma river in the upper reaches near Keiskammahoek (see Figure 4) flows through an area where erosion is clearly discernible with up to 25% of the area having lost its original topsoil through sheet, rill or gully erosion. This area commonly includes parts in which the original topsoil is still present and others where it has been partly removed. In the middle reaches, near Middeldrift, the Keiskamma river flows through an area in which the land has been eroded to the point where there is an intricate pattern of moderately deep or deep gullies and up to 100% of the original topsoil has been removed (Hill et al 1977). In the lower reaches the river flows through an area

in which erosion is clearly discernible and includes parts where the original topsoil is still present and others where it has been partly removed (Hill et al 1977).

Severe erosion has led to increased siltation of the Keiskamma river. There is evidence that siltation can threaten certain fish species (Gaigher 1978). This aspect will be dealt with in detail in section 2.3.

2.1.3 Sampling stations

A survey of the Keiskamma was undertaken in June 1983. The survey was undertaken in June, a period which falls within the dry season when the water flow was slow which aided sampling. Fifteen stations were selected and these are shown in Figure 4. A variety of habitats (according to Allen 1951) such as stickles, shallow runs (Figure 6), deep runs (Figure 7), pools and weirs (Figure 8) were sampled.

2.2 The Tyume river system

2.2.1 Topography, climate and vegetation

The Tyume river arises from several small streams in the Winterberg mountain range on the Hogsback ($32^{\circ} 35' S : 26^{\circ} 55' E$) at an altitude of 1500m ASL. These small streams flow together to form two main streams which plunge over an escarpment as a number of waterfalls down to an altitude of 800m ASL and then flow together to form the Tyume. The river flows down a gradient of approximately 1 : 40 to its confluence with the Keiskamma river ($32^{\circ} 55' S : 26^{\circ} 54' E$), at an altitude of 350m ASL. The Tyume is joined by annual tributaries along its course and, as in the Keiskamma, these streams drain severely eroded land with the result that the substratum changes from rocky or sandy in the upper reaches to silt-laden in the lower reaches. Along the course of the river there are twelve weirs, all of which are silt-laden. Some of these weirs are about four meters high (Figure 9) and could serve as barriers to fish movement and hence fish distribution. The length of the Tyume river from Hogsback to the confluence with the Keiskamma is approximately 86 km.

The climatic conditions of the Tyume river basin are similar to those of the Keiskamma basin. There are two flow gauging weirs along the Tyume river, one of which marks the upper limit of sampling station 4 and the other the upper limit of sampling station 6. The mean annual run-off for the period 1953 - 1976 was $18.53 \text{m}^3 \times 10^6$ at the former gauging weir and $24 \text{m}^3 \times 10^6$ for the period 1928 - 1976 at the latter.

The catchment area of the Tyume drainage area is approximately 946 km^2 . The drainage area above the escarpment and along the slopes of the mountain is covered with evergreen forests and grasslands whereas in the river valley, below the escarpment, they are replaced by Acacia karoo and arid macchia (Euryops spp. and Pteronia incana). Agriculture in the river valley, below the escarpment, consists mainly of maize lands and citrus plantations and stock farming with cattle, sheep and goats is also practised.

2.2.3 Sampling stations

Fourteen sampling stations were selected along the Tyume river (Figures 4 & 14).

Station 1 : Approximately 3 km downstream from the escarpment. It consists of fast-flowing stickles and pools approximately 4 m wide and 1 m deep.

Station 2 : shallow run with a rocky substratum approximately 5 m wide and 60 cm deep and sandy pools approximately 1 m deep.

Station 3 : consists of a series of runs approximately 80 cm deep and 4 m wide with stickles in between. The substratum consists of boulders and sand.

Station 4 : consists of a few sandy pools approximately 1 m deep with a width that ranges from 6 m to 15 m. At the ends of the pools are rocky, slow-flowing, shallow runs approximately 60 cm deep and rocky fast-flowing stickles.

Station 5 : Largely rocky shallow runs approximately 50 cm deep and 8 m wide with a few stickles in between them.

Station 6 : this station is directly below a weir. It consists of sandy pools approximately 8 m wide and 1 m deep. Stickles from these pools lead into shallow runs approximately 70 cm deep. The substratum of the runs is solid bedrock.

Station 7 : a sandy run with abundant tree cover. It is approximately 8 m wide and 1 m deep.

Station 8 : directly below a weir and consists of pools approximately 12 m wide and 1 m deep. The deeper ends of the pools are sandy and the shallow ends are rocky. There are rocky stickles between the pools.

Station 9 : a deep sandy to muddy pool approximately 12 m wide.

Station 10 : directly below a weir. This site consists of pools with a sandy to muddy substratum. The pools are approximately 12 m wide and 1 m deep. Stickles from these pools change into runs that are approximately 60 cm deep with a substratum that consists largely of boulders.

Station 11 : a shallow rocky run between two deep pools.

Station 12 : consists of deep pools approximately 15 m wide. The substratum consists of bedrock and some sand. Sampling was confined to the shallow ends of the pools.

Station 13 : consists of sandy to muddy pools approximately 15 m wide and 1 m deep. The pools are joined to each other by rocky runs approximately 5 m wide and 70 cm deep.

Station 14 : consists of stony shallow runs that lead into a long deep sandy pool at the confluence of the Tyume and Keiskamma rivers.

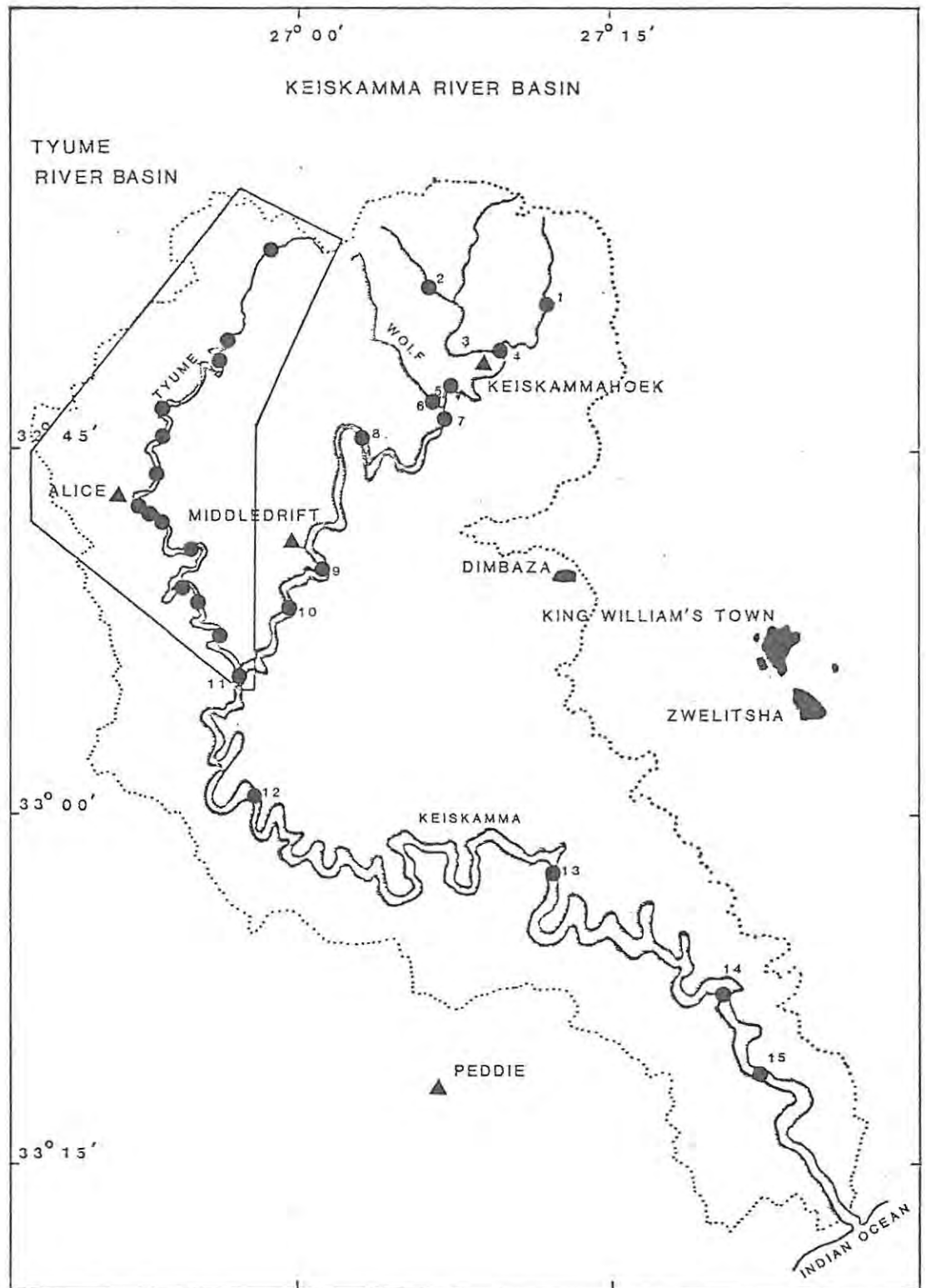


Figure 4. Map of the Keiskamma river system showing sampling stations (●).

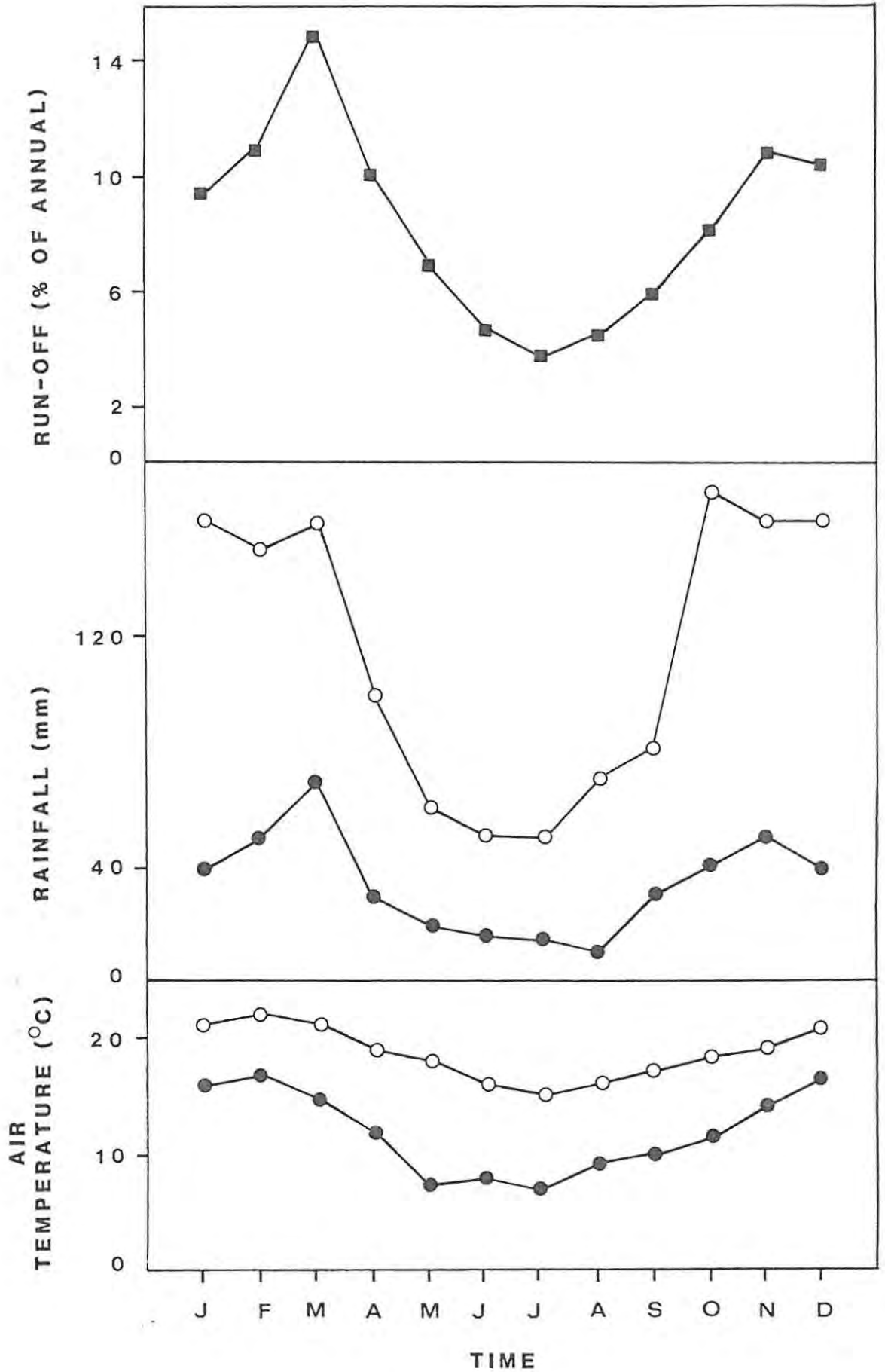


Figure 5. The average monthly variation in minimum (●) and maximum (O) air temperature, rainfall and run-off in the Keiskamma river basin for the period 1928 - 1976.

Table 1. The average monthly variation in the minimum and maximum air temperature, rainfall and run-off in the Keiskamma river basin for the period 1928 - 1976. (After Hill et al 1977)

Months	Air temperature (°C)		Rainfall (mm)		Run-off Mean monthly variation (% of annual)
	Average monthly variation		Average monthly variation		
	Minimum	Maximum	Minimum	Maximum	
January	16	21	40	160	9,2
Feb	17	22	50	150	10,9
March	15	21	70	160	14,9
April	12	19	30	100	10
May	7	18	20	60	6,8
June	8	16	15	50	4,7
July	7	15	15	50	3,7
August	9	16	10	70	4,4
September	10	17	30	80	5,9
October	11	18	40	170	8,1
November	14	19	50	160	10,9
December	16	21	40	160	10,5



Figure 6. A shallow run in the Keiskamma river.



Figure 7. A deep run in the Keiskamma river.



Figure 8. Sampling a weir in the Keiskamma river.



Figure 9. A weir in the Tyume river.

2.2.4 The physical and chemical characteristics of the water

Water analysis was carried out at monthly intervals from March 1983 to July 1984 at stations 1, 4, 6, 9 and 14 (see Figures 4 & 14).

Air and water temperatures were measured with a standard mercury thermometer, pH with a Kane May 7001 pH meter, conductivity with an Anikem conductivity meter Model MC 20, oxygen concentration by the Winkler-Azide titration method and turbidity by an absorptometric method using a DR-EL/2 Hach instrument.

The monthly changes in the physical and chemical characteristics of the water are summarized in Table 2 and Figure 10. The altitude related changes in the physical and chemical characteristics of the water are shown in Figure 11.

There is a close positive correlation between air and water temperatures. The highest air temperature recorded was 27°C in November 1983 and January 1984 whilst the lowest was 16°C in June and July 1983. The highest water temperatures of 23°C and 21°C were recorded in March 1983 and January 1984 respectively whilst the lowest temperature of 13°C was recorded in June 1983 and July 1984. The air temperature was constant along the course of the river whereas water temperature increased with decreasing altitudes. This is common in many rivers (Moyle & Cech 1982).

The pH was constant within the range 7.17 - 8.30 although an inexplicable value of 6.94 was recorded in November 1983. The pH was found to increase with decreasing altitude. There was a positive relationship between pH and turbidity (Figure 10).

pH was positively related to turbidity which was found to increase with decreasing altitude. Dissolved oxygen was within the range 7 - 8 mg/l although values of 4 mg/l and 9 mg/l (see Table 2 for temperature values) were occasionally obtained at certain sampling stations. Dissolved oxygen was positively related to altitude, decreasing with decreasing altitude and inversely related to water temperature.

Although the data are incomplete it is clear from Figure 10 that turbidity increases during the rainy season. The highest value of 225 FTU was obtained in April 1984. The lowest values of 20 FTU and 29 FTU were obtained in September and June 1984 respectively. As with the other parameters, there was an altitude related profile showing an increase in turbidity with decreasing altitude was observed.

Table 2. The monthly changes and range in the physical and chemical characteristics of the water.

Month	Air temp °C	Water temp °C	O ₂ mg/l	pH	Conductivity ms/m.	Turbidity (FTU)
March	27 (25-29)	23 (20-25)	7 (5-8)	8,30 (8,25-8,35)	2,06 (.60-3,30)	42 (22-75)
April	20 (20-28)	21 (15-24)	7 (4-9)	8,30 (8,28-8,42)	1,90 (.65-3,50)	53 (20-90)
May	17 (15-20)	14 (13-15)	8 (7-10)	8,20 (7,72-8,42)	1,43 (.60-3,20)	58 (20-110)
June	16 (15-20)	13 (13-14)	8 (8-9)	8,26 (8,20-8,40)	1,45 (.60-3,10)	58 (25-110)
July	16 (15-19)	14 (11-16)	8 (8-9)	8,09 (7,55-8,20)	1,85 (.90-3,10)	42 (25-110)
August	23 (21-24)	15 (13-18)	8 (8-9)	7,95 (7,60-8,80)	1,72 (.70-5,00)	36 (18-110)
September	21 (20-23)	18 (17-20)	7 (6-9)	8,13 (7,82-8,45)	3,27(1,00-7,00)	20 (10-80)
October	25 (23-28)	19 (18-21)	7 (6-8)	7,90 (7,00-8,80)	2,00 (.80-4,00)	60 (40-60)
November	26 (24-27)	19 (19-20)	8 (7-9)	6,94 (6,85-7,00)	0,90 (.60-1,30)	80 (40-110)
December	25 (22-26)	19 (17-21)	8 (7-9)	8,02 (7,98-8,06)	0,87 (.55-1,10)	- - -
January	20 (18-23)	21 (18-23)	7 (7-8)	7,45 (7,39-7,48)	1,40 (.62-2,30)	- - -
February	19 (18-21)	18 (17-21)	7 (7-8)	7,40 (7,30-7,49)	1,30 (.70-1,60)	45 (10-100)
March	20 (19-22)	19 (17-20)	7 (6-8)	7,30 (7,07-7,49)	1,14 (.60-1,50)	- - -
April	19 (16-22)	17 (15-19)	7 (7-8)	7,17 (7,08-7,54)	1,52(1,00-2,50)	70 (8-225)
May	18 (17-19)	14 (13-16)	8 (7-8)	7,59 (7,09-7,92)	2,08 (.80-3,00)	51 (18-70)
June	16 (15-17)	14 (12-15)	8 (7-8)	7,94 (7,63-8,56)	2,61 (.13-4,00)	29 (24-44)
July	17 (15-18)	13 (12-15)	8 (7-8)	7,93 (7,54-8,31)	2,36 (.50-5,00)	50 (35-70)

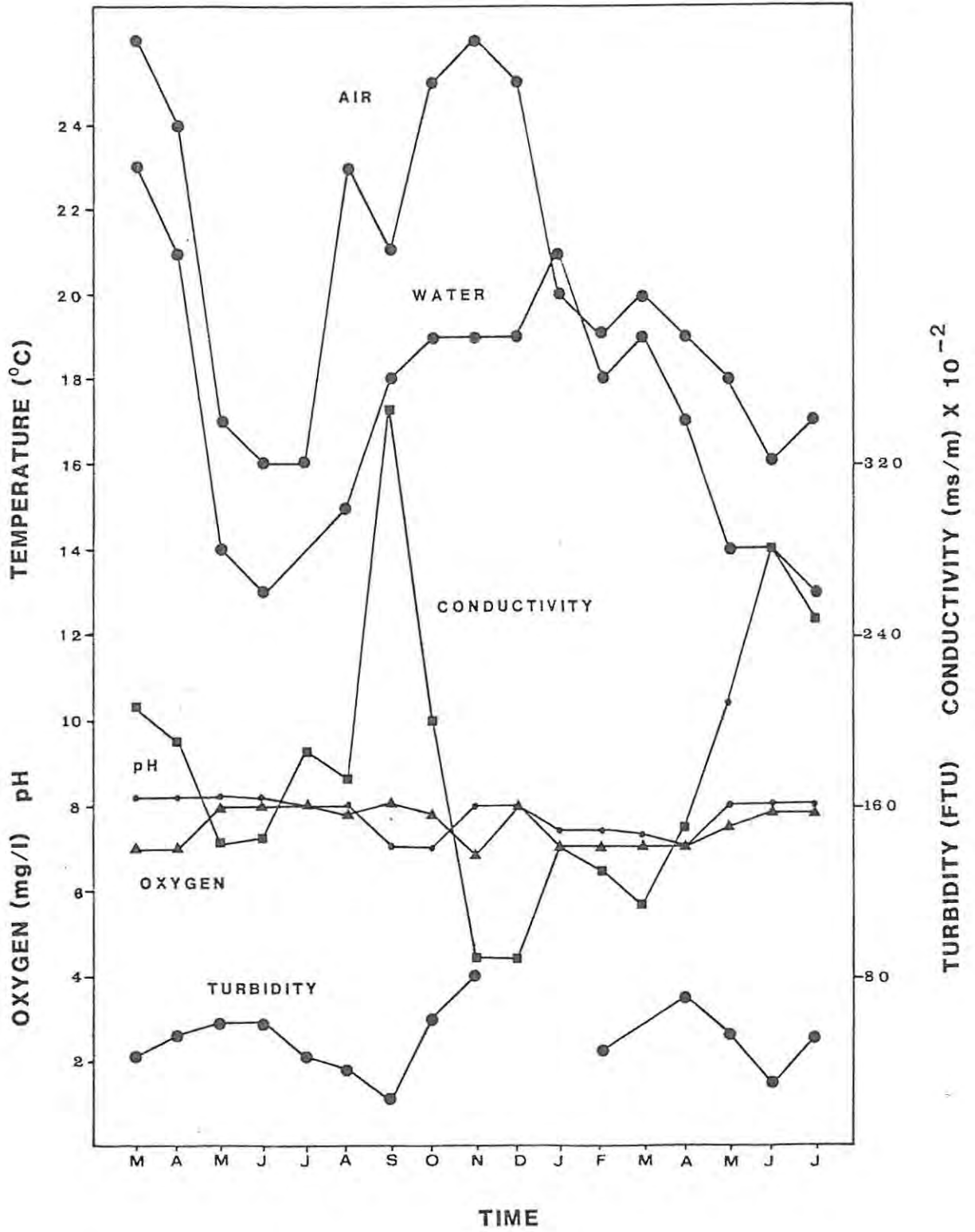


Figure 10. The mean monthly changes in the physical and chemical characteristics of water in the Tyume river.

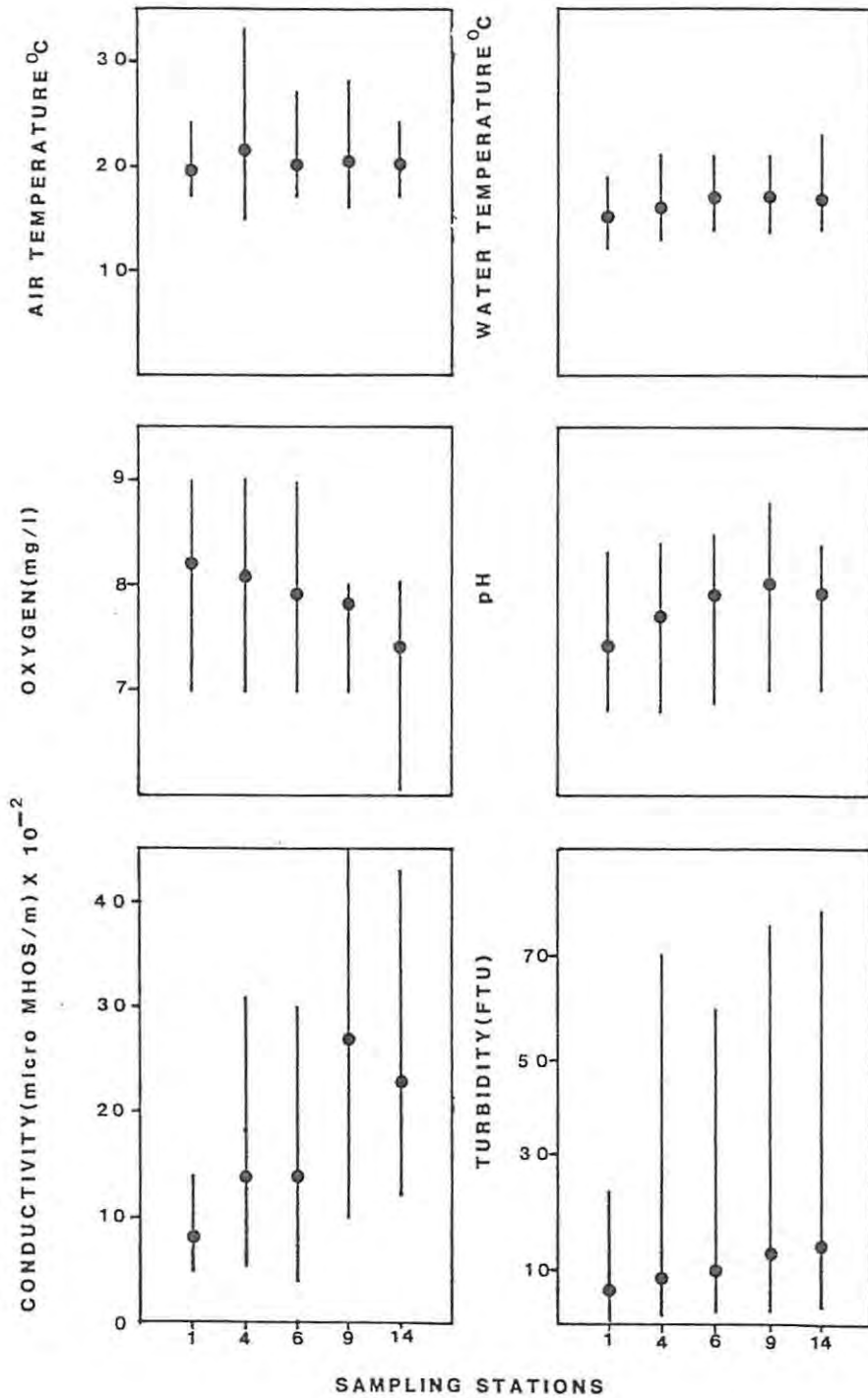


Figure 11. The physical and chemical characteristics of water at different sampling stations in the Tyume river from March 1983 to July 1984. The data are given as means (●) and ranges (vertical lines).

Conductivity fluctuated over the months and showed peaks during the dry season in June and September. There is no relationship between these peaks and agricultural activities in the river valley. Ntusi (1983) obtained a similar result in the Tyume river and concluded that conductivity is related to rainfall. Rainfall decreases conductivity possibly by dilution of the salts and minerals in the water. This contention is supported by the findings of this study in which an inverse relationship was found between conductivity and turbidity.

2.3 DISCUSSION

The distribution and survival of fishes is influenced by a number of natural as well as man-made constraints. The most important natural constraint in the Keiskamma river is river flow. This is a very important constraint throughout the eastern Cape where long periods of drought are common. During these periods the Tyume river, for example ceases to flow and fishes become confined to isolated pools where they are subjected to a number of stress factors such as overcrowding, exposure to predation and disease and possibly decreased food availability.

Some of the most important man-made constraints are :

(i) High suspensoid loads and siltation

High suspensoid loads and the resultant water turbidity are directly related to the soil erosion status of a catchment area. The main cause of soil erosion in the Keiskamma river system was discussed in section 2.1.2. The effect of suspensoids on fish are reduced growth rate, a decrease in size at first maturity and maximum size, and size of the population (Bruton 1985). This can be ascribed to the following factors, (a) reduction in light penetration and of photosynthesis in micro- and macrophytes, resulting in reduced food availability and plant biomass, (b) reduced visibility of pelagic food and (c) reduced availability of benthic food due to smothering (Bruton 1985). Gaigher (1978) cites siltation as one of the most important factors threatening B. trevelyani, an endangered species in the Tyume river.

(ii) Construction of dams and weirs.

According to Skelton (1983) the construction of weirs affects (not necessarily detrimentally) the character of rivers and streams in South Africa. There is no doubt, however, that weirs have a detrimental effect on migratory fish such as Myxus capensis (Bok 1983). On the other hand weirs may affect fishes favourably in the following ways :

- (a) provide reservoirs and refuges during a dry season (Skelton 1983);
- (b) may provide a suitable muddy habitat for some fishes such as Labeo umbratus;
- (c) may provide a relatively silt-free habitat immediately downstream because they act as silt traps.

The Keiskamma river system has a climate that can be described as temperate to warm with a definite rainy summer season which reaches its peak in March. The river catchment is severely eroded due to effects associated with settled agriculture. From the water analysis data the Tyume river can be described as a well-oxygenated, slightly alkaline stream with a wide summer and winter temperature range and a fluctuating ion content. There are no natural physical barriers to fish movement but twelve weirs have been erected along the course of the river which in all probability severely inhibit the migration of certain species.

CHAPTER 3

THE DISTRIBUTION, HABITAT PREFERENCES, ABUNDANCE, SEX RATIO AND POPULATION STRUCTURE OF SANDELIA BAINsii IN THE TYUME RIVER.

