Observations on the feeding habits of larvae, juvenile and adult stages of the African clawed frog, *Xenopus laevis*, in impoundments in Transkei

HJ Schoonbee[1]*, JF Prinsloo[2] and JG Nxiweni[3]
[1]*Department of Zoology, Rand Afrikaans University, PO Box 524, Johannesburg 2000, South Africa*
[2]*Limnological Research Unit, Department of Zoology, University of the North, Private Bag X1106, Sovenga 0722, Transvaal, South Africa*
[3]*Department of Zoology, University of Transkei, Private Bag X5092, Umtata 5100, Transkei*

Abstract

The feeding habits of tadpoles, juvenile and adult stages of the African clawed frog or platanna, *Xenopus laevis* (Daudin) in small impoundments in Transkei were investigated. An analysis of the stomach contents of developmental stages of the larvae showed that the initial diet is mainly phytophagous, consisting predominantly of unicellular algae and diatoms. A change in the diet of the larvae coincides with the transformation of the tadpole during the climax stage of metamorphosis when its head-shape assumes that of a juvenile frog. At this stage food of animal origin begins to appear in its diet.

The stomach contents of the frogs analysed showed that they feed mainly on benthic macro-invertebrate fauna which occur in or on the substrate of the impoundments as well as amongst the submerged and marginal vegetation. The results also confirmed that *X. laevis* can be cannibalistic, taking its own eggs and larvae as food.

Introduction

In recent years much progress has been made in South Africa towards the large-scale spawning and larval rearing of a number of warm-water fish species intended for use in aquaculture (Schoonbee et al., 1978; 1980; Brandt and Schoonbee, 1980; Hecht, 1981, 1982; Hecht and Viljoen, 1982; Hecht et al., 1982; Prinsloo and Schoonbee, 1986; Schoonbee and Prinsloo, 1984; Uys and Hecht, 1985; Polling et al., 1987; 1988). In most cases the necessary steps are usually taken to eradicate parasites and diseases from spawners and juvenile fish (Schoonbee et al., 1978; Brandt et al., 1981; Polling et al., 1987). However, when it comes to the nursing of juvenile fish in outside ponds at hatcheries, substantial losses may occur due to predation by the clawed frog, or platanna, *Xenopus laevis* (Daudin) (Hey, 1945; Jubb, 1980; Prinsloo et al., 1981; Schramm, 1987). Schoonbee et al. (1979) also found that the nektonic larval stages of *X. laevis* may compete for food with fish such as the Chinese grass carp, *Hypophthalmichthys molitrix* (Val.), affecting its growth in fish ponds (Nxiweni, 1982; Schramm, 1987). This information indicates that this frog, which commonly occurs in rivers and impoundments throughout Southern Africa (MacNae et al., 1973; Passmore and Carruthers, 1979), may pose a serious threat to warm-water pond fish culture in the areas where it occurs naturally.

Although research workers like McCoid and Fritts (1980a, b) have described the diet of a feral population of *X. laevis* in Californian waters, where it has been present since 1968 (Fritts and McCoid, 1976; Zacuto, 1975), little work has been done on the feeding ecology of the various developmental stages of this frog in Southern Africa where it naturally occurs (Hey, 1945; Jubb, 1980). It was therefore decided to investigate the dietary habits of *X. laevis* and that of its larvae in five small cattle watering ponds near Umtata, Transkei where this frog is usually found in large numbers. The ponds investigated were all less than 0,5 ha in size and on average less than 1 m deep. Fringing vegetation largely consisted of grass and other terrestrial plants bordering the impoundments. The impoundments investigated contained no fish life.

The investigation which was done on a monthly basis over a period of six months, commenced in March 1981 (autumn) when water temperatures were still comparatively high, continued throughout winter when the feeding intensity was expected to be at its lowest, and was terminated in September 1981 (spring) when water temperatures were on the increase and when the feeding intensity of the platanna was expected to have already taken place. Owing to severe drought conditions which prevailed at that time, three of the five ponds used in the investigation dried out, while the shallow water in the other ponds became so turbid because of cattle watering activities, that the investigation had to be prematurely terminated before a summer survey could also be undertaken. Sufficient data were, however, obtained to merit the publication of the findings of this study.

Materials and methods

Physical and chemical conditions of the impoundments investigated

A Hach model Dr-EL/2, single-beam spectrophotometer, designed to provide direct read-outs of the values of the various chemical substances, was used for the analysis of nitrate, ammonia, orthophosphate, total alkalinity, calcium hardness and total hardness. Analysis of the water was done according to *Standard Methods* (1980).

Collection and analysis of the benthic macroinvertebrate and marginal vegetation fauna of the ponds

In order to determine the frogs' food preferences, it was necessary to compare these data with information on the availability of organisms in the ponds. One set of macro-invertebrate fauna, sampled from the bottom sediments, as well as marginal vegetation during spring, was collected during the same period when frogs and tadpoles were sampled for analysis.

*To whom all correspondence should be addressed.

