

The feeding and reproductive biology of a south african Anabantid fish, Sandelia bainsii

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ABSTRACT

Sandelia bainsii is a euryphagous and opportunistic predator whose diet depends on available food. The species matures during the second year and breeds repeatedly from October to February. The breeding season coincides with increased water temperatures, rainfall and increased feeding intensity. Some life history traits of the species are compared with those of other anabantids.

KEY WORDS : Fish — Fresh waters — Africa — Anabantidae — *Sandelia* — Distribution.

RÉSUMÉ

ALIMENTATION ET BIOLOGIE D'UN ANABANTIDAE D'AFRIQUE DU SUD, *SANDELIA BAINsii*

Sandelia bainsii est un prédateur euryphage opportuniste. Il atteint sa maturité sexuelle à deux ans et se reproduit plusieurs fois entre octobre et février. La saison de reproduction est étroitement liée aux augmentations de température et des précipitations et s'accompagne d'une augmentation de l'alimentation. Certains grands traits de la biologie de cette espèce sont comparables à celles d'autres Anabantidae.

MOTS-CLÉS : Poissons — Eau douce — Afrique — Anabantidae — *Sandelia* — Répartition.

INTRODUCTION

The Anabantidae is a small Afro-Asian family of fishes with three genera. The two species of the genus *Sandelia* are restricted to the Cape Province of South Africa while the genus *Ctenopoma* with some 26 species (GOSSE, 1986) occurs in west central, central and south eastern Africa. The Asian genus *Anabas* is monotypic (but see RAMASESHIAH & DUTT, 1984)

and is restricted to south east Asia (LIEM, 1963) (fig. 1).

This paper describes the feeding and reproductive biology of *Sandelia bainsii*. The study was undertaken during 1983 and 1984 primarily to ascertain its conservation status and as a contribution towards understanding of the life history styles of southern hemisphere fishes. Contributions to the understanding of the demography, age and growth and on the conservation status of *Sandelia bainsii* have been

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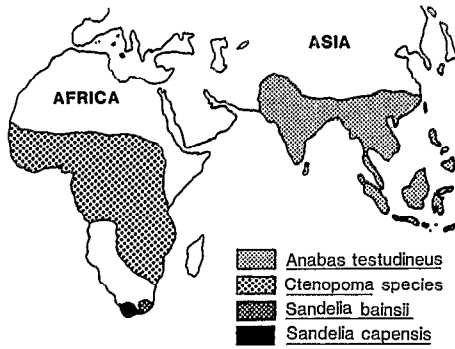


FIG. 1. — The world distribution of anabantid fishes. Répartition des Anabantidés dans le monde.

published previously (MAYEKISO & HECHT, 1988a & b).

The study area

The Tyume river is the main tributary of the Keiskamma river system. It was chosen as the study area because it is central within the known distributional range of the species (fig. 2). The Tyume river arises in the Winterberg mountain range (32° 35' S: 26° 55' E) at an altitude of 1500 meters above sea level (m ASL). At a gradient of 1: 40, the Tyume

river flows into the Keiskamma (32° 55': 26° 54'), at an altitude of 335 m ASL. On the basis of altitude and species composition the Tyume can be divided into upper (731-676 m ASL), upper middle (676-574 m ASL), middle (574-478 m ASL), lower middle (478-382 m ASL) and lower (382-335 m ASL) reaches (see fig. 5).

The climate of the area is subtemperate. The average air temperature during the summer months is 16° C in the upper reaches and 20° C in the lower reaches and during the winter months 9° C and 14° C in the upper and lower reaches respectively. The rainy season extends from October to March and the mean annual rainfall is 1200 mm in the upper reaches and 500 mm in the lower reaches (HILL *et al.*, 1977). The climatic data for the entire Keiskamma river system is summarised in figure 3. From the water analysis data (MAYEKISO, 1986) the river can be described as well-oxygenated, slightly alkaline with a wide summer and winter temperature range and a fluctuating ion content (50-700 mhos/cm).

METHODS

Electro-fishing gear (220 V AC), seine nets and gill nets were used to catch fishes at 14 sampling stations along the length of the Tyume river on a monthly basis from March 1983 to August 1984. To obtain an