3.1 INTRODUCTION

The broad distribution of S. bainsii in the rivers of the eastern Cape is well documented (Harrison 1952, Jubbs 1971, Cambray 1980, Bok 1983) but the only detailed study is that of Bok (1983) in the Kowie river.

Before any biological study of a fish species can be undertaken, accurate knowledge of its distribution in that particular system is necessary. For this purpose and because of the possible endangered status of S. bainsii, surveys of the Tyume (February 1983) and the Keiskamma rivers (June 1984) were undertaken. The purpose of the surveys was to determine as accurately as possible the distribution, factors that affect the distribution, abundance and the habitat preferences of S. bainsii in the Keiskamma river system. It was envisaged that this information together with the biological data would clarify the conservation status of S. bainsii and provide the basis for the development of a conservation strategy.

3.2 Materials and methods

Electro-fishing gear (220V AC), seine nets and gill nets were used to catch fishes. The two operators of the electro-fishing apparatus worked upstream together approximately 1.5 m apart. Once the fish were stunned they would surface and immediately be caught with hand-held dip nets. Fishes not caught by the dip nets were caught by a stop net placed downstream. This was the main fishing method and was particularly effective when catching fishes in shallow rocky sections of the river. This method is also regarded as the least selective method of fishing (Boccardy & Cooper 1963). In all cases the fishing time and the distance covered were noted.

Seining of pools up to a depth of approximately 1.5 m was performed with

a small bag seine net, 9 m long, 1.52 m deep, a cod end 1.82 m long and a stretched mesh size of 12 mm. The net was mounted with PVC floats and sinkers spaced at 30 cm intervals. Wooden poles were fitted at the end of each wing. Two operators pulled the net upstream to catch fishes. This method of fishing was especially useful for sampling sections of the river with a sandy or muddy substratum. Sampling of wide, deep pools and dammed up sections of the river above weirs was done with the aid of a larger seine net, 40 m long, 2.5 m deep, cod end 2 m long, and a 27 mm stretched mesh size. The net was mounted with PVC floats and sinkers spaced at 70 cm intervals.

Gill nets whose mesh size ranged from 35 - 57 mm were also used in sections of the river where neither seining nor electro-fishing could be performed. In all cases the nets were set overnight. This was the least successful method of catching S. bainsii.

Estimation of abundance

The relative abundance of organisms can be calculated by enumerating the number caught over a certain period of time (Odum 1983). During the course of this study the number of fishes caught over a period of 150 minutes was used to calculate relative abundance. Relative abundance was used to calculate the importance value index (IVI) using Odum's (1983) formula :

$$IVI = \frac{\text{relative abundance of a fish species}}{\text{total number of fishes}} \times 100$$

Sex ratio and population structure

The sex ratio can provide information about the reproductive potential of a population as populations in which the sex ratio is biased towards females will have higher total reproductive outputs than populations with more equal sex ratios if all females have access to the fertilizing capacity of males (Wootton 1982).

Population structure refers to the frequency of occurrence of various age or size classes that constitute a population (Weatherley 1972).

Population structure in this chapter refers only to the frequency of occurrence of the various size classes as age and growth are discussed in Chapter 4. Population structure can provide information on a number of population parameters such as growth, maximum size, mortality and longevity, as well as the contribution of the various size classes to population fecundity if the size at maturity is known (Lagler 1982).

In order to study the sex ratio and population structure, all S. bainsii caught monthly at the various stations were killed by placing them on ice in a cooler bag and taken to the laboratory for analysis. In the laboratory the standard length (SL) of the fish was measured to the nearest 1 mm using a measuring board and they were weighed to the nearest 0.1g using a Mettler balance. The fish were sexed after dissection of the abdomen.

3.4 RESULTS

3.4.1 Fish distribution and abundance

3.4.1.1 Keiskamma river

Although S. bainsii is widely distributed in the Keiskamma river (Figure 12) it is not common in any locality. S. bainsii is first encountered near Keiskammahoek at an altitude of 740 m ASL, and at other localities at lower altitudes, but is not found at altitudes lower than 230 m ASL.

The different fish species found in the Keiskamma and their importance value indices at each sampling station are shown in Table 3 and the relative abundance-altitude relationship is shown in Figure 13. S. bainsii is not common at altitudes higher than 624 m ASL and lower than 340 m ASL but is commonly caught at intermediate altitudes.

3.4.1.2 Tyume river

The Tyume river can be divided into the upper, upper middle, middle, lower middle and lower reaches on the basis of altitude. S. bainsii is the most widely distributed fish in the Tyume river. It is found from approximately 3 km below the escarpment (700 m ASL) to the confluence

with the Keiskamma (350 m ASL) (Figure 14).

The importance value indices of fishes in the Tyume river are shown in Table 4 and the altitude related changes in abundance in Figure 15. In the upper reaches (station 1, 700 m ASL) Barbus trevelyani is the most abundant fish while S. bainsii and S.gairdneri are relatively scarce. In the upper middle reaches (station 5, 560 m ASL), S. bainsii is the most abundant fish, B. trevelyani is still abundant and Tilapia sparrmanii and Labeo umbratus appear for the first time. In the middle reaches (station 7, 520 m ASL) S. bainsii and L. umbratus are most abundant whereas T. sparrmanii and B. trevelyani are scarce. In the lower middle reaches (station 11, 420 m ASL), S. bainsii is scarce, M. salmoides appears for the first time although it is not abundant, T. sparrmanii and Lepomis macrochirus are fairly abundant while L. umbratus is the most abundant fish.

Clarias gariepinus has been excluded from Figure 15 because the importance value indices on which the figure is based were calculated on data of fishes caught over a two year period. C. gariepinus was caught for the first time in the Tyume in March 1985 and the data are not sufficient to calculate its importance value indices.

As in the Keiskamma, S. bainsii in the Tyume river is most common within a narrow range of altitudes. The relative abundance-altitude relationship is shown in Figure 13. Similar to the distribution pattern in the Keiskamma, the species is not common at high altitudes (>650 m ASL) and at lower altitudes (<350 m ASL). The limits of distribution of S. bainsii and the sections of the river in which it is least abundant do not coincide only with low and high altitudes but also with the occurrence of the two alien predatory species, S. gairdneri and M. salmoides in the upper and lower reaches respectively. This aspect is discussed further in section 3.5.

3.4.2 Habitat preferences

The findings of this study agree with those of Harrison (1952) who also observed the preference of this species for rocky habitats. A typical S. bainsii habitat is shown in Figure 16.

S. bainsii is common in habitats just below weirs. In Chapter 2 it was mentioned that weirs tend to trap silt which causes the substratum below weirs to be relatively free of silt and the water relatively clear. The abundance of S. bainsii in these habitats suggests that it prefers habitats where water is clear and the substratum free of silt. This is supported by the absence of this species in weirs where the water is turbid and the substratum muddy.

S. bainsii was caught mostly in shallow runs where the substratum consisted of rock, gravel, or sand. The preference for shallow water is shown by the fact that large specimens (> 150 mm SL) were caught in water that was 30-60 cm deep. The few specimens that were caught in deep runs and pools of 1 m and deeper were caught underneath stones along the side margins of the stream and never in open water. Although a few specimens were caught underneath stones in midstream where the current is strong, S. bainsii prefers habitats where the water flow is relatively slow.

Both juveniles and adults were caught in similar habitats. Juveniles, however, prefer habitats with an even slower flow than adults. They were caught in quiet, rocky, temporary side waters and shallow ends of pools (Figure 17).

The two predatory aliens, S. gairdneri and M. salmoides, share the same habitat preference as S. bainsii. They prefer a habitat with a rocky or sandy rather than a muddy substratum. S. gairdneri, however, prefers fast-flowing water. This is probably due to their similar feeding strategies (see section 5.4 Chapter 5).

3.4.3 Sex ratio and population structure

The overall sex ratio of 365 S. bainsii caught in the Tyume river was 1:1.96 in favour of females. The length frequency distribution of 123 males and 242 females is shown in Figure 18. Females were more abundant than males in all size classes up to 130 mm SL. Female S. bainsii did not exceed 136 mm SL whereas males reach a size of 172 mm SL.

The length frequency distribution of 928 fish of both sexes is skewed to

the right (Figure 19), which may indicate a high mortality of older fish. The figure includes an underestimate of juvenile fish (10 mm - 50 mm SL) as no attempt was made to catch all these fish during sampling. The rest of the figure, however, gives an adequate representation of the population structure. With a view of also using the population structure to study growth, a separate figure showing the monthly length frequency distribution of 558 young fish of SL < 80 mm was prepared (Figure 31). Clear modes are not apparent from the catches, indicating a prolonged recruitment period (see Chapter 6).

TABLE 3. The importance value indices (IVI) of various fish species in the Keiskamma river.

STATION NO.	FISH SPECIES AND IMPORTANCE VALUE INDICES								
	<u>Barbus</u> <u>trevelvani</u>	<u>Sandelia</u> <u>bainii</u>	<u>Labec</u> <u>undulatus</u>	<u>Tilapia</u> <u>sparrmanii</u>	<u>Lepomis</u> <u>macrochirus</u>	<u>Micropterus</u> <u>salmoides</u>	<u>Micropterus</u> <u>golomieu</u>	<u>Glossobius</u> <u>tenuiformes</u>	<u>Myxus</u> <u>cadensis</u>
1	100								
2	100								
3	100								
4	75	25							
5	100								
6	90	10							
7	86	14							
8	86	14							
9		13	86						
10			86	11					
11		0,3	95	1,5	1,5	0,6	0,3		
12			93	3	2	1,5			
13		0,4	99						
14			27	36				36	
15			14					74	11

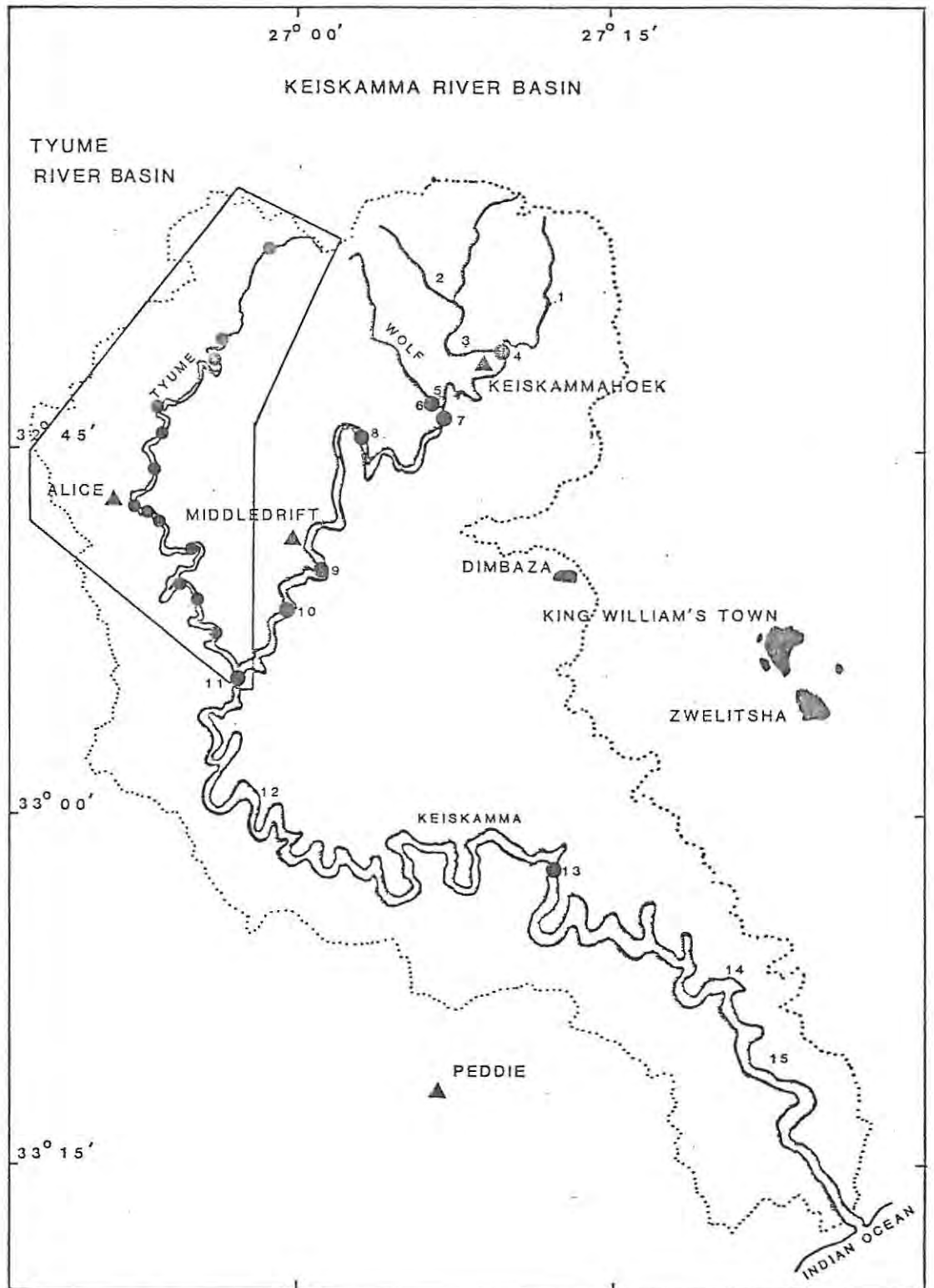


Figure 12. Map of the Keiskamma river system showing the distribution of *S. bairnsii* (●).

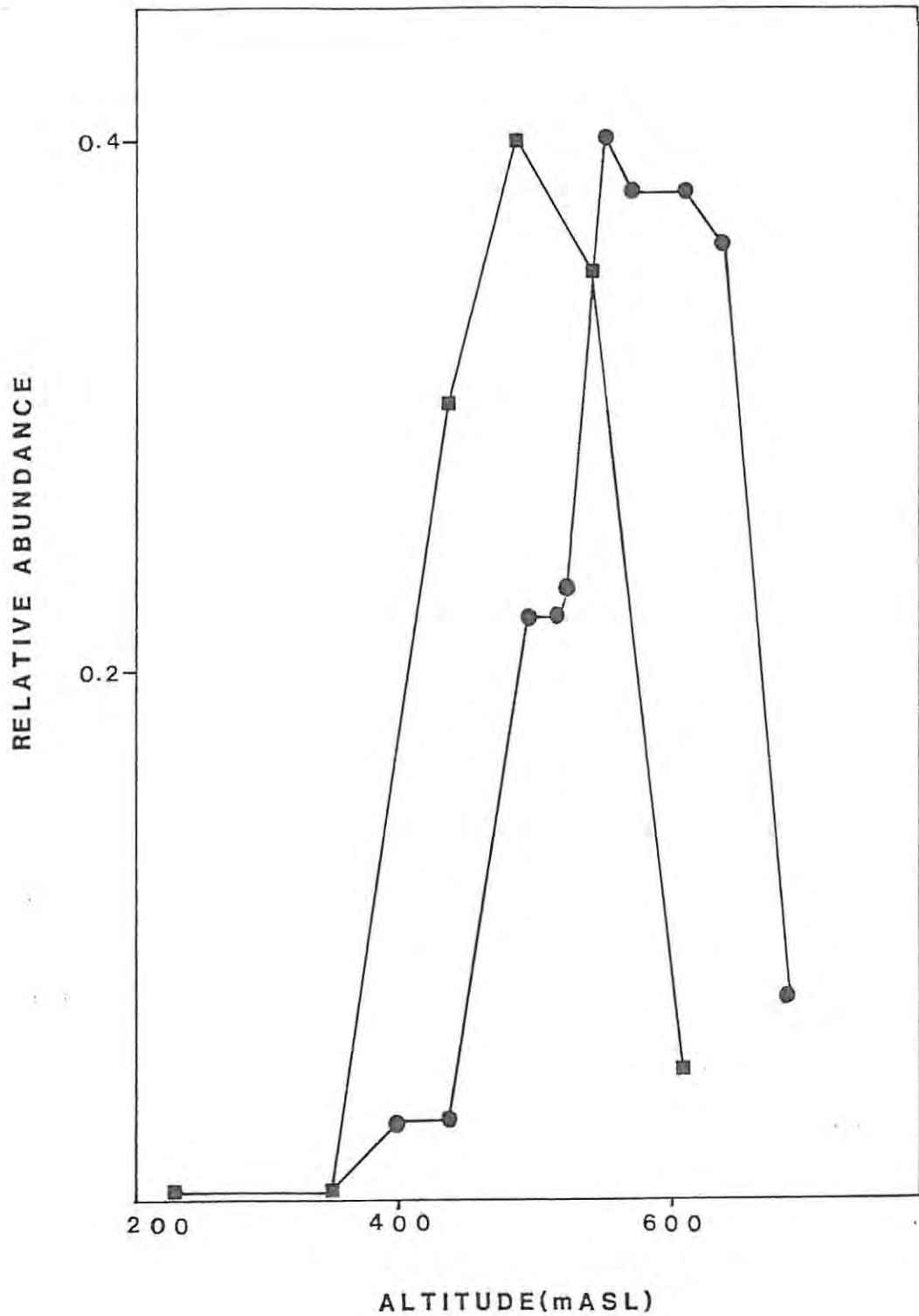


Figure 13. The relationship between the abundance of *S. bainsii* and altitude in the Tyume (●) and Keiskamma (■) rivers.

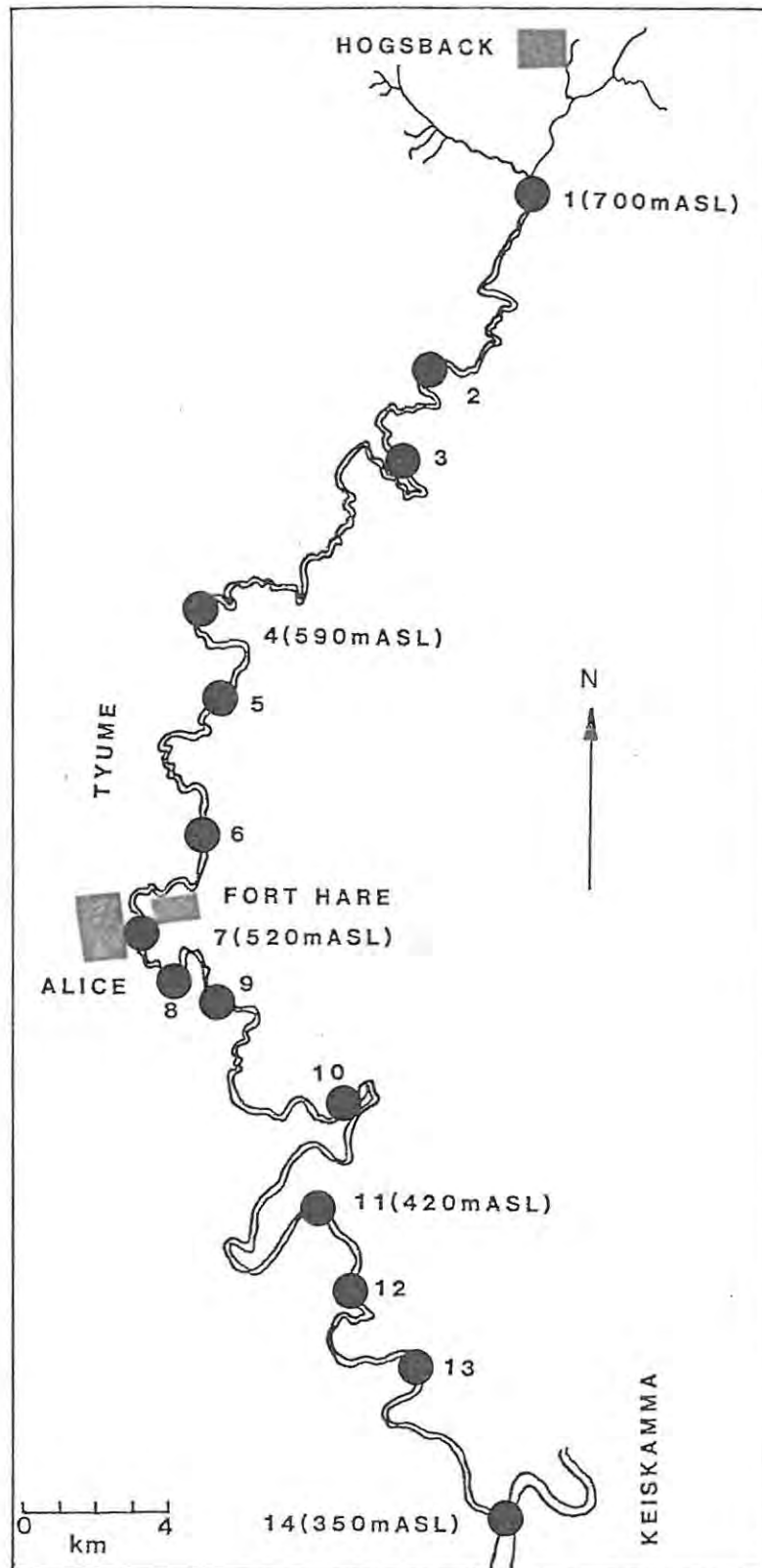


Figure 14. Map of the Tyume river system showing the distribution of S. bainsii.

TABLE 4. The importance value indices (IVI) of various fish species in the Tyume river.

STATION NO.	FISH SPECIES AND IMPOTANCE VALUE INDICES								
	<u>Salmo</u> <u>gairdneri</u>	<u>Barbus</u> <u>trevelyani</u>	<u>Sandelia</u> <u>bainsii</u>	<u>Tilapia</u> <u>sparmanii</u>	<u>Labeo</u> <u>umbratus</u>	<u>Lepomis</u> <u>machrochirus</u>	<u>Micropterus</u> <u>salmoides</u>	<u>Clarias</u> <u>gariepinus</u>	<u>Anguilla</u> <u>mossambica</u>
1	6,8	79,5	13,6						
2		62	34						2,5
3		62	36						1,2
4		70	27						1,8
5		37	44,4	7,4	11,1				
6		0,6	12	17	69		+		0,6
7		2,8	47,8	7	42,2		+		
8			19	40	40				
9			1,8	25	72	1,8		+	
10			7	23	67				1,3
11			1,2	19,1	63,6	12,7	3,18		
12			1,4	17	73	8,8	1,4		
13			1,3	13	78	7,8			
14			0,2	5,7	86	5,7	1,4		

+ C.gariepinus found

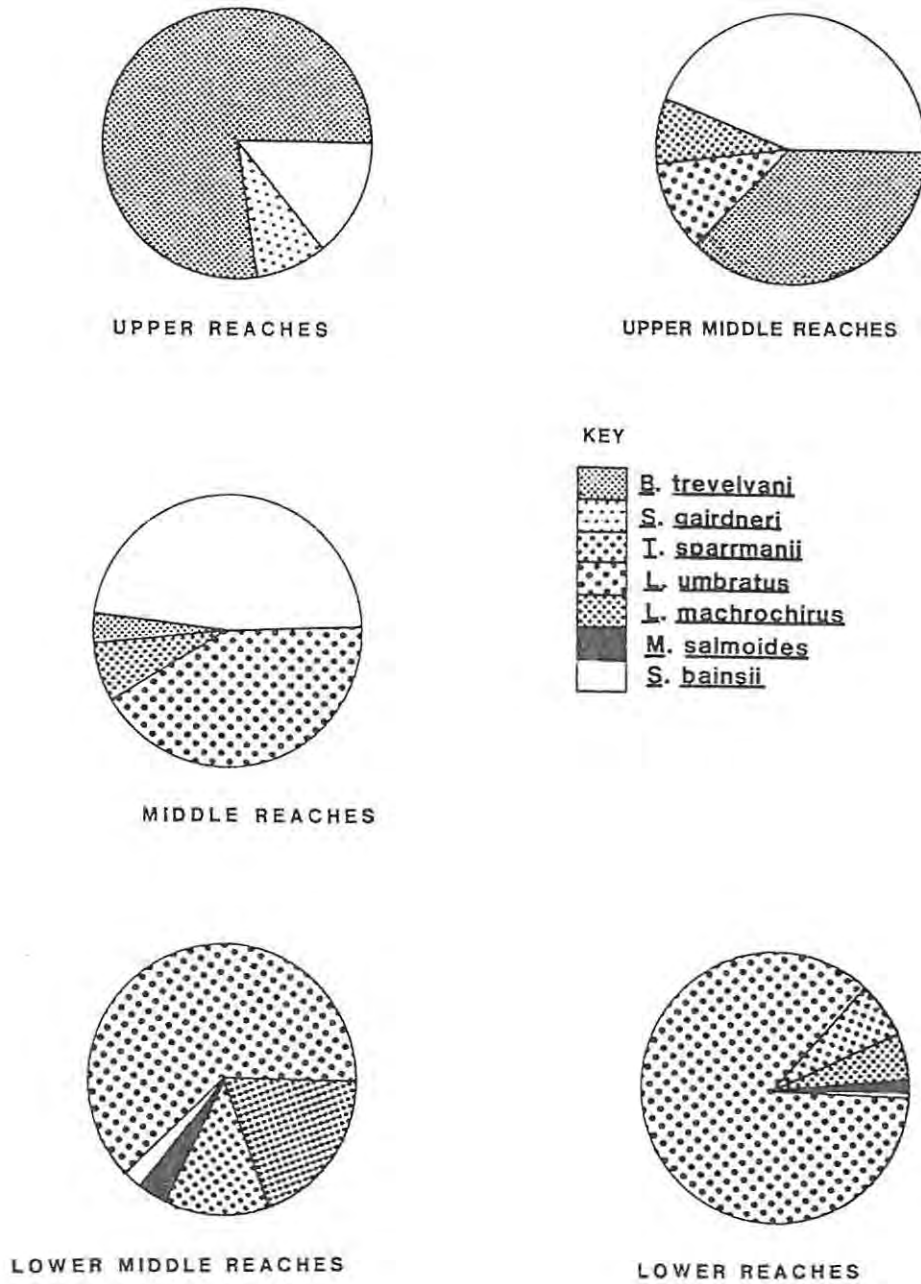


Figure 15. The changes in the relative abundance of fishes at different altitudes in the Tyume River.



Figure 16. The typical habitat of S. bainsii in the Tyume river.



Figure 17. The typical habitat of juvenile S. bainsii in the Tyume river. (The photograph was taken during the dry season).

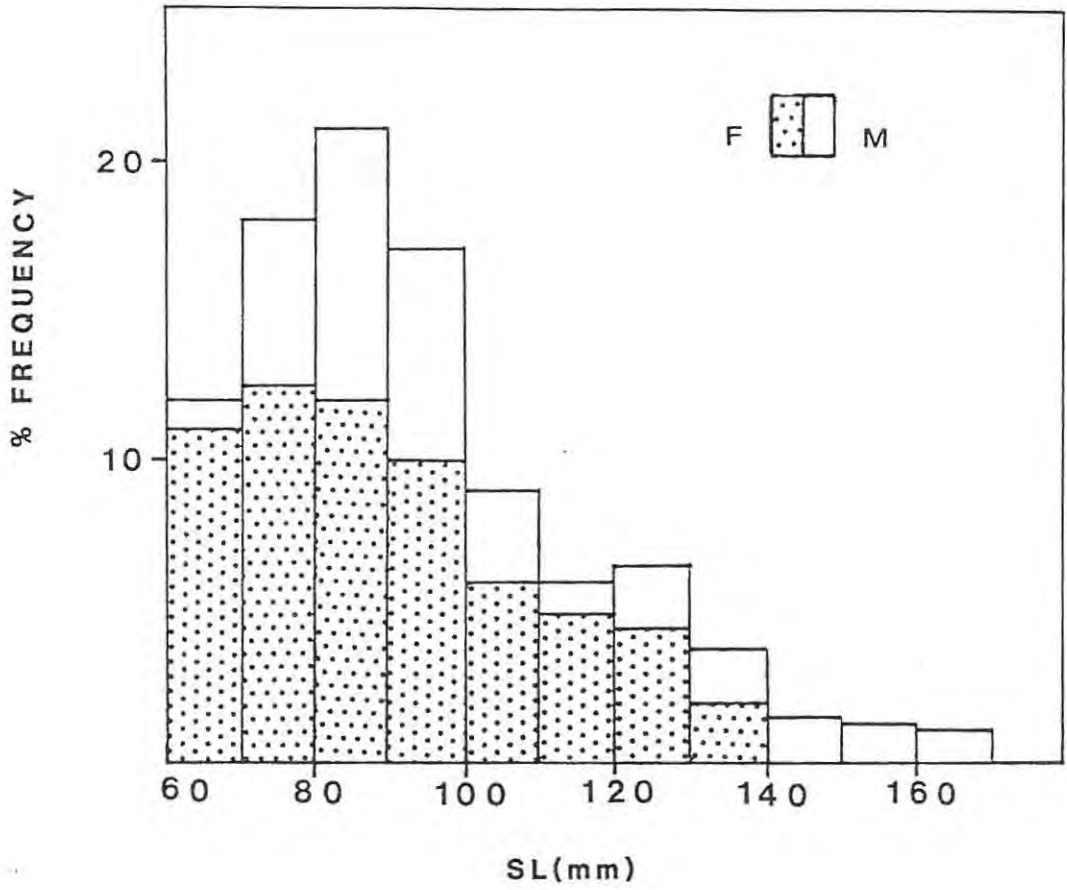


Figure 18. The percent sex composition of the different size classes of *S. bairdii*.