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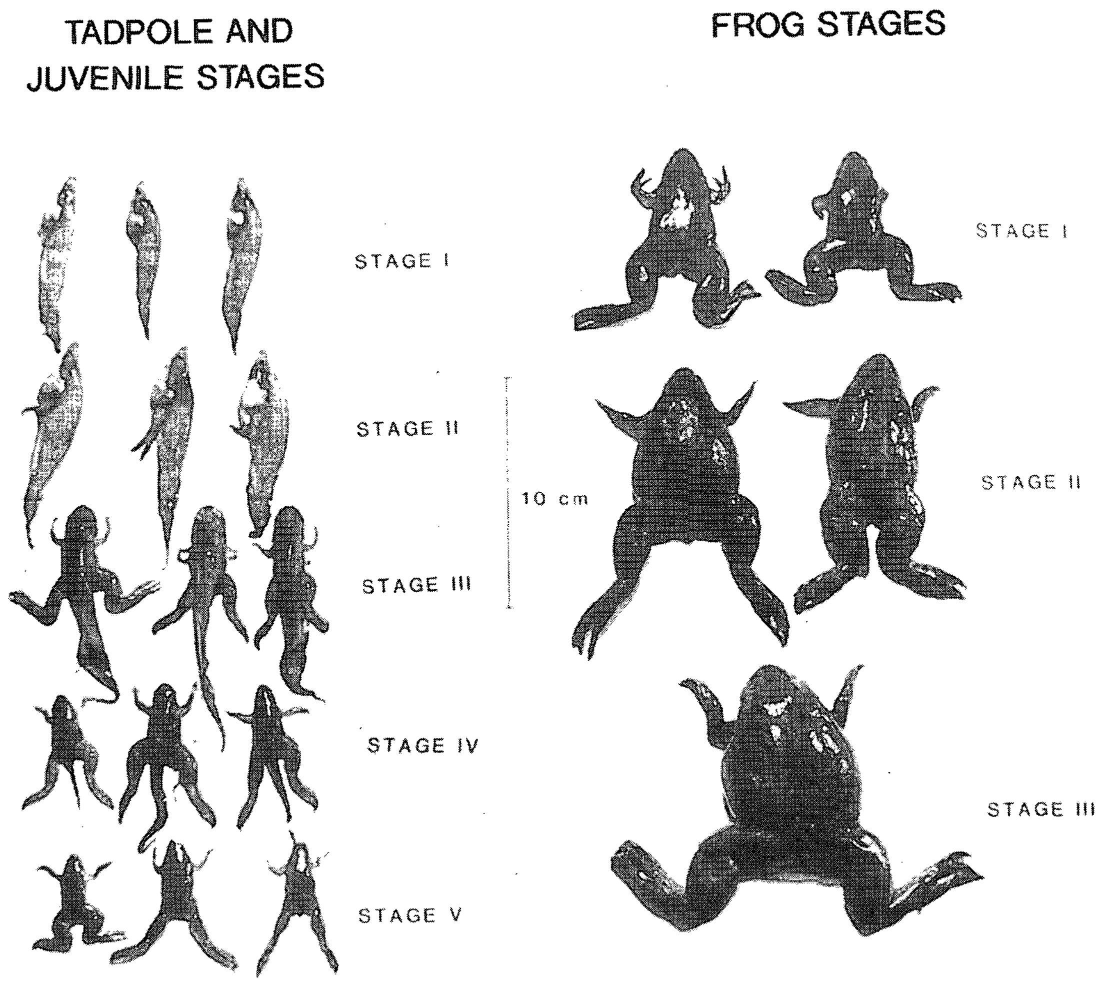

Figure 1
Subdivision of developmental stages of larvae and juveniles and frog sizes of Xenopus laevis *used for the purpose of determining possible changes in their dietary habits*

Random samples of the fauna of the bottom sediments were collected with a Birge-Eckman grab, while the fauna of the marginal vegetation was sampled with a fine mesh handnet. Each faunal sample collected was first rinsed through a 500 µm sieve to remove silt. The organic matter and organisms which remained behind were then preserved in 10% formalin, labelled and stored for sorting, identification and counting of organisms at a later stage.

Collection of tadpoles and frogs for stomach contents analysis

A 60 m seine net of stretched mesh size of 5 mm was used to collect specimens from each impoundment. A random sample of 15 to 25 frogs was collected monthly from each of 5 impoundments investigated within the specified period of investigation. Five hundred frogs were thus collected during the entire study period, of which approximately 350 were eventually dissected and their gut contents analysed.

For the qualitative analysis of the gut contents of the tadpoles of which there were five developmental groups (see below), a total sample of 20 per group was collected during the first sampling period only.

All specimens were killed with chloroform immediately after collection and preserved in 10% formalin. Each frog was later weighed to 0,1 g before the stomach contents were removed. Each stomach was carefully opened and the contents transferred to a labelled vial, containing 70% alcohol, for later analysis. Each frog's stomach contents was then individually examined in full without subsampling and food items were identified. Results on each were separately recorded.

The tadpoles and juvenile frogs (Table 1) were dissected and each gut carefully removed. The foregut, in the case of tadpoles, and stomachs in juvenile frogs were opened and their contents emptied individually into petri-dishes, containing 70% alcohol. A representative number of subsamples from each stomach were put on microscope slides and the food items identified, using a light microscope.

Subdivision of the life cycle of *X. laevis* into tadpole developmental stages and frog size groups

The results obtained on the food ingested were analysed separately for the five tadpole developmental stages and the three frog size groups (Table 1; Fig. 1).

Results and discussion

Physical and chemical conditions of impoundments

The results obtained on the water chemistry of the impoundments sampled for *X. laevis* are contained in Table 2.

Water temperatures showed a considerable fluctuation with a winter minimum of 8°C. Since samples were collected during the day it can be assumed that temperatures in the shallow impoundments may have declined even more during the winter months. During the warmer months of the sampling period (autumn and spring) water temperatures were usually found to exceed 25°C.

Dissolved oxygen concentrations in the impoundments were found to fluctuate greatly from impoundment to impoundment, largely depending on the time of day when the samples were taken. No anoxic conditions were, however, found to occur, with the oxygen concentrations in some impoundments tending towards saturation. The pH values obtained from these impoundments clearly reflect the general alkaline conditions of waters in Transkei. On most occasions pH values exceeded 7,0, increasing to almost 10,0 in some impoundments during the day in the ponds where algal densities were high. Values obtained for conductivity, with a maximum of 690 $\mu S \cdot cm^{-1}$, are typical for cattle watering impoundments in Transkei, where evaporation is high and where a build-up of mineral solutes may occur. This phenomenon is also clearly illustrated by the alkalinity and hardness of the water which, in the latter case, on occasion exceeded 100 $mg \cdot \ell^{-1}$ for these parameters. Nitrogen and phosphate concentrations were sufficiently high to cause algal blooms in some of these impoundments. Most of the impoundments were fairly turbid as a result of cattle activity.