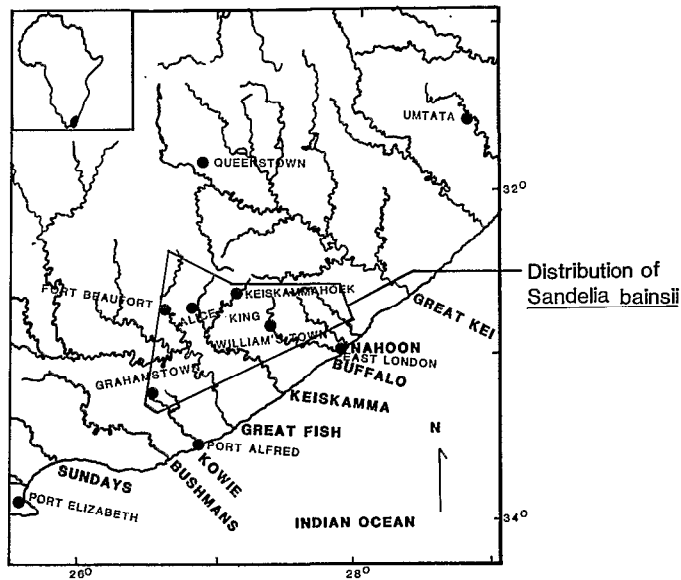


FIG. 2. — The distribution of *Sandelia bainsii* in the Nahoon, Buffalo, Keiskamma, Great Fish and the Kowie river systems in South Africa. Répartition de *Sandelia bainsii* dans divers bassins d'Afrique du Sud : fleuves Nahoon, Buffalo, Keiskamma, Great Fish et Kowie.

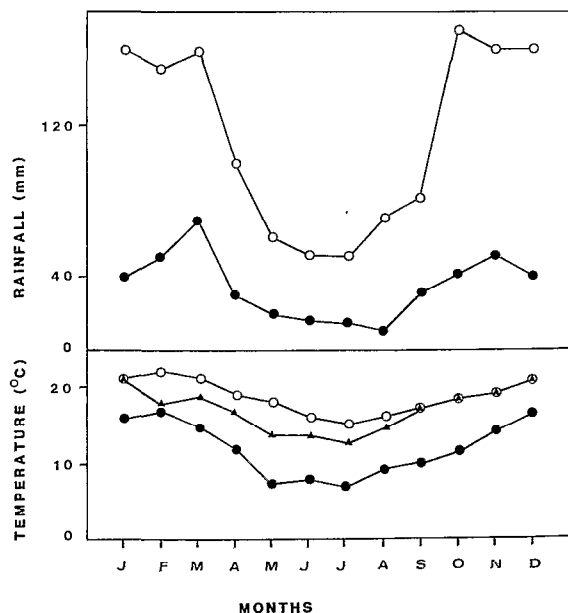


FIG. 3. — Monthly air temperature (maxima \circ , minima \bullet) average water temperature (\blacktriangle) and rainfall (maxima \circ , minima \bullet) in the entire Keiskamma river basin (1928-1977). *Données climatiques moyennes sur l'ensemble du bassin du fleuve Keiskamma pour la période 1928-77. Température mensuelle de l'air (maximum et minimum) et température de l'eau (triangles), et précipitations mensuelles (minimum et maximum).*

overview of the distribution of *S. bainsii* in the entire Keiskamma river system, a survey of the Keiskamma was undertaken in June 1984. The number of fishes caught over a period of 150 minutes with the electro-fishing gear represents the relative abundance (RA). This value was used to calculate the Importance Value Index (IVI) using ODUM's (1983) equation:

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

The stomach contents of 331 fish caught on a monthly basis at the various sampling stations were analysed. Specimens of all size classes as well as other predators found in the Tyume were killed by placing them in ice. The methods used to analyse stomach contents were based on those of HYNES (1950), WINDELL (1971) and HYSLOP (1980), namely the numerical (NA), frequency of occurrence (FO) and the dry weight (DA) methods. 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 percentages 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*. The diets of the other predators caught in the Tyume river were evaluated using only the numbers and frequency of occurrence methods. Diet similarities between the different species were analysed using correlation values and clustering by average distance according to the method of DIXON, (1981).

The condition factor (CF) of *S. bainsii* was calculated using the following equation:

$$CF = \frac{Tw - Gw}{L^b} \times 100$$

where Tw = total fish weight (g), Gw = gonad weight (g), L = standard length (cm) and b = exponent derived from the length/weight relationship (3.0281) (MAYEKISO, 1986).

In order to determine the periodicity of spawning, the gonads were classified according to KESTEVEN's (1960) scale of maturity. The gonads were then removed, weighed to the nearest 0.01 g and preserved in 10% formalin. The gonadosomatic index (GSI) was calculated using the equation:

$$GSI = \frac{\text{gonad weight (g)}}{\text{total fish weight (g) - gonad weight}} \times 100$$