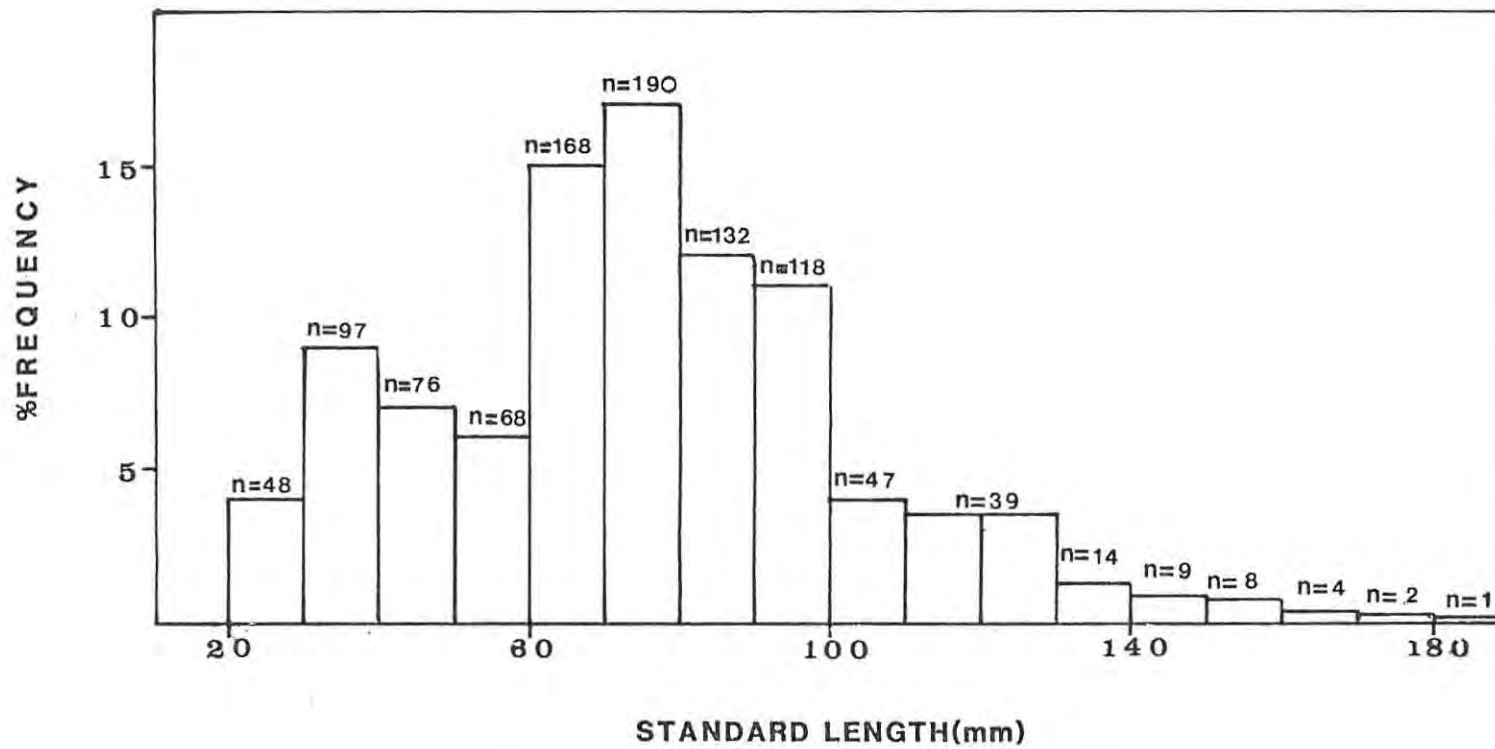


Figure 19. The length frequency distribution of all *S. bairdii* caught during the period March 1983 to August 1984.

3.5 DISCUSSION

Surveys of the Keiskamma river system have shown that S. bainsii is a relatively widespread species which is abundant only in relatively restricted sections of the river system depending on the type of substratum. These findings are the same as those of Bok (1983) who found that in the Kowie S. bainsii is rare in the head waters, abundant in the upper middle and middle reaches, fairly common in the lower middle reaches and absent just above and in the ebb and flow section of the river. The distribution of S. bainsii is not uniform throughout its range as they are most abundant only in shallow rocky areas.

The habitat preference data indicates that weirs may benefit the species as they provide a habitat relatively free of silt. Moreover S. bainsii is a "sedentary" species (see section 6.3.3, Chapter 6) and is unlikely to be seriously affected by physical barriers.

From the data on abundance, it appears that S. bainsii still occurs in numbers that suggest that the species has not been seriously affected by the threats mentioned earlier. The effect of siltation has probably been minimized by the exploitation of a habitat sustained by man-made physical barriers (weirs). This might justify the statement by Gaigher *et al* (1980 p.79) that "Sandelia bainsii ... has a restricted distribution but is abundant and does not seem to be seriously affected by man induced changes to the rivers".

The threat of predation by or competition with the two alien species has probably been avoided by altitude-related partial separation along the stream (S. gairdneri in the upper reaches, M. salmoides in the lower reaches and S. bainsii in the middle reaches). Moreover Bok (1983) questions the significance of the effects of predation by one of the alien species M. salmoides on Myxus capensis because the number of these predators in the Cape rivers is low. The effects of predation of M. salmoides may, however, vary from one prey species to the other. Moreover, it will be shown in Chapter 5 that S. bainsii probably competes with the alien species for food.

Some aspects of the life history of S. bainsii such as the prolonged

recruitment period are likely to play an important role in the survival of the species. A prolonged recruitment period tends to have a "buffering" effect in certain fish species against failure of recruitment as a result of adverse climatic conditions (Wallace 1975).

The preceding discussion suggests that S. bainsii is not endangered in the Tyume river. S. bainsii, however, deserves to be included in the list of "vulnerable" species because of the following reasons :

- (i) S. bainsii is endemic to the Cape where it has a restricted distribution;
- (ii) agricultural activities in the river catchment are likely to increase, causing increased siltation and a reduction in suitable habitats for S. bainsii;
- (iii) there is a danger that one or both alien species, S. gairdneri and M. salmoides may establish themselves in the sections of the river in which S. bainsii is still abundant. Whilst sampling in February 1984 one adult and four juveniles of M. salmoides were caught at station 6 which is outside the range of the species according to all previous records (Ntloko 1973, Gaigher 1975, Gaigher 1978). The origin of these specimens has not been established but sampling in some of the farm dams in the Tyume basin has yielded some specimens of M. salmoides. It is probable that the specimens found their way from the dams into the stream during floods. Besides having to contend with the threat posed by the two aliens, S. bainsii has also to contend with an indigenous, translocated predator viz. the sharptooth catfish C. gariepinus which seems to have recently established itself in the middle and lower reaches. No specimens of C. gariepinus were caught during 1983 and 1984 but some specimens including juveniles were caught in 1985.

CHAPTER 4

AGE AND GROWTH

4.1 INTRODUCTION

Age and growth studies are an important component in the study of the biology of fishes. The ability to age fish allows determination of the growth rate and the age structure of a population. The age structure can give indications on some population parameters such as mortality, longevity and age at sexual maturity (Tesch 1968). Also, by monitoring growth rates of various age classes in a population, it is possible to identify fast- and slow-growing seasons or years. This information can be used to establish correlations with environmental factors (Smith 1974, Lagler 1982).

No previous age and growth studies have been undertaken on anabantids. As S. bainsii is a fish of doubtful conservation status, it was envisaged that an understanding of its age and growth would be needed for the formulation of a conservation strategy.

It was decided to treat age and growth of S. bainsii before the other biological aspects that have been studied (eg feeding and reproduction), as these are related to or determined by the age of the fish. The most frequently used method of age determination in fishes is the counting of growth zones or checks which appear in their hard parts such as scales, otoliths, vertebrae, spines and opercular bones (De Bont 1967). The following discussion is confined to scales and otoliths as these were the only hard parts that were examined in this study.

An increase in length of a fish is usually associated with periods of active feeding which in turn coincide with the period of circulus deposition in scales (Bilton 1974). A check or ring is formed on a scale if there is a disruption in the regular arrangement of circuli (Tesch 1968). The check is formed when there is an increase in the growth rate in summer or decrease in growth rate in winter and is conspicuous in fishes of the temperate regions of the world (Bilton 1974). The formation of a check on the scale during one season in the

year forms the basis of the use of scales in ageing fish. This method of ageing fish is, however, unreliable in ageing slow-growing and older fish (Casselman 1983). Furthermore, in some fish populations checks may be formed more than once a year, or not at all (Bruton 1979a).

Otoliths have been successfully used in age determination in recent years (Liew 1974, Pannella 1974, Williams & Bedford 1974, Brothers et al 1983). The preference of the otolith method over other methods employing hard parts is a result of its reliability and consistency even in the ageing of older fish (Casselman 1983). The otolith of a fish consists of alternating opaque and translucent zones (under reflected light) whose separation is more conspicuous in fishes of the temperate regions of the world (Pannella 1974). The opaque zones are usually wider and are associated with fast growth, whereas the translucent zones are narrower and are associated with slow growth (Liew 1974, Williams & Bedford 1974). In age determination one opaque zone and one translucent zone are together regarded as an annulus.

In order to obtain reliable information from age and growth studies, validation of the accuracy of estimates obtained from scales and otoliths is essential. Methods of validation of age estimates involve examining hard parts of fish of known age, mark and recapture methods (Casselman 1983) and the Petersen's length frequency method (Weatherley 1972). In this study, mark and recapture data obtained from studies on migration as well as monthly length frequency distribution data were used in an attempt to validate length-at-age data obtained from scales and otoliths.

4.2 MATERIALS AND METHODS

4.2.1 Removal, preparation and interpretation of age marks on scales and otoliths.

Scales : S. bainsii has both cycloid and ctenoid scales (see Chapter 1). Cycloid scales are found on the ventral side and dorsally on the head. Ctenoid scales, on the other hand, occur on the trunk region. The ctenoid scales immediately posterior to the operculum and just below the lateral line were selected for age and growth studies because of

their large uniform size, better symmetry and legibility. Six scales from each fish were stored in gelatin capsules and cross-referenced to fish number. The scales were later soaked overnight in lukewarm water and then washed in cold water after which they were mounted between two microscope slides and cross-referenced to fish number and stored. In order to estimate age from scales they were projected through a microfiche reader at 36X magnification.

In order to determine the periodicity of check formation in scales, the number of circuli in the marginal increment on the anterior median axis were counted. The marginal increment is that area on the scale between the most recent check and the outer margin (Figure 20). The number of circuli in the marginal increment depends on the time of sampling (Hecht 1980a). The scale of a fish sampled shortly after check formation has the check on or near the margin of the scale, hence only a few or no circuli occur in the marginal increment. Therefore, if a large sample of scales is taken at different times throughout the year and the number of circuli in the marginal increment of each scale is determined, the time of check formation on the scale and the number of checks formed per year can be established. The number of circuli in the marginal increment of scales from 225 S. bairdii falling in the size class 35 mm-80 mm SL was determined monthly. The determination of the periodicity of check formation was restricted to one size class because the number of circuli between checks decreases with age (Hecht 1980a).

The monthly changes in the mean number of circuli in the marginal increment of scales is shown in Figure 21. The following periods can be distinguished :

- (i) the period during which the mean number of circuli is relatively constant extending from March to September, a period of slow growth;
- (ii) the period during which the mean number of circuli is low extending from October to November, the period of check formation;
- (iii) the period during which there is a progressive increase in the mean number of circuli extending from November/December to March, a period of accelerated growth.

It is evident from these data that one annual check (annulus) is formed per year in October.

The annulus in the scales of S. bairdii is formed when a zone of closely spaced circuli is followed by a zone of widely spaced circuli. The annulus is at the outer border of the closely spaced circuli (Figures 20 & 22). Checks which did not extend from the lateral field across the anterior field and into the opposite lateral field were regarded as false annuli and were not used for age estimation.

Otoliths : The sagittal otoliths were removed from a subsample of fish by dissection of the cranium. They were stored in gelatin capsules and cross-referenced to fish number. The otoliths were later examined with the aid of a stereo-microscope at 40X magnification in xylol in a black dish under reflected light.

In order to determine the periodicity of growth zone formation in otoliths the size of the marginal increment (the distance from the most recent translucent zone to the margin of the otolith on the anterior median axis) (Figure 23) was measured monthly. As with scales the size of the marginal increment depends on the time of sampling. The otolith of a fish sampled at the beginning of Spring has a translucent zone on or near the margin of the otolith. If a large number of otoliths is taken at different times throughout the year and the size of the marginal increment is determined, the time of formation of each zone can be established. The size of the marginal increment of 131 otoliths of S. bairdii falling in the size class 35 mm-80 mm SL was determined monthly. The determination of the periodicity of zone formation was restricted to one size class because it was observed that the size of the marginal increment decreases with age.

The monthly changes in the size of the marginal increment of otoliths is shown in Figure 24. Three periods can be distinguished namely :

- (i) the period during which the mean size of the marginal increment is relatively constant extending from March to August, a period of slow growth;
- (ii) the period during which the mean size of the marginal increment is

small in October, a period of cessation of the deposition of the translucent zone and beginning of the deposition of the opaque zone, ie check formation;

- (iii) the period during which there is a progressive increase in the mean size of the marginal increment extending from November to March, a period of growth acceleration.

It is evident from these data that one translucent zone and one opaque zone are formed per year. The deposition of the translucent zone ceases at the end of the cold dry season in September. The deposition of the opaque zone begins in October and probably ceases in April/May.

The otoliths of S. bairdii have a nucleus surrounded by alternating wide opaque zones and narrow translucent zones. One opaque zone and one translucent zone together form an annulus.

4.2.2 Backcalculation of length-at-age

Backcalculation can be defined as the process of determining how large an individual fish was at some previous age (Smith 1974). This is achieved by comparing a standard dimension of some calcified parts such as scales or otoliths with a standardized measure of the overall size of the body such as standard length. If the growth zones on the calcified part can be related to a time scale, it is possible to trace the growth history of an individual fish (Smith 1974). If the relationship between the body and the calcified part is linear and their growth directly proportional, the formula of Lea (1910) is used to backcalculate length-at-age. If, on the other hand the relationship between the body and calcified part is linear but their growth not directly proportional, the formula of Fraser (1916) and Lee (1920) is used to backcalculate length-at-age.

Scales : For purposes of backcalculation of length-at-age the following were determined for each scale :

- (i) the number of annuli;
- (ii) the distance from the focus to the anterior lateral margin (Figure 20);

- (iii) the distance from the focus to each annulus along the lateral radius. The lateral radius was chosen as the annuli along this radius are more widely spaced than elsewhere on the scale. This practice facilitated measurement of the distance between annuli.

In order to determine whether the length at previous ages could be backcalculated, the lateral radii of 367 scales were plotted against standard length by the method of least squares (Tesch 1968). The relationship obtained is described by the equation :

$$y = 0.03x \quad (r^2 = 0.94 \quad p < 0.005)$$

where y = scale radius (mm)

x = standard length of fish (mm)

The relationship is shown in Figure 25. The regression was linear and passed through the origin, permitting the use of Lea's (1910) formula :

$$l_n = \frac{S_n \times l}{S}$$

where l_n = length of fish when annulus "n" was formed

l = length of fish at the time the scale sample was obtained

S_n = radius of annulus "n" at length " l_n "

S = total scale radius

Otoliths : On a similar basis the following were determined for purposes of backcalculation of length-at-age :

- (i) the number of annuli;
- (ii) the distance from the focus to the mid-anterior margin using a micrometer eye-piece;
- (iii) the distance from the nucleus to the outer edge of each annulus.

In order to determine whether the previous length-at-age can be backcalculated the anterior longitudinal radii of 224 otoliths were plotted against standard length by the method of least squares. The relationship obtained is described by the equation :

$$y = 0.0220x + 0.6365 \quad (r^2 = 0.89 \quad p < 0.005)$$

The relationship is shown in Figure 26. The regression is linear but not directly proportional and backcalculations were therefore made using

the Frazer and Lee formula (Frazer 1916, Lee 1920) :

$$l_n - c = \frac{S n (1 - c)}{S}$$

where l_n = length of fish when annulus "n" was formed

l = length of fish at capture

$S n$ = radius of annulus "n" at length " l_n "

S = total otolith radius

c = intercept on length axis

4.2.3 Calculation of growth rate using scales and otoliths

To enable generalized comparative descriptions of growth, the data from scales and otoliths were fitted to the von Bertalanffy growth model

(Ricker 1975) in the form of :

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

where L_t = length at age t

L_∞ = the maximum theoretical length a fish can attain

K = the rate at which L_∞ is attained

t_0 = the time at which the fish would have been zero length if it had always grown according to the equation

e = the Neperian constant 2.71828

Ricker (1975) considers the von Bertalanffy model as a useful empirical descriptive expression because it is usually close to the observed growth curves. The adequacy of the von Bertalanffy growth equation was tested using Ford-Walford plots (Ford 1933, Walford 1946). Ford-Walford plots of length at age " t " against " $t+1$ " were calculated by regression analysis using the method of least squares. The straight line data points of the Ford-Walford line bisect the 45 diagonal which permits expression of the growth of *S. bairdii* using the von Bertalanffy equation. This is indicative of an initial period of fast growth followed by a decrease in the growth rate. The y axis intercept of the Ford-Walford line equals $L_\infty (1-k)$ and L_∞ can be obtained where $K = e^{-k}$. From the slope (k) of the Ford-Walford line, K was calculated from the relationship :

$$K = -\log_e k$$

The parameter " t_0 " was calculated by the regression of " t " on $\log_e(L_\infty - l_t)$ by the method of least squares. By equating $\log_e L_\infty + Kt_0$ with the y axis intercept of the regression line, " t_0 " can be calculated.

4.2.4 Age-length key

In order to obtain an approximate estimate of the age distribution of S. bainsii, an age-length key was constructed as described by Ricker (1975). Using the length-at-age data obtained from scale and otolith analysis (Table 11 & 12), the percentage of each age among fish of a given length group was calculated. Males and females were considered separately.

An important requirement when constructing an age-length key is that the data are from a representative sample of fish from the population being aged (Ricker 1975). All the conditions for construction of an age-length key (Ricker 1975) were met.

4.2.5 Validation of age and growth estimates

Mark and recapture method

A mark and recapture programme was undertaken primarily to study migration but the data were also used to validate age estimates and growth rate (Casselman 1983). The tagging procedure is described in Chapter 6 (section 6.2.3).

Length frequency distribution method

The length frequency distribution (Petersen method) can also be used to validate age and growth estimates of fish (Weatherley 1972, Linfield 1974). Populations of fish that reproduce seasonally are characterized by regular influxes of recruits that, if adequately sampled, usually reveal a size structure in the form of modes, which indicate the presence of several age groups, especially in the first few years of life. Should individuals from such age groups bear on their calcified structures checks corresponding to the order of fish in the size structure of the population, this may be taken as evidence of the

validity of the checks (Weatherley 1972). An attempt was thus made to validate age and growth estimates obtained from scales and otoliths data using the Petersen method.

"Known" age method

Use of fish of known age is one of the methods of validation of age and growth estimates obtained from hard parts (Casselman 1983).

At the beginning of this study, juvenile S. bainsii (30-40 mm SL) caught in the Tyume river were released into an irrigation dam at Fort Hare. Unfortunately the dam was drained and all the fish were lost. An attempt was made to validate the age estimates obtained from hard parts using a fish of "partially known" age. A fish of 181 mm SL caught in August 1983 which had three scale rings was kept in an aquarium (1350 X 750 X 1250 cm deep). The temperature of the water was kept constant at 16°C. The fish was sacrificed in June 1985 when it had attained a length of 192 mm and its scales and otoliths were examined for annuli.

4.2.6 Length-weight relationship

The length-weight relationship of a fish is calculated for a number of reasons. Firstly, in the description of the growth of a fish it is often necessary to state whether a fish exhibits isometric or allometric growth (Ricker 1975) and this can be established by determining the length-weight relationship. Secondly, knowledge of the length-weight relationship has practical value since it allows conversion of length into weight and weight into length (Lagler 1982). Thirdly, it is used to determine the co-efficient of condition with the objective of expressing the condition of a fish in numerical terms (see section 5.2.3, Chapter 5). The relationship between length (L) and weight (W) can be described by the formula :

$$W = aL^b \quad (\text{Tesch 1968})$$

where "a" and "b" are constants. If the exponent "b" = 3 then growth is isometric, ie if the specific gravity of the fish remains constant, so will the shape of the body (Ricker 1975). If on the other hand "b" ≠ 3, the body form will change with size and growth is allometric. The length-weight relationship was calculated on data of 643 S. bainsii.

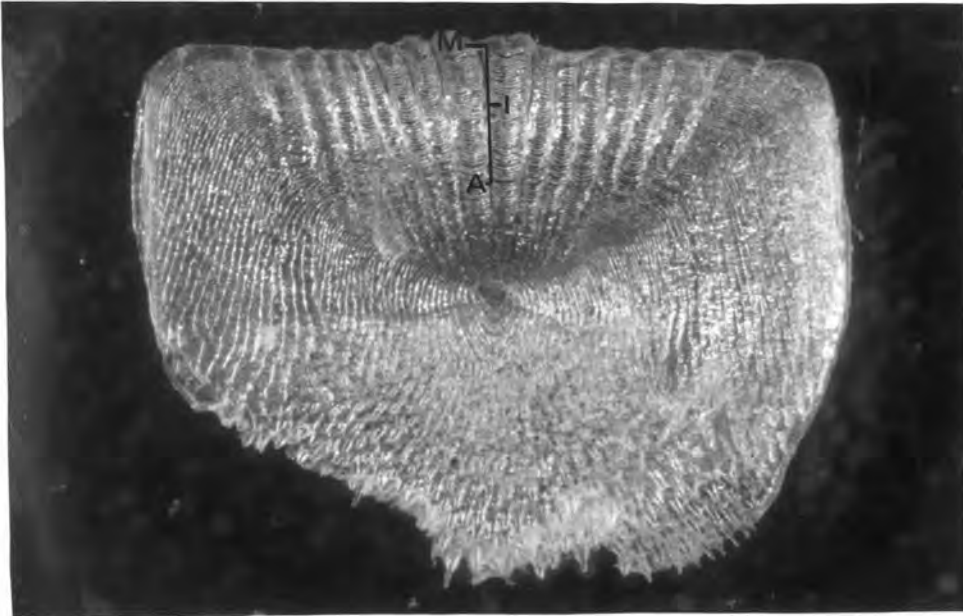


Figure 20. Scale of 1+ year old *S. bairdii* showing the annulus (A), anterior median margin (M) and marginal increment (I). (20x).

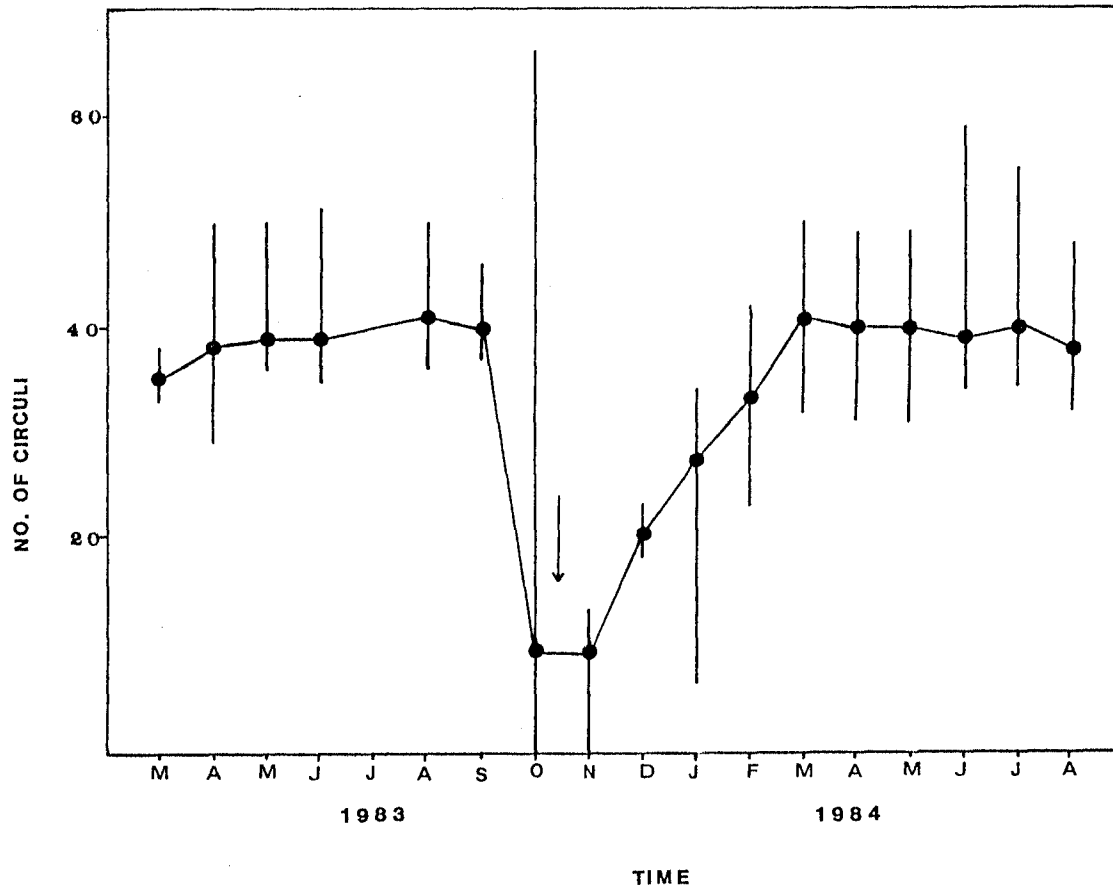


Figure 21. The monthly changes in the mean number of circuli in the marginal increment of scales of *S. bairdii*. The vertical lines show the range. The arrow indicates the time of annulus formation.

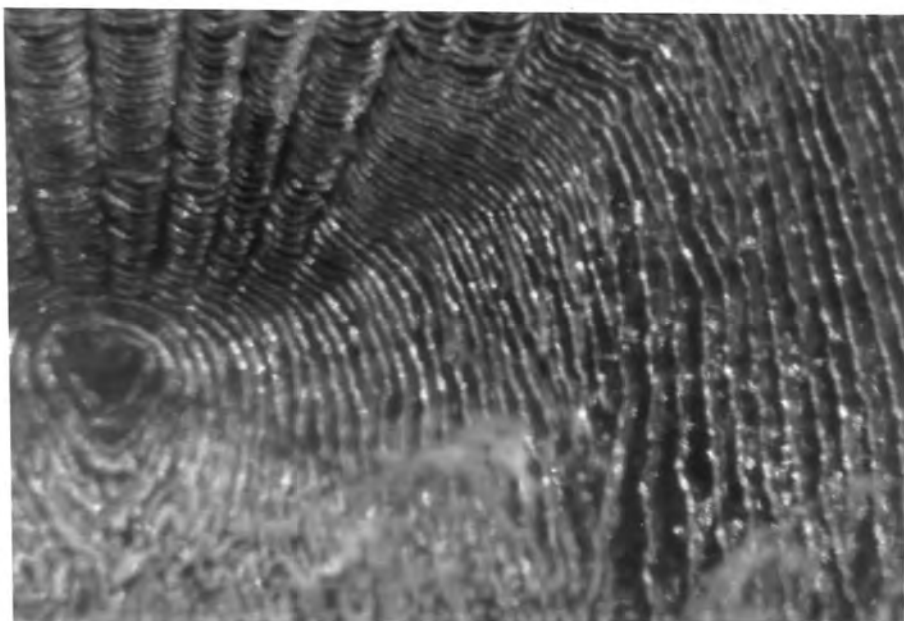


Figure 22. The anterior portion of *S. bainsii* scale showing the annulus. (75x).