TABLE 1
TADPOLE STAGES AND FROG SIZE GROUPS USED FOR GUT CONTENT ANALYSIS. CORRESPONDING DEVELOPMENTAL STAGES OF THE LARVAE AND JUVENILE FROGS ACCORDING TO NIEUWKOOP AND FABER (1956) AND KING AND MILLAR (1981) ARE ALSO INCLUDED

Tadpole stages	Corresponding developmental stages
I. Without limbs	Premetamorphosis 1-46
II. With hind limbs only	Premetamorphosis 46-55
III. With fore- and hind limbs	Premetamorphosis 56-59
IV. Well developed fore- and hind limbs. Head-shape changed to that of juvenile frog. Shortening and narrowing of tail.	Climax 60-65
V. Juvenile frogs (froglets). Tail almost or completely resorbed	Post-climax 66-

Frog stages (sizes)
I. Mass less than 30 g.
II. Mass greater than 30 g but less than 60 g.
III. Mass greater than 60 g.

TABLE 2
SUMMARY OF PHYSICAL AND CHEMICAL CONDITIONS OF THE FIVE IMPOUNDMENTS FROM WHICH *XENOPUS LAEVIS* TADPOLES AND FROGS WERE COLLECTED FOR ANALYSIS

Analysis	n	$\bar{x}$	Range Min	Range Max
Temperature (°C)			8	27
Dissolved oxygen (% saturation)	30	59,8	27	90
pH	30		6,74	9,88
Conductivity $\mu S \cdot cm^{-1}$	30	259,5	114	690
Turbidity, Secchi disc (in cm)	25	8,2	2,0	36,5
Alkalinity as $CaCO_3$ $mg \cdot \ell^{-1}$	30	51,0	10	100
Calcium hardness as $CaCO_3$ $mg \cdot \ell^{-1}$	30	38,8	10	105
Total hardness as $CaCO_3$ $mg \cdot \ell^{-1}$	30	67,8	20	165
Nitrate (NO_3^-) $mg \cdot \ell^{-1}$	30	0,471	tr	1,35
Ammonia (NH_3) $mg \cdot \ell^{-1}$	30	2,683	tr	6,44
Orthophosphate (PO_4^{3-}) $mg \cdot \ell^{-1}$	30	0,562	0,15	1,79

Macroinvertebrate fauna of the substrate and marginal vegetation of the cattle watering ponds

The results listed in Table 3 can be summarised as follows:

There is a wide variety of organisms present in the ponds. The numerically dominant groups amongst the zoobenthos during all seasons sampled are the Annelida (38%), Crustacea (47%) and Diptera (11%), comprising 96% of the total number of macro-invertebrate organisms during autumn. A similar pattern exists during winter and spring, when these groups still comprise the numerically dominant organisms amongst the benthic macro-invertebrate fauna of the ponds.

In the marginal vegetation a decline occurs amongst the Annelida while the Crustacea, mainly represented by the Ostracoda, Copepoda and Cladocera which are numerically dominant, constitute 83% of the total number of macro-invertebrate fauna in this habitat type. Diptera comprised less than 2% of the macro-invertebrates whilst Gastropods such as *Bulinus, Lymnaea* and *Ferrisia*, absent from bottom sediments, featured in the samples collected from the marginal vegetation. This also applies to the larger predatory insects such as *Pseudagrion, Trithemis*, Notonectidae, Corixidae, Nepidae and Gerridae.

Feeding habits of the larval stages of *X. laevis*

The following food items were identified from the different developmental stages of the larvae of *X. laevis* (Table 4).

Results showed that tadpoles initially feed primarily on phytoplankton, (stages I to III) but change their diet during metamorphosis, when they become zooplankton feeders (Stages IV to V). The change in diet occurs during the climax stage (Table 1) when the tadpole head-shape is transformed to that of the juvenile frog.

Feeding habits of *Xenopus laevis* frogs

As mentioned, the feeding habits of the different developmental stages of the *Xenopus* frogs were studied over a period of seven months. The results obtained on this part of the investigation are listed in Tables 5 to 7.

Nematodes, which occurred in the stomachs of the frogs during autumn (Table 5), were only present in Stages I and II, when they were represented by 1,3% and 4,4% of the frequency of occurrence in the stomachs analysed, respectively. These nematodes seem to occur in a parasitic association with the frogs. In contrast to the nematodes, the Annelida were represented by the earthworm *Microchaetus* in the stomachs of the frogs during autumn. It is interesting to note that *Microchaetus* became progressively more important in the diet of the frogs as they grew bigger. In fact, it occurred as a food item in 20% of the stomachs of Stage III frogs analysed.

The Hydracarina only occurred in the diet of Stage I frogs and may have been taken with other food items as these organisms are generally small.

TABLE 3
MACROINVERTEBRATE FAUNA OF THE BOTTOM SEDIMENTS AND MARGINAL VEGETATION OF IMPOUNDMENTS USED FOR COLLECTION OF *X. LAEVIS* TADPOLES AND FROGS: MARCH TO SEPTEMBER 1981. RESULTS EXPRESSED IN NUMBERS OF ORGANISMS/m² POND BOTTOM (BENTHIC ORGANISMS) OR 2 m MARGINAL VEGETATION SAMPLED