In order to determine whether the species exhibits sexual dimorphism, the body colouration of the sexes and the area of the operculum immediately posterior to the eyes was examined for contact organs. The absolute fecundity (BAGENAL & BRAUM, 1968) of *S. bainsii* was estimated from 11 fish in Stage V (KESTEVEN, 1960). For this purpose the ovaries were preserved in Gilson's fluid for three months. Three subsamples of over 200 ova were counted and weighed to the nearest 0.01 mg. The total number of ova per fish was calculated as the mean of the replicate subsamples. To determine the size frequency distribution of ova, random subsamples of approximately 500 ova from nine fish were measured with a micrometer eye-piece to 0.01 mm and 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. A tagging programme was initiated in February 1984 in order to establish whether *S. bainsii* undertakes a spawning migration. Plastic anchor tags (Floy FD-67) and a Mark II Pistol grip tagging gun were used to tag the fish. In order to monitor tag loss and tag induced mortality 36 fish were tagged and kept in aquaria (1350 × 750 × 1250 cm deep) for a period of

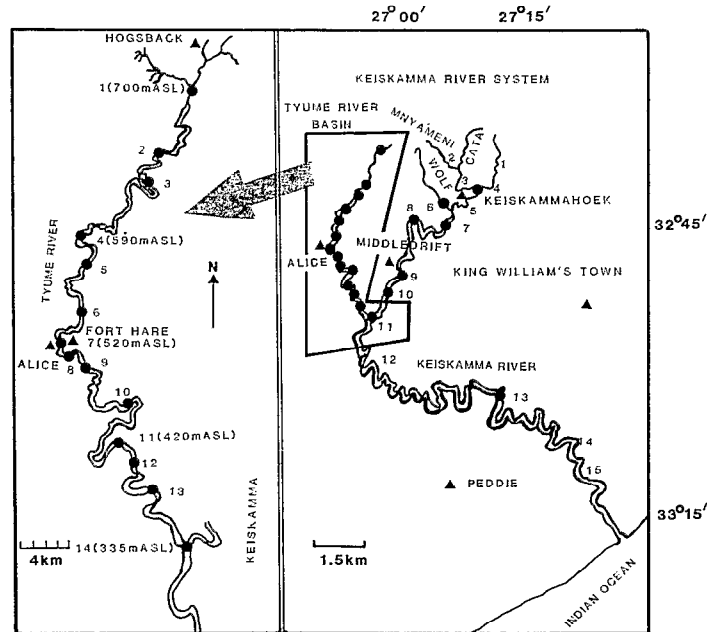


FIG. 4. — The distribution (●) of *Sandelia bainsii* in the Keiskamma river system. The numbers indicate sampling stations. Répartition de *Sandelia bainsii* (●) dans le bassin du Keiskamma. Les numéros indiquent les points d'échantillonnage.

18 months. In the field a total of 375 fish were tagged and released.

RESULTS AND DISCUSSION

Distribution, abundance and growth

Sandelia bainsii is widely distributed in the Keiskamma and Tyume rivers (fig. 4). The altitude-related changes in the IVI of fishes in the Tyume are shown in figure 5. *Sandelia bainsii* is not common (RA = 0.08) in the upper reaches, abundant (RA = 0.4) in the upper middle reaches, common (RA = 0.22) in the middle reaches and rare (RA = 0.001) in the lower middle and lower reaches. The fish were caught mostly below weirs in shallow runs (maximum depth = 60 cm) where the substratum consisted of rock, gravel or sand. The upper and lower limits of the distribution of *S. bainsii* fall within the distribution ranges of two alien species, *Salmo gairdneri* and *Micropterus salmoides* in the upper and lower reaches respectively. Surveys of the Tyume river between March 1985 and March 1987 have now also revealed the presence of a breeding population of a translocated indigenous species

Clarias gariepinus (sharp-tooth catfish) in the middle and lower reaches. The possible effect of the alien species and *C. gariepinus* on the population of *S. bainsii* was discussed by MAYEKISO & HECHT (1988a).

Age and growth of *S. bainsii* in the Tyume river is described by MAYEKISO & HECHT (1988b). Briefly, growth rings were deposited annually in spring. Males grow faster, reach a larger size (190 mm SL) and have a longer lifespan (5 years) than females (134 mm SL, 3 years). Based on otoliths the growth of males is described by $L_t = 287(1 - e^{-0.186(t-0.15)})$ mm SL and that of females by $L_t = 214(1 - e^{-0.223(t-0.18)})$ mm SL.

