

# Diet of feral *Xenopus laevis* (Daudin) in South Wales, U.K.

G. J. Measey

School of Biological Sciences, University of Bristol, Bristol BS8 1UG, U.K.

(Accepted 30 March 1998)

## Abstract

African clawed frogs (*Xenopus laevis*) in a South Wales pond ate a wide variety and size range of prey. Zoobenthos and zooplankton made the greatest contribution to diets, both numerically and by weight. Terrestrial invertebrates made up a small proportion of the diet numerically but a large proportion of the diet mass during the spring and summer. Nektonic prey were present throughout the year but made up a very small proportion of diet. Cannibalism was important when eggs and larvae were present in the pond. Electivity values were consistently positive for chironomids (larvae and pupae) and daphnids but were consistently negative for tubificids. In addition, electivity increased for larger sizes and pupae of *Chironomus plumosus*, but was low for the largest size class (> 12 mm). Electivity of other taxa showed an increase when densities of chironomids and daphnids were reduced. Mean sizes of daphnids and cyclopods were consistently larger in frog stomach contents than in the water column, indicating that predation on zooplankton by *Xenopus laevis* is size-selective.

**Key words:** African clawed frogs, ecology, benthic invertebrates, invasive amphibians, predation, diet selectivity

## INTRODUCTION

Predation in aquatic communities is now widely considered to be of profound importance in structuring prey species diversity, species composition, distribution, feeding and activity levels, and production rates (e.g. see Sih, 1979; Peckarsky & Dodson, 1980; Walde & Davies, 1984) and thus impacting on all aspects of freshwater ecology. Power, Marks & Parker (1992) revealed a four-level trophic cascade in a north American stream where omnivorous fish preferentially consumed predatory invertebrates over chironomid larvae which spun silk-reinforced retreats. These retreats protected the larvae from top (fish) but not intermediate (invertebrate) predators. The introduction of exotic aquatic predators to natural water bodies may prompt such trophic cascades, significantly altering the native species diversity and composition. Invasions into aquatic habitats by fish are frequently instigated by humans and many studies have shown the undesirable effects that introductions have had on natural freshwater ecosystems (e.g. Nile perch in Lake Victoria, see Miller, 1989).

Studies of anuran diets are surprisingly scarce. Those that exist mainly concern examination of gut contents of preserved material (e.g. see Inger & Marx, 1961; Grant, 1996). Other workers have collected faeces for dietary

analysis (Denton & Beebee, 1994). Most studies show that anurans are typically opportunistic generalist predators of invertebrates (Duellman & Trueb, 1986). Ecological studies of diet related to environmental prey availability are absent for a wide range of anurans (but see Cornish *et al.*, 1995). Conversely, numerous dietary studies of aquatic urodeles have contributed to a much greater understanding not only of their diet, but also of amphibian prey selection within a habitat. These investigations have concentrated on predation of either zooplankton (Nuutinen & Ranta, 1986; Zerba & Collins, 1992), zoobenthos (Parker, 1993; 1994), or both (Griffiths, 1986; McWilliams & Bachmann, 1989). Predation by urodeles has been shown to strongly influence the size and distribution of prey (Dodson, 1970), although such studies have largely concentrated upon experimental manipulation of zooplankton sizes, following work based on optimal foraging by fish (Werner & Hall, 1974).

*Xenopus laevis* (Daudin) has been the subject of intensive study in the areas of developmental, cell and molecular biology (Gurdon, 1996). However, ecological studies of this principally aquatic amphibian remain scarce. Examination of gut contents has shown this aglossan genus to have mainly aquatic dietary components of zoobenthos and zooplankton (McCoid &

Fritts, 1980; Schoonbee, Prinsloo & Nxiwini, 1992; Tinsley, Loumont & Kobel, 1996) making them more similar to fish than to other anuran genera. Other investigations have found terrestrial prey to form a significant element of the diet (Kazadi, DeBruyn & Hulselmans, 1986; DeBruyn, Kazadi & Hulselmans, 1996). Laboratory maintenance has been made easy by the ability of *Xenopus* to detect and feed on carrion, although there are few records of this occurring naturally in gut contents. Cannibalism of offspring is also widely reported and may make a significant nutritional contribution, as well as exploiting an otherwise unavailable dietary niche (see Tinsley, Loumont *et al.*, 1996). *Xenopus* species in sub-Saharan Africa inhabit virtually all waterbodies, including large rivers and lakes, as well as permanent and temporary ponds over a wide range of altitudes and temperatures (Tinsley, Loumont *et al.*, 1996). This flexibility in both diet and habitat type has probably contributed to the exploitation by *X. laevis* of newly constructed waterbodies in its native southern Africa, and also to the establishment of feral populations in the United States, Chile, Ascension Island, mainland Europe and the United Kingdom (Tinsley & McCoid, 1996).

Feeding mechanisms of most anuran amphibians involve detection of prey by visual cues followed by capture and retrieval with the tongue (Lauder & Reilly, 1994 and references therein). Aglossan *Xenopus* exhibit a variety of feeding mechanisms corresponding to the diverse components of their diet. Sokol (1969) reported the use of a hyobranchial pump by which planktonic and nektonic prey is captured. Benthic invertebrates are believed to be separated from the sediment by a mechanism involving the forelimbs and hyobranchial ingestion. Detection of the prey is believed to be by the use of the extremely sensitive lateral line organs which are distributed over the head and trunk (Elepfandt, 1996). The eyes are adapted for vision in air (Elepfandt, 1996), and their orientation suggests that they play a minimal part in aquatic prey detection. However, recent studies on the mechanism of terrestrial prey capture in *X. laevis* suggests that terrestrial prey detection is primarily visual. Here prey capture is achieved with a fast body lunge out of the water grasping the prey with the forelimbs and mouth, followed by a fast retreat into the water where the prey is ingested (Measey, 1998). Detection of carrion is primarily through olfaction, although it may also involve lateral line detection of foraging conspecifics (Frye & Avila, 1979). Once located, carrion prey is gripped with the mouth, and pieces are broken for ingestion with the use of the claws on the hindlimbs with a powerful overhead kick (Avila & Frye, 1978).

The aim of this study was to compare the availability of potential food within an aquatic environment to the stomach contents of adult *X. laevis* throughout a year in a small stock pond in South Wales, U.K. Dietary composition and seasonal changes in the diet as well as selective predation for both prey type and prey size are considered.

## MATERIALS AND METHODS

### Study site

The stock pond lies in pastoral land 0.8 km from a small river in South Wales. Water depth varies seasonally (0.8–0.2 m) with 0.8 m of mud lining the deepest areas. Hawthorn (*Crataegus monogyna* Jacq.) and field maple (*Acer campestre* L.) overhang approximately one-third of the water surface. The pond is split into four areas by walls in which holes allow access into each adjacent area. The water is clear in the winter and a dense growth of opposite leafed pondweed (*Groenlandia densa* (L.)) fills 20% of the pond in spring. This is overtaken in summer by duckweed (*Spirodela polyrhiza* (L.)) which covers two-thirds of the surface, dying back in the autumn. For a complete description of the pond and its natural history, see Measey (1997).

### Sampling of *X. laevis* and stomach contents

From August 1995 to August 1996, *X. laevis* were collected by trapping with 6 modified fyke nets (funnel traps) baited with lambs liver contained within a mesh bag. Traps were set at dusk and collected at dawn on 2 consecutive nights. The frogs were freeze-branded (see Daugherty, 1976) and transported to a bench, where they were sexed, weighed, and the snout–vent length (SVL) was measured. All frogs were sexed on their secondary sexual characteristics: protruding labial lobes in females and formation of nuptial pads on the forearms of males. *X. laevis* were aged using skeletochronology and categorized into ‘young’ and ‘old’ (see Measey & Tinsley, 1998).