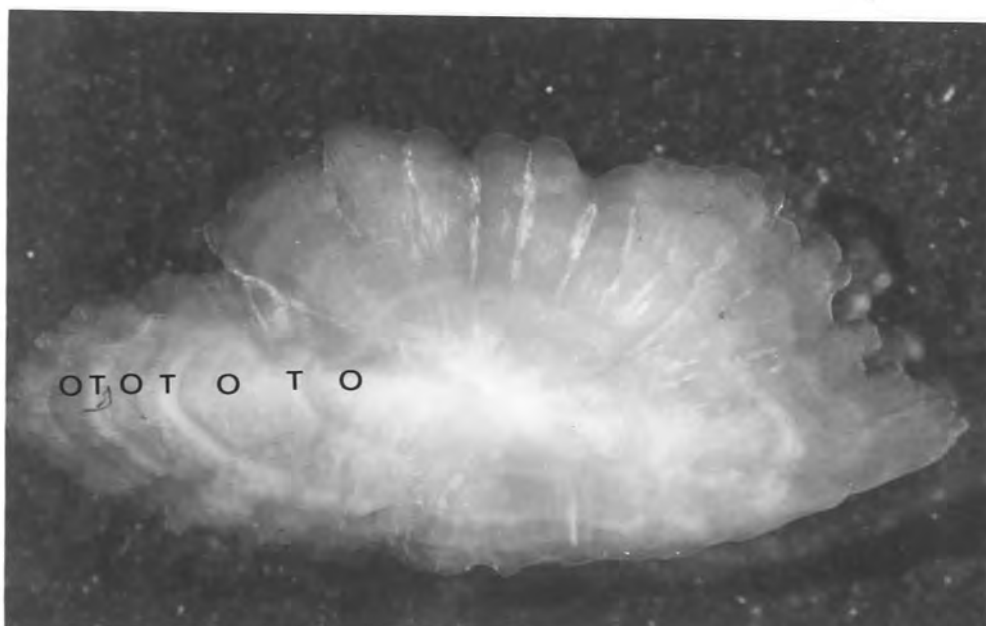


Figure 23. Otolith of 3+ year old *S. bainsii* showing opaque (O) and translucent (T) zones. (75x).

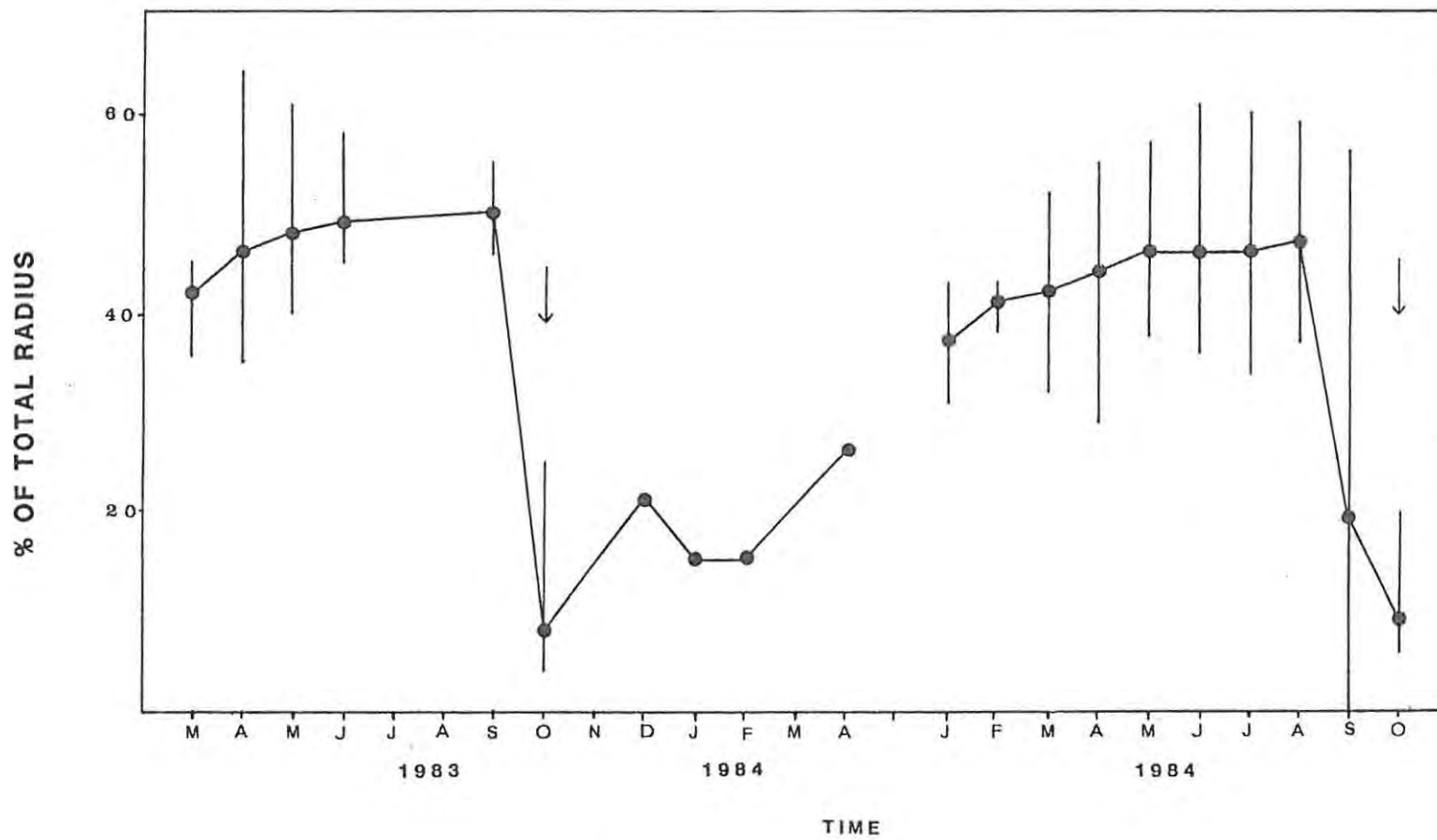


Figure 24. The monthly changes in the mean size of the marginal increment of otoliths of *S. bairdii*.

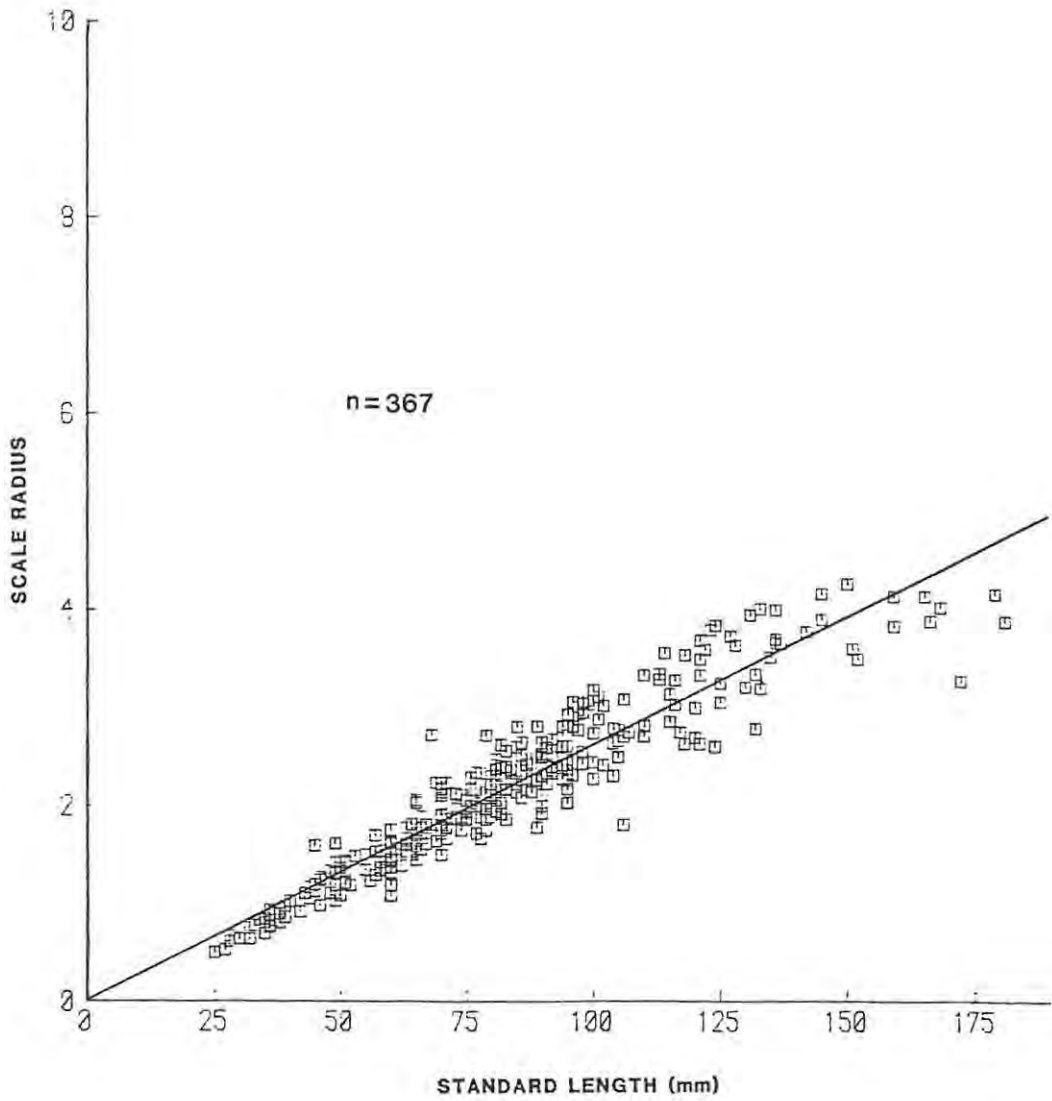


Figure 25. The relationship between fish length and anterior lateral scale radius for *S. bairdii* from the Tyume river.

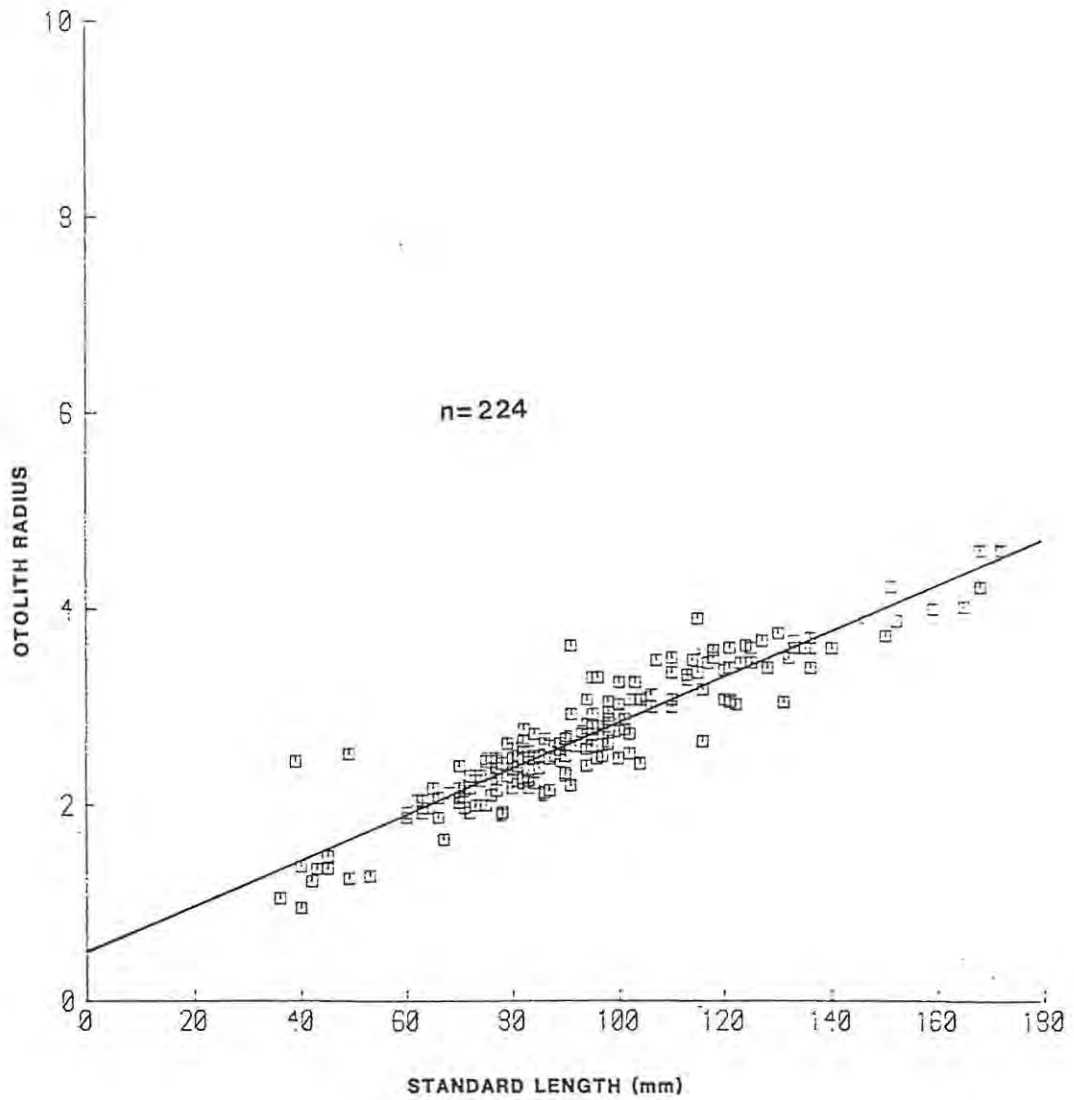


Figure 26. The relationship between fish length and anterior median otolith radius for *S. bairdii* from the Tyume river.

4.3 RESULTS

4.3.1 Age and growth rate

The backcalculated length-at-age and the observed length-at-age data for male and female S. bairnsii based on scales and otoliths are shown in Tables 5 - 8.

Table 5. The mean backcalculated standard length-at-age(SL), standard error(SE), annual length increment(Δ SL) of male S. bairnsii based on scales(S) and otoliths(O).

Age	Backcalculated		SE		N		Δ SL	
	S	O	S	O	S	O	S	O
1	38	43	0.9	1.1	118	101	38	43
2	79	86	2.6	2.6	35	41	41	43
3	112	118	4.8	3.4	15	13	33	32
4	148	149	7.1	1.7	6	4	36	31

Table 6. The mean backcalculated standard length-at-age(SL), standard error(SE) and annual length increments(Δ SL) of female S. bainsii based on scales(S) and otoliths(O).

Age	Backcalculated		SE		N		Δ SL	
	SL(mm)							
Year	S	O	S	O	S	O	S	O
1	33	35	0.7	0.9	146	112	33	35
2	71	72	1.5	1.4	48	38	38	37
3	98	97	3.7	2.1	16	16	27	27
4	125	122	-	-	1	1	27	25

Table 7. The mean observed length-at-age(SL), standard error(SE) and annual length increments(Δ SL) of male S. bainsii based on scales and otoliths.

Age	Observed		SE		N		Δ SL	
	SL(mm)							
Year	S	O	S	O	S	O	S	O
1	84	85	1.2	1.2	80	70	84	85
2	112	117	3.6	3.7	23	19	28	32
3	143	141	4.7	4.6	10	9	31	24
4	163	168	6.7	1.4	6	4	20	27

Table 8. The mean observed length-at-age(SL), standard error(SE), and length increments(Δ SL) of female S. bainsii based on scales(S) and otoliths(O).

Age	Observed SL(mm)		SE		N		Δ SL	
	S	O	S	O	S	O	S	O
1	73	76	1.1	1.2	95	63	73	76
2	98	102	2.3	2.2	32	31	25	26
3	117	116	2.0	2.2	16	16	19	14
4	136	136	-	-	1	1	19	20

There is a big difference between the backcalculated length-at-age data and the observed length-at-age data particularly in the one year old fish. This is possibly due to the near continuous recruitment of this species. This aspect is discussed in section 4.4.

The values of the von Bertalanffy equation calculated from the data derived from scales and otoliths are given in Table 9.

Table 9. The values of the constants in the von Bertalanffy growth model and correlation coefficients from Ford-Walford plots as fitted to the length-at-age data of S. bainsii.

	Sex	L	K	r^2	t_0
Scales	Males	603	0.073	0.99	0.14
	Females	236	0.198	0.99	1.26
Otoliths	Males	287	0.186	0.99	0.15
	Females	214	0.223	0.99	0.18

The values of " t_0 " are generally close to zero and the correlation

coefficients (r^2) for the Ford-Walford regressions were 0.99, both indicating a good fit. The Ford-Walford plots of males and females of S. bainsii are shown in Figure 27.

The calculated von Bertalanffy lengths-at-age are shown in Table 10 and the growth of S. bainsii is shown in Figures 28 and 29.

Table 10. The calculated von Bertalanffy standard lengths-at-age (SL) and annual increments (Δ SL) of males(M) and females(F) of S. bainsii based on scales and otoliths.

Age	Scales				Otoliths			
	SL(M)	Δ SL	SL(F)	Δ SL	SL(M)	Δ SL	SL(F)	Δ SL
1	41.9	41.9	32.6	32.6	47.4	47.4	41.2	41.2
2	76.6	34.7	71.2	38.6	88.0	40.7	75.8	34.5
3	113.6	37.1	99.1	27.9	121.8	33.8	103.4	27.6
4	148.1	34.5	123.6	24.6	149.9	28.0	125.5	22.1

4.3.2 Age-length key

The age-length keys of S. bainsii based on scales and otoliths are shown in Tables 11 & 12 respectively. The population age structure of S. bainsii is shown in Figure 30. There is some overlap between the lengths of consecutive age groups. The overlaps in the lengths-at-age are not excessive in spite of the apparent continuous recruitment in this species. A possible explanation may be that, although the species has a protracted breeding season, there is a pronounced spawning peak in Spring. As this is the time of annulus formation, these fish will form their first annulus after a full season's growth. Fish spawned in summer or autumn (relatively younger in months at annulus formation) are probably small in number and have not had an appreciable effect on the length-at-age data.

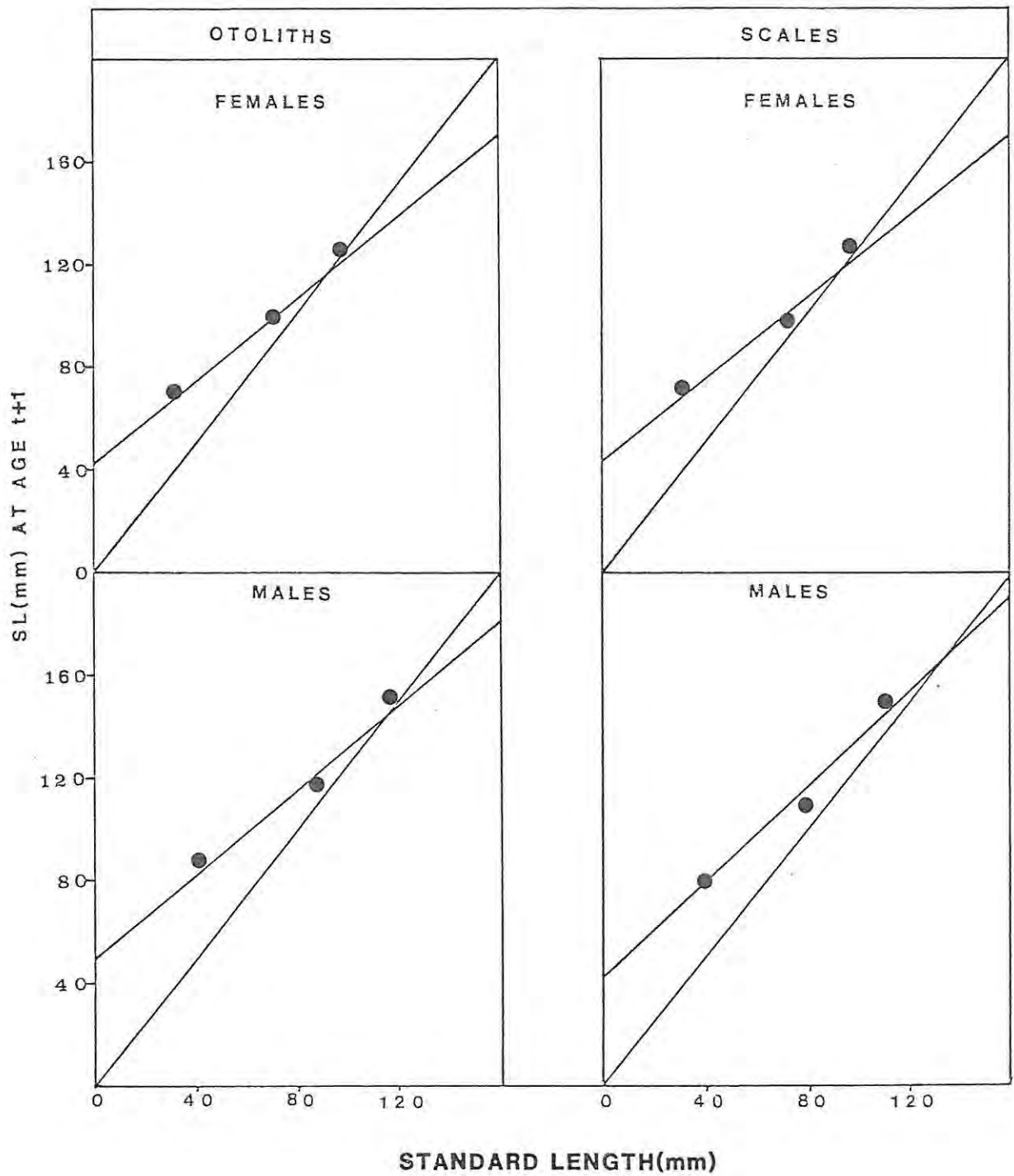


Figure 27. Ford-Walford plots of male and female *S. bairdii* based on otoliths and on scales.

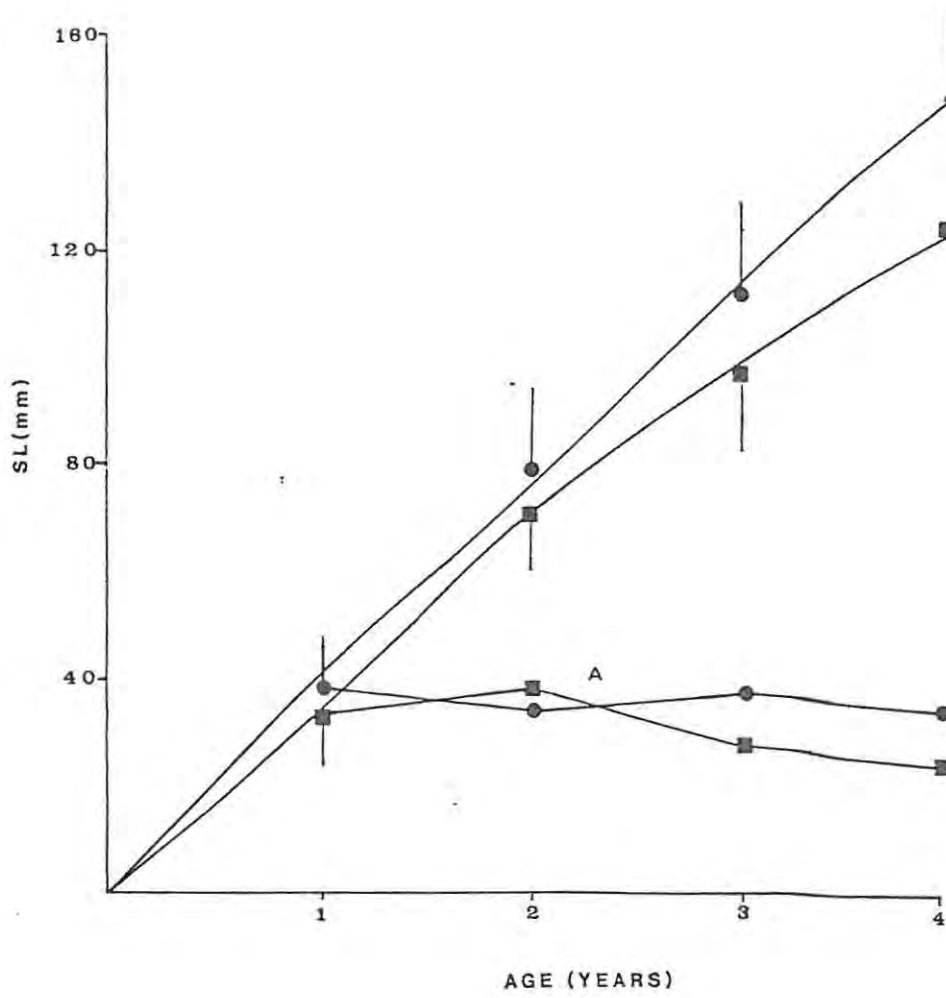


Figure 28. Growth in length of male (●) and female (■) *S. bairdii* based on scales. The data are given as means and half standard deviation (vertical lines). The annual length increments are shown (A).

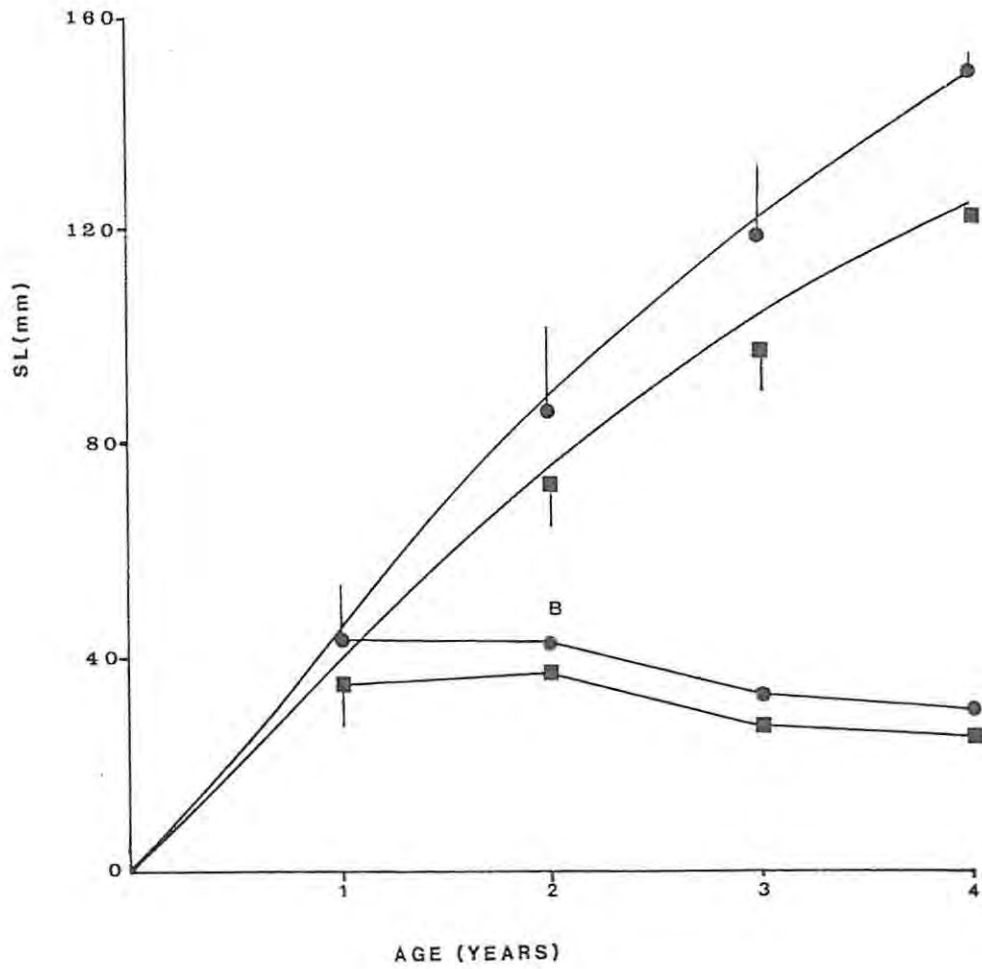


Figure 29. Growth in length of male (●) and female (■) *S. bainsii* based on otoliths. The data are given as means and half standard deviation (vertical lines). The annual length increments are shown (B).

4.3.3 Validation of age and growth estimates

Mark and recapture method

A total of 372 fish were tagged and released to determine whether the species undertakes a spawning migration (see section 6.2.3, Chapter 6). Of these 24(6.5%) were recaptured and the monthly increments attained are shown in Table 13.

Table 13. Growth in length of S. bainsii using marked fishes.

Fish no.	SL at tagging	SL at recapture	$\Delta t(\text{days})$	Monthly increment
1	65	69	51	2.3
2	80	80	38	0.0
3	69	69	24	0.0
4	78	81	37	2.4
5	92	92	37	0.0
6	68	70	24	2.4
7	87	91	24	4.8
8	77	79	37	1.6
9	72	72	24	0.0
10	65	65	33	0.0
11	83	85	33	1.8
12	68	70	33	1.8
13	67	67	123	0.0
14	96	103	123	1.7
15	87	93	108	1.7
16	62	63	123	0.2
17	75	78	123	0.7
18	96	104	186	1.3
19	75	78	186	0.5
20	62	63	186	0.2
21	88	96	213	1.1
22	67	70	216	0.4
23	65	69	216	0.6
24	71	79	216	1.1

As the tagged fish were neither sexed nor aged at the time of tagging, it was impossible to use the data to validate the growth estimates based on scales and otoliths.

Length frequency method

The length frequency distribution of young fish, <80 mm SL, caught monthly from February 1983 to August 1984 is shown in Figure 31. Clear modes are not apparent from the catches and it was not possible to determine the growth rate from these data. This can be attributed to the protracted breeding season and consequently near continuous recruitment in this species. This aspect is discussed in section 6.3.1 of Chapter 6.