Feeding

Most of the *S. bainsii* stomachs examined (71 %) contained food. A total of 25 different prey species were identified (table I). Individual stomachs, however, never contained more than three different prey species. The percent contribution of the three major prey groups to the diet of different size classes is shown in figure 6. Fish below 59 mm SL are predominantly insectivorous whereas those in the length range 60-90 mm SL have a diet that is largely insectivorous with crustaceans and fish only occasio-

TABLEAU I

The food of various size groups of *Sandelia bainsii*
 Les aliments des diverses classes de taille de *Sandelia bainsii*

Food species or group	No.	% of Total	F.O.	%F.O.	Weight	%total weight	IRI
20-59 mm SL (n=74)							
CRUSTACEA	2	.43	1	1.4	.0004	.12	.7
Ostracoda	2	.43	1	1.4	.0004	.12	.7
INSECTA	467	99.6	74	100	.3390	99.9	19950
Baetidae G.1	126	26.9	28	37.8	.0849	25	1962
Baetidae G.2	20	4.3	7	9.5	.0150	4.4	83
Odonata	8	1.7	8	10.8	.0665	19.6	230
Coleoptera	6	1.3	2	2.7	.0041	1.2	7
Notonectidae	9	1.9	5	6.8	.0161	4.7	45
Nemouridae	16	3.4	3	4.1	.01007	3	26
Unidentified	7	1.5	6	8.1	.0129	3.8	43
Ceratopogonidae	274	58.4	20	27	.1290	38	2603
larvae							
Coleoptera	1	.2	1	1.4	.00045	.12	.4
larvae							
60-90 mm SL (n = 183)							
PISCES	3	.2	2	1.1	.0566	3.8	4
<i>T. sparrmanii</i>	1	.08	1	.5	.0363	2.5	1
Unidentified	2	.2	2	1.1	.0203	1.4	2
CRUSTACEA	166	13.1	41	22.4	.3991	27.1	900
<i>P. sidneyi</i>	10	.8	10	5.5	.2723	18.5	106
<i>Mysis</i> sp.	36	2.8	7	3.8	.0371	2.5	20
<i>Daphnia</i> sp.	14	1.1	4	2.2	.0128	.9	4
Amphipoda	8	.6	8	4.4	.0654	4.4	22
Cladocera	80	6.3	1	.5	.01	.7	4
Ostracoda	18	1.4	3	1.6	.0015	.1	2
INSECTA	1097	86.4	157	86	1.0116	68.6	13330
Baetidae G.1	809	63.8	86	47	.4652	31.6	4484
Baetidae G.2	4	.3	4	2.2	.0046	.3	1
Notonectidae	67	5.3	14	7.7	.1474	10	118
Nemouridae	34	2.7	10	5.5	.0655	4.4	39
Odonata	8	.6	6	3.3	.1039	7	25
Coleoptera	8	.6	7	3.8	.0134	.9	6
Unidentified	43	3.4	30	16.4	.0892	6	36
Ceratopogonidae	116	9.1	9	5	.0926	6.3	77
larvae							
Insect larvae	2	.2	2	1.1	.0006	.04	.3
Coleoptera	3	.2	3	1.6	.0176	1.2	2
larvae							
Insect pupae	3	.2	2	1.1	.0116	.8	1
MOLLUSCA	3	.2	3	1.6	.0071	.5	1
<i>Ferrissia</i> sp.	3	.2	3	1.6	.0071	.5	1
100-139 mm SL (n=61)							
PISCES	17	5.4	15	24.6	1.0994	37.6	1343
<i>B. trevellyani</i>	4	1.3	4	6.6	.2739	9.4	71
<i>S. bainsii</i>	4	1.3	2	3.3	.07	2.4	12
<i>T. sparrmanii</i>	5	1.6	5	8.2	.6701	22.9	201
<i>L. macrochirus</i>	1	.3	1	1.6	.04	1.4	3
Unidentified	3	1	3	5	.0454	1.6	13
CRUSTACEA	43	13.7	17	26.2	1.2603	43.1	1488
<i>Mysis</i> sp.	17	5.4	2	3.3	.0031	.1	18
Ostracoda	8	2.6	1	1.6	.0008	.03	4
INSECTA	253	80.8	39	64	.5630	19.3	6406
<i>Macrotermes</i> sp.	26	8.3	4	6.6	.2884	9.9	120
Baetidae G.1	182	58.1	17	27.9	.1507	5.2	1766
Notonectidae	21	6.7	8	13.1	.0398	1.4	106
Nemouridae	5	1.6	5	8.2	.0663	2.3	32
Odonata	4	1.3	4	6.6	.0032	.1	9
Coleoptera	1	.3	1	1.6	.0022	.07	.6
Unidentified	8	2.6	5	8.2	.0093	.3	24
Ceratopogonidae	3	1	1	1.6	.0028	.1	2
larvae							
Coleoptera	2	.6	1	1.6	.0002	.007	1
larvae							
Insect larva	1	.3	1	1.6	.00005	.002	.5
140-180 mm SL (n=13)							
PISCES	4	6.8	3	23.1	2.027	61.4	1575
<i>S. bainsii</i>	1	1.7	1	7.7	1.3464	40.8	327
<i>T. sparrmanii</i>	1	1.7	1	7.7	.1656	5	52
<i>B. trevellyani</i>	1	1.7	1	7.7	.4305	13	113
Unidentified	1	1.7	1	7.7	.0845	2.6	33
CRUSTACEA	18	30.5	9	69.2	1.2564	38.1	4747
<i>P. sidneyi</i>	7	11.9	6	46.2	1.2494	37.8	2296
<i>Mysis</i> sp.	3	5.1	2	15.4	.0064	.19	81
Ostracoda	8	13.6	1	7.7	.0006	.09	105
INSECTA	37	62.7	5	38.5	.0179	.54	2435
Baetidae G.1	12	20.3	1	7.7	.0055	.17	158
Notonectidae	24	40.7	3	23.1	.0119	.36	948
Coleoptera	1	1.7	1	7.7	.0005	.02	13