Stomach contents were removed from 20 *X. laevis* (or as many as numbers captured permitted) by stomach flushing (Legler & Sullivan, 1979) within 4 h of capture. Frogs were sampled in a randomized fashion from all those caught, removing individual animals from a bucket. Each frog was stomach-flushed using a 50 ml syringe, with a 120-mm long, 3-mm diameter plastic tube. A small piece of moist cardboard was used to gently open the frog’s mouth, and the plastic tube was inserted carefully into the mouth and then into the stomach where 50 ml of dechlorinated water was injected slowly. Stomach contents were flushed out, captured in a plastic container and immediately preserved in 10% formalin. If no items were flushed from the stomach, the procedure was repeated twice. In the laboratory, all prey were identified and chironomid larvae were sorted with a dissecting microscope into 1 of 4 size categories (0–4, 4–8, 8–12, >12 mm) representing approximate instars of this most abundant benthic invertebrate item. After enumeration, prey were blotted on tissue paper, and the formalin-wet-biomass of all organisms in each taxon was determined to the nearest 0.01 g (Sartorius BA 310P). Numbers of zooplankton were estimated by evenly distributing and averaging counts of 3 areas of 10 mm<sup>2</sup> multiplied by the total area

covered. A small sample of zooplankton was taken with a wide-bore pipette (12 mm<sup>2</sup>), and the body length (not including spines in daphnids and from head to furcal rami in cyclopods) of the first 5 individuals of each species present were measured to the nearest 0.01 mm with a calibrated ocular micrometer fitted to a binocular microscope.

### Sampling of available prey

Within 24 h of collecting all *X. laevis*, 3 benthic invertebrate samples and 4 zooplankton samples were collected in a random fashion from regular sampling areas around the pond. Each benthic invertebrate sample was made up of 10 cores of mud of 0.00125 m<sup>2</sup> to a depth of 0.1 m, pooled in a 250 µm mesh net and washed. Zooplankton samples were taken with single vertical hauls from the sediment to the surface with a 250 µm zooplankton net in a known water depth, and samples were immediately fixed in 10% formalin. In the laboratory, live benthic invertebrates were sorted by eye from small portions of mud resuspended in water in a white tray and fixed in 10% formalin. To facilitate constant searching effort, the tray contents were agitated and searched 3 times after the last benthic invertebrate found. Fixed samples were then identified, enumerated and weighed (see above). A sub-sample of 6 ml of zooplankton was taken from each sample for enumeration and identification.

### Data analysis

To examine the relationships of prey usage between sexes and between frogs of different ages, Wilcoxon matched-pairs signed ranks tests were conducted on averaged data. Spearman rank correlations and Wilcoxon matched-pairs signed ranks tests were used to test whether available prey and prey eaten were related for common benthic and zooplankton prey. For  $\chi^2$  tests of gender differences, occasions on which individuals were sampled more than once were deleted.

To examine size-selection by *X. laevis*, comparisons were made in the size distribution of chironomids, cyclopods, and daphnids between the stomach contents and samples from the pond. Analysis was restricted to these groups as they were most abundant in stomach contents throughout the study.

A measure of relative abundance of prey in the diet compared to relative abundance of zooplankton ( $n$  per m<sup>3</sup>) and benthic invertebrates ( $n$  per m<sup>2</sup>) in the pond was made using Vanderploeg & Scavia's (1979) (see Lechowicz, 1982 for justification) relativized electivity index ( $E^*$ ):

$$E^* = \frac{W_i - \frac{1}{n}}{W_i + \frac{1}{n}} \quad \text{with} \quad W_i = \frac{r_i}{\sum r_i p_i}$$

where  $r_i$  is the relative abundance of prey type  $i$  in the diet,  $p_i$  is the relative abundance of prey type  $i$  in the environment and  $n$  is the number of prey types included in the analysis. This index gives a value (from +1 to -1) of the over- or under-representation of prey in the diet in proportion to their relative abundance in the environment. Values near zero represent neutral selectivity.

### RESULTS

In the field, over 27 sampling occasions from August 1995 to August 1996, *X. laevis* from the pond were stomach-flushed a total of 406 times, representing 21% of total captures during that period. Individual frogs were flushed a total of one to six times (1 = 177; 2 = 49; 3 = 28; 4 = 9; 5 = 1; 6 = 1). After three stomach-flushes, 12.6% yielded no prey or skin. No *X. laevis* died, nor were the frogs found to have suffered any deleterious effects immediately after stomach flushing. No significant difference was found in the recapture rates of *X. laevis* which had been stomach-flushed ( $F_{1,926} = 0.357$ ,  $P = 0.550$ ). Of stomachs flushed, 85.2% contained prey

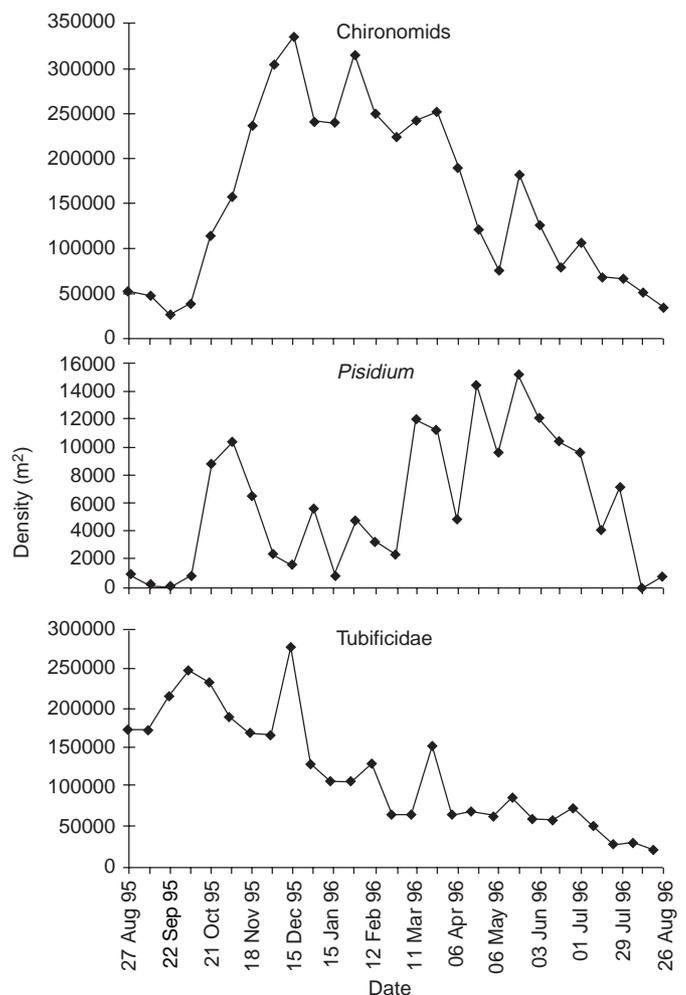
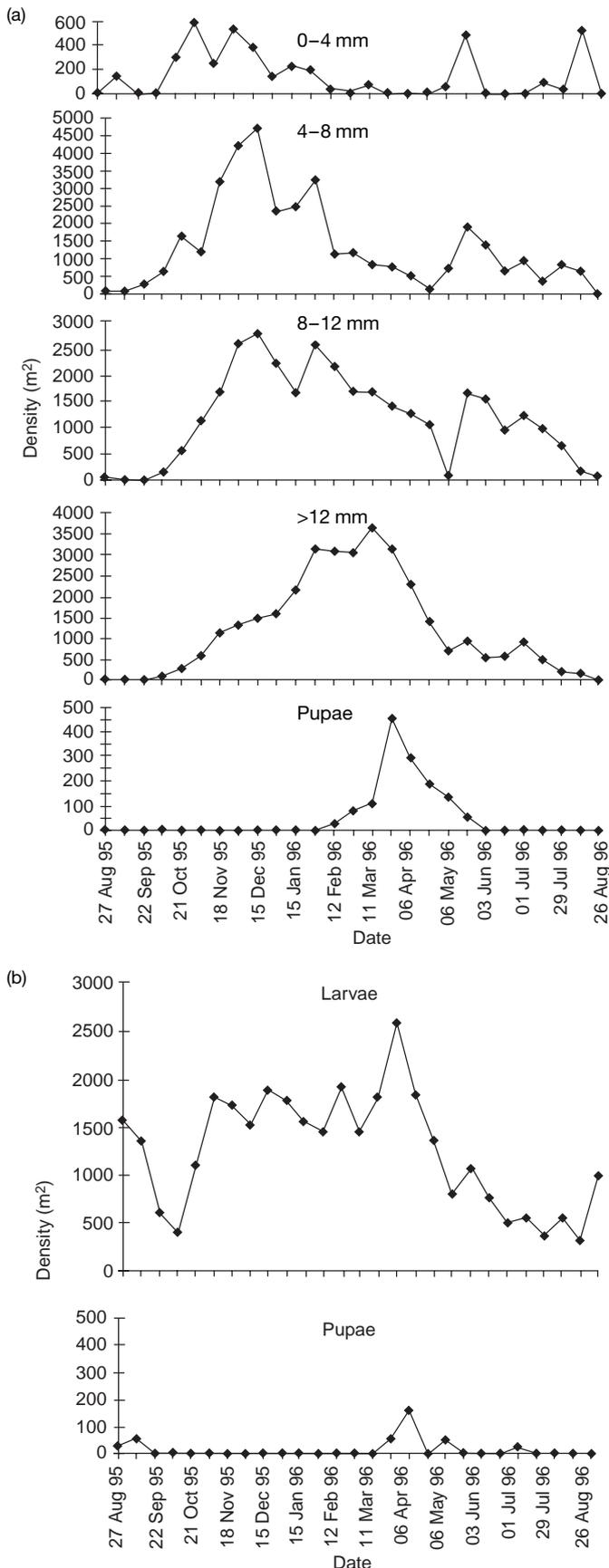