"Known" age method

The scales as well as otoliths of the fish that was captured in August 1983 and kept in an aquarium had five annuli when it was killed in June 1985. This suggests that, in addition to the three annuli present in August 1983, one annulus was added late in 1983 and a second one in 1984. Although this result is consistent with observations on scales and otoliths, the data do not validate estimates based on the hard parts as the data are derived from one fish. Moreover, extrapolation of data from an aquarium-reared fish might be misleading.

4.3.4 Length-weight relationship

The length-weight relationship of S. bairdii is shown in Figure 32. The value of the exponent "b" from the relationship $W = aL^b$ is 3.0281. S. bairdii therefore exhibits near isometric growth. The relationship is described by the equation :

$$\text{Weight} = 0.2366 \times 10^{-4} \text{ Length}^{3.0281} \quad (r^2 = 0.89, p < 0.005).$$

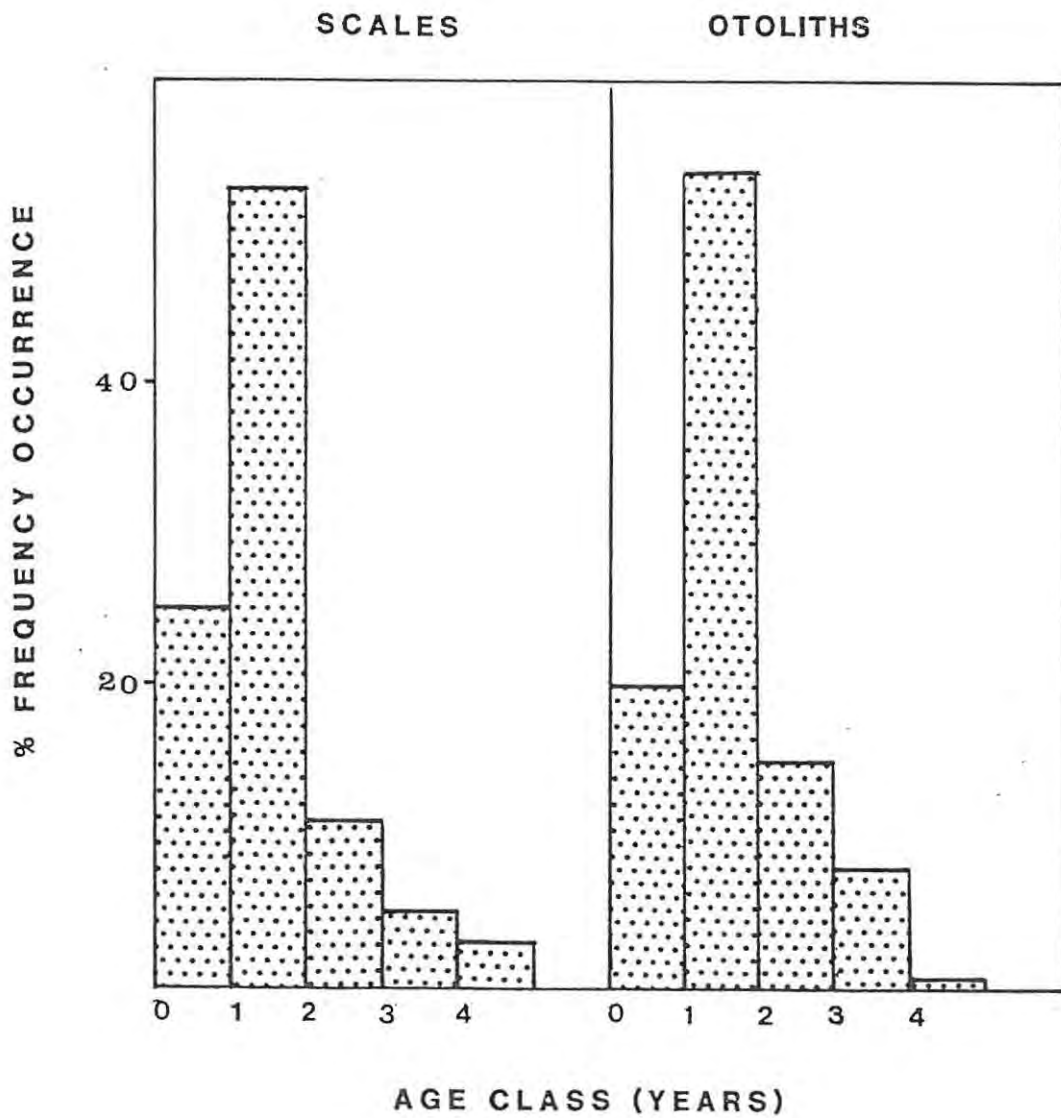


Figure 30. The population age structure of *S. bairdii*. Values were calculated using length-age-keys (Ricker 1975).

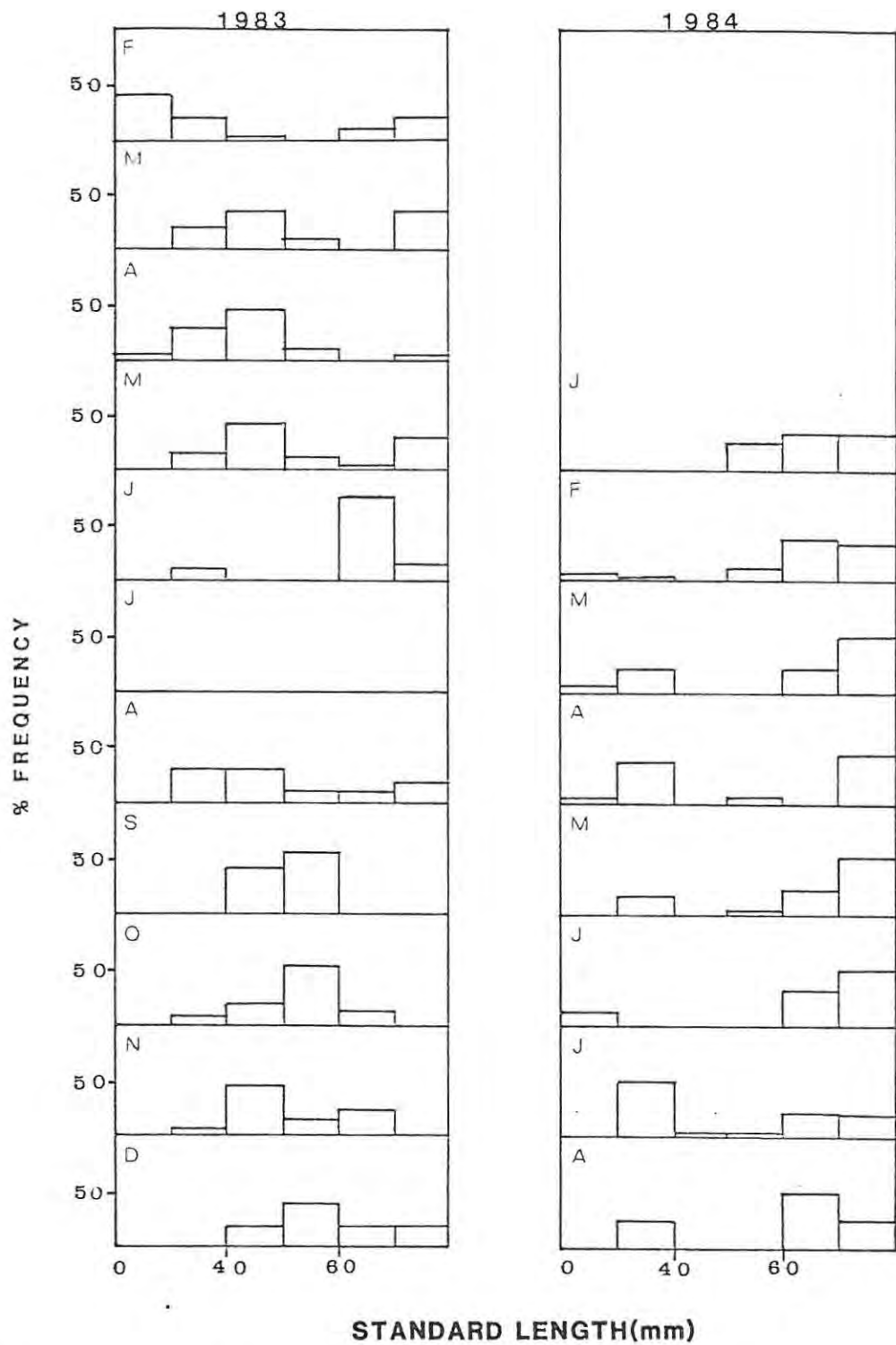


Figure 31. The monthly length frequency distribution of young *S. bairdii* (SL < 80mm).

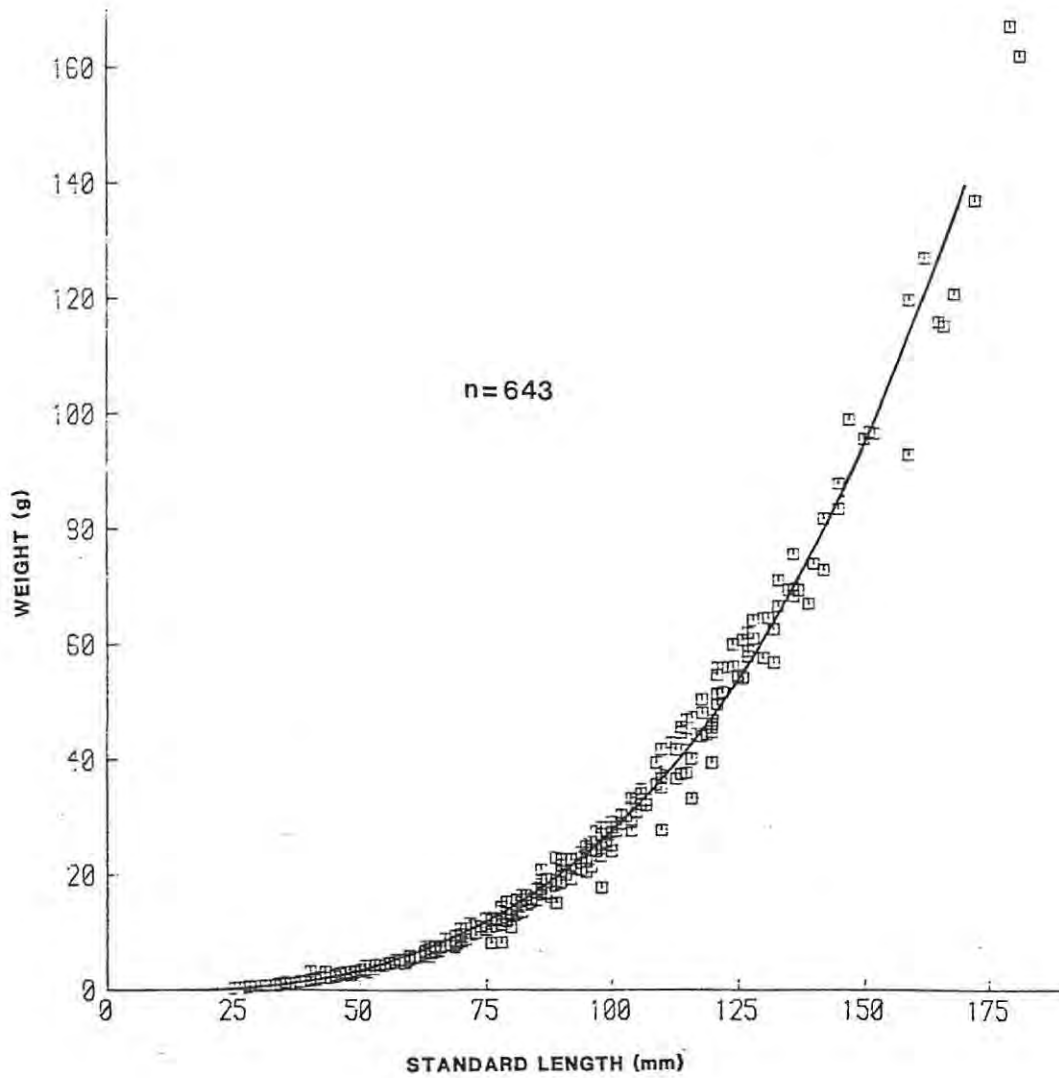


Figure 32. The length-weight relationship of *S. bairdii* from the Tyume river.

4.4 DISCUSSION

The factors involved in the process of annulus formation are not clear. The annulus may be formed by temporal food availability (Bilton 1974, Bruton & Allanson 1974), determined by an "endogenous biological rhythm" (Balon 1975) or may be a spawning mark.

Examination of the scales of S. bainsii shows that the annulus is formed by a discontinuity in the pattern of circuli caused by a wider spacing of circuli than is normally the case. If the increase in length of the fish is isometric, as is the case in S. bainsii (see section 4.3.4), the annulus is formed at a time of rapid body and scale growth. Rapid scale growth results in the wider spacing of circuli. Wide spacing of the circuli would result if the basal plate of the scale showed a growth acceleration which tended to separate the circuli (Bruton & Allanson 1974). On the other hand, slow growth would result in closely spaced circuli (Figure 22).

There are three events coinciding with scale annulus formation that have been observed during the course of this study namely :

- (i) increase in water temperature (Table 2) and the beginning of the rainy season (Figure 5);
- (ii) the beginning of the breeding season (Figure 42);
- (iii) increase in the stomach fullness index (Figure 37).

It seems that scale annulus formation therefore occurs when the fish grow rapidly in response to increased food availability, which in turn is determined by factors such as temperature and rainfall. A study of the monthly change in the condition factor shows that the females are in poor condition in October (Figure 39), a period during which gonadal maturity is achieved. This observation suggests that scale annulus formation is a result of post breeding growth acceleration as it is unlikely that fish in poor condition (just prior to breeding) will show rapid growth. This does not mean, however, that the annulus is a spawning ring because immature fish, < 60 mm SL, also form an "annulus". It would seem that scale annulus formation is primarily controlled by environmental factors such as temperature and rainfall. The observation that S. bainsii forms annuli under constant environmental conditions,

however, suggests that environmental conditions are not the only controlling factors. It is possible that annulus formation in S. bainsii is controlled by an "endogenous rhythm" that is regulated by environmental factors as suggested by Balon (1975).

The otolith annulus of S. bainsii consists of one opaque zone and one translucent zone. The opaque zone is formed during a period of increased water temperature, high rainfall, and fast postbreeding growth. The translucent zone on the other hand appears on the otolith during a period of lower water temperature and low rainfall prior to breeding, when the fish are in poor condition. As with the scales, it would appear that the formation of the opaque and translucent zones is controlled by environmental factors only. The observation that the two zones are formed under constant environmental conditions, however, suggests that an "endogenous rhythm" is involved as well.

Both the scale and otolith methods of ageing are adversely affected by the near continuous recruitment in this species. These fish form a ring (annulus ?) irrespective of "age" in months. This is evidenced by the observation that some fish that are 35 mm and others that are 95 mm in length have one annulus and are thus interpreted to be one year old fish in spite of the large difference in length. This length difference in fish of the same age (both 1+) is more striking in view of the maximum length of 172 mm SL at age four. The conclusion reached is that the fish form a ring (annulus ?) in Spring irrespective of "age" in months. This is probably a result of the near continuous recruitment in this species which is also possibly responsible for the large difference between the backcalculated lengths-at-age and the observed lengths-at-age.

On closer examination of both the scales and the otoliths of S. bainsii and the data presented in Table 7 and Figures 28 and 29, a number of points emerge that show that otoliths are more suitable than scales for age determination in this species :

- (i) the greater difficulty of reading scales of 3 and 4 year old fish as the rings become crowded in the anterior and lateral fields;
- (ii) the von Bertalanffy parameter L_{∞} of 603 mm and 236 mm for males

and females respectively calculated on the data from scales is improbable when it is compared with the observed maximum length of 190 mm and 136 mm attained by males and females respectively. The L_{∞} values of 287 mm and 214 mm for males and females respectively calculated on the data from otoliths are a better estimate;

- (iii) the erratic nature of the growth in length based on scales shown in Figure 28 compared to the more uniform growth pattern which conforms to the expected norm shown in Figure 29 which is based on otoliths.

According to Casselman (1983) otoliths are preferred because they are more reliable and interpretations based on them more closely approximate the "true" age of fish because zonation is usually more distinct and more easily recognised, even in older fish.

The advantage of using scales over otoliths is that fish do not necessarily have to be killed. This means that scales can be used in mark and recapture experiments to generate useful data. Conversely however, if a fish species that is rare or vulnerable is to be studied, it is imperative that ageing be done as accurately as possible as this is one of the most important parameters upon which recommendations for management will be based.

Male and female fish often grow at different rates. Bruton & Allanson (1974) and Hecht (1980a) found that males of cichlids show a faster growth rate than females. The results obtained in this study (Figure 28 and Figure 29) show that the males of S. bainsii also grow at a faster rate than the females. Females, however, had a higher growth coefficient (K) but a lower L_{∞} than males. According to Kingsley (1980) the higher K value and lower L_{∞} are characteristic of the sex that matures earlier and at a smaller size. In Chapter 6 it will be shown that females of S. bainsii mature at a smaller size than males.

The maximum observed length of S. bainsii in the Keiskamma river system was 190 mm SL which approximates that of the larger anabantids such as A. testudineus. The maximum length reached by the Ctenopoma species is 155 mm SL (Daget 1961) whereas A. testudineus reaches 250 mm TL

(Forselius 1957) and S. capensis reaches 220 mm TL (Bruton et al 1982).

The oldest fish caught in this study was 4 years old. There is some evidence that S. bainsii lives to a greater age as a single specimen* (190 mm SL) whose age was estimated to be 5 years old was caught in the Keiskamma river in 1984.

* Specimen number RUSI 20094 housed in the J L B Smith Institute of Ichthyology, Grahamstown.

CHAPTER 5

FEEDING

5.1 INTRODUCTION

Feeding is one of the most important activities of an organism because all the other basic activities such as growth, reproduction and development utilize energy which enters the organism in the form of food (Nikolsky 1963).

A major objective of feeding studies is to determine the diet of the species concerned. Determination of the diet of a species usually includes a qualitative and quantitative assessment of the kinds and amounts of food consumed and the way in which food habits are influenced by habitat preferences, season, fish size and competitor species (Windell 1968). The diet information can then be used to determine the trophic level and niche of the species within a community (Hyslop 1980). This allows for comparison of the nutritional role of the species in its ecosystem with other different but trophically comparable species in the same or other systems (Weatherley 1972).

S. bainsii occurs in the Tyume river together with an indigenous insectivore, B. trevelyani (Gaigher 1975), an indigenous predator, Anguilla mossambica (Bruton et al 1982), an omnivore, T. sparrmanii (Bruton et al 1982) and very recently a translocated indigenous omnivorous predator, C. gariepinus (Bruton 1979b) and two alien predators, S. gairdneri and M. salmoides (Crass 1963).

Co-habitation of several species with similar dietary requirements often gives rise to speculation on the possible competitive interactions between them. These interactions have received attention from ecologists studying fish assemblages in many parts of the world. Some consider that the competitive exclusion principle does not apply in some situations where food is overabundant (Hartley 1948, Larkin 1956, Fryer & Iles 1972). More recently it has been suggested that interspecific and intraspecific differences in ecology reduce competition for food (Keast 1980).

Dietary overlap among species does not necessarily result in intense competition as it has been observed that the species tend to subdivide and share resources (Lowe-McConnell 1975). The subdivision of the resources can be explained in terms of horizontal and vertical distribution patterns, habitat preferences, mouth size and changes in diet with size. However, the extent to which these factors reduce competition for food is unknown (Bennett et al 1983). This non-competitive sharing of resources probably occurs in assemblages of indigenous fishes where there are no introduced species.

Previous studies of feeding in anabantids have shown that S. capensis feeds on insects, crustaceans and aquatic snails (Siegfried 1963), C. multispinis on insects, crustaceans, snails and small fish (Bruton 1979a) and A. testudineus on insects, microcrustaceans and small fish (Singh & Samuel 1981). No detailed feeding studies have previously been undertaken on S. bainsii. The main objective in studying the feeding of S. bainsii was to collect data that can be used to determine the trophic level of the species and also to relate the data to other aspects of its biology in order to obtain a composite picture of its life history strategy. The feeding data would also be used to determine whether there is an overlap between the diet of S. bainsii and that of the other predators found in the Tyume river and the possible effect of this on S. bainsii.

5.2 MATERIALS AND METHODS

Fish of which the stomach contents were analysed were caught using electro-fishing gear and seine nets on a monthly basis at the different sampling stations along the Tyume river from March 1983 to August 1984. Specimens of all size classes of S. bainsii and other predators were killed by placing them in crushed ice.

5.2.1 Laboratory analysis

Immediately on arrival in the laboratory the fish were measured, weighed and the alimentary canal removed. The stomachs were rated for fullness using an arbitrary estimation. Points were allocated as follows :

<u>Visual estimation of fullness</u>	<u>Points</u>
Distended	10
Full	8
$\frac{3}{4}$ Full	6
$\frac{1}{2}$ Full	4
$\frac{1}{4}$ Full	2
Trace	1
Empty	0

The stomachs were preserved in 10% formalin and cross-referenced to fish number.

5.2.2 Food analysis

Food analysis was restricted to the stomach as the food in the intestine was at an advanced stage of digestion and its inclusion in the analysis would have biased the results in favour of less digestible food items.

The methods used to analyse food in this study are based on those described by Hynes (1950), Windell (1968) and Hyslop (1980), namely the numerical (NA), frequency of occurrence (FO) and the dry weight (DW) methods. These methods are described briefly below.

Numerical method : The number of individuals of each food type in each stomach was counted. These were summed to give totals for each kind of food item in the whole monthly sample, and then a grand total of all items obtained. The quotient of these gave the percentage representation.

Frequency of occurrence method : Stomach contents were examined and individual food items identified and sorted. The number of stomachs in

which each food item occurred was recorded and expressed as a percentage of the total number of stomachs which had food.

Dry weight method : The different food items were identified, sorted and then dried in an oven at 95°C for 15 hours. The dry weight of each food item was taken to the nearest 0.00001g. Weight values for the various kinds of items were expressed as percentages of the total weight of all the samples.

Each of the above methods, if used alone, has inherent disadvantages (Windell 1968, Hyslop 1980). For example the numerical method does not give a good representation of the importance of food items of different prey size. Similarly, the frequency of occurrence method is biased in favour of small food items, whereas the dry weight method favours large items which take longer to digest completely.

All the above mentioned methods were used to assess the importance of different food items in the diet of the fish. Windell (1971) considers indices which combine values obtained from different methods as more representative of the diet of a fish. Such an index or measure is the "index of relative importance" (IRI) (Pinkas et al 1971, Prince 1975) which incorporates percentage by number (NA), dry weight (DA) and frequency of occurrence (FO) in the formula :

$$IRI = (\%NA + \%DA) \times \%FO$$

The above formula was used to compare the relative importance of different food items in the diet of S. bainsii.

Calorific content of food

Preliminary analyses to compare the calorific content of the most important prey items were undertaken. The aim of the analyses was to determine whether S. bainsii "selects" (Ivlev 1961) food items that have a high calorific content or not. For this purpose the calorific content of the most common and "important" food items, Baetidae nymphs, Potamon sidneyi, juvenile B. trevelyani and T. sparrmanii was determined using a Gallenkamp bomb calorimeter.

5.2.3 Condition factor

The condition factor (K) gives an indication of the feeding intensity of a fish by revealing the "fatness" and can be used to investigate seasonal and habitat differences (Tesch 1968). The condition factor can be calculated using the formula :

$$K = \frac{W}{L^b} \times 100 \quad (\text{Lagler 1982})$$

where W = weight(g)

L = length(cm)

b = exponent derived from the length-weight relationship (3.0281).

At the onset of the breeding season the gonad weight in fishes increases markedly with the result that the high values for the condition factor obtained during this period reflect an increase in gonad weight rather than an improvement in the condition of the fish. To exclude this error the above formula was modified as follows :

$$K = \frac{T_w - G_w}{L^b} \times 100$$

where T_w = total fish weight(g)

G_w = gonad weight(g)

L = length(cm)

b = exponent 3.0281

5.3 RESULTS

5.3.1 General food preferences

The food preferences of all S. bainsii examined are given in Table 14. The indices of relative importance are also shown in Figure 33.

Insects were the dominant food item by number (87%) followed by crustaceans (11.5%), fish (1.3%) and molluscs (0.2%). Of the insects, the Baetidae nymphs Genus 1 were the dominant food item (58.3%) followed by Ceratopogonidae larvae (16.1%).

Similarly insects were the dominant food item by frequency (80.6%) followed by crustaceans (20.7%), fish (7.2%) and molluscs (1.0%). Baetidae nymphs were the most common food item (42.8%) followed by Ceratopogonidae larvae (10.5%).

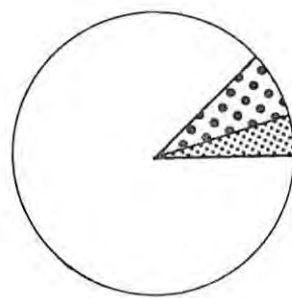
Fishes were the dominant food item by weight (60.9%) followed by crustaceans (23.2%), insects (17.1%) and molluscs (0.1%). The dominant food items were B. trevelyani (20.7%), S. bainsii (29.3%) and P. sidneyi (19.3%).

When the values obtained from the three methods of food analysis were combined to give the "index of relative importance" (Pinkas et al 1971, Prince 1975) insects emerged as the most important food item (8386) followed by the crustaceans (719), fish (449) and molluscs (0.2). The most "important" individual food item in the diet of S. bainsii were the Baetidae Genus 1 nymphs (2868) followed by P. sidneyi (192) and Ceratopogonidae larvae (189).

Table 14. The food of S.bainsii

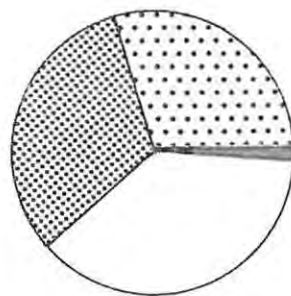
Food species or group	N.A.		F.O.		D.W.A.		IRI
	No.	% of Total	Freq. of Occurrence	% F.O.	Total Weight	% of total dry weight	
PISCES	25	1,28	22	7,23	5,27927	60,89	449
<u>B.trevelyani</u>	6	0,30	5	1,64	1,79547	20,71	34
<u>T.sparmani</u>	8	0,41	8	2,63	0,84513	9,74	26
<u>L.macrochirus</u>	2	0,10	2	0,65	0,09348	1,07	0,76
<u>S.bainsii</u>	5	0,25	3	0,98	2,54337	29,33	28
Unidentified	4	0,20	4	0,32	0,00182	0,02	0,07
CRUSTACEA	224	11,52	63	20,72	2,01375	23,22	719
<u>P.sidneyi</u>	30	1,54	28	9,21	1,67552	19,32	192
<u>Mysis sp.</u>	75	3,85	11	3,61	0,12992	1,49	19
Cladocera	93	4,78	6	1,97	0,02125	0,24	9
Copepoda	13	0,66	6	1,97	0,00299	0,03	1
Amphipoda	12	0,61	11	3,61	0,03856	0,44	3
INSECTA	1692	87	245	80,59	1,47803	17,06	8386
Ephemeroptera	1145	58,89	136	44,73	0,76185	8,78	3026
Baetidae G. 1	1135	58,38	130	42,76	0,75541	8,71	2868
Baetidae G. 2	10	0,51	6	1,97	0,00644	0,07	1
Hemiptera	47	2,41	20	6,57	0,03385	0,39	18
Notonectidae	47	2,41	20	6,57	0,03385	0,39	18
Plecoptera	56	2,88	17	5,59	0,10154	1,17	22
Nemouridae	56	2,88	17	5,59	0,10154	1,17	22
Isoptera	30	1,54	4	1,31	0,1239	1,42	3
<u>Macrotermes sp.</u>	30	1,54	4	1,31	0,1239	1,42	3
Aeshnidae	19	0,97	15	4,93	0,17341	2,0	14
Coleoptera	14	0,71	11	3,61	0,03187	0,36	3
Dystiscidae	8	0,41	5	1,64	0,01715	0,19	0,98
Corixidae	6	0,30	6	1,97	0,01472	0,16	0,90
Unidentified	45	2,31	26	8,55	0,05135	0,59	24
Insect larvae	330	16,97	46	15,13	0,18896	2,17	289
Diptera	313	16,10	32	10,52	0,16795	1,93	189
Ceratopogonidae	313	16,10	32	10,52	0,16795	1,93	189
Odonata	1	0,05	1	0,32	0,00017	1,001	0,01
Coleoptera	10	0,51	8	3,28	0,0199	0,22	2
Unidentified	6	0,30	5	1,64	0,00094	0,01	0,5
Insect pupae	3	0,15	3	0,98	0,01159	0,13	0,27
Trichoptera	1	0,05	1	0,32	0,00138	0,01	0,01
Unidentified	2	0,10	2	0,65	0,01021	0,11	0,20
MOLLUSCA	3	0,15	3	0,98	0,00702	0,08	0,22
Gastropoda	3	0,15	3	0,98	0,00702	0,08	0,22
<u>Ferrisia sp.</u>	3	0,15	3	0,98	0,00702	0,08	0,22

No. of S.bainsii examined = 426No. of S.bainsii with stomach contents = 304



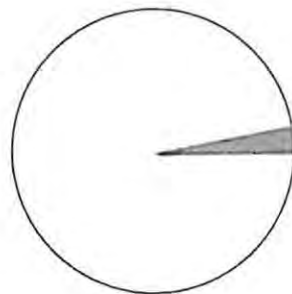
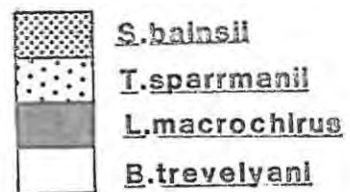
A

MAJOR PREY CLASSES



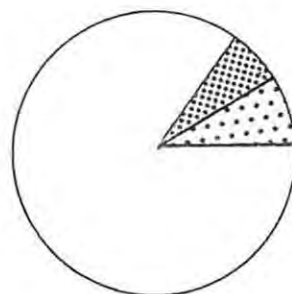
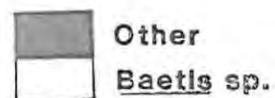
B

FISH



C

INSECTS



D

CRUSTACEANS

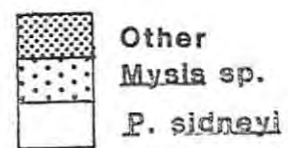


Figure 33. The percent contribution of the major prey classes (A), fish species (B), insect groups (C) and crustaceans (D) to the diet of *S. bairdii* based on the IRI.