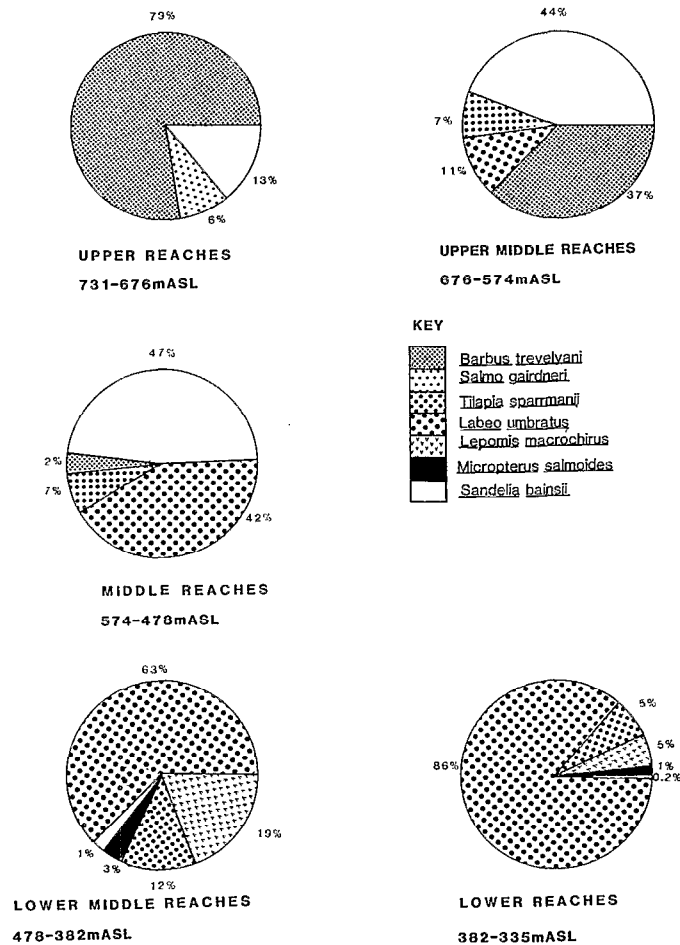


FIG. 5. — The Importance Value Indices of fish species in the various reaches of the Tyume river. *Composition du peuplement (indice d'importance) dans les différentes sections du fleuve Tyume.*

nally taken. The relative importance of fishes and crustaceans increases in fish in the length range 100-139 mm SL although insects are still the dominant prey item. Crustaceans, particularly *Potamon sidneyi* and fishes become more important in the size class 140-180 mm SL with insects becoming less dominant. The change in composition of the diet discussed above reflects an ability to take larger food items as the fish increase in size. Intraspecific competition is therefore reduced because different size classes rely on different food categories. The most "important" food item in the diet of *S. bainsii* were Baetidae nymphs (see table I). In order to determine whether *S. bainsii* "selects" the Baetidae nymphs, samples of aquatic insects were taken from a typical *S. bainsii* habitat. On analysis it was found that 85% of the insects were Baetidae nymphs. This

observation suggests that *S. bainsii* does not "select" particular prey items but exploits an abundant food supply (facultative opportunism). The Baetidae nymphs are relatively small insects with a high calorific content (MAYEKISO, 1986). In the majority of predators, the number of prey items found together in the stomach usually decreases as the fish increases in size, while the relative size of the separate food items increases because the amount of energy expended on the capture of numerous small prey may exceed their calorific value (NIKOLSKY, 1963; BRUTON, 1979b). It seems reasonable, however, to assume that a relatively small predator like *S. bainsii* may continue to take small prey if it is abundant and has a high calorific content.