Fig. 1. Density of major benthic invertebrate fauna sampled at fortnightly intervals from August 1995 to August 1996.



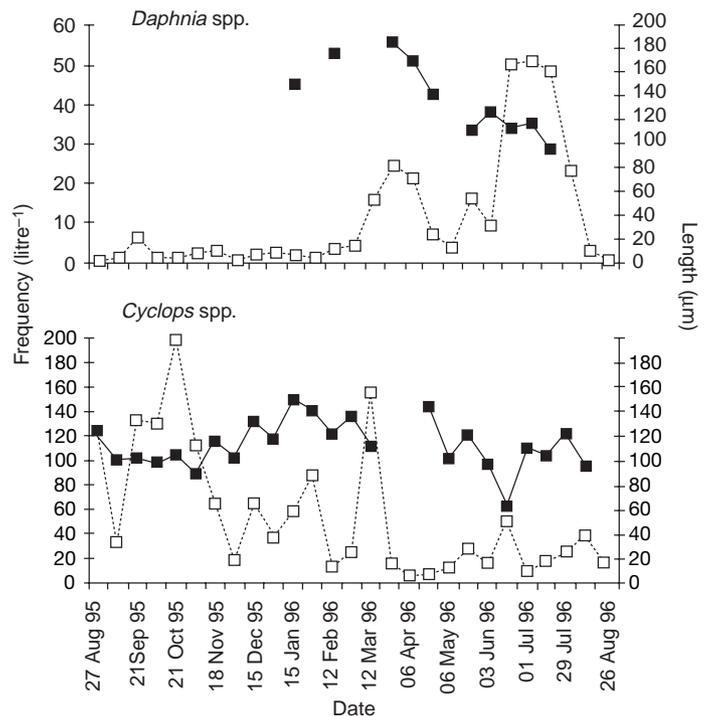
**Fig. 2.** Seasonal abundance of pupae and various size classes (0–4, 4–8, 8–12, >12 mm) of chironomid larvae sampled at fortnightly intervals from August 1995 to August 1996: (a) *Chironomus plumosus*, (b) *Anatópynia varia*.

and 13.3% sloughed skin (nine of which had only skin). There was no significant difference in the presence of ingested skin between males (57%) and females (43%) ( $\chi^2$  test,  $P > 0.05$ ). The percentage of stomachs containing sloughed skins sharply increased in June 1996. Many stomachs contained detritus and some vegetative fronds (turions) of the duck-weed *Spirodela polyrhiza*, but no floating forms of *S. polyrhiza*. No other vegetation was found.

**Prey availability**

Densities of common benthic invertebrates were seen to fluctuate from August 1995 to August 1996 (Fig. 1). The major components were tubificid worms (whose abundance peaked in autumn), chironomid larvae (*Chironomus plumosus* L. and *Anatópynia varia* Fabricius) (whose abundance peaked in winter), and pea mussels (*Pisidium amnicum* (Müller)) (whose abundance peaked in summer). Densities of *C. plumosus* and *A. varia* were further divided into larval size classes (for *C. plumosus*) and pupae (Fig. 2), which shows the growth of a cohort of *C. plumosus*. Pupae of both species peaked in the spring with pupae of *A. varia* showing a smaller second peak in autumn.

The densities of zooplankton composition were seen to fluctuate from August 1995 to August 1996 (Fig. 3). The major components were cladocerans, whose abundance peaked in early summer, and copepods, whose abundance peaked in autumn. Zooplankton sizes varied



**Fig. 3.** Open squares, density of major zooplankton taxa sampled at fortnightly intervals from August 1995 to August 1996; closed squares, sizes of zooplankton found from August 1995 to August 1996.

**Table 1.** The contribution of each prey habitat group to the diet of *X. laevis* in a pond in South Wales from August 1995 to August 1996. (See Table 2 for composition of each prey habitat group)