ORGANISMS	BENTHIC FAUNA											MARGINAL VEG. FAUNA	
	AUTUMN					WINTER				SPRING		SPRING	
	MAR	APR	MAY	x	%	JUN	JUL	x	%	SEPT	%	SEPT	%
CNIDARIA													
Hydrozoa													
Hydra	-	178	-	59	0,3	178	44	111	0,5	-	-	1	<0,1
NEMATODA	845	1022	44	637	2,8	711	311	511	7,3	409	2,5	117	4,8
ANNELIDA													
Tubificidae (unclassified)	1510	1022	444	992	4,4	4533	2088	3311	14,9	5911	30,2	4	0,2
Branchiura sowerbyi	2089	4089	177	2118	9,4	1466	2711	2089	9,5	1555	8,0	1	<0,1
Limnodrilus	3200	1245	-	1482	6,6	1199	1289	1244	5,6	1910	9,8	1	<0,1
Naididae (unclassified)	-	12000	-	4000	17,8	-	-	-	-	-	-	196	8,0
ARACHNIDA													
Hydracarina	-	-	-	-	-	-	-	-	-	-	-	2	0,1
CRUSTACEA													
Cladocera (unclassified)	-	-	-	-	-	-	-	-	-	-	-	60	2,5
Simocephalus	977	3467	1422	1955	8,7	222	177	200	0,9	3111	15,9	2	0,1
Daphnia (ephippium)	-	6534	89	2208	9,8	17778	88	8933	40,2	-	-	91	3,7
Ilyocryptus	88	533	-	207	0,9	222	44	133	0,6	44	0,2	2	0,1
Copepoda													
Calanoid copepods	44	177	-	74	0,3	-	-	-	-	-	-	261	10,6
Cyclopoid copepods	-	89	-	30	0,1	-	-	-	-	-	-	-	-
Mysidacea (Opossum shrimps)	-	-	44	15	0,1	-	44	22	0,1	-	-	-	-
Ostracoda	711	17289	355	6118	27,3	2355	266	1311	5,9	1200	6,1	1618	66,1
INSECTA													
Odonata													
Pseudagrion	-	-	-	-	-	-	-	-	-	-	-	3	0,1
Aeschna	-	-	-	-	-	-	-	-	-	-	-	1	<0,1
Ephemeroptera													
Cloeon nymphs	-	-	-	-	-	-	-	-	-	-	-	5	0,2
Caenis nymphs	-	-	-	-	-	-	-	-	-	-	-	1	<0,1
Hemiptera													
Notonectidae	-	-	-	-	-	-	-	-	-	-	-	8	0,3
Corixidae	-	-	-	-	-	178	-	89	0,4	-	-	2	0,1
Micronecta	-	-	44	15	0,1	44	-	22	0,1	-	-	2	0,1
Sigara nymphs	-	-	-	-	-	-	-	-	-	-	-	3	0,1
Nepidae (*Ranatra*)	-	-	-	-	-	-	-	-	-	-	-	1	0,1
Gerridae	-	-	44	15	0,1	-	-	-	-	-	-	7	0,3
Coleoptera													
Dytiscidae larvae	-	-	-	-	-	-	-	-	-	-	-	2	0,1
Hydraenidae	-	-	-	-	-	-	-	-	-	-	-	1	<0,1
Orthoptera (terrestrial)	-	-	-	-	-	-	-	-	-	-	-	1	<0,1
Diptera													
Chironomidae larvae (excl. *Chironomus*)	88	622	534	415	1,8	1289	355	822	3,7	2532	13,0	30	1,2
Chironomidae pupae	-	89	-	30	0,1	-	-	-	-	-	-	4	0,2
Chironomus larvae	711	178	44	311	1,4	222	177	200	0,9	311	1,6	-	-
Pentaneura	578	2221	1867	1555	6,9	4223	1200	2712	12,2	1867	9,5	7	0,3
Rheotanytarsus	311	111	-	141	0,6	-	-	-	-	-	-	-	-
Heleidae (*Palpomyia*)	44	44	89	59	0,3	177	133	155	0,8	177	0,9	1	<0,1
Culicidae larvae	-	-	-	-	-	-	-	-	-	-	-	1	<0,1
MOLLUSCA													
Bivalvia													
Pisidium	-	-	-	-	-	444	222	333	1,5	444	2,3	1	<0,1
Gastropoda													
Bulinus	-	-	-	-	-	-	-	-	-	-	-	4	0,2
Lymnaea natalensis	-	-	-	-	-	-	-	-	-	-	-	6	0,3
Ferrissia	-	-	-	-	-	-	-	-	-	-	-	2	0,1
TOTAL	11196	50910	5197	22436		35241	9149	22198		19551		2449	

A comparison of the Crustacea as food for the various stages (sizes) of the platanna suggests that the younger frogs (Stage I) feed on the widest variety of species occurring in the pond. With increasing frog size, the species variety declined markedly with the larger organisms being taken as food by Stage III frogs. Important Crustacea which served as food include Mysidacea, Ostracoda and the decapod *Potamon*. One food item, which remained important in the diet of all three frog sizes, occurring in more than 40% of the stomachs of Stage I frogs, and declining to 20% in Stage III, are the Ostracoda, which are not necessarily large but which were found to be common amongst the benthos in the impoundments. The large Crustaceans, which include the opossum shrimps and *Potamon*, clearly became the dominant food items in the stomachs of Stage III frogs, where their frequency of occurrence was 60% and 40%, respectively.

Amongst the Odonata, *Pseudagrion* which primarily dwells among the submerged and marginal vegetation in impoundments, as well as *Aeschna* and *Trithemis*, also occurred in the diets of Stages I and II frogs. *Aeschna* and *Trithemis* were found in 8,7% and 4,4% respectively, of the stomachs of Stage II frogs analysed. Ephemeroptera, presented by *Cloeon*, were also eaten by Stages I and II frogs and were more important as a food item in the younger frogs.

The Hemiptera as a group remained an important food item of *X. laevis*, especially among Stages I and II of the frogs. *Micronecta, Sigara* and notonectids were all represented in Stages I and II, with the latter being the dominant food item. The larger Stage III frogs still fed actively on *Micronecta* and *Sigara*. The naucorids were also consumed by Stages I and II frogs. Amongst the Coleoptera, the dytiscid larvae were consumed by Stages I and II frogs, but were absent from the diet of the largest frogs. Land insects, like grasshoppers, were also consumed by Stages I and II frogs.