S. bainsii occasionally consumed large numbers of a single prey item. One fish had consumed 80 larvae

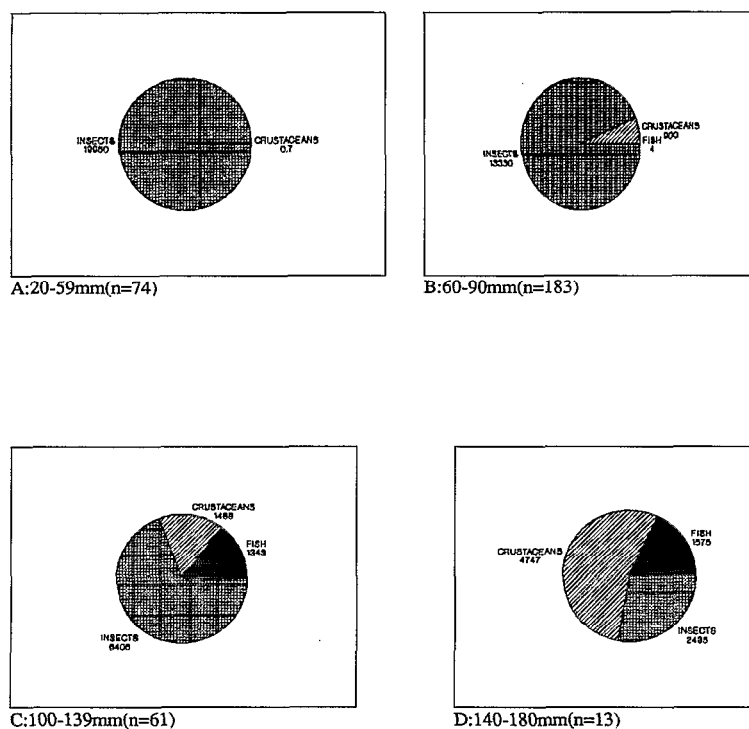


FIG. 6. — The percent contribution of the three major prey classes to the diet of the different size classes of *Sandelia bairdii* based on the index of relative importance (IRI). *Contribution des trois types de proies à l'alimentation des différentes classes de taille de Sandelia bairdii calculées par l'indice d'importance relative.*

and another 53 Baetidae nymphs indicating concentrated feeding. This ability is of value because it enables the fish 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 two fish caught at that locality, it was found that they had consumed 30 flying termites. The data therefore suggests that *S. bairdii* is a euryphagous and opportunistic predator whose diet is determined by available prey items. NIKOLSKY (1963) associates euryphagy with unstable feeding conditions resulting from a variable food supply.

The diet and feeding habits of *S. bairdii* are similar to those of the other anabantids (SIEGFRIED, 1963; BRUTON, 1979a; SINGH & SAMUEL, 1981). The similarity in the diet of *S. bairdii* and that of the other species caught in the Tyume river is shown in figure 7. The low % similarity between the diet of *S. bairdii* and that of the other indigenous fishes (except *Barbus trevelyani*) suggests resource partitioning among them and the higher % similarity with the diet of most alien species on the other hand

suggests competition between them. Although the diet of *C. gariepinus* was not analysed during this study, the data on feeding of this species presented by BRUTON (1979b) suggests a high likelihood of competition between the two species.

The condition factor of both sexes is low in winter (June-July) and increases thereafter with that of males reaching a peak early in the breeding season (October) whereas that of females reaches a peak later in the breeding season (November-December) (fig. 8). In general the condition factor of males is higher than that of females possibly because of a larger energy investment in gonadal tissue in the case of females.

Reproduction

Based on the GSI and visual maturity stage analysis the gonads of *S. bairdii* begin to mature in August and September. The majority of the population is ripe from October to February (figs. 9 & 10). The spawning season, starting in October, coincides with the beginning of the rainy season and increased

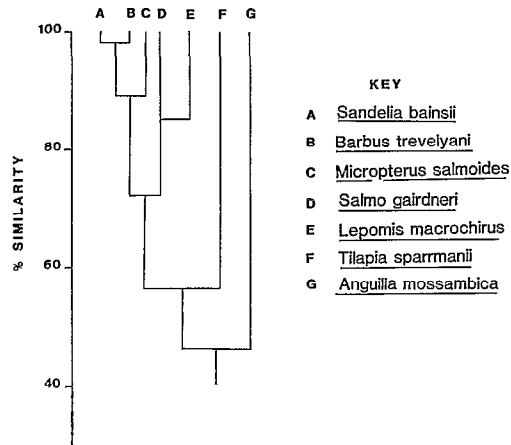


FIG. 7. — The diet similarity of the various fish species found in the Tyume river. *Similitude du régime alimentaire des diverses espèces de poissons du fleuve Tyume.*