Dates	Nos. stomachs	Weight of stomach cont. g/frog (No./frog)	% Mass benthic in sample (% frequency)	% Mass zooplankton in sample (% frequency)	% Mass nektonic in sample (% frequency)	% Mass <i>X. laevis</i> in sample (% frequency)	% Mass terrestrial in sample (% frequency)
26 Aug 95	9	0.0 (222.9)	3.8 (0.1)	11.5 (99.7)	5.2 (0.0)	0.0 (0.0)	79.5 (0.1)
09 Sep 95	11	0.0 (3.0)	43.9 (78.8)	0.0 (0.0)	1.7 (6.1)	0.0 (0.0)	54.4 (15.2)
21 Sep 95	18	0.1 (44.7)	22.6 (10.3)	6.6 (87.0)	5.6 (0.1)	0.0 (0.0)	65.2 (2.6)
07 Oct 95	16	0.1 (613.3)	48.6 (0.6)	36.5 (99.4)	0.0 (0.0)	0.0 (0.0)	14.9 (0.0)
21 Oct 95	19	0.1 (298.5)	13.5 (1.4)	68.5 (98.4)	1.3 (0.1)	0.0 (0.0)	16.7 (0.1)
03 Nov 95	20	0.1 (300.2)	19.3 (1.6)	63.5 (98.3)	10.8 (0.0)	0.0 (0.0)	6.4 (0.1)
17 Nov 95	20	0.1 (289.2)	56.1 (8.0)	19.4 (91.6)	0.6 (0.1)	0.0 (0.0)	23.8 (0.3)
02 Dec 95	0	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
14 Dec 95	0	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
03 Jan 96	14	0.0 (62.1)	62.7 (9.0)	32.4 (90.8)	0.4 (0.1)	0.0 (0.0)	4.6 (0.1)
15 Jan 96	20	0.2 (117.8)	49.2 (20.6)	40.0 (79.0)	0.8 (0.2)	0.0 (0.0)	10.1 (0.3)
30 Jan 96	10	0.2 (169.3)	35.0 (11.4)	65.0 (88.6)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
11 Feb 96	0	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
26 Feb 96	1	0.8 (3.0)	1.2 (66.7)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	98.8 (33.3)
10 Mar 96	9	0.1 (98.8)	49.5 (21.0)	49.9 (78.7)	0.6 (0.2)	0.0 (0.0)	0.0 (0.0)
25 Mar 96	8	0.2 (21.4)	79.6 (98.8)	0.0 (0.0)	1.3 (0.6)	0.0 (0.0)	19.2 (0.6)
06 Apr 96	10	0.3 (110.1)	70.6 (26.8)	26.1 (72.7)	3.3 (0.5)	0.0 (0.0)	0.0 (0.0)
22 Apr 96	21	0.5 (19.4)	12.8 (49.1)	1.7 (49.1)	0.0 (0.2)	0.0 (0.0)	85.5 (1.5)
06 May 96	14	0.1 (14.7)	90.3 (95.1)	0.0 (0.0)	9.7 (4.9)	0.0 (0.0)	0.0 (0.0)
21 May 96	19	0.2 (241.5)	19.4 (4.8)	75.6 (94.8)	4.1 (0.4)	0.0 (0.0)	0.9 (0.1)
02 Jun 96	12	0.2 (41.0)	30.8 (34.8)	0.0 (0.0)	1.5 (0.8)	57.5 (64.0)	10.2 (0.4)
18 Jun 96	14	0.1 (37.8)	37.2 (21.0)	39.4 (75.6)	0.8 (0.6)	0.4 (0.2)	22.2 (2.6)
02 Jul 96	20	0.3 (236.5)	33.7 (13.7)	56.2 (84.8)	5.4 (0.8)	1.3 (0.6)	3.5 (0.1)
14 Jul 96	14	0.4 (443.4)	21.4 (8.3)	74.8 (91.0)	2.7 (0.6)	0.0 (0.0)	1.0 (0.0)
29 Jul 96	20	0.2 (57.2)	31.9 (34.5)	16.0 (63.1)	2.7 (1.7)	0.1 (0.1)	49.3 (0.6)
12 Aug 96	17	0.1 (717.5)	72.6 (1.5)	16.6 (98.4)	7.0 (0.0)	0.0 (0.0)	3.7 (0.0)
26 Aug 96	17	0.1 (61.2)	18.4 (4.4)	1.6 (70.0)	10.5 (1.3)	0.0 (0.0)	69.4 (24.2)
Means	13.1	0.2 (156.5)	34.2 (23.1)	26.0 (59.7)	2.8 (0.7)	2.2 (2.4)	23.7 (3.0)

during the year, with sizes of both daphnids and cyclo-pods greater in the winter than the summer (Fig. 3).

### Composition of stomach content

Data on stomach contents have been divided up into groups by prey habitat and consequently by the probable mechanism of predation (see Table 1). The prey category '*X. laevis*' has been placed in a separate group which comprises larvae and eggs of *X. laevis*. The mean weight of full stomach contents was constant throughout the year ( $0.16 \pm 0.03$  g), although composition of prey varied. Zoobenthos and zooplankton consistently made up the largest components of stomach contents, with terrestrial prey peaking in spring and summer. *X. laevis* made an important contribution to stomach contents only during summer 1996, when breeding occurred in the pond (Measey & Tinsley, 1998). The contribution of nektonic prey was consistently low throughout the year. From combined data, contributions of each prey habitat group to the diet of *X. laevis* over one year has been estimated (Table 1). Each group shows a large taxonomic range of invertebrate (and vertebrate) prey, but the majority of prey is made up of very few taxonomic groups. The availability of the most important dietary components was sampled

quantitatively (benthic invertebrates and zooplankton) and made up 65% of the total weight and 98.7% of the numbers of individual prey in the diet. Prey of terrestrial origin also appear to be of importance (25.4% of weight) but are made of very few (0.5%) items (see Table 1).

Vertebrate prey were found in the stomachs of four (1%) *X. laevis* from the pond. The front leg and scapula of a bank vole (*Clethrionomys glareolus* (Schreber)) was found to be intact (and the flesh still pink) and feathers in sheaths of a chick (unidentified) were found in the stomachs of three frogs which had also ingested terrestrial maggots (see Table 2).

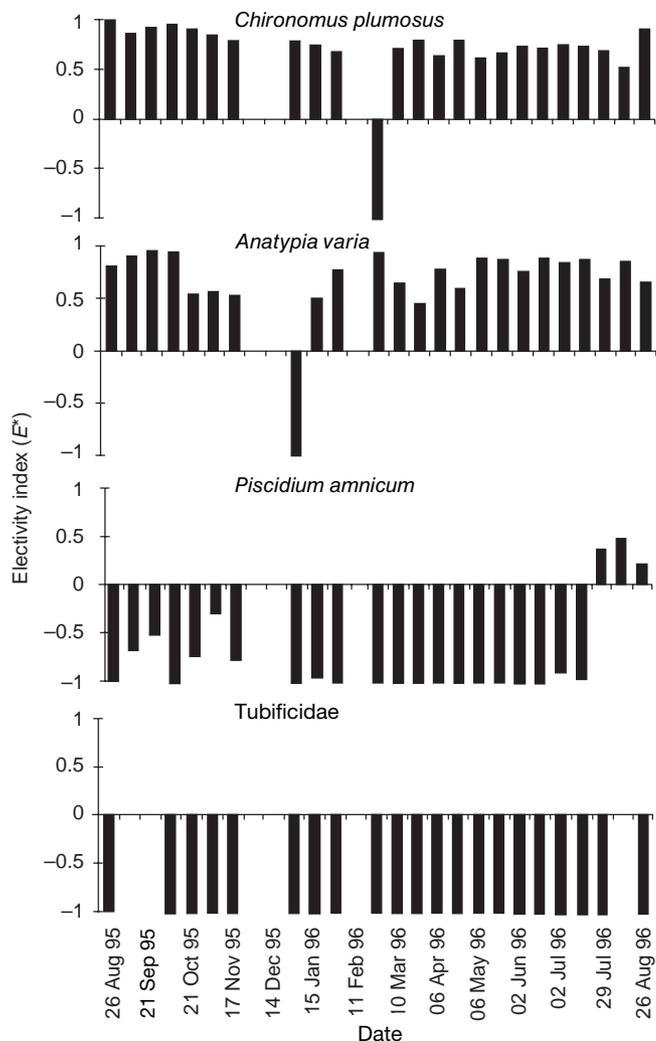
There were no significant differences between the sexes ( $W=19$ ,  $n=10$ ,  $P=0.415$ ) or between ages ( $W=19$ ,  $n=10$ ,  $P=0.415$ ) for numbers of zoobenthos and zooplankton food types. However, mean weights of these prey were found to be significantly greater in females than males ( $W=0.0$ ,  $n=10$ ,  $P=0.006$ ) and greater in younger than older ( $W=0.0$ ,  $n=10$ ,  $P=0.006$ ) individuals.