The benthic dwelling Chironomidae were clearly among the important food items in the diets of all sizes of the frogs of *X. laevis*. *Pentaneura* larvae, which could easily be distinguished from other chironomidae larvae, also formed an important food item in the case of Stage I frogs. Even though the ceratopogonid *Palpomyia* is a thin, small larva, it was still identifiable amongst the food items. It occurred frequently in the gut contents of the larger frogs.

The presence of the molluscs *Pisidium* and *Bulinus* in the diet of *Xenopus*, clearly confirms the benthic feeding habits of this frog.

All three *Xenopus* frog sizes were cannibalistic with a definite increase in incidence in tadpoles eaten as the frog grew bigger. Among the largest (Stage III) frogs, for instance, *Xenopus* tadpoles occurred in 60% of the stomachs analysed. Where tadpoles were taken as food, they usually constituted the bulk of the diet.

A comparison of the feeding habits of the *Xenopus* frogs during winter (Table 6) with those in autumn (Table 5) shows the following major tendencies:

- There was a general decline in the variety of Crustacean species ingested with Stage I frogs still utilising the largest numbers of Crustacea as food.
- The Ostracoda again comprised the food items with the highest frequency of occurrence among the Crustacea during winter, being particularly important in the diet of Stage I frogs.
- No significant decline occurred in the species variety of the Hemiptera taken, which occurred in the diet of both Stages I and II frogs analysed.
- The notonectids again were among the most preferred food item, occurring between 32% and 50% of the stomachs of the analysed frogs (Table 6).
- A slight increase occurred in the importance of Coleoptera as food compared to autumn.
- The value of Chironomidae as a preferred source of food for the *Xenopus* frogs was again confirmed.
- The molluscs *Bulinus* and *Pisidium* again featured in the diet of the frogs during the winter period.
- *X. laevis* tadpoles again constituted an important food item in the diet of both Stages I and II frogs.

TABLE 4
FOOD ITEMS FROM THE FOREGUT OF THE DIFFERENT DEVELOPMENTAL STAGES OF THE LARVAE OF *X. LAEVIS*

Larval stage	Food items
I	*Scenedesmus* (3 spp.), *Ankistrodesmus, Crucigenia, Phacus, Agmenellum, Cyclotella, Staurastrum, Coelastrum, Trachelomonas, Pediastrum, Microcystis, Oocystis*, diatoms and pollen grains.
II	*Scenedesmus* (3 spp.), *Ankistrodesmus, Crucigenia, Phacus, Agmenellum, Cyclotella, Trachelomonas, Pediastrum, Microcystis*, diatoms and pollen grains.
III	*Scenedesmus, Ankistrodesmus, Crucigenia, Cyclotella, Trachelomonas, Oocystis*, diatoms and pollen grains.
IV	*Chelomonas*, ciliates, insect remians and pollen grains.
V	*Daphnia*, cyclopoid copepods and insect remains.

The Cladocera, which appeared in the diet of Stages I and II frogs during spring (Table 7) assumed a sub-dominant position as preferred food item after *Potamon* amongst the Crustacea, followed by the calanoid Copepoda. The almost entire absence of the Crustacea in Stage III frogs may be misleading as only two frogs of this size group were collected and analysed during this season.

The absence of opossum shrimps in winter as well as in spring may be related to the seasonal fluctuations in numbers of this crustacean in the impoundments, which in turn affected the feeding pattern of *Xenopus* for this specific food item during certain times of the year.

The Odonata, especially *Pseudagrion* and *Aeschna*, assumed increasing importance as food items with increasing frog size. The Ephemeroptera, represented by *Cloeon* and *Caenis*, occurred more frequently in Stage I and II frogs in spring than during the preceding season (Tables 5 and 6). The Hemiptera again featured high on the list as a preferred food source, especially *Micronecta* (Stages I and II) and Notonectidae, which were taken as food by all three frog sizes. The Coleoptera occurred in the diet of Stages I and II of *Xenopus* with the widest variety of species being consumed by the younger frogs. Terrestrial insects, such as locusts, were also eaten when available. The Chironomidae, which occurred in more than 90% of all the analysed samples, again confirmed the benthic feeding habits of the frogs. *Pentaneura* larvae also occurred in no less than 50% of all the stomachs analysed.

During this season *Lymnaea natalensis* replaced *Bulinus* as a food item whilst *Pisidium*, which occurs in the sediments in impoundments, was again eaten by the smaller frogs.

The increase in percentage occurrence of *Xenopus* tadpoles as a food item was again substantiated by the analysis of the stomach contents of the frogs collected during spring (Table 7).

TABLE 5
ANALYSIS OF THE STOMACH CONTENTS OF *XENOPUS LAEVIS* FROGS CAUGHT IN IMPOUNDMENTS IN TRANSKEI DURING AUTUMN (MARCH-MAY) 1981