temperatures. These two environmental factors also lead to an increase of 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 increase during this period (MAYEKISO, 1986), suggesting a relationship between feeding and gonadal maturation. The size frequency distribution of ova of fish caught during the breeding season shows up to six significantly different ($p > 0.005$, Chi Square Test) size classes of ova (fig. 11). Fish caught early during the breeding season (October) have mature eggs and high GSIs whereas those caught in December and January still have mature eggs but lower GSIs suggesting that the ova in one ovary mature and are released at different times during the breeding season. These observations together with the prolonged recruitment period (MAYEKISO, 1986) suggest repeated spawning. The multiple spawning habit may be in response to the risk associated with spawning at a particular time. This may be the case if the survival of ova and fry is dependent on unpredictable factors (MURPHY, 1968) such as the erratic river flow in the eastern Cape. Repeated spawning has been reported in *A. testudineus* (BREDER & ROSEN, 1966), some *Ctenopoma* species (BERNS & PETERS, 1969) and *Sandelia capensis* (SIEGFRIED, 1963). The fecundity (F) of *S. bainsii* is related to the standard length ($F = 94.55 \text{ SL}$, $r^2 = 0.87$, $p < 0.005$) as is typical in fish (BAGENAL, 1973). The maximum fecundity of 85 ova/mm SL in *S. bainsii* is lower than the estimate of 318 ova/mm SL in *A. testudineus* reported by CHANCHAL & PANDEY (1980) but higher than the

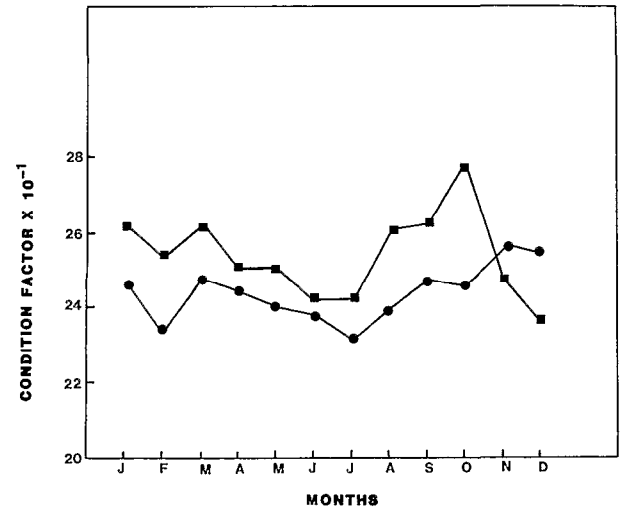


FIG. 8. — Changes in the mean condition factor of male (■) and female (●) *Sandelia bainsii*. *Évolution saisonnière du coefficient de condition chez les mâles (■) et les femelles (●) de Sandelia bainsii.*

estimate of 56 ova/mm SL in *Ctenopoma kingsleyae* reported by ALBARET (1982). The species matures during the second year (MAYEKISO & HECHT, 1988a) although males mature at a larger size (80-90 mm) than females (60-69 mm). Maturity in *S. bainsii* is delayed compared to other anabantids such as *A. testudineus* (CHANCHAL & PANDEY, 1978), some *Ctenopoma* sp. (BERNS & PETERS, 1969) and *Sandelia capensis* (SIEGFRIED, 1963) which mature during their first year.

Sexual dimorphism based on the occurrence of contact organs and colouration during the breeding season was observed and the former can be used to distinguish between the sexes in larger fish. All females and 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 larger than 90 mm SL. Sexual dichromatism was observed with respect to general body colouration only during the breeding season. The females retain the drab, olive green colour throughout, whereas males assume an attractive pale green (or lemon) colour during the breeding season. The tints of orange on the fins are also accentuated in males during this period. BERNS & PETERS (1969) associate this form of sexual dimorphism with territoriality in males in some African anabantids.

Of the 375 fish that were tagged 15.8 % were recaptured within 95 metres of the place of release irrespective of season. This may suggest that the

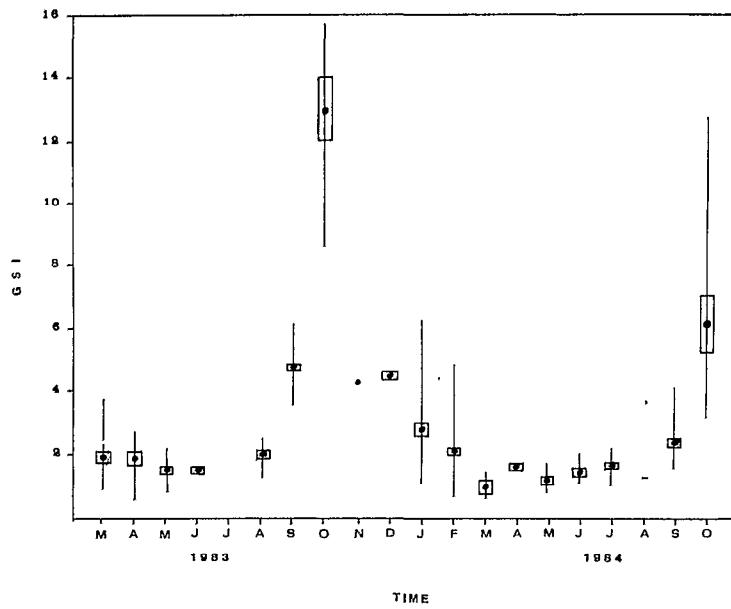


FIG. 9. — Changes in the gonadosomatic index of female *Sandelia bainsii*. The data are given as means (●), standard errors (blocks) and ranges (vertical lines). *Évolution de l'indice gonado-somatique des femelles de Sandelia bainsii*; moyenne, écart-type (rectangle) et valeurs extrêmes.