### Prey preferences

Electivities for benthic prey numbers (Fig. 4) showed marked preferences for chironomid larvae throughout

**Table 2.** The total contribution of prey types ((a) terrestrial, (b) benthic, (c) zooplankton, (d) *X. laevis*, (e) nektonic) found in the stomach contents of *X. laevis* from Black Shed Pond, South Wales (data collected August 1995 to August 1996). Estimates are based on the sum of all sampling dates. Generally identification was made to the lowest taxonomic level, but due to the state of decomposition of some items, this was not always possible. Some species were not identified to species due to a constraint upon time and expertise available

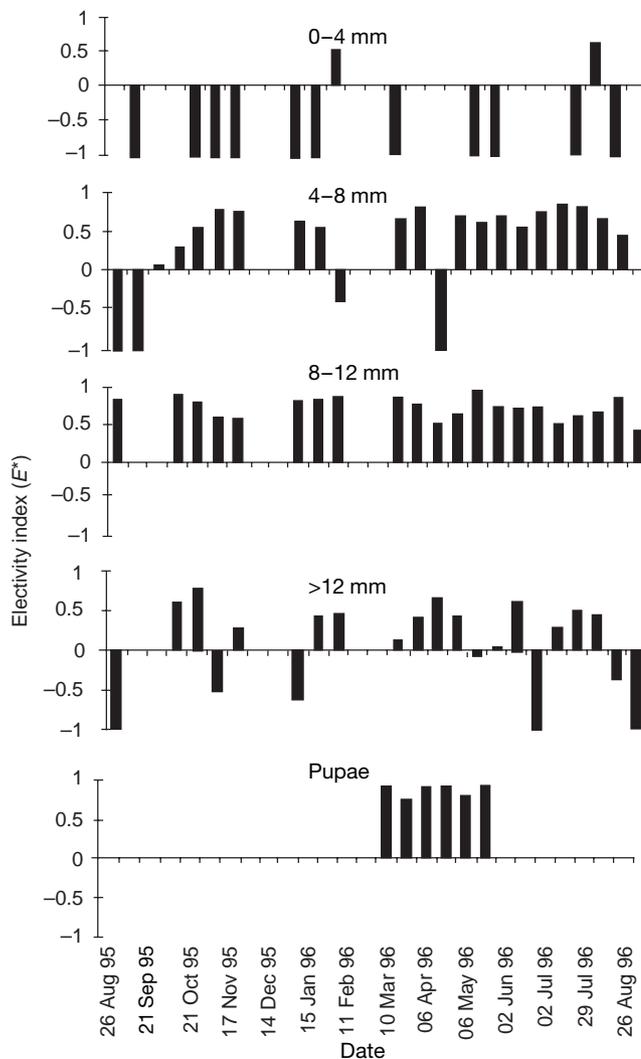
Prey	Common name	% of sample dates ( <i>n</i> = 27) prey occurred in diet	% of total terrestrial food ( <i>n</i> = 366)	% of weight total terrestrial food (total = 15.2g)	% <i>X. laevis</i> eating item ( <i>n</i> = 366)	Mean no. items ingested
<b>Terrestrial</b>						
Invertebrates						
ANNELEIDA						
<i>Lumbricus</i> sp	Earthworm	33.3	4.10	69.07	3.55	1.15
CHELICERATA						
Arachnida	Spider	7.4	1.09	0.11	1.09	1.00
Chilopoda	Centipede	7.4	0.55	0.65	0.55	1.00
CRUSTACEA						
<i>Porcellio spinicornis</i>	Woodlouse	44.4	12.57	7.61	6.56	1.92
UNIRAMIA						
Diptera	Adult Fly	25.9	5.46	0.95	3.55	1.54
	Larvae	11.1	8.20	2.55	1.64	5.00
<i>Forficula auricularia</i>	Earwig	22.2	3.01	3.03	2.19	1.38
Coleoptera, (e.g. <i>Leistus rufomarginatus</i> )	Ground beetle	18.5	2.46	2.40	2.74	1.13
Lepidoptera	Larvae Caterpillar	3.7	0.82	0.51	0.82	1.00
<i>Rhopalosiphum nymphaeae</i>	Aphid	7.4	61.38	0.34	2.46	24.25
Vertebrates						
AVES						
Unidentified	Chick	3.7	0.30	20.3	1.09	0.01
MAMMALIA						
<i>Clethrionomys glareolus</i>	Bank Vole	3.7	0.06	10.75	0.27	0.25
<b>Benthic</b>						
PLATYHELMINTHES						
<i>Polycelis tenuis</i>		7.41	0.27	0.13	0.82	1.00
ANNELEIDA						
Tubificidae		0.0	0.00	0.00	0.00	0.00
MOLLUSCA						
<i>Pisidium amnicum</i>		40.7	2.92	5.59	8.47	4.61
CRUSTACEA						
<i>Asellus aquaticus</i>		37.04	0.06	0.44	2.73	1.30
UNIRAMIA						
<i>Chironomus plumosus</i>	0-4 mm	7.4	0.10	0.01	0.55	2.50
	4-8 mm	74.1	26.88	9.16	36.07	9.96
	8-12 mm	81.5	29.31	28.27	46.45	8.44
	>12 mm	70.4	9.71	20.32	30.05	4.32
	Pupae	59.3	4.64	7.85	21.04	2.95
<i>Anatopynia varia</i>	Larvae	81.5	17.03	13.90	43.72	5.21
	Pupae	63.0	9.63	14.31	25.68	5.01
<b>Zooplankton</b>						
CRUSTACEA						
<i>Daphnids</i>	Water flea	63.0	36.02	57.36	13.11	472.38
<i>Cyclopods</i>	Copepods	37.0	63.97	42.59	9.84	1118.47
UNIRAMIA						
<i>Chaoborus</i> sp.	Phantom midges	11.0	0.01	0.05	1.64	1.00
<b><i>X. laevis</i></b>						
Skin	African clawed frog	92.59	12.78	66.49	13.93	1.00
Larvae		3.7	0.25	0.48	0.27	1.00
Eggs		18.5	86.97	33.03	2.73	34.70
<b>Nektonic</b>						
UNIRAMIA						
<i>Cloeon dipterum</i>	Larvae Mayfly	25.9	27.85	7.55	4.64	2.59
<i>Limnephilus</i> sp.	Larvae Caddisfly	3.7	0.63	0.22	0.27	1.00
<i>Corixa punctata</i>	Water boatman	25.9	5.70	16.36	.46	1.00
<i>Gerris lacustris</i>	Adult Pond skator	3.7	0.63	1.78	.27	1.00
<i>Notonecta</i> sp.	Adult Backswimmer	7.4	3.80	6.96	1.09	1.50
Coleoptera (e.g. <i>Hygrobia hermani</i> )	Adult Water beetle	51.9	40.51	40.93	8.74	2.00
	Larvae	29.6	17.72	23.83	4.37	1.75
Zygoptera	Larvae Damselfly	7.4	1.27	0.96	0.55	1.00



**Fig. 4.** Vanderploeg & Scavia's (1979) electivity index ( $E^*$ ) for common benthic invertebrate taxa selected by *X. laevis* in a pond in South Wales.

the year, while *P. amnicum* seemed to be selected when other prey densities were low. Figure 5 shows electivities for numbers of different size classes of *C. plumosus*. Positive electivities are particularly prominent for 4–8 and 8–12 mm size classes, as well as pupae when present. Spearman rank correlation coefficients show no correlation between relative abundances of benthic and zooplankton prey in the environment and in the diet ( $r_{25} = 0.071$  (chironomids), 0.294 (pea-mussels), 0.448 (cyclopods);  $P > 0.05$ ), except for daphnids ( $r_{25} = 0.333$ ;  $P < 0.05$ ).