In order to determine whether S. bainsii "selects" the Baetidae nymphs, a sample of insects was taken from a typical habitat of S. bainsii. On analysis of the sample it was found that 85% of the insects were Baetidae Genus 1 nymphs. This observation suggests that S. bainsii does not "select" particular food items but rather exploits an abundant food supply.

5.3.2 Food preferences of different size classes

The food preferences of S. bainsii of different size classes for the major prey classes based on the "index of relative importance" are presented in Table 15 and Figure 34.

- (i) 20-30 mm SL : Insect nymphs and larvae.
(0+)
- (ii) 40-50 mm SL : Insect nymphs and larvae.
(0+)
- (iii) 60-79 mm SL : Insects and small crustaceans.
(1+)
- (iv) 80-99 mm SL : Insects and crustaceans.
(0+ & 1+)
- (v) 100-119 mm SL : Insects were the dominant prey class. Juvenile
(1+, 2+ & 3+) fish and crustaceans were also taken.
- (vi) 120-139 mm SL : Insects, P. sidneyi and juvenile fish.
(2+, 3+ & 4+)
- (vii) 140-172 mm SL : Insects and P. sidneyi and fish. Fish
(2+, 3+ & 4+) formed a more "important" component of the diet than in all the other size classes.

Insect larvae (Ceratopogonidae) were the most "important" prey item in the size class 20-59 mm SL whereas Baetidae nymphs were the most "important" in the size class 60-172 mm SL.

Table 15. The percentage contribution of the major prey classes to the diet of the different size classes on the basis of the IRI.

Size class(mm)	% IRI		
	Insecta	Crustacea	Pisces
20-39	100	0	0
40-59	100	0	0
60-79	81	19	0
80-99	63.4	33.7	0
100-119	65.8	11.6	22.6
120-139	73.9	12.5	13.5
140-172	36.7	36.9	26.5

5.3.3 Food preferences during different seasons

The percentage contribution of the three major classes of prey to the diet of S. bairnsii based on the IRI during different seasons is presented in Table 16 and Figure 35. Insects were the most important prey group contributing more than 80% of the total prey during all four seasons. Fish and crustaceans were taken in low proportions throughout the year. The highest intake of fish was in Spring and Summer whereas that of crustaceans was in Autumn.

Table 16. The seasonal percentage contribution of the three major prey classes to the diet during the four seasons based on the IRI.

Prey class	Summer	Autumn	Winter	Spring
Insecta	92.3	88.3	97.0	92.6
Crustacea	3.0	11.7	0.5	1.7
Fish	4.7	0.1	2.5	5.7

5.3.4 Prey diversity and numbers

A total of 25 different prey species/groups comprised the diet of S.

bainsii. Individual stomachs, however, never contained more than 3 different food species or group.

The monthly change in prey diversity in all stomachs and the number of prey per stomach are shown in Figure 36. Prey diversity was highest in March/April and October/November and lowest in June/July. The periods of high prey diversity coincide with the warm rainy season whereas the period of low prey diversity coincides with the cold dry season (Figure 5). A similar trend was observed on analysis of the monthly changes in the number of prey items per stomach.

S. bainsii occasionally consumed large numbers of a single prey item. For example one fish had consumed 80 Ceratopogonidae larvae and another 53 Baetidae nymphs. These examples indicate concentrated feeding. This ability is of value because it enables S. bainsii to exploit a transitory but abundant food supply. This ability is confirmed by an observation in November 1983, a day after heavy rains when a large number of terrestrial flying termites (Macrotermes sp.) were seen drifting in the water. On examination of stomach contents of fish caught at that locality, two fish had consumed 30 Macrotermes sp. to satiation. That this food item was transitory is confirmed by the fact that the Macrotermes sp. was never encountered again in the stomach contents of S. bainsii during the course of this study.

5.3.5 Calorific content of food

The results of preliminary studies of the calorific content of some of the prey items of S. bainsii are given below :

Baetidae nymphs	18.654 j/g
<u>B. trevelyani</u>	19.036 j/g
<u>T. sparrmanii</u>	15.317 j/g
<u>P. sidneyi</u>	8.387 j/g

These values are comparable to the values obtained by Warren & Davies (1968) for similar organisms. The most important prey group in the diet of S. bainsii has a high calorific content.

5.3.6 Stomach fullness index

Stomach fullness indices can give an insight into the intensity and periodicity of feeding (Popova 1967). The changes in the monthly mean values of the stomach fullness index are shown in Figure 37. The monthly stomach fullness indices of both juveniles and adults fluctuated but show a peak in summer and a trough in winter. The summer peak probably reflects a period of intense feeding activity as a result of higher water temperatures and the trough in winter, low feeding activity due to low water temperature. Generally the feeding intensity of adults is not high, and with the exception of fish caught in November-January, stomachs were less than half-full (Figure 37). Juvenile fish on the other hand had higher and relatively constant stomach fullness indices.

5.3.7 Condition factor

The changes in the monthly mean condition factor of both sexes combined is shown in Figure 38 and that of males and females separately is shown in Figure 39. From Figure 38 it is clear that the condition factor of S. bainsii is low in winter over the period June-July and increases thereafter remaining high during the main breeding season (October-February) reaching a peak in March. This pattern is similar to that of the males, whose condition factor, in addition to the peak in March reaches another in October. The condition factor of females on the other hand is relatively low at the beginning of the breeding season and increases thereafter reaching a peak also in March. Ripe females with high gonosomatic indices have low condition factors early in the breeding season (October) whereas those with recovering ovaries have higher condition factors.

5.3.8 Competition for food

The percentage frequency of occurrence of the different food items in the stomachs of various predators in the Tyume river is shown in Table 17. The food analysis studies were primarily directed at S. bainsii with the result that the samples of the other predators were not sufficient to allow application of statistical tests to determine the degree of similarity or dissimilarity with the food of S. bainsii.

Nonetheless the following points emerge from the data :

- (i) S. bairnsii was the only indigenous species that consumed fish.
All the alien species consumed fish.
- (ii) Baetidae nymphs were taken by most predators (6 out of 7)
and were the most common food item in 6 out of 7.
- (iii) Baetidae nymphs which were the most "important" food item in the
diet of S. bairnsii were the most common food item in two out
of three alien species and in one out of three indigenous species.

Table 17. The frequency of occurrence of the different food items in the stomachs of the various predators in the Tyume river.

Food item	Frequency of occurrence in the stomachs						
	<u>S.</u> <u>bairnsii</u>	<u>S.</u> <u>gairdneri</u>	<u>M.</u> <u>salmoides</u>	<u>T.</u> <u>sparmanii</u>	<u>B.</u> <u>trevelyani</u>	<u>A.</u> <u>mossambica</u>	<u>L.</u> <u>macrochirus</u>
<u>B. trevelyani</u>	1.64	20		-	-	-	-
<u>T. sparmanii</u>	2.63		8.33				25
<u>L. macrochirus</u>	0.65	-	-	-	-	-	-
<u>S. bairnsii</u>	0.98						
<u>P. sidneyi</u>	9.21		16.67	-	-	75	-
Baetidae	42.76	60	42	12.5	70		25
Notonectidae	6.57	-	25	-	-	50	-
Nemouridae	3.59	-	-	-	-	-	-
Coleoptera	3.61	20	8.33	12.5	-	-	25
Diptera larvae	10.52	60	-	12.5	10	-	50
Odonata	0.32	-	8.33	-	-	-	-
Macrophytes	-	-	-	50	-	-	25
Algae	-	-	-	12.5	-	-	-

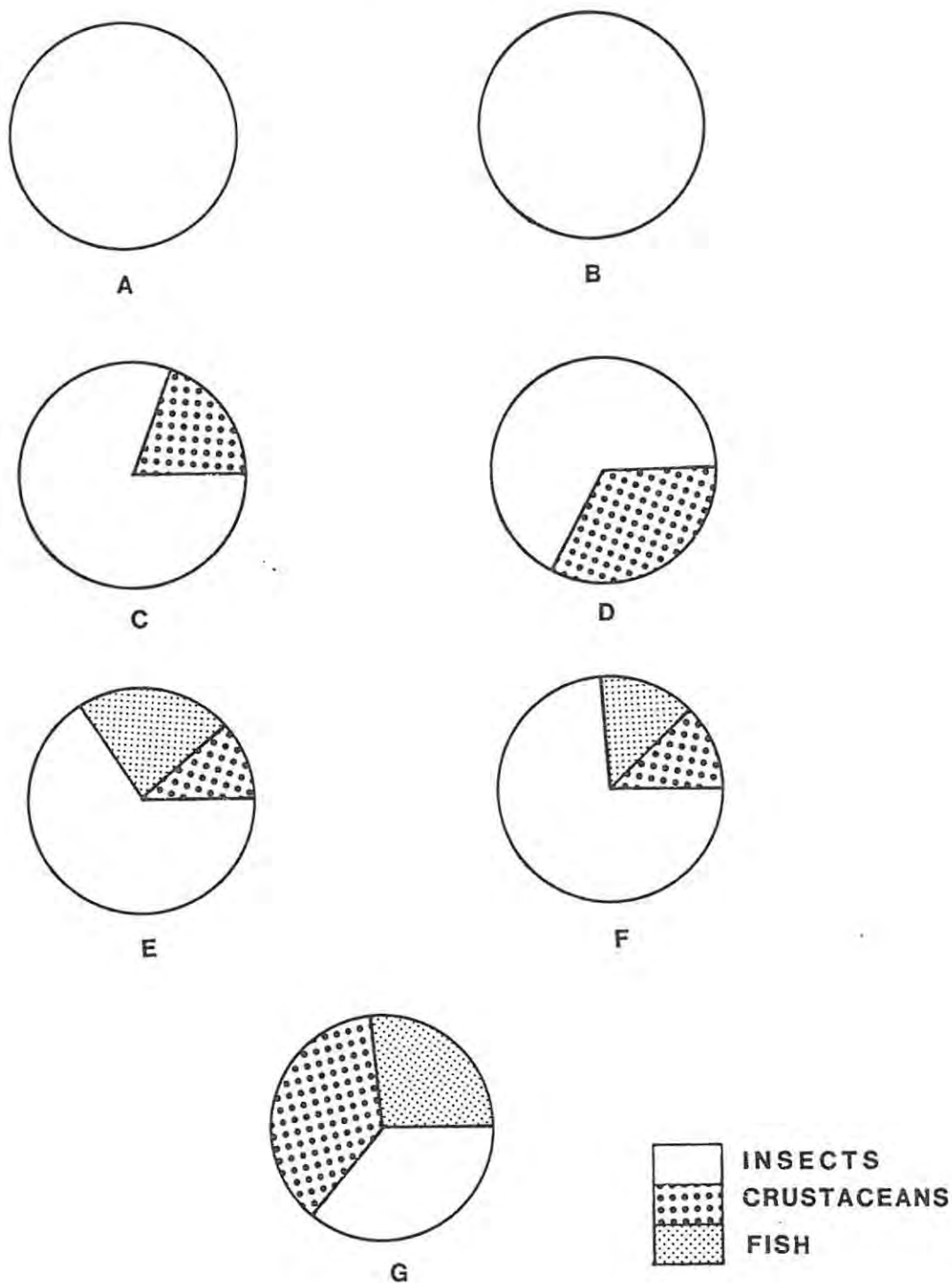


Figure 34. The percent contribution of the three major prey classes to the diet of different size classes of *S. bairdii* based on IRI.

A : 20 - 30 mm
 B : 40 - 59 mm
 C : 60 - 79 mm
 D : 80 - 99 mm

E : 100 - 119 mm
 F : 120 - 139 mm
 G : 140 - 172 mm

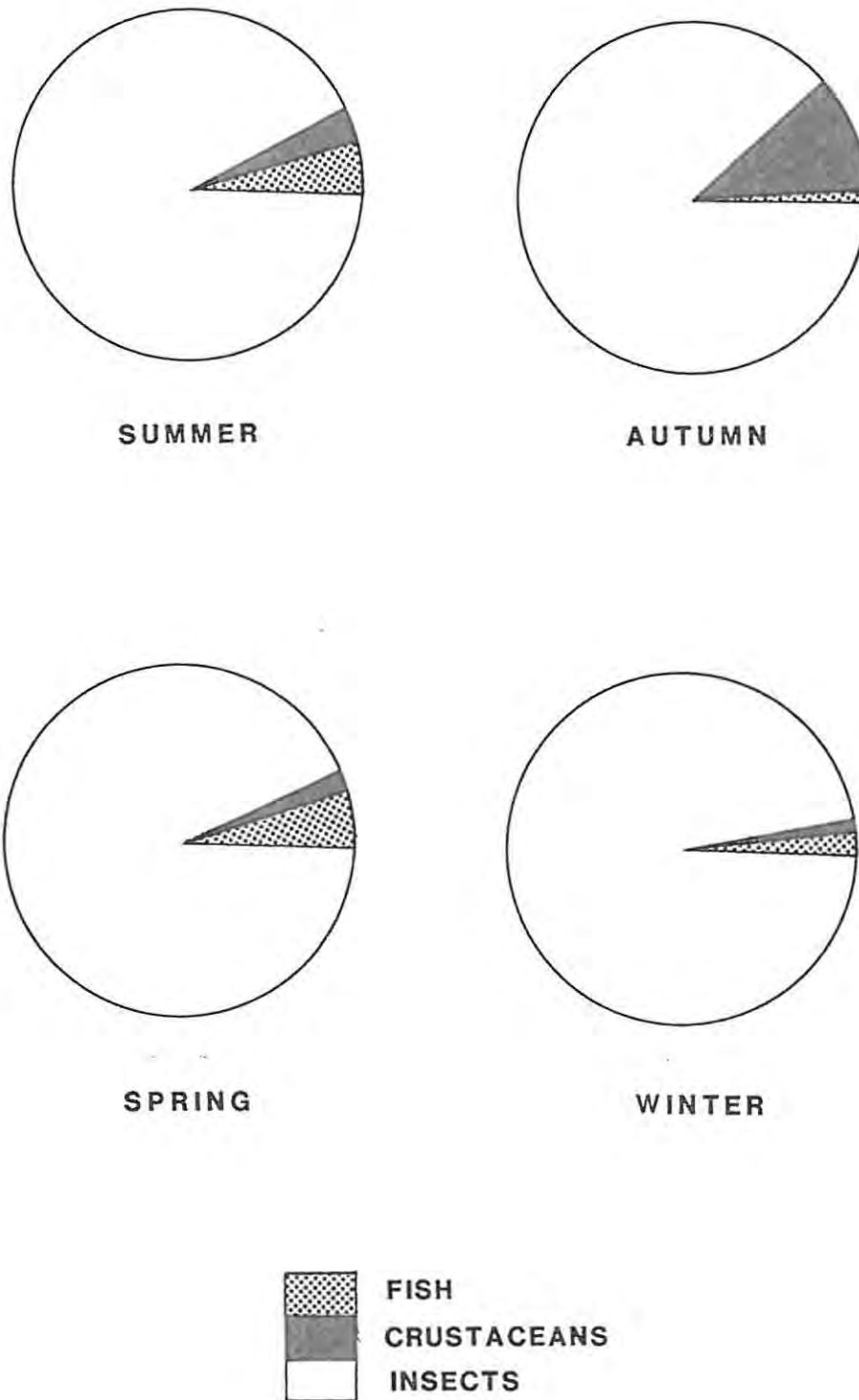


Figure 35. The percent contribution of the three major classes of prey to the diet of *S. bairdii* during different seasons based on the IRI.

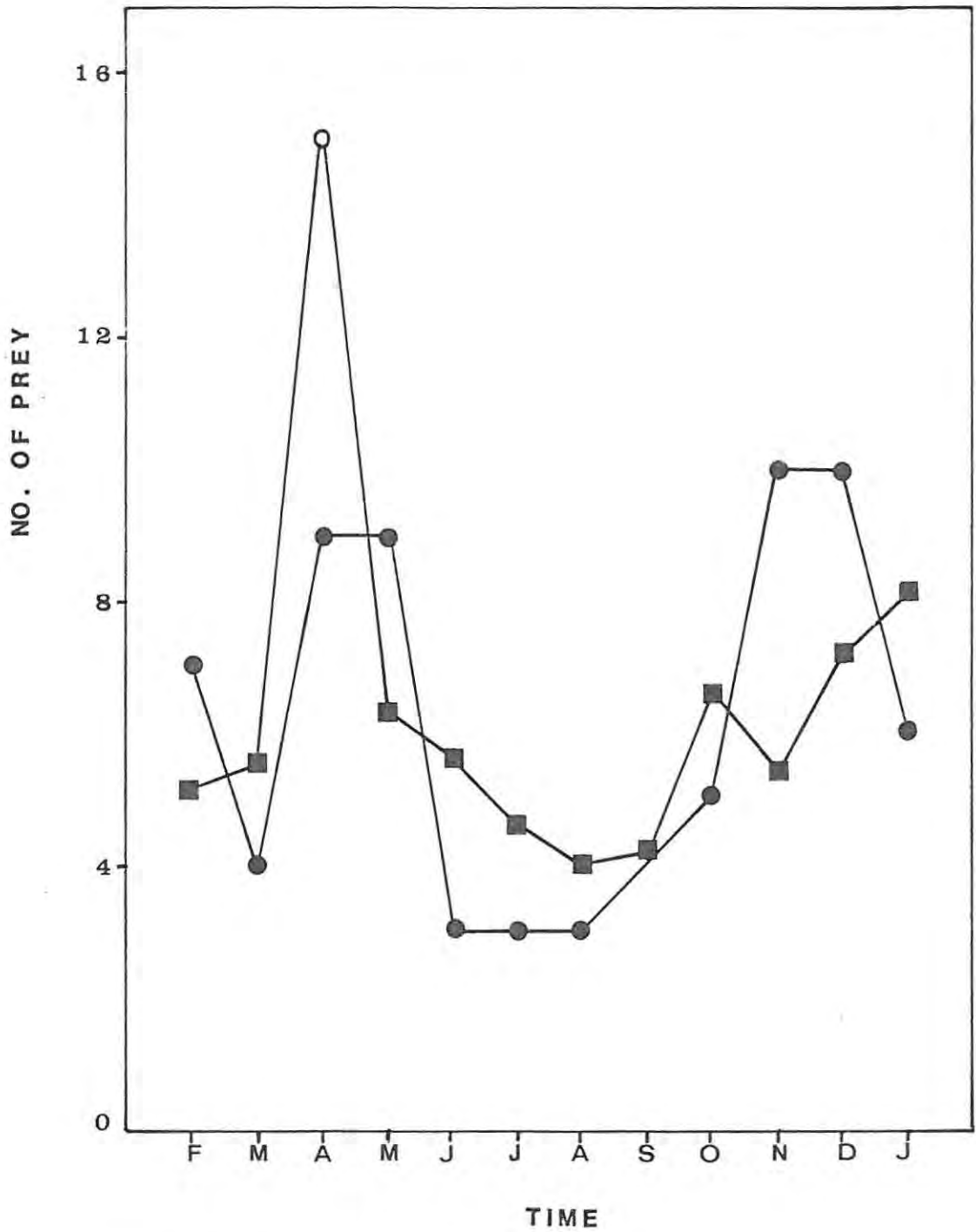


Figure 36. The monthly changes in prey diversity (●) and the monthly change in the number of prey items per stomach (■).

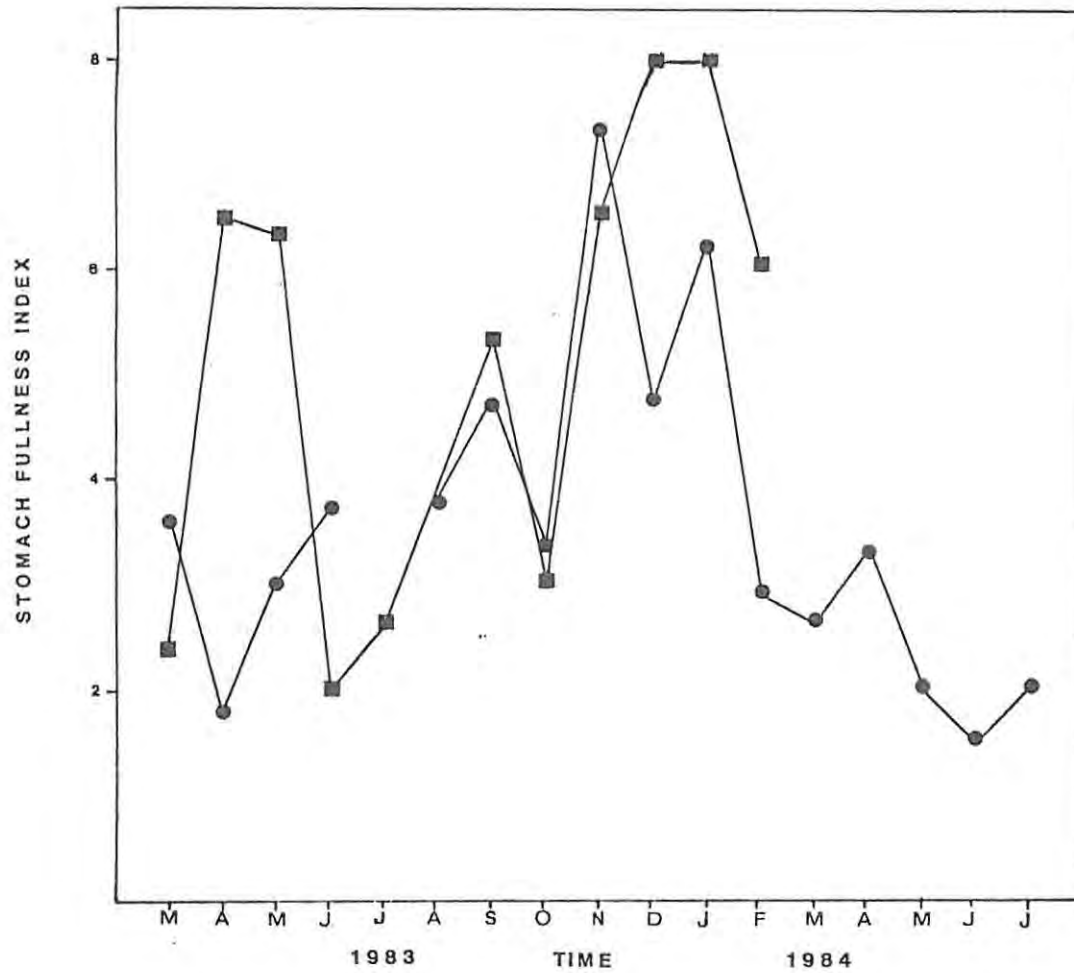


Figure 37. The monthly changes in the mean values of the stomach fullness index of juvenile (■) and adults (●) *S. bairdii*.

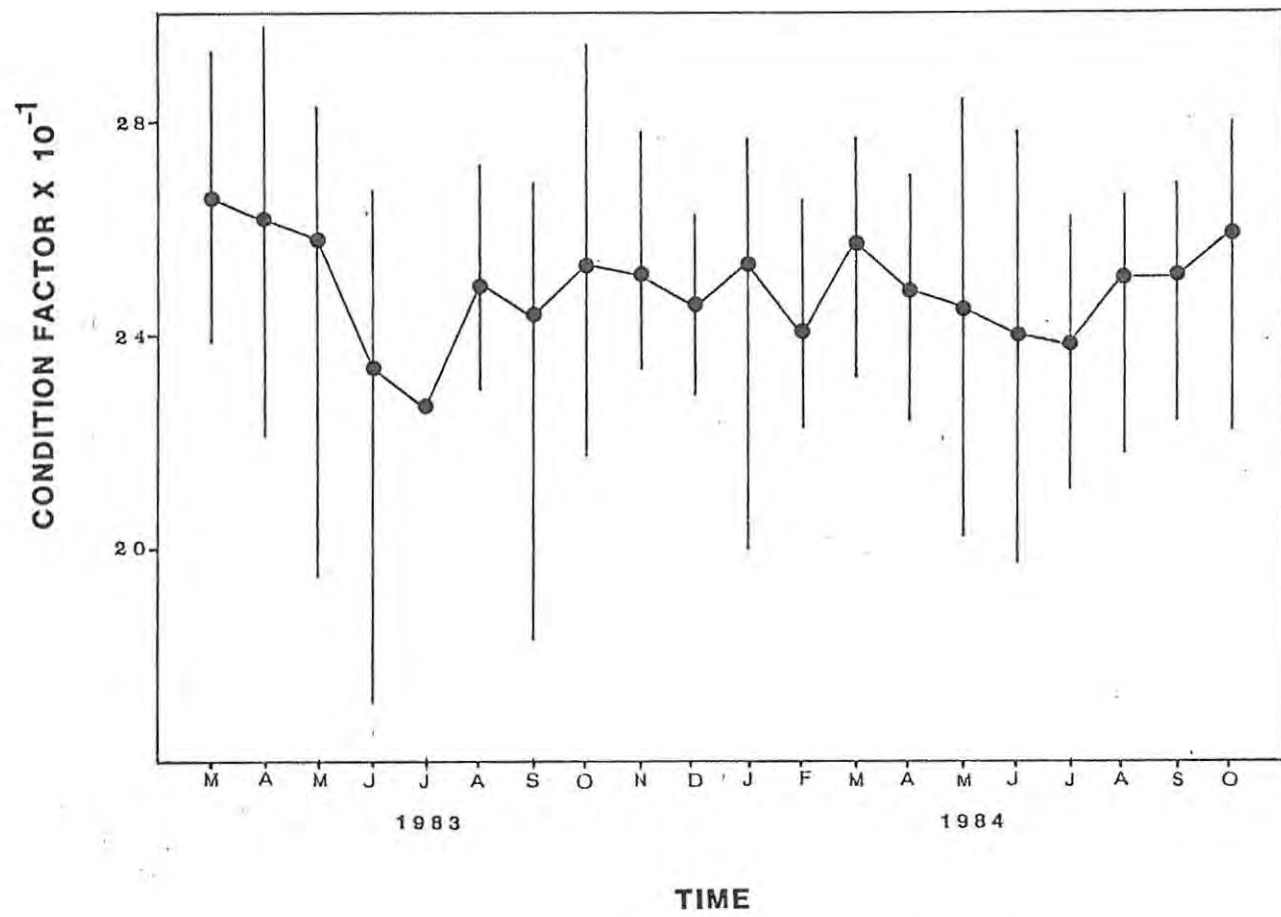


Figure 38. The monthly changes in the condition factor of *S. bainsii* (males and females combined). The data are given as means (●) and ranges (vertical lines).