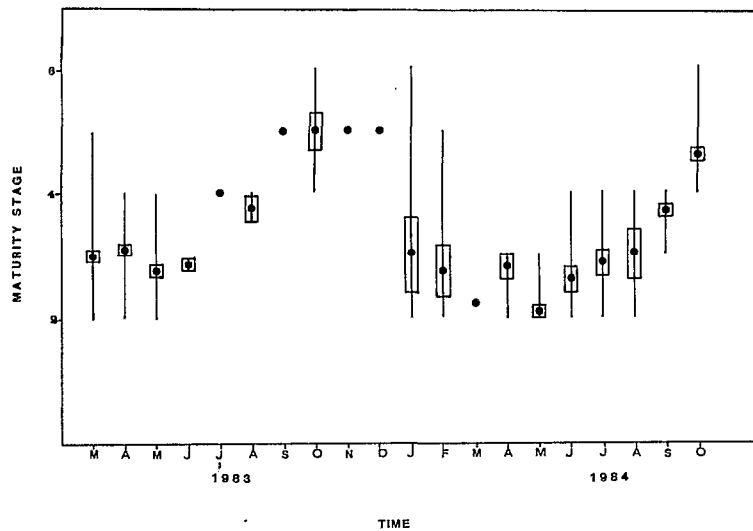


FIG. 10. — Changes of the gonad maturity stages of *Sandelia bainsii*. The data are given as means (●), standard errors (blocks) and ranges (vertical lines). *Évolution des stades de maturité des gonades de Sandelia bainsii*; moyenne, écart type (rectangles), et valeurs extrêmes observées.

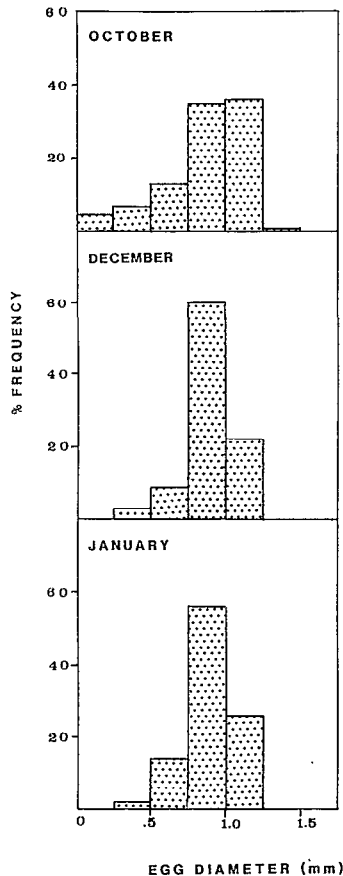


FIG. 11. — The frequency distribution of egg sizes of *Sandelia bainsii* in October, December and January 1983/1984. *Distribution des fréquences de tailles des œufs de Sandelia bainsii en octobre et décembre 1983 et janvier 1984.*

species is "sedentary" and, thus, is not seriously affected by man made physical barriers such as weirs which are common in eastern Cape rivers.

SUMMARY

The annual life cycle of *S. bainsii* can be described as follows: in winter *S. bainsii* shows a decline of prey diversity in diet, number of prey items per stomach and in stomach fullness indices (MAYEKISO, 1986). 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 (MAYEKISO & HECHT, 1988b), the last two being indicative of slow growth (BRUTON & ALLANSON, 1974; PANELLA, 1974). The rainy season begins in spring accompanied by an increase in water temperature, prey diversity in the diet, number of prey items per stomach and stomach fullness indices, suggesting an increased food supply and increased feeding intensity. During this season the gonads develop rapidly to reach a peak in October indicating the beginning of the breeding season. At this time the opaque zone is deposited on the otoliths and the circuli become widely spaced (MAYEKISO, 1986), suggesting growth acceleration (BRUTON & ALLANSON, 1974; PANELLA, 1974). Breeding continues throughout summer and there is an increase in the condition factor of the fish, the size of the opaque zone on the otoliths and the number of circuli in the marginal increment of the scales. Autumn marks the end of the rainy season and of breeding. 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 spring. The conclusion reached is that feeding, growth and reproduction, in common with other subtemperate and temperate fishes, are closely synchronized with and influenced by seasonal environmental conditions particularly temperature, rainfall and food supply.

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