Electivities for numbers of zooplankton taxa (Fig. 6) show positive selection of daphnids for most of the year, while cyclopods show positive selection mostly in the autumn (when density peaked, see Fig. 4). The mean sizes of zooplankton in the stomachs of *X. laevis* sampled were found to be consistently higher than those available, irrespective of sex or age of the frog (daphnids,  $W = 33.0$ ,  $n = 8$ ,  $P = 0.042$ ; cyclopods,  $W = 126.0$ ,  $n = 16$ ,  $P = 0.003$ , Fig. 7).



**Fig. 5.** Vanderploeg & Scavia's (1979) electivity index ( $E^*$ ) for different size classes of *Chironomus plumosus* selected by *X. laevis* in a pond in South Wales.

## DISCUSSION AND CONCLUSION

*Xenopus laevis* are generalist predators that consume a wide variety and size range of invertebrate prey. In this study, zoobenthos and zooplankton consistently made the greatest contribution to diets, both numerically and by weight. This is consistent with other studies of the stomach contents of *X. laevis* in an impoundment in its native Transkei (Schoonbee *et al.*, 1992) and from a stream in California (McCoid & Fritts, 1980). Principal prey in Transkei were chironomids, notonectids, and ostracods, but no estimate of the of bulk of these items was recorded. Ostracods contributed very little to the diet of *X. laevis* in this study, and their abundance was seasonal. Live ostracods which had passed through the guts of *X. laevis* were found when individuals, collected when ostracods were most abundant in the autumn, were screened for *Protopolystoma xenopodis* (Price) eggs (see Measey, 1997). The ability of these small crustaceans to survive passage through predators' digestive

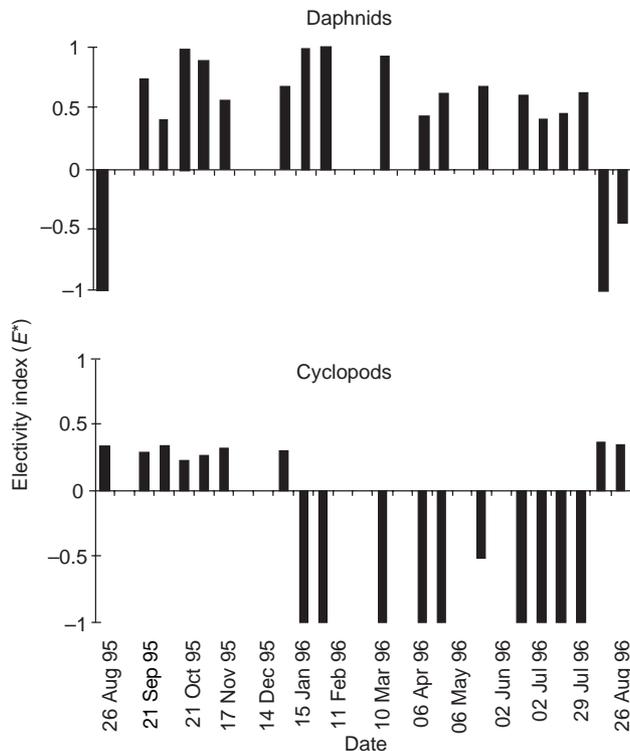


Fig. 6. Vanderploeg & Scavia's (1979) electivity index ( $E^*$ ) for common zooplankton taxa selected by *X. laevis* in a pond in South Wales.

systems is known elsewhere (H. I. Griffiths, pers. comm.). This suggests that although ostracods may be ingested in large quantities in the Transkei, the amount they contribute to the nutrition of individual *X. laevis* may be very low. In common with the present study, tubificids found to be abundant in the environment were completely absent from stomach contents. This phenomenon has been observed in fish diets, and is attributed to the unavailability of tubificids which are found to move deeper into the sediment in the presence of predators (Kornijów & Moss, 1998). The opposite was found to be true of *Asellus* which were extremely scarce in zoobenthos samples, but not infrequent in stomach contents. The size of *Asellus aquaticus* L. ingested was very small (1–3 mm). This may be because the *A. aquaticus* population had been heavily predated by *X. laevis*. Similar observations have been made for fish predation of benthic invertebrates (see Northcote, 1988).

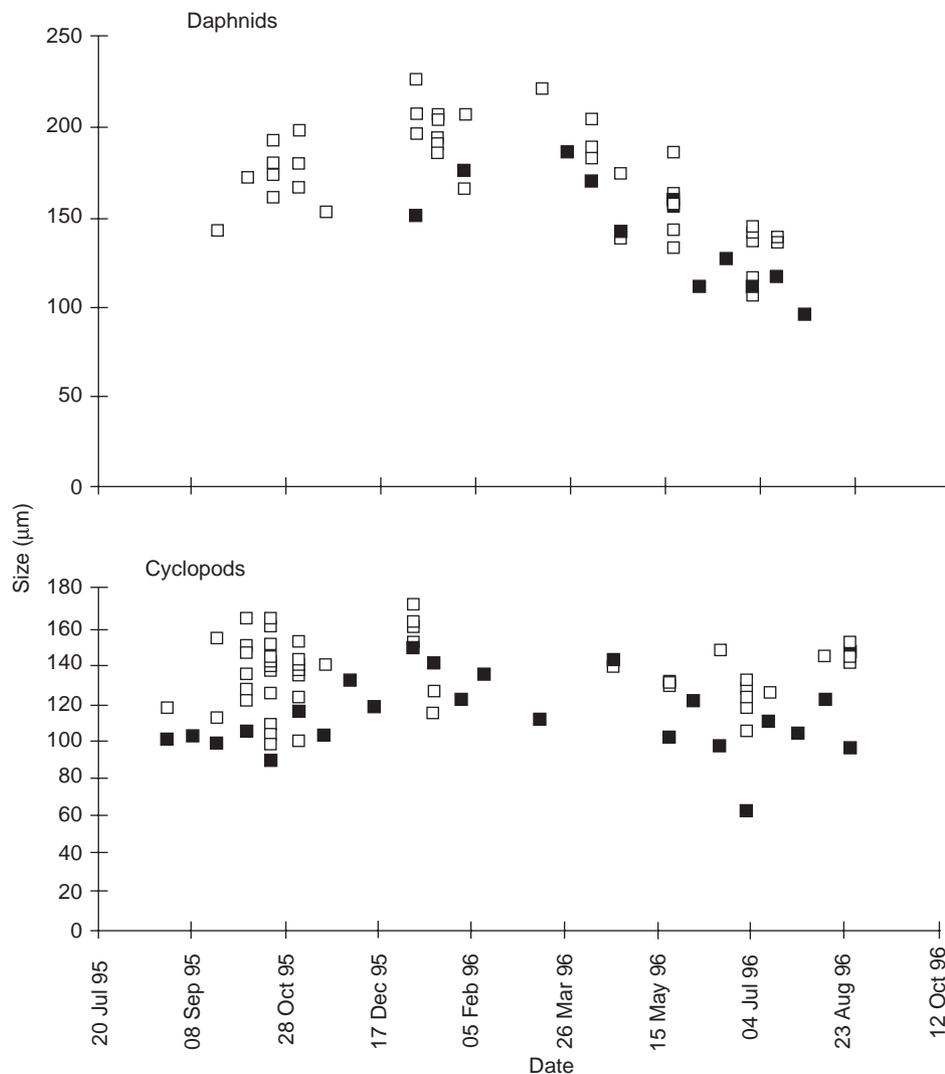
The study of McCoid & Fritts (1980) in California involved *X. laevis* from a stream which would have provided a different availability of potential prey. However, McCoid & Fritts (1980) found that *X. laevis* preyed principally on benthic invertebrates and zooplankton. Fish (*Eucyclogobius newberryi* Girard, *Gambusia affinis* Baird & Girard, and *Clevelandia ios* (Jordan & Gilbert)) were found in the gut contents of Californian *X. laevis* inhabiting the estuary of the Santa Clara River (Lafferty & Page, 1997). No fish were present in the pond during this study. Schoonbee *et al.*