ORGANISMS	DEVELOPMENTAL STAGES OF FROGS STAGE I (n=77) % of total number of food items x = 1169	% frequency of occurrence	STAGE II (n=23) % of total number of food items x = 314	% frequency of occurrence	STAGE III (n=5) % of total number of food items x = 207	% frequency of occurrence	% of total number of food items x = 1690	% frequency of occurrence
NEMATODA	0,1	1,3	0,6	4,4	-	-	0,2	1,9
ANNELIDA								
Microchaetus	0,1	1,3	0,6	8,7	0,5	20,0	0,2	3,8
Cocoons	0,3	1,3	-	-	-	-	0,2	1,0
ARACHNIDA								
Hydracarina	0,1	1,3	-	-	-	-	0,1	1,0
CRUSTACEA								
Cladocera								
Daphnia	0,6	3,9	-	-	-	-	0,4	2,9
Daphnia (ephippium)	0,6	3,9	-	-	-	-	0,4	2,9
Simocephalus	-	-	-	-	-	-	-	-
Ilyocryptus	0,1	1,3	-	-	-	-	0,1	1,0
Alona	0,5	3,9	-	-	-	-	0,4	2,9
Copepoda								
Calanoid copepoda	0,3	3,9	0,3	4,4	-	-	0,3	3,8
Mysidacea (Opossum shrimps)	1,3	11,7	1,6	13,0	3,4	60,0	1,6	14,3
Ostracoda	38,2	40,3	6,1	26,1	0,5	20,0	27,6	36,2
Decapoda								
Potamon (complete)	0,2	2,6	1,0	13,0	1,0	40,0	0,4	6,7
Potamon (remains)	0,2	2,6	0,3	4,4	-	-	0,2	2,9
INSECTA								
Odonata								
Pseudagrion	0,1	1,7	-	-	-	-	0,1	1,0
Aeschna	0,2	2,6	0,6	8,7	-	-	0,2	3,8
Trithemis	0,1	1,3	0,3	4,4	-	-	0,1	1,9
Ephemeroptera								
Baetidae (Cloeon) nymphs	0,6	9,1	0,3	4,4	-	-	1,5	7,6
Hemiptera								
Micronecta (adults)	2,3	16,9	3,5	21,7	0,5	20,0	4,3	18,1
Sigara (adults)	3,9	24,7	3,2	26,1	1,5	40,0	3,5	25,7
Sigara (nymphs)	0,9	10,4	-	-	-	-	0,7	7,6
Notonectidae (adults)	7,4	40,3	8,6	56,5	-	-	0,8	41,9
Naucoridae	0,1	1,3	0,3	4,4	-	-	0,1	1,9
Coleoptera								
Dytiscidae larvae	1,5	16,9	1,9	26,1	-	-	1,4	18,1
Orthoptera								
Locust	0,1	1,3	0,3	4,4	-	-	0,1	1,9
Diptera								
Chironomidae larvae (incl. *Chironomus*)	29,1	70,1	61,2	78,3	87,9	60,0	42,3	71,4
Chironomidae (pupae)	2,3	16,9	1,9	17,4	0,5	20,0	2,0	17,1
Pentaneura (larvae)	4,8	39,0	1,6	13,0	-	-	3,7	31,4
Culicidae larva	-	-	-	-	-	-	-	-
Chaoborus	0,1	1,7	0,3	4,4	-	-	0,1	1,9
Heleidae (*Palpomyia*)	0,3	15,2	1,0	8,7	1,0	20,0	0,5	6,7
MOLLUSCA								
Bivalvia								
Pisidium	0,1	1,3	-	-	-	-	0,1	1,0
Gastropoda								
Bulinus	1,6	8,0	1,0	4,4	-	-	1,3	6,7
AMPHIBIA								
Xenopus tadpoles	1,8	24,7	3,5	47,8	3,8	60,0	2,3	31,4

TABLE 6

ANALYSIS OF THE STOMACH CONTENTS OF *XENOPUS LAEVIS* FROGS CAUGHT IN IMPOUNDMENTS IN TRANSKEI DURING WINTER (JUNE-AUGUST) 1981

	DEVELOPMENTAL STAGES OF FROGS					
	STAGE I (n=91)		STAGE II (n=14)		TOTAL (n=105)	
ORGANISMS	% of total number of food items x = 1184	% frequency of occurrence	% of total number of food items x = 169	% frequency of occurrence	% of total number of food items x = 1353	% frequency of occurrence
NEMATODA	0,1	1,1	-	-	0,1	1,0
ANNELIDA						
Microchaetus	0,9	12,0	-	-	0,8	10,5
Cocoons	-	-	-	-	-	-
CRUSTACEA						
Cladocera						
Daphnia	3,6	3,3	-	-	3,2	2,9
Alona	0,3	1,1	-	-	0,2	1,0
Copepoda						
Calanoid copepoda	0,2	2,2	-	-	0,2	1,9
Ostracoda	49,6	42,9	8,9	14,3	44,5	39,1
Decapoda						
Potamon (complete)	-	-	0,6	7,1	0,1	1.0
Potamon (Remains)	-	-	-	-	-	-
INSECTA						
Odonata						
Pseudagrion	0,6	7,7	-	-	0,5	6,7
Ephemeroptera						
Baetidae (Cloeon) nymphs	1,4	9,9	3,0	28,6	1,6	12,3
Caenis nymphs	-	-	0,6	7,1	0,1	1,0
Hemiptera						
Micronecta (adults)	1,8	13,2	6,5	35,7	2,4	16,2
Micronecta (nymphs)	0,2	2,1	-	-	0,2	1,9
Sigara (adults)	0,4	3,3	1,2	14,3	0,5	4,8
Sigara (nymphs)	0,2	1,1	0,6	7,1	0,2	1,9
Notonectidae (adults)	5,8	31,9	14,8	50,0	7,0	34,3
Veliidae	0,3	2,2	-	-	0,2	1,9
Belostomidae (Sphaerodema)	0,1	1,1	-	-	0,1	1,0
Nepidae (Ranatra)	-	-	-	-	-	-
Coleoptera	0,8	7,7	0,5	7,1	0,5	7,6
Dytiscid adult	-	-	0,6	7,1	0,1	1,0
Dytiscid larvae	0,3	3,3	0,6	7,1	0,3	3,8
Orthoptera						
Locust	0,2	2,2	-	-	0,2	1,9
Diptera						
Chironomidae larvae (incl. Chironomus)	28,0	65,9	47,9	85,7	30,5	68,6
Chironomidae (pupae)	0,3	3,3	0,6	7,1	0,3	3,8
Pentaneura (larvae)	3,0	24,2	10,1	42,9	3,9	26,7
Culicidae larvae	0,1	1,1	-	-	0,1	1,0
Heleidae (Palpomyia)	0,6	6,6	-	-	0,5	5,7
MOLLUSCA						
Bivalvia						
Pisidium	1,0	2,2	-	-	0,9	1,9
Gastropoda						
Bulinus	0,1	1,1	0,6	7,1	0,2	1,9
AMPHIBIA						
Xenopus tadpoles	0,4	5,5	3,0	35,7	0,7	9,5