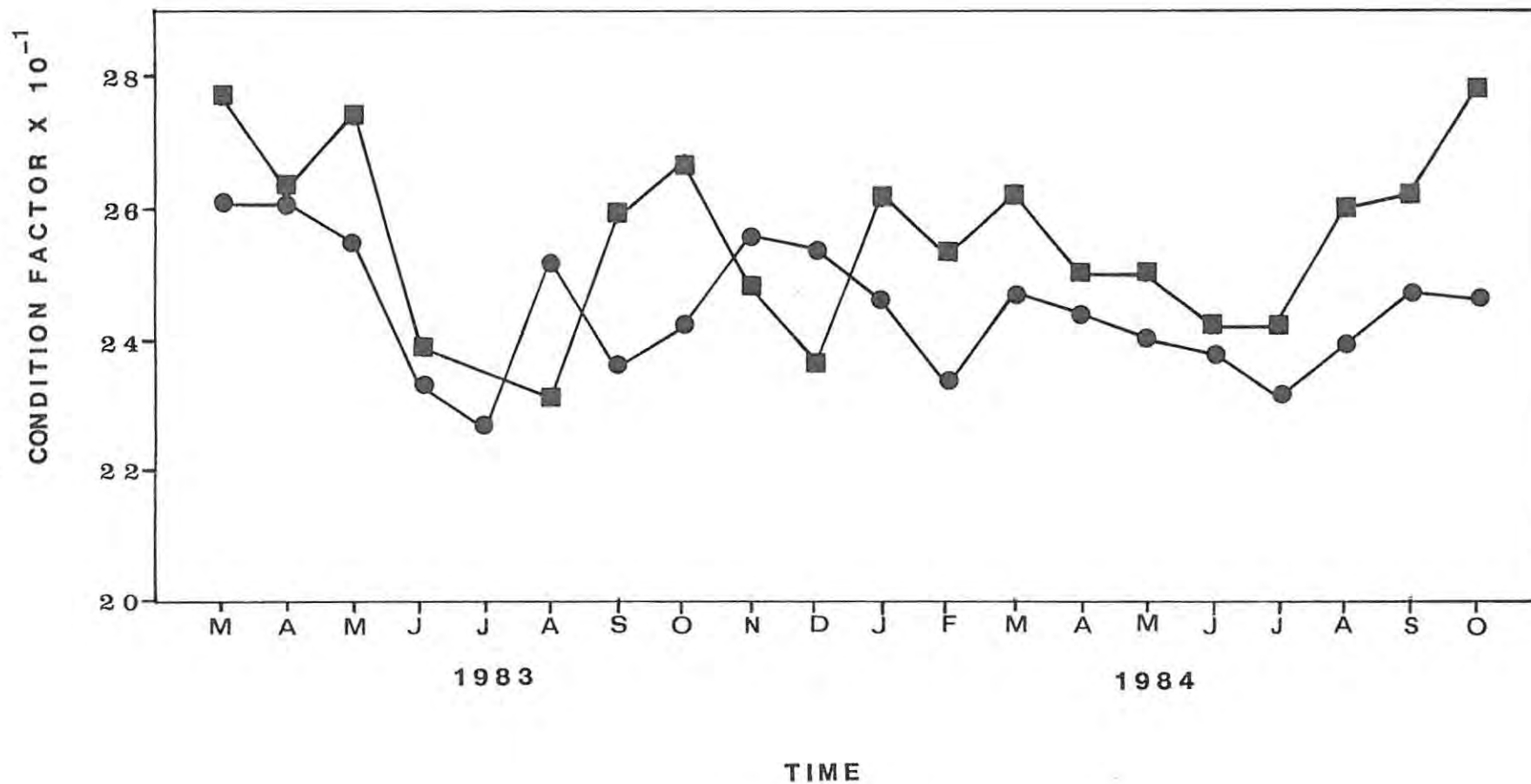


Figure 39. The monthly changes in the mean condition factor of males (■) and females (●) of *S. bairdii*.

5.4 DISCUSSION

S. bainsii is an euryphagous and opportunistic predator which varies its diet according to food availability. Nikolsky (1963) associates euryphagy with unstable feeding conditions resulting from a variable food supply. The diet and feeding habits of S. bainsii are similar to those of the other anabantids described by Siegfried (1963), Bruton (1979a), Singh & Samuel (1981). Results obtained in this study also indicate that S. bainsii does not "select" particular food items but exploits an abundant food supply (see pg. 85) on a seasonal basis.

S. bainsii less than 59 mm SL are insectivorous. Those in the length range 60-129 mm SL have a diet that is largely insectivorous but crustaceans and fish are occasionally taken. The relative importance of insects decreases, however, in fish in the length range 130-172 mm SL, with crustaceans (P. sidneyi) and fishes becoming more important. The change in the composition of the diet discussed above reflects an ability to take larger food as the fish increase in size. Intraspecific competition is therefore reduced by virtue of the fact that different size classes rely on different food categories.

The most "important" food item in the diet of S. bainsii in the Tyume river was the Baetidae which are relatively small insects with a high calorific content. In the majority of predators, the number of food items found together in the stomach usually decreases as the fish grows, while the relative size of the separate food objects increases because the amount of energy expended on the capture of numerous small prey may exceed their calorific value (Nikolsky 1963). A similar result was found by Bruton (1979b) in Clarias gariepinus in Lake Sibaya. It seems reasonable, however, to assume that a relatively large predator like S. bainsii may benefit from taking small prey if that prey is abundant and has a high calorific content.

The high stomach fullness indices observed during the summer months probably reflect increased prey diversity and density brought about by increased temperature and rainfall. An increase in temperature results in increased food consumption and hence growth (Allen & Wootton 1982). This period coincides with the formation of the scale annulus, the

deposition of the opaque zone on the otolith as well as the beginning of the breeding season.

The condition factor of S. bainsii is low during the winter months but increases thereafter and seems to be related and influenced by the same environmental factors as the stomach fullness index. High condition factors in females are attained after breeding slightly later than in males. This can be explained in terms of the larger energy investment of females in gonadal tissue than males. Termination of breeding permits re-allocation of resources which previously went to gonad development to somatic growth (Wootton 1982), hence the improvement of the condition after breeding and the concomitant deposition of the opaque zone on the otolith.

A comparison of the diets of the predators in the Tyume river presented in Table 17, shows that there is a greater overlap in the diet of S. bainsii with that of the two alien species, S. gairdneri and M. salmoides, compared to the indigenous species. More extensive sampling of the stomach contents of the aliens would have yielded more shared food items. According to Johnson (1977) where a dietary overlap occurs such that the frequency of occurrence of a food item exceeds 25% in two or more predators, competition is likely. The Baetidae nymphs occurred in 42% of S. bainsii stomachs, in 60% of S. gairdneri and in 42% of M. salmoides. These findings therefore indicate the possibility that there is competition for food between S. bainsii and the two alien species.

The studies of Crass (1963) on the diet and feeding habits of S. gairdneri provide further evidence of trophic similarities between this species and S. bainsii. Crass (1963) found that S. gairdneri is an euryphagous and opportunistic predator that feeds on dragonfly nymphs, mayfly nymphs, crabs and fish.

Their similar diet and feeding habits indicate that S. bainsii and S. gairdneri probably occupy the same trophic level. The mountain stream environment in which the two species co-exist is nutrient poor or oligotrophic with a low carrying capacity (Gaigher et al 1980). The scarcity of resources in this environment is likely to enhance the likelihood of competition.

The diet of trout in the Cape Province and Natal is similar to the diet of trout in other parts of the world (Allen 1961, Frost & Brown 1967). The reason for this is that aquatic life in mountain streams has a general similarity whether they are American, European or African (Crass 1963). It is therefore surprising that S. gairdneri was introduced without any apparent consideration of possible deleterious competitive (and other) effects on indigenous species.

The second alien species, M. salmoides, also has a diet and feeding habit similar to that of S. bairdii. It is an opportunistic predator and smaller bass feed on small crustaceans and insects while fish, crabs and frogs form their staple diet as they grow older. Large bass feed exclusively on fish (Crass 1963). There is thus a strong possibility of competition for food with S. bairdii, at least in the smaller size classes (<120 mm).

As mentioned in Chapter 1, the Anabantidae is the most primitive of the anabantoid families. Liem (1963) considers the predatory mode of feeding as the most primitive in the Anabantoidei and identifies the following gradual changes correlated with changing feeding habits in the suborder :

- (i) increase in protrusibility of the jaws;
- (ii) reduction in the dentition of the parasphenoid;
- (iii) increase in the number and change in the form of gill rakers.

These evolutionary changes are shown in Figure 40. The progressive changes shown in Figure 40 are correlated with diet : the Anabantidae are predatory, the Belontiidae are omnivorous, the Helostomatidae are plankton feeders and the Osphronemidae are herbivorous. The findings of this study on S. bairdii show that the species has retained the ancestral and predatory feeding mode.

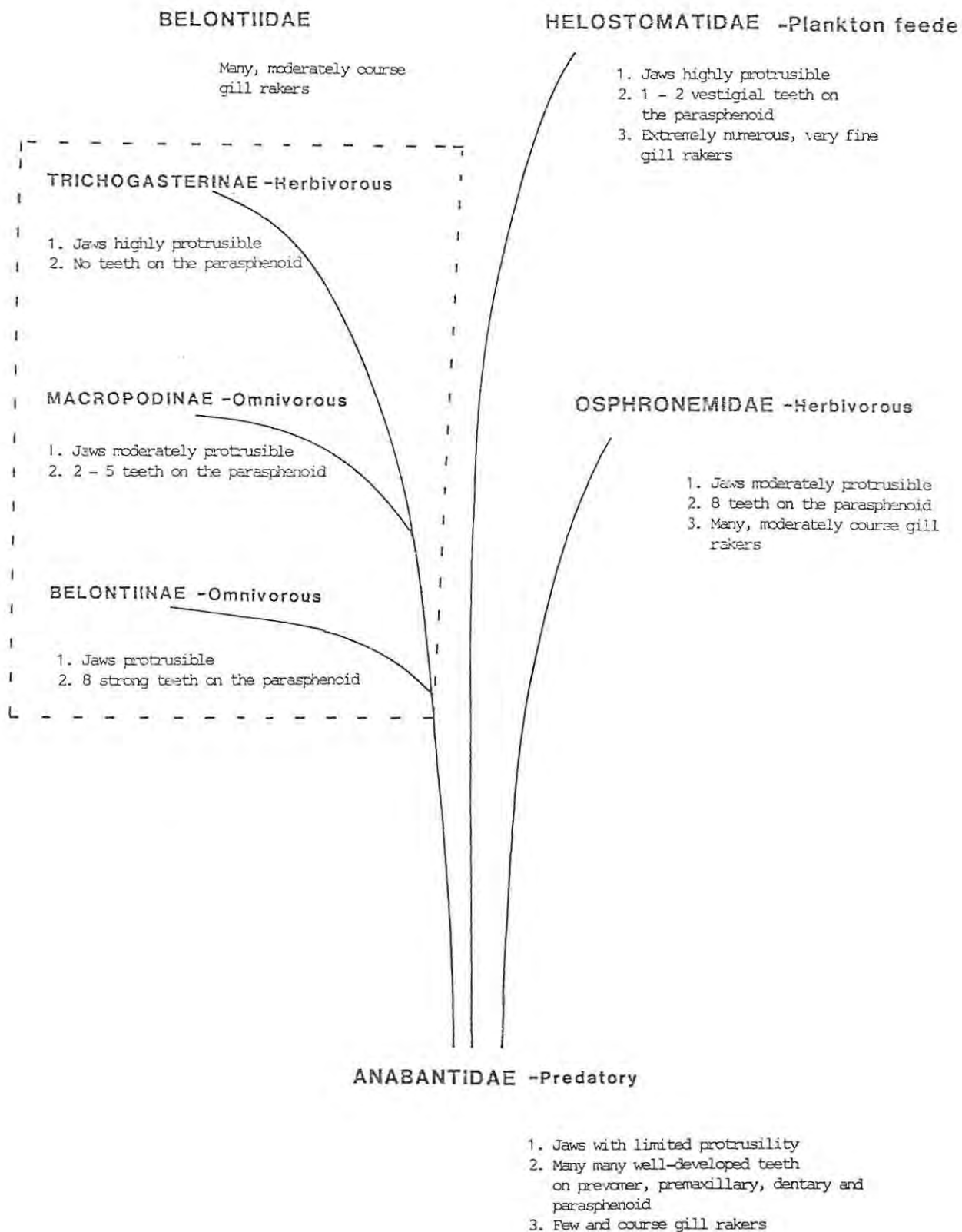


Figure 40. The evolutionary changes correlated with changing feeding habits in the Anabantoidei (after Liem 1963).

CHAPTER 6

REPRODUCTIVE BIOLOGY

6.1 INTRODUCTION

The success of any fish species is ultimately determined by the ability of its members to reproduce successfully in a fluctuating environment and thereby to maintain viable populations. Since each fish species occurs under a unique set of ecological conditions, it has a unique reproductive strategy with special adaptations (Moyle & Cech 1982).

The first objective of the study of the reproductive biology of S. bainsii was to understand the styles that the species has evolved in the eastern Cape in an environment which, according to Heydorn & Grindley (1982), has an erratic river flow owing to the frequent droughts. The second objective was to relate the data on reproductive strategies to other aspects of the natural history of the species in order to obtain a composite view of its life history strategy. It was also envisaged that an understanding of the reproductive biology of this species (of uncertain conservation status), would perhaps reveal constraints imposed by the environment on its reproductive success. Knowledge of these constraints and their effect on reproductive success would be of value for conservation proposals, as shown by Bok (1983) in the case of Myxus capensis.

6.2 MATERIALS AND METHODS

6.2.1 Fish capture and laboratory analysis

Specimens were caught at the different sampling stations on a monthly basis. In the laboratory the fish were measured, weighed, sexed, the maturity stages noted, gonads removed and weighed to the nearest 0.01g. The gonads were preserved in 10% formalin and cross-referenced to fish number. The area of the operculum immediately posterior to the eyes was examined to determine the occurrence or absence of contact organs. The colouration of the different sexes was examined for indications of sexual dichromatism.

6.2.2 Gonadal maturation, size at maturity and fecundity

A record of the state of maturity of a fish can be used to determine the proportion of the stock that is mature, or the size or age at first maturity as well as the time and duration of the breeding season (Bagenal & Braum 1968).

The gonads of all fish caught were examined and gonadal maturity stages based on those of Kesteven (1960) allocated (Table 18). The testes showed little macroscopic development during early stages of gonad development (I - III) and these stages were often difficult to distinguish accurately. Analysis of gonadal development was therefore confined to female fish. It is reasonable to assume that for successful spawning the sexual development of male and female fish is synchronized (Scott 1979).

The reproductive effort of a fish is a measure of the amount of energy and time invested in reproduction. A rough estimate of this effort, at least among fish that do not provide any parental care, is the gonosomatic index (GSI) (Moyle & Cech 1982). Determination of the changes in GSI during the year also gives information on the periodicity (Honma & Chiba 1982) and the duration of the breeding season. The GSI was calculated using the formula :

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

The size frequency distribution of ova in the ovary can also provide information on the spawning behaviour (whether a total or a multiple spawner) of a fish (Hecht 1980b). This information is important for an understanding of the life history style.

To determine the size frequency distribution of ova of S. bainsii, random subsamples of approximately 500 ova from nine fish were measured with a micrometer eye-piece to 0.01 mm and the ova belonging to different size classes counted. Six of the fish were caught in October 1983, two in December 1983 and one in January 1984. The ovaries of all the fish were in Stage V of development and exhibited the highest GSI values during the three months.

The length at sexual maturity was established by macroscopic examination of the gonads after identifying the six stages of gonadal activity. To eliminate possible bias these data were collected during the peak period of gonadal activity to avoid the masking effect of fish with gonads in the recovering stage (Bok 1983). Fishes with gonads in Stages I and II were regarded as immature, and those with gonads in Stages III to VI were considered to be sexually mature.

Fecundity refers to the number of eggs maturing in the ovary of a female fish prior to spawning (Bagenal & Braum 1968) and is a measure of the reproductive potential of a fish.

To determine the absolute fecundity (Bagenal & Braum 1968) of S. bainsii, ovaries of 11 fish (66-134 mm SL) in Stage V were preserved in Gilson's fluid for at least three months to facilitate hardening of the ova and separation from the ovarian tissue. After three months the ova were separated from the ovarian tissue and rinsed repeatedly in tap water. The ova were dried for 15 hours in an oven at 40°C. Three subsamples of over 200 ova were counted and weighed to the nearest 0.00001g. The total number of eggs per fish was calculated by proportion for each subsample. The final fecundity was calculated as the mean of the replicate subsamples.

6.2.3 Migration

S. bainsii belongs to the primary division of fish (Darlington 1957, Hoffmeyer 1966). Any migration that this species undertakes would be of a potamodromous nature (Myers 1949) ie, migrating "wholly within freshwater". The most common and critical migration in the life cycle of a potamodromous fish is the upstream migration to the spawning grounds and migration downstream to the feeding grounds (Harden-Jones 1968). According to Harden-Jones (1968) this pattern has the following advantages : it greatly increases the probability of larval stages finding their way to the proper habitats, it reduces the likelihood of intraspecific competition for food among the different age classes, and it reduces the probability of cannibalism.

The potential detrimental effect of dam walls and weirs on migration of

freshwater fishes of the eastern Cape is well-documented (Gaigher *et al* 1979, Skelton 1983, Bok 1983). In order to determine whether obstacles to migration were responsible for the reported decline in the numbers of S. bainsii in the Tyume river, a tagging programme was started in February 1984 to determine whether S. bainsii undertakes spawning migrations.

Plastic anchor tags (Floy FD-67C) and a Mark 11 Pistol grip tagging gun were used to tag fish. The tags were inserted into the dorsal musculature between the pterygiophores, posterior to the spiny section of the dorsal fin. The position of the tag on the fish is shown in Figure 41.

In order to monitor tag loss and tag induced mortality 36 fish were brought to the laboratory where they were tagged and kept in aquaria (1350 X 750 X 1250 cm deep). In the field 375 fishes were captured, measured, tagged and released during February 1984. The standard length of the fishes was measured whereupon they were returned to the water. In addition to the routine sampling programme a more intensive sampling programme was undertaken at the beginning of the breeding season (October 1984). The section of the river between the lower limit of station 3 and station 2 (see Figure 14) were sampled thoroughly for tagged fish. A total of 126 fish had been tagged and released at these stations. This section of the river was selected because it has no man-made barriers to fish migration such as weirs.

6.3 RESULTS

6.3.1 Gonadal maturation length at maturity and fecundity

The monthly changes in the mean gonadal maturity values are shown in Figure 42. In general, gonads of S. bainsii are in the resting stage during March, April, May and June and begin maturing in August and September. The bulk of the population is ripe from October to February. The latter period coincides with the rainy season (Figure 5) and increased water temperatures (Table 2).

The monthly changes in the mean gonosomatic index are shown in Figure

43. The gonosomatic index is low from March to August increasing sharply in September, reaching a peak in October and decreasing thereafter. This pattern is generally similar to the one shown in Figure 42.

A comparison of Figure 42 and Figure 43 shows that although the GSI values are relatively low in December, January, and February, the fish still have ripe ova and thus the gonads retain the same maturity status as the gonads of fish caught in October which have higher GSI values. This suggests that either the gonads of some fish mature late in the breeding season or the fish spawn repeatedly over a long period.

The size frequency distribution of ova of 9 fish caught during the breeding season is shown in Figure 44. The following points emerge :

- (i) there are up to six different size classes of eggs in one ovary prior to spawning. The difference between the size classes is significant (Chi Square Test, $\chi^2 = 606.32 >$ critical value 21.026 at 5% level of significance and with 12 degrees of freedom).
- (ii) the ova reach a maximum size with a diameter of between 0.99 mm and 1.24 mm;
- (iii) the fish with the highest GSI values have the majority of their ova in the 0.99 mm - 1.24 mm diameter range;
- (iv) the fish caught in December and January with lower GSI values have a large proportion of their ova in the diameter range 0.74 - 0.99 mm.

The monthly changes in the mean of the gonadal maturity values, the monthly changes in the GSI and the size frequency distribution of ova during the breeding season suggest that S. bairdii spawns repeatedly. The ova are released when their wet diameter is in the 0.99 - 1.24 mm range. It appears that the first spawning is followed by a period during which some of the remaining ova in the ovary increase in size (mature). During this period the GSI value is lower than before the first spawning. As soon as the ova attain the mature size and conditions are favourable, another batch of ova is probably spawned. The repeated spawning is probably responsible for the observed near continuous recruitment in this species.

The length at sexual maturity of males and females is shown in Figure 45. Females attain 50% sexual maturity at lengths between 60 and 69 mm. Males on the other hand attain 50% maturity at lengths between 80 and 89 mm. Forty percent of the males are, however, already mature at lengths between 70 and 79 mm. Reference to Figure 18 in Chapter 3 will show that the modal length of females and males is 70 - 79 mm and 80 - 89 mm respectively which means that a large proportion of the fishes at any given time are sexually mature and thus contribute to population fecundity. Reference to Table 10 in Chapter 4 will show that both males and females become sexually mature during their second summer.

The fecundity of S. bainsii is related exponentially to standard length (Figure 46) as is typical in fish (Bagenal 1973). The line of best fit for the sample of 11 S. bainsii is described by the expression :

$$y = 10 \times 9.45^{SL} \quad (r^2 = 0.87 \quad p < 0.005)$$

where y = absolute fecundity

6.3.2 Sexual dimorphism

Sexual dimorphism based on the occurrence of contact organs was observed in S. bainsii. The contact organs in S. bainsii, as is the case with other anabantids, consist of groups of scales which have only a few long ctenii (Peters 1976) unlike ordinary ctenoid scales which have many fine spikes (ctenii).

The frequency of occurrence of contact organs in different size classes is shown in Figure 47. Females caught during the course of this study did not have contact organs. Contact organs are rare in females occurring only in large females (185-190 mm total length) (Cambray 1980). Males less than 70 mm SL did not have contact organs. Larger males had contact organs in varying frequencies depending on size : 13% in the 70 - 79 mm SL class, 68% in the 80 - 89 mm SL class and in all males whose length exceeded 90 mm SL. The development of contact organs seems to coincide with the attainment of sexual maturity (see Figures 45 & 47). From these data it is clear that the occurrence of contact organs can be used to differentiate between sexes only in the size range 90 - 179 mm SL.

Table 18. Gonadal maturity stages of male and female of S. bainsii as modified from Kesteven (1960).

Stage I Immature virgin

Ovaries and testes small, colourless to grey. The gonosomatic index (GSI) of females : < 1.0 .

Stage II Developing virgin

Ovaries and testes translucent, grey-red. Ova invisible to the naked eye but visible at 20X magnification. GSI of females ranges from 1.0 - 1.8 .

Stage III Developing

Testes opaque. Ovaries opaque, orange-red, with conspicuous blood capillaries : granular whitish ova visible to the naked eye. GSI of females ranges from 1.8 - 2.5 .

Stage IV Developing

Testes and ovaries occupy most of the body cavity. Testes reddish-white, no milt drops appear under pressure. Ovaries orange and ova opaque. GSI of females ranges from 2.5 - 6.5 .

Stage V Gravid

Gonads fill the body cavity : females have a distended body cavity. Testes white, drops of milt exuded with pressure. Ova completely round, some already translucent and ripe. GSI of females range from 6.5 - 15.9 .

Stage VI Spawning

Roe and milt run with slight pressure. Most ova translucent. GSI of females ranges from 12.0 to 15.9 .



Figure 41. The position of the tag on S. bairdii.

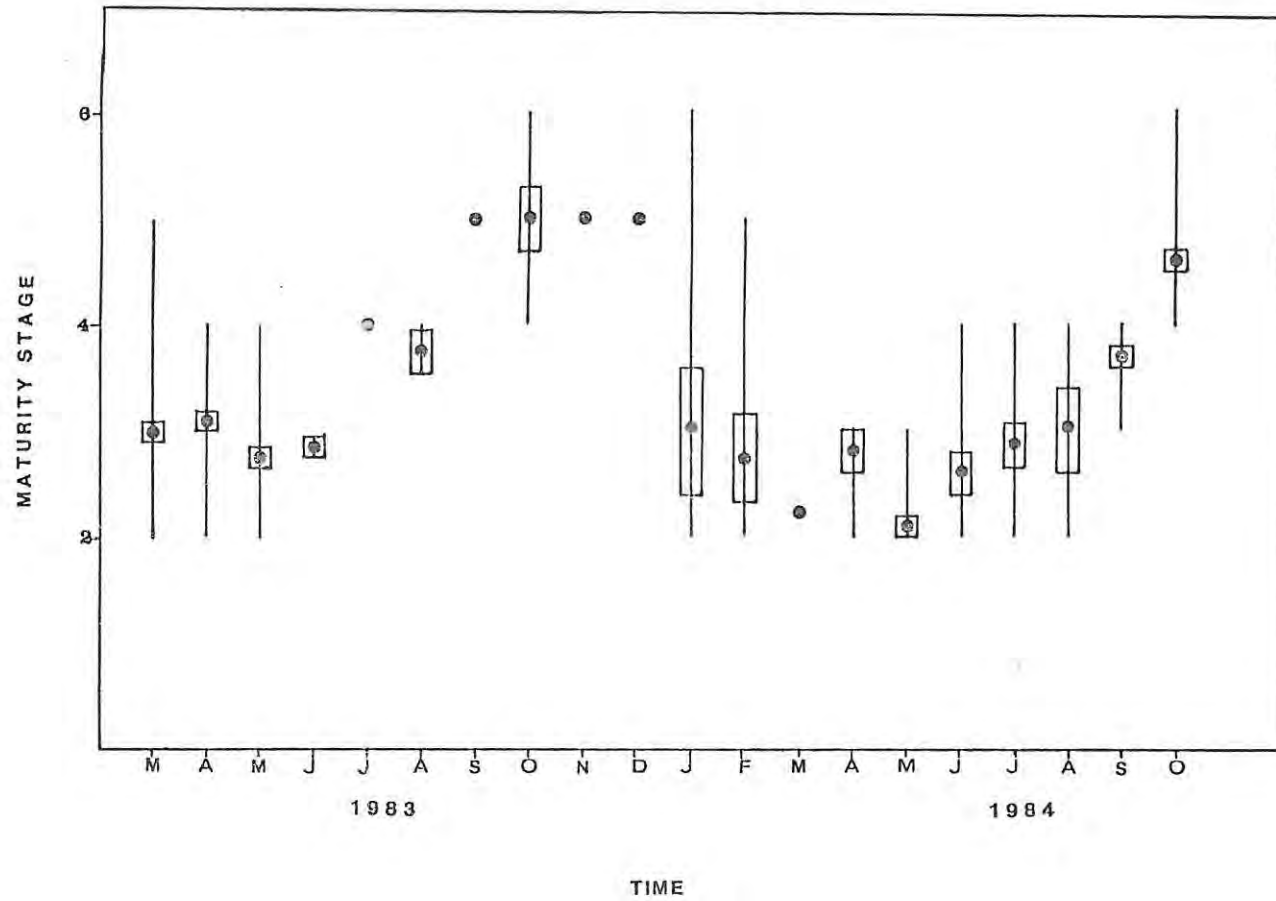


Figure 42. The monthly differences in the maturity values of *S. bairdii*. The data are given as means (●), standard errors (blocks) and ranges (vertical lines).

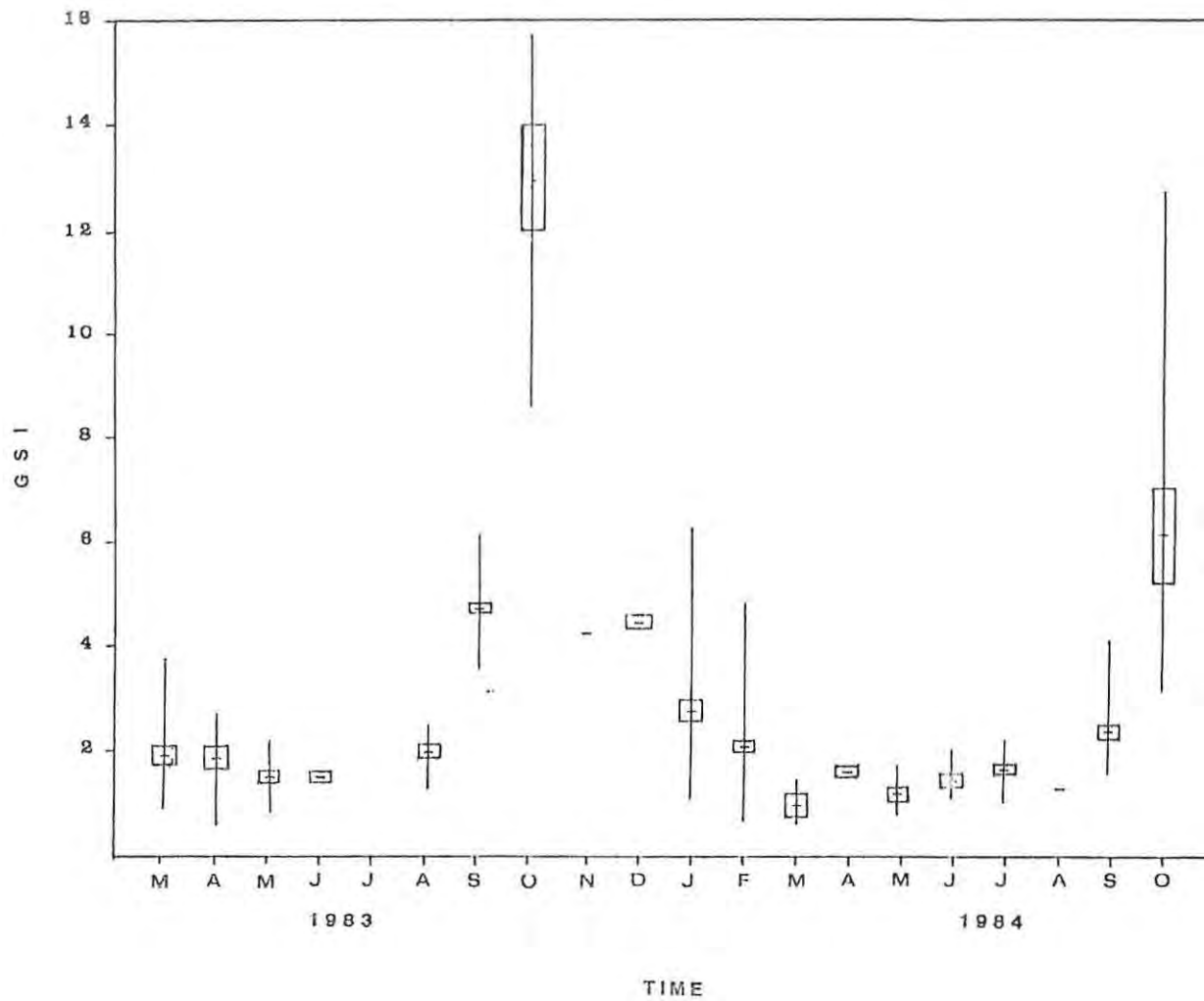


Figure 43. The monthly differences in the gonosomatic index of female *S. bairdii*. The data are given as means (-), standard errors (blocks), and ranges (vertical lines).