(1992) did not state whether fish were present in the Transkei impoundment, but the ability of *X. laevis* to catch a range of nektonic prey suggests that had fish been present they may have been consumed. Small fish are easily caught by *X. laevis* when they pass close to a waiting individual (G. J. Measey, pers. obs.). This sit and wait method of capturing nektonic prey may explain their consistently low proportion in the diet. However, this study conflicts with the conclusions of McCoid & Fritts (1980) and Avila & Frye (1978) that *X. laevis* is a clumsy predator adapted for capturing sessile or slow-moving items. Laboratory studies are needed to investigate the ability of *X. laevis* to consume nektonic prey, and the extent to which pursuit of these items is related to the individual condition of the frog.

Tissue of a bank vole (*C. glareolus*) found in the stomach of one *X. laevis* was still pink, suggesting that it had been taken from a whole animal that was either alive or recently dead. However, the presence of maggots with the chick infers substantial decomposition of this vertebrate prior to ingestion by *X. laevis*. The opportunity to feed on carrion prey in the pond was noted to exist with the presence of a dead bird (September 1996) and rabbit (November 1994) floating in the water, and avian bones found in benthic samples.

Evidence of cannibalism in the diet of *X. laevis* is well reported in the literature (see Tinsley *et al.*, 1996). In the pond the incidence of cannibalism was restricted to one period during this study when frogs were known to be mating. *X. wittei* Tinsley, Kobel & Fischberg females have been observed to eat their own eggs immediately after spawning (Measey & Tinsley, 1997; also see Dreyer, 1913). In the present study, most incidents of cannibalism were of eggs, 95% of which were eaten by females. It is probable that the numbers of tadpoles found in the diet (one record) under-represented the extent to which predation occurred. Tadpole densities were very high for 4 weeks after the first matings were observed, and then declined rapidly. Although predation of tadpoles by coleopterans and odonates is thought to be high (Azevedo-Ramos *et al.*, 1992; Tejedo, 1993), it is probable that the high density of *X. laevis* adults caused the sudden disappearance of tadpoles. In January 1995, *Rana temporaria* L. spawned in the pond and numbers of larvae were monitored. As no *R. temporaria* larvae were found in stomach contents of *X. laevis*, there is no conclusive evidence of predation on *R. temporaria*. However, no tadpoles or metamorphs of *R. temporaria* could be found by April, 1995 (Measey, 1997). Low numbers of *Triturus cristatus* Laurenti and *T. helveticus* Razoumowsky were also found in the pond during the study, but as none was recaptured, populations could not be monitored (see Measey, 1997).

Although the diet of the frogs was dominated numerically by aquatic organisms, terrestrial organisms consistently contributed a large proportion to the total mass of prey consumed. In a recent review of diet in *Xenopus*, the large amount of terrestrial prey reported in stomach contents has been considered unlikely to have arisen solely from animals that have fallen or been



**Fig. 7.** Sizes of daphnids and cyclopods compared to those eaten by *X. laevis*. Solid symbols, prey available; open symbols, prey eaten.

swept from overhanging vegetation into the water (Tinsley *et al.*, 1996). Terrestrial prey were found to account for 57% of the numbers of food in the stomachs of adult *X. fraseri* Boulenger (see DeBruyn *et al.*, 1996). DeBruyn *et al.* (1996) made no study of available prey, although reported stomach contents were not similar in composition to those in the present study or in Schoonbee *et al.* (1992) and McCoid & Fritts (1980). In the present study, items of terrestrial origin make up a quarter of the weight of all ingested prey. It is assumed that not all of these items were caught by *X. laevis* while in their terrestrial habitat. Many may have been ingested after falling inadvertently into the pond, where they may have become trapped by the surface tension or, in the case of *Lumbricus* sp., fallen to the bottom. However, as there are such high numbers of woodlice in the diet, it is plausible that they were taken from outside the pond (see Measey, 1998).

Griffiths (1986) found a marked increase in the numbers of sloughed newt skins in the stomachs of Welsh newts in March, which he attributed to their

return to the water. It is not known how often *X. laevis* slough their skins, although some preliminary observations suggest that moulting occurred once a week (Bouwer, Ewer & Shiff, 1953). *X. laevis* showed an increase in the frequency of sloughed skin in stomachs at the beginning of June 1996, which coincided with the onset of mating. No significant difference was found between males and females, suggesting that the frequency of skin sloughing increased for both sexes prior to mating.

Turions of *S. polyrhiza* were found in the benthos throughout the year, although they were most abundant during the winter and spring when floating thalli were absent from the surface. Their occurrence in the stomach contents of *X. laevis* is believed to be accidental during ingestion of benthic invertebrates. However, large numbers of aphids (*Rhopalosiphum nymphaeae* L.) were found in *X. laevis* stomachs in August 1996 which were available in abundance, feeding on top of the floating thalli of *S. polyrhiza*. This suggests that *X. laevis* are able to separate these small ingested prey and

avoid ingestion of vegetation. Laboratory studies have shown that *Xenopus* readily separate terrestrial prey from *Lemna minor* L. thalli when feeding at the surface (see Measey & Tinsley, 1997).

Results in this study clearly demonstrate the size-selective nature of predation by *X. laevis* on zoobenthic and zooplanktonic prey. Prey preferences show *X. laevis* to be selecting against the smallest (0–4 mm) and largest (>12 mm) *C. plumosus* larvae and to be positively selecting pupae (Fig. 5). The smallest size class occurred in very low numbers in the benthic samples because hatchlings are pelagic (Oliver, 1971). However, owing to the method and frequency of sampling, larvae <2 mm were probably underestimated (see Kornijów, 1997). Positive electivities in Fig. 5 (0–4 mm) and a negative electivity (4–8 mm) are spurious results due to low numbers of available or actual prey. The largest *C. plumosus* size class (>12 mm) made up the greatest portion of the weight of all *C. plumosus* available (Fig. 2) and yet was not selected. Similar results have been found for sculpin, perch, and bluegills, and it has been suggested that small tube-building chironomids are most available because they are least proficient at tube building and are probably closer to the sediment surface (Werner, Mittelbach *et al.*, 1983; Hershey, 1985; Kornijów, 1997). Larger tube-dwelling chironomids burrow deeper with increasing size, such that small bluegills contained virtually no chironomids greater than 12 mm in their stomach contents (Werner *et al.*, 1983). Larger chironomids burrow deeper into the sediment during winter, especially if they are not feeding (Oliver, 1971). This would suggest that these most profitable larger *C. plumosus* are not easily available to *X. laevis*, even though they make up a very large part of the available biomass (Fig. 2). Furthermore, *X. laevis* stomachs found to contain this largest size class of *C. plumosus* were also found to have the silk tubes and sediment in their stomachs.