TABLE 7
ANALYSIS OF THE STOMACH CONTENTS OF *XENOPUS LAEVIS* FROGS CAUGHT IN INPOUNDMENTS IN TRANSKEI DURING SPRING (SEPTEMBER) 1981

ORGANISMS	DEVELOPMENTAL STAGES OF FROGS: STAGE I (n=87) % of total number of food items x = 3781	STAGE I (n=87) % frequency of occurrence	STAGE II (n=16) % of total number of food items x = 512	STAGE II (n=16) % frequency of occurrence	STAGE III (n=2) % of total number of food items x = 20	STAGE III (n=2) % frequency of occurrence	TOTAL (n = 105) % of total number of food items x = 4313	TOTAL (n = 105) % frequency of occurrence
NEMATODA	<0,1	1,2	-	-	5,0	50,0	0,1	1,9
ANNELIDA								
Microchaetus	<0,1	1,2	-	-	-	-	<0,1	1,0
CRUSTACEA								
Cladocera								
Daphnia	11,0	5,8	16,6	-	-	11,6	6,7	
Daphnia (ephippium)	<0,1	1,2	-	-	-	-	<0,1	1,0
Simocephalus	<0,1	1,2	-	-	-	-	<0,1	1,0
Alona	0,9	6,9	-	-	-	-	0,7	5,7
Copepoda								
Calanoid copepoda	0,6	14,9	0,2	6,3	-	-	0,5	13,3
Ostracoda	0,1	3,5	-	-	-	-	0,1	56,2
Decapoda								
Potamon (complete)	52,4	64,4	46,1	18,8	-	-	51,4	56,2
Potamon (remains)	0,1	2,3	0,2	6,3	-	-	0,1	2,9
INSECTA								
Odonata								
Pseudagrion	0,3	12,6	2,3	25,0	10,0	50,0	0,6	15,2
Aeschna	<0,1	1,2	0,4	12,5	10,0	50,0	0,1	3,8
Trithemis	<0,1	1,2	-	-	-	-	<0,1	1,0
Ephemeroptera								
Baetidae (Cloeon) nymphs	0,4	12,6	2,3	17,5	-	-	0,7	16,2
Caenis nymph	0,1	4,6	0,2	6,3	-	-	0,1	4,8
Hemiptera								
Micronecta (adults)	1,6	31,0	0,2	6,3	-	-	1,4	26,7
Micronecta (nymphs)	<0,1	1,2	0,4	12,5	-	-	0,1	2,9
Sigara (adults)	0,1	3,5	-	-	-	-	0,1	2,9
Notonectidae (adults)	2,1	44,8	2,3	37,5	15,0	50,0	2,2	42,9
Notonectidae (nymphs)	0,1	2,3	-	-	-	-	0,1	1,9
Coleoptera (unclassified)	0,1	5,8	-	-	-	-	0,1	4,8
Dytiscidae adults	<0,1	1,2	-	-	-	-	<0,1	1,0
Dytiscid larvae	0,1	4,6	0,2	6,3	-	-	0,1	4,8
Hydrophilidae	<0,1	1,2	-	-	-	-	<0,1	1,0
Orthoptera								
Locust	0,1	3,5	0,2	6,3	-	-	0,1	3,8
Diptera								
Chironomidae larvae (incl. Chironomus)	16,3	95,4	13,9	93,8	35,0	100,0	16,1	95,2
Chironomidae (pupae)	0,7	20,7	1,4	31,3	-	-	0,7	21,9
Pentaneura (larvae)	12,5	69,0	9,2	56,3	10,0	50,0	12,1	66,7
Culicidae larvae	<0,01	1,2	~0,1	6,3	-	-	0,1	1,9
Heleidae (Palpomyia)	<0,1	1,2	1,0	12,5	-	-	0,1	2,9
Tabanidae larvae	0,2	10,3	1,2	18,8	10,0	50,0	0,4	12,4
MOLLUSCA								
Gastropoda	0,1	2,3	-	-	-	-	0,1	1,9
Bulinus	-	-	-	-	-	-	-	-
Lymnaea natalensis	0,1	2,3	~0,1	6,3	-	-	0,1	2,9
Ferrissia	-	-	-	-	-	-	-	-
AMPHIBIA								
Xenopus tadpoles	<0,1	1,2	0,6	18,8	5,0	50,0	0,1	4,8

X. laevis frogs are, according to the present study, primarily benthic feeding organisms which can also utilise fauna associated with submerged aquatic and fringing vegetation, overhanging the water. The present findings indicate without doubt that the platanna is cannibalistic. By arranging the food items according to the percentage frequency of occurrence in the gut contents of all the frogs analysed with the results obtained for the autumn season as a basis for the purpose of comparison, fluctuations in the diet of *X. laevis* and tendencies in its possible food preferences can be illustrated. Figure 2 shows that the food items which occurred in more than 30% of the stomachs of frogs in the impoundments, included Chironomidae larvae, which not only remained numerically the dominant food item but occurred in more than 69% of the stomachs analysed during all three seasons. Other important food items are notonectid adults, Ostracoda, *Pentaneura* larvae and *Xenopus* tadpoles. During winter and spring, notonectids, Ostracoda, and *Pentaneura* larvae remained the sub-dominant items, which coincides with the onset of the platanna spawning season, *Xenopus* tadpoles declining to 5% in the stomachs of frogs in spring. *Sigara*, which occurred in 25% of the stomachs analysed during autumn, declined to less than 5% in spring. *Micronecta* on the other hand, remained an important food item, increasing to more than 25 % in its frequency of occurrence as food for frogs in spring. Even though the opossum shrimps varied considerably as a food of the frogs from one season to another, the importance of its relative size as a food item, like that of *Xenopus* tadpoles, must be taken into consideration where it appears in the stomach of frogs. This also applies to the freshwater crab *Potamon* and to a certain extent to the large terrestrial earthworm, *Microchaetus* in the diet of *X. laevis*.