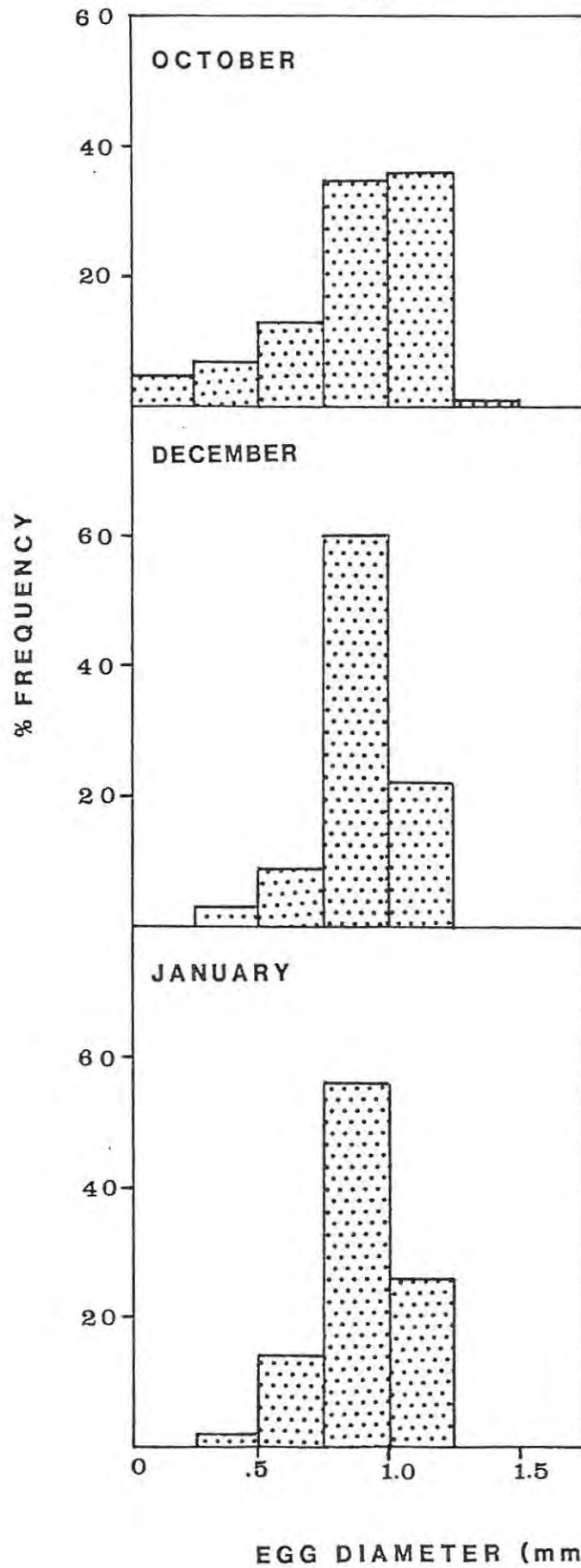


Figure 44. The frequency distribution of egg sizes in ovaries of ripe fish caught in October, December 1983 and January 1984.

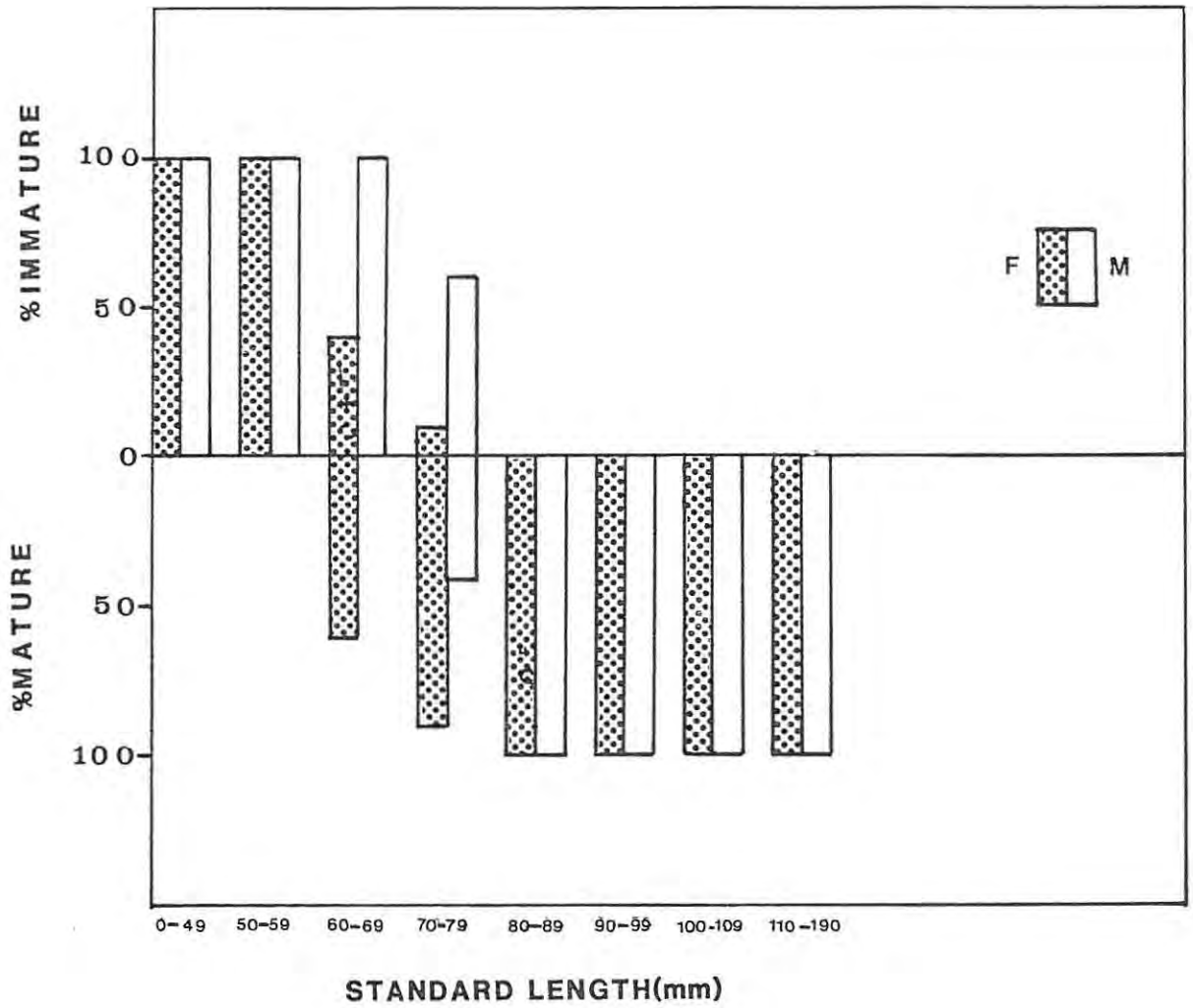


Figure 45. Length at sexual maturity of male and female *S. bairdii*.

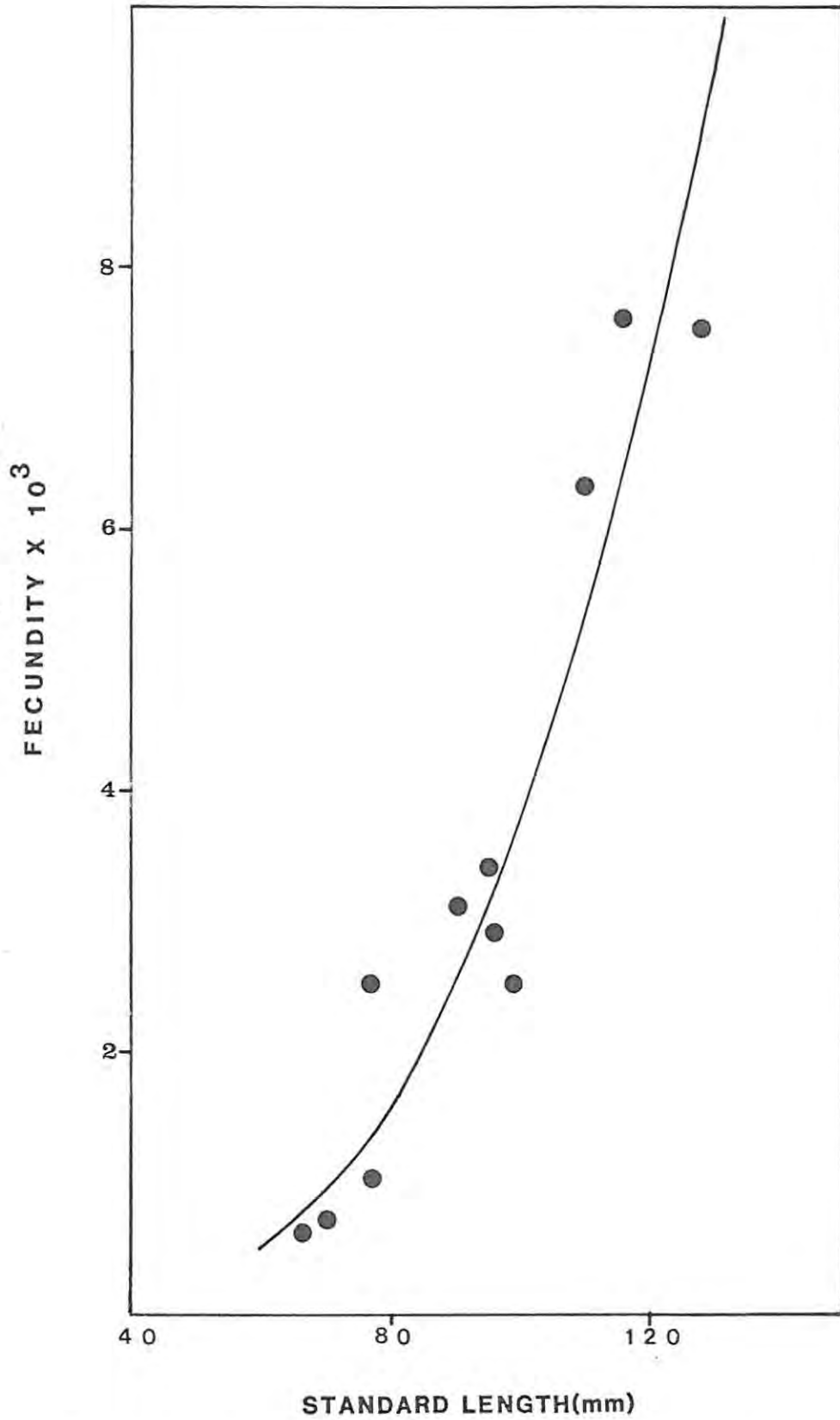


Figure 46. The relationship between absolute fecundity and standard length in *S. bairdii*.

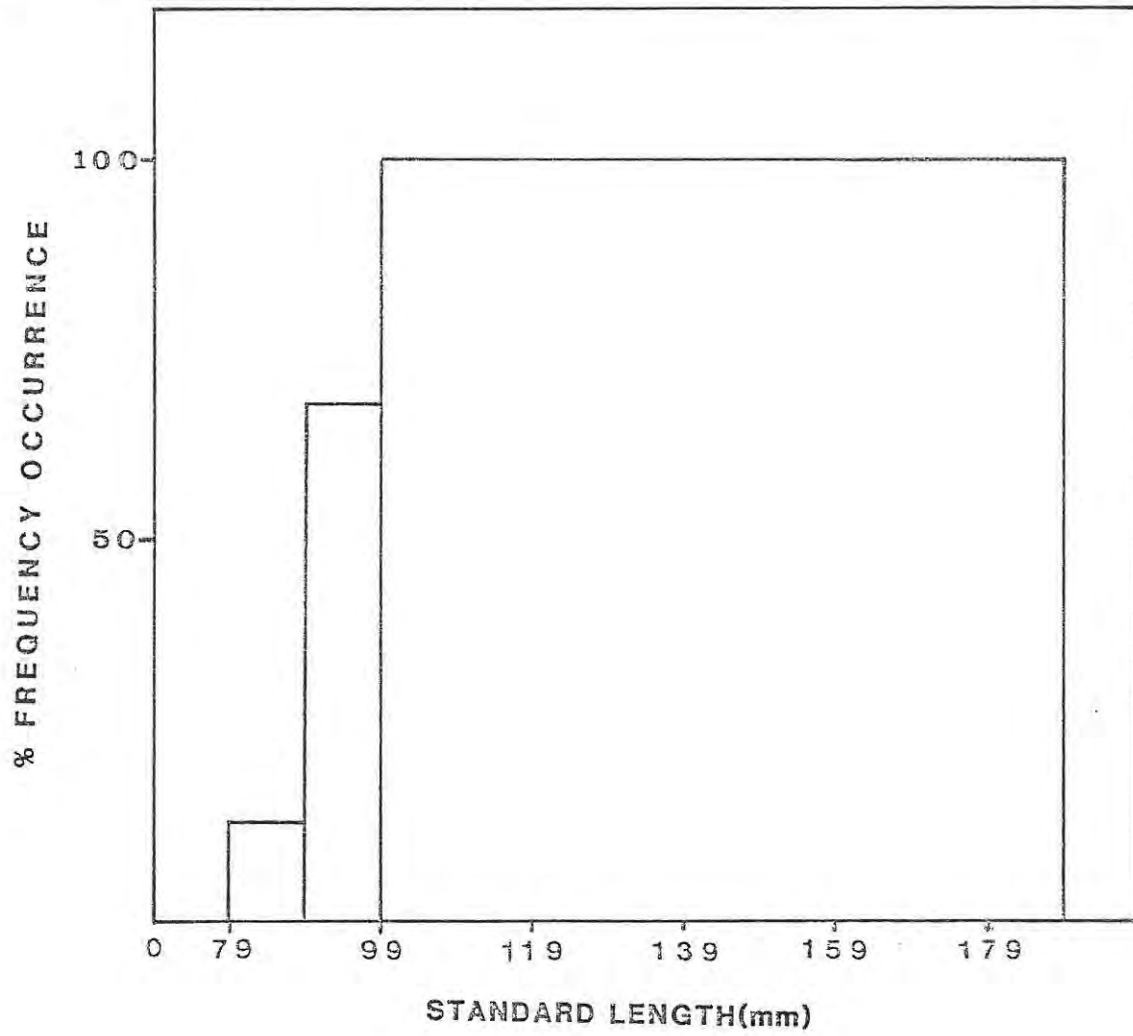


Figure 47. The frequency of occurrence of the anterior contact organs in the different size groups of males of S. bairdii.

Sexual dimorphism was observed in S. bainsii also with respect to general body colouration during the breeding season. The females retain the drab, olive green colour throughout the year whereas males assume an attractive pale light green (or lemon) colour during the breeding season. The tints of orange on the fins were also accentuated during this period. Berns & Peters (1969) associate this form of sexual dimorphism in some African anabantids with territoriality in males.

6.3.3 Migration

Of the 36 S. bainsii that were tagged and maintained in aquaria, 7(19%) had lost their tags and 10(27%) had died after a period of 18 months.

Of the 126 fishes that were tagged at station 2 and 3, twenty fishes (15.8%) were recaptured. All the tagged fish were caught within 95 meters of the place where they were released after tagging. Moreover three of these fishes that were tagged in February 1984 were recaptured twice at the same locality in June and in October 1984. These fishes were sacrificed in October to determine their sex. Two of the fishes were males and the other was a ripe female. These findings suggest that S. bainsii is a "sedentary" species and that none of the sexes undertakes a spawning or feeding migration. This means that S. bainsii is not necessarily affected by man-made obstacles such as dam walls and weirs.

6.4 DISCUSSION

The gonads of S. bainsii mature in Spring (October) at a time of increased water temperature and at the beginning of the rainy season (Figure 5). These two environmental factors also affect food supply. Gonadal development is known to be affected by both temperature and feeding levels in some fish (Richter et al 1982). Feeding levels in S. bainsii, as revealed by the stomach fullness indices (Figure 37) increase during this period, suggesting a relationship between feeding and gonadal maturation.

The results of this study show that S. bainsii spawns mainly over a

period of five months (October - February). The size frequency distribution of ova during the breeding season indicates that S. bainsii is a multiple spawner (Bagenal 1973). According to Lowe-McConnell (1975), production of several batches of eggs must have an advantage if the first batch is at risk. The evolution or retention of the multiple spawning in S. bainsii, as opposed to the total spawning habit characteristic of temperate fish (De Bont 1967), may indicate an important survival strategy in the conditions under which this species lives. A short, well-defined spawning period is associated with a high survival rate of progeny during the particular spawning period (Lowe-McConnell 1975). Multiple spawning, on the other hand, is probably in response to the risk associated with spawning at a particular time. This may be the result if the survival of the eggs and fry is dependent on unpredictable environmental factors. The extended recruitment period of S. bainsii is probably associated with a need for this species to recruit into a harsh and unpredictable environment. The harshness and unpredictability of the environment in which S. bainsii is found arises mainly from the frequent droughts and erratic river flow.

The multiple spawning habit of S. bainsii observed during this study is common in anabantids. Siegfried (1963) observed "incomplete spawning of females of S. capensis at repeated intervals over a prolonged period". Breder & Rosen (1966) also reported that spawning occurs several times a year in A. testudineus. Berns & Peters (1969) observed 73 spawning series over a period of seven months in C. muriei and 7 spawning series over three months in C. damasi.

Anabantids exhibit two types of reproductive behaviour. One group does not show any parental care. This group includes A. testudineus (Breder & Rosen 1966), C. muriei, C. argentoventer, C. kingsleyae and C. oxyrhynchum (Berns & Peters 1969). The other group shows parental care and includes froth nest builders and substrate spawners whose spawn is guarded. This group includes C. ansorgei, C. fasciolatum, C. nanum, C. damasi (Berns & Peters 1969) and S. capensis (Siegfried 1963). It is also of interest that the former group has contact organs whereas the latter group does not have them (Peters 1976).

There are no previous detailed studies on the reproductive behaviour of

S. bainsii. Preliminary aquarium studies indicate that S. bainsii lays demersal eggs that are not guarded (Berns & Peters, personal communication). These findings suggest that S. bainsii belongs to the group that does not take care of its brood.

There are few studies on anabantids that give estimates of fecundity. Chanchal et al (1978) estimated that the fecundity of A. testudineus ranges from 3434 ova (61 mm SL) to 42564 ova (134 mm SL). Albaret (1982) estimated the fecundity of C. kingsleyae at 6390 ova (115 mm SL) SL. Richter (1977) observed that the froth-nest builder C. ansorgei lays up to 400 ova. From these data, it appears that anabantids that show parental care lay fewer ova than those that abandon their broods. Fecundity estimates of S. bainsii caught during this study ranged from 2078 for a fish of 66 mm SL to 10500 eggs for a fish of 134 mm SL (Figure 46). This estimate is lower than that of A. testudineus which lays pelagic eggs but similar to that of the Ctenopoma species that do not guard their spawn.

According to Wootton (1982), the minimum age at first reproduction is genetically determined, although in a few cases it is possible to infer the environmental factors that have led to the evolution of an observed age. Alm (1959) observed that within a population faster growing fish tended to mature at an earlier age than the slower growing fish. Growth rate is susceptible to the effect of environmental factors such as food supply and temperature (Wootton 1982). S. bainsii reaches maturity during its second summer of life. There are no data on age at maturity of other S. bainsii populations nor data on other anabantids to compare with.

CHAPTER 7

FINAL DISCUSSION

The most important threats to the fish in the Tyume river are habitat alteration and introduced species. The introduced species that may threaten the survival of S. bainsii by predation or competition are the two aliens, S. gairdneri and M. salmoides and a recently translocated indigenous species, C. gariepinus. The data on abundance of S. bainsii, however, indicates that the species has not yet been seriously affected by these threats. In spite of this S. bainsii deserves to be included in the list of "vulnerable" species of Skelton (1977) for the following reasons :

- (i) the world-wide distribution of S. bainsii is restricted to a few eastern Cape rivers;
- (ii) the inevitable increase in the human population in the area with the concomitant increase in agricultural activities in the river catchment is likely to increase suspensoid load and siltation which will further reduce clear water rocky habitats preferred by the species;
- (iii) there is a danger that the introduced species may eventually establish themselves in sections of the river where S. bainsii is still abundant resulting in a reduction of its population.

Mark and recapture experiments have shown that S. bainsii is a "sedentary" species which is therefore unlikely to be seriously affected by barriers to migration. Habitat preference data indicate that weirs, which act as silt traps, may benefit S. bainsii by creating suitable habitats below.

The species exhibits sexual dimorphism during the breeding season with males adopting nuptial dress and developing contact organs. Berns & Peters (1969) associate sexual dimorphism in Ctenopoma species with territoriality. The sedentary nature of this species (see section 6.3.3, Chapter 6) may be one of the reasons for the observed euryphagous and opportunistic feeding habit. It seems that S. bainsii, because of its sedentary nature, depends to a large extent on organisms drifting

downstream for food. These organisms are referred to as the "living drift" by Frost & Brown (1967). According to Nikolsky (1969), euryphagy is a characteristic of fish experiencing unstable feeding conditions.

In Winter S. bainsii shows a decline in prey diversity, number of prey items per stomach and in stomach fullness indices (Figures 36 & 37). This can be attributed to low water temperatures which must affect the metabolic rate and feeding intensity. Towards the end of Winter, the condition factor declines, a translucent zone is deposited on the otoliths and the circuli on the scales become closely spaced, the last two being effects of slow growth (Bruton & Allanson 1974, Panella 1974). The rainy season begins in Spring accompanied by an increase in water temperature, prey diversity, number of prey items per stomach and stomach fullness indices, suggesting an increased food supply. During this season the gonads develop rapidly to reach a peak in October, indicating the beginning of the breeding season. During this time the opaque zone is deposited on the otoliths and the circuli on the scales become widely spaced, forming an annulus, suggesting growth acceleration (Bruton & Allanson 1974, Panella 1974). Breeding continues throughout Summer and there is an increase in the condition factor, the size of the opaque zone on the otolith and the number of circuli in the marginal increment of the scales. Autumn marks the end of the rainy season and of the breeding season. The opaque zone on the otoliths has attained maximum size and remains relatively constant until the following Spring. Similarly, the scales show the maximum number of circuli which remains relatively constant until the following Spring. The conclusion reached is that feeding, growth and reproduction, in common with other temperate fishes, are closely synchronized with and influenced by seasonal environmental conditions particularly temperature, rainfall and food supply.

In his review of theories pertaining to life history strategies, Stearns (1976) points out that a life history trait or a combination of co-evolved traits may be explained in terms of several plausible hypotheses. One of these is that of r- and K- selection (MacArthur & Wilson 1967), as developed by Pianka (1970). The theory predicts that species occupying unstable or unpredictable habitats will be comparatively r- selected and those in stable, predictable habitats

comparatively K- selected. At the r- endpoint of the r-K continuum there is a theoretical ecological vacuum in which there are no density effects or competition, while the K- endpoint represents a situation where density effects are at a maximum and competition is keen. Thus the optimum r- strategy involves maximization of productivity by reducing body size, age at sexual maturity, parental care, size of the young and generation time, by increasing fecundity and by the evolution of semelparity. The optimum K- strategy maximizes efficiency of resource utilization and competitive ability by increasing body size, longevity, parental care, size of the young and generation time, by delaying reproduction, by reducing fecundity and by iteroparity. Logically, no species ever achieves either the r- or K- endpoint, but each achieves a compromise position at some point along the r-K continuum (Pianka 1970).

Interpretation of life history tactics according to r-K theory poses certain problems. Life-histories are dynamic in time, both in a unidirectional evolutionary sense, in response to long-term environmental change, and in the sense of adaptive shifts to accommodate short-term environmental variability (Stearns 1976). A second difficulty is that when the correlates of r- and K- selection are examined in terms of an alternative hypothesis, named bet-hedging by Stearns (1976), predictions are generated which differ markedly from those of Pianka (1970). In essence, the bet-hedging hypothesis distinguishes between environmental impact (in unstable environments) on juvenile and adult mortality, predicting that when juvenile mortality is high, selection favours increased longevity and reduced reproductive effort, but when adult mortality is high selection occurs for reduced longevity and increased reproductive effort (Stearns 1976). There is at present little evidence to support this hypothesis and the data on the life history strategy of S. bainsii is therefore interpreted in terms of r- and K- theory because this theory has been the most widely used.

The life history traits which are interpreted in terms of the r- and K- theory are the age at first maturity, fecundity, maximum body size, frequency of reproduction and longevity (Table 19). The interpretation of the life history traits of S. bainsii in the r-K continuum is based on a comparison with life-history traits of other anabantids where data

are available. Where data on anabantids are not available, as in the case of age at maturity and longevity, general fish traits are considered.

Table 19. Some correlates of r- and K- selection (modified after Pianka 1970) and some life-history traits of S. bainsii in the Tyume river.

Correlates	r-selected	K-selected	Environment and traits of <u>S. bainsii</u>	Position in r-k continuum
Habitat	Less stable	More stable	Less stable	Favours r
Maturity	Early	Late	2nd year-early	Towards r
Fecundity	Higher	Lower	Max. 10500-high	Towards r
Maximum size	Smaller	Larger	Max. 190mm-small	Towards r
Reproduction	Semelparity	Iteroparity	Iteroparous	Towards K
Longevity	Shorter	Longer	5 years-short	Towards r

Table 19 shows that S. bainsii matures early, has a high fecundity, a small body size, is iteroparous and has a short lifespan. The early maturity, small body size and short lifespan and high fecundity suggest that the species is a r- strategist whereas iteroparity suggests that it is a K- strategist. These findings are, with the exception of iteroparity, consistent with predictions based on the r- and K- theory, that organisms found in unstable/unpredictable habitats would be selected more towards the r- side of the r-K continuum. The iteroparity is inconsistent with the theory of r- and K- selection although it may have evolved as a response to the harsh environment of this species. According to Wilbur et al (1974) natural selection modifies each of the life-history parameters " to produce a life-history strategy that results in the highest individual fitness and reflects a compromise between many selection pressures".

The life history traits of S. bainsii were also evaluated in terms of the theory of altricial and precocial life styles, which states that the early life-history of an organism will be of critical importance and has

the primary determining influence on the entire life-history (Noakes & Balon 1982). This theory assumes that the reproductive style or guild of each species is determined by factors related to oxygen supply for the developing young and predation upon them. Further, it is proposed that, in general, evolution will proceed from altricial (generalists) to precocial (specialists) forms. This is based on the assumption that communities will tend towards a more mature competitive condition, favouring a more precocial life style. Changes in the relative timing and duration of developmental intervals within a guild allow species to adapt somewhat more towards an altricial or a precocial life history style (Balon 1981). The characteristics of altricial and precocial forms are similar to the components of r and K- selection respectively. Moreover, altricial forms are thought to occupy habitats with persistent fluctuations whereas precocial forms are suited for stable conditions and the resultant competition (Noakes & Balon 1982).

Similar to the case with r- and K- selection theory, S. bainsii exhibits traits expected of both altricial and precocial life styles. Traits such as early maturity, high fecundity, small body size and short lifespan are characteristic of altricial forms whereas iteroparity is characteristic of precocial forms. These observations can perhaps be explained in terms of ontogenetic shifts which allow flexibility and adaptability and shifts between altricial and precocial life styles.

The relatives of Sandelia are found in tropical regions of the world. Most of them are K- selected and precocial. S. bainsii found in subtemperate South Africa is selected more towards the r- side of the r-K continuum and exhibits an altricial life style. These findings confirm the hypothesis that the geographic distribution of S. bainsii has resulted in this species adopting a life history style which is different from that of its relatives.

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