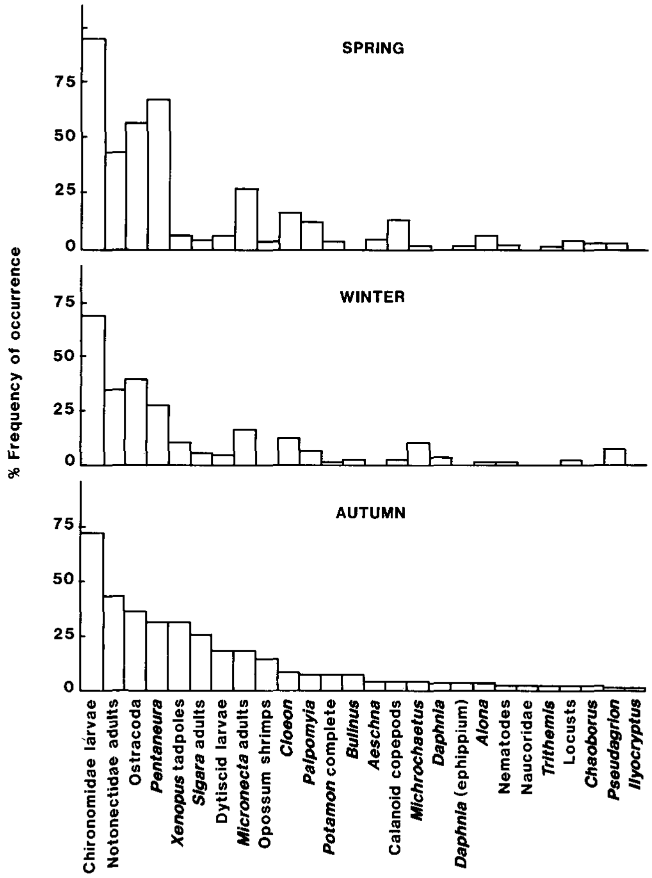

Figure 2
Percentage frequency of occurrence of food items in the diet of Xenopus laevis *adults from impoundments in Transkei*

General discussion

The results show that the early larval stages of *X. laevis* feed on phytoplankton organisms but that a change in the diet occurs after the tadpole has fully developed fore- and hind limbs and has undergone a change in its head-shape. This change in diet corresponds with the larval developmental stages 60 to 65 (Nieuwkoop and Faber, 1956) and climax stage (King and Millar, 1981). At this stage of larval development histomorphological changes must have also taken place in the alimentary canal of the larvae as well as the diet then largely contains macroinvertebrate organisms instead of phytoplankton.

The diet of *X. laevis* adults also shows some changes with growth and increase in size, especially between frogs smaller than 80 g and the larger frogs. The young frogs appear to be capable of utilising a wider variety of the smaller macro-invertebrate fauna compared to a somewhat more specific and selective diet among the larger frogs.

The tendency to eat its own larvae and juveniles, which has also been pointed out by Leslie (1980), and McCoid and Fritts (1980a; b) has again been substantiated by the present study. A comparison of the present results with that of investigators such as McCoid and Fritts (1980a) also showed that the food preferences of the platanna *X. laevis* remain the same, irrespective of where it is found in the world under natural environmental conditions. For instance, where it is found in Southern Californian waters (McCoid and Fritts, 1980b), gastropods, chironomidae, amphipods, Cladocera and ostracods are usually well represented amongst the food items found in its diet. Specific food items which may at times occur in large numbers in a single stomach of a frog are Cladocera and Ostracoda.

Where *X. laevis* occurs in waters in Africa and elsewhere in the world where it has been introduced, this frog has been shown to take small and juvenile fish as food (Lesley, 1980; Hey, 1945; FAO/EPTA, 1965; Schoonbee et al., 1979; Jubb, 1980; McCoid and Fritts, 1980a). Judging by its food preferences in the present study, both the larval and adult frogs of *X. laevis* will directly compete with phytophagous and benthic feeding fish (Schoonbee, 1969; Matlak and Matlak, 1976; Cremer and Smitherman, 1980; Crivelli, 1981; Opuszinski, 1981; Schramm, 1987). Because of this, various measures have been taken in the past with variable degrees of success, either to eradicate *Xenopus* or to prevent this frog from entering fish ponds. Largemouth bass, *Micropterus salmoides* (Lacépéde) have been used as predators of *X. laevis* in waters in the Cape (Hey, 1945) and Transkei (Prinsloo et al., 1981). Barriers were constructed around ponds (Schoonbee, et al., 1979; Jubb, 1980; Prinsloo et al., 1981) while traps were also found to be successful in reducing *X. laevis* populations in trout waters (Jubb, 1980) and in fish ponds at certain hatcheries (Schramm, 1987).

From the preceding discussion it is clear that *X. laevis* possesses a number of characteristics which make this frog one of the most successful aquatic dwelling lower vertebrates in Africa. Its successful adaptation to a wide variety of environmental conditions is one of them. It has been shown to survive desiccation in nature by burrowing into the mud of streams and impoundments (Millard and Robinson, 1967; Jubb, 1980). It is known to leave areas which may be unfavourable to it and to migrate over land to colonise other water bodies (Hey, 1945) and even to migrate actively at night between fish ponds despite an abundance of water (FAO/EPTA 1965; Schoonbee, personal observations). For breeding purposes, *X. laevis* thrives in highly eutrophic conditions where there is an abundance of phytoplankton which serves as food for its larvae (Schoonbee, personal observations). Furthermore, the platanna is a very popular bait organism used to fish for sharptooth catfish, *Clarias gariepinus* (Burchell). In addition, it is one of the most widely used laboratory animals at institutions for dissection purposes and a range of biological studies. In view of this, it is felt that much more work should be done to exploit the potential of this animal further.

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