The extent to which predation on *C. plumosus* pupae is recorded may greatly under-represent true quantities as sampling represents only a few hours of each fortnight. The pupal stage of chironomids has a very short duration, from a few hours to a few days, after which the pharate ascends from the sediment to the surface and is especially vulnerable to predation (Oliver, 1971). *A. varia* are shown to be selected over *C. plumosus* (Fig. 4): this may be because these animals are predatory, spending more time at the sediment surface (Oliver, 1971) and when disturbed are far more active swimmers than *C. plumosus* (G. J. Measey, pers. obs.). Hershey (1987) showed that predation of chironomid larvae is strongly influenced by their behaviour. Further laboratory studies are needed to fully explain the observed results, in particular to describe the precise mechanism by which these chironomids are extracted from the sediment.

Seasonal effects in preferences are not shown for many of the generally preferred prey (e.g. chironomids and cladocerans). However, items with lower overall

electivities showed seasonal effects when availability of other items were decreased. This indicates that certain food are preferred (e.g. chironomids and cladocerans) over less desirable ones (e.g. pea-mussels and copepods). Thus *X. laevis* displayed size-selective predation as well as preference of certain taxa over others.

It is likely that the exact restructuring of the aquatic macroinvertebrate community by *X. laevis*, recorded in this study, would not occur in the absence of this invading species, or by any native species. Native piscine predators of benthic macroinvertebrates are often absent from smaller lentic habitats in the U.K., unless artificially stocked. This is partly due to the extremes of physical conditions which such water bodies undergo, both daily and seasonally. Physical conditions, such as low dissolved oxygen concentrations, do not affect air breathing *X. laevis*. Diel and seasonal fluctuations in such small freshwater habitats pose severe physiological constraints for many organisms, but are poorly studied (Everard, 1997). More knowledge about the differences in prey detection and capture between native and feral species is essential to predict possible trophic cascades caused by invasive predators on natural habitats.

The exact mechanisms involved in catching different prey found in the diet of *X. laevis* in the pond are not known. For most items of terrestrial origin, prey may have been detected visually (Measey, 1998), or by detection of waves in the surface tension (Elepfandt, 1996). As the eyes are adapted for vision in air, detection and selection of benthic, nektonic, and zooplanktonic prey may have been primarily by the use of lateral line organs. Activity of *X. laevis* is known to be crepuscular and nocturnal (see Tinsley & Kobel, 1996), which corresponds to high activity levels of some of their most important prey (Hershey, 1987). Lannoo (1986) found that vision was not necessary for *Ambystoma maculatum* (Shaw) larvae to be size-selective in their predation of zooplankton. He further suggested that lateral line organs may be primarily responsible for zooplanktivory in enucleated salamander larvae. The generalisation made in analyses that all prey are equally available is probably not realistic for *X. laevis* which detects some prey with its lateral line system. Prey may not only be distributed at different depths in the sediment, but may produce different intensities of detectable movement. For example, Power *et al.* (1992) suggested that the fish in their study could not detect the chironomid larvae within their retreats, in contrast to their invertebrate predators. Unequal evaluation of individual prey may account for some of the observed selectivity of both benthic and zooplanktonic prey. *X. laevis* is known to have two distinct classes of olfactory receptors, enabling the frogs to detect airborne odours as well as water-soluble odorants (Freitag *et al.*, 1995). However, it is not known to what extent olfaction aids in detection of prey other than carrion. Extensive laboratory studies are needed for elucidation on these important points.

## Acknowledgments

The author thanks R. Tinsley, P. Miller and G. Jones for comments on an earlier draft of this manuscript, and R. Griffiths and R. Kornijów for constructive reviews. This study was funded by a NERC studentship.

## REFERENCES

- Avila, V. L. & Frye, P. G. (1978). Feeding behaviour of the African clawed frog (*Xenopus laevis* Daudin): (Amphibia, Anura, Pipidae): effect of prey type. *J. Herpet.* **12**: 391–396.
- Azevedo-Ramos, C., Van Shuys, M., Hero, J. M. & Magrus, J. (1992). Influence of tadpole movement on predation by odonate naiads. *J. Herpet.* **26**: 335–338.
- Bouwer, S., Ewer, D. & Shiff, C. (1953). Frequency of moulting in Anura. *Nature* **172**: 408.
- Cornish, C. A., Oldham, R. S., Bullock, D. J. & Bullock, J. A. (1995). Comparison of the diet of adult toads (*Bufo bufo* L.) with pitfall trap catches. *Herpetol. J.* **5**: 236–238.
- Daugherty, C. H. (1976). Freeze-branding as a technique for marking anurans. *Copeia* **1976**: 836–838.
- DeBruyn, L., Kazadi, M. & Hulselmans, J. (1996). Diet of *Xenopus fraseri* (Anura Pipidae). *J. Herpet.* **30**: 82–85.
- Denton, J. S. & Beebee, T. J. C. (1994). The basis of niche separation during terrestrial life between two species of toad (*Bufo bufo* and *Bufo calamita*): competition or specialisation? *Oecologia* **97**: 390–398.
- Dodson, S. I. (1970). Complementary feeding niches sustained by size-selective predation. *Limnol. Oceanogr.* **15**: 131–137.
- Dreyer, T. F. (1913). The “plathander” (*Xenopus laevis*). *Trans. R. Soc., S. Afr.* **3**: 341–355.
- Duellman, W. E. & Trueb, L. (1986). *Biology of amphibians*. New York: McGraw-Hill.
- Elepfandt, A. (1996). Sensory perception and the lateral line system in the clawed frog, *Xenopus*. In: *The biology of Xenopus*: 177–193. Tinsley, R. C. & Kobel, H. R. (Eds). Oxford: Oxford University Press.
- Everard, M. (1997). Encouragement for work on small aquatic systems. *Freshwater Forum* **9**: 61–62.
- Freitag, J., Krieger, J., Strotmann, J. & Breer, H. (1995). Two classes of olfactory receptors in *Xenopus laevis*. *Neuron* **15**: 1383–1392.
- Frye, P. G. & Avila, V. L. (1979). Food-initiated behaviour of the African clawed frog (*Xenopus laevis*): effect of population density. *Herpetologica* **35**: 30–37.
- Grant, G. S. (1996). Prey of the introduced *Bufo marinus* on American Samoa. *Herpet. Rev.* **27**: 67–69.
- Griffiths, R. A. (1986). Feeding niche overlap and food selection in smooth and palmate newts, *Triturus vulgaris* and *Triturus helveticus*, at a pond in mid-Wales. *J. Anim. Ecol.* **55**: 201–214.
- Gurdon, J. B. (1996). Introductory comments: *Xenopus* as a laboratory animal. In: *The biology of Xenopus*: 3–6. Tinsley, R. C. & Kobel, H. R. (Eds). Oxford: Oxford University Press.
- Hershey, A. E. (1985). Effects of predatory sculpin on the chironomid communities in an Arctic Lake. *Ecology* **66**: 1131–1138.
- Hershey, A. E. (1987). Tubes and foraging behavior in larval Chironomidae – implications for predator avoidance. *Oecologia* **73**: 236–241.
- Inger, R. & Marx, H. (1961). The food of amphibians. *Explor.-Parc natn. Upemba* **64**: 1–85.
- Kazadi, M., DeBruyn, L. & Hulselmans, J. (1986). Notes ecologiques sur les contenus stomacaux de une collection de *Xenopus laevis* (Daudin 1803) (Amphibia: Anura) du Ruande. *Annals Soc. r. zool. Belg.* **116**: 227–234.
- Kornijów, R. (1997). The impact of predation by perch on the size-structure of *Chironomus* larvae—the role of vertical distribution of the prey in the bottom sediments, and habitat complexity. *Hydrobiologia* **342**: 207–213.
- Kornijów, R. & Moss, B. (1998). Vertical distribution of in-benthos in relation to fish and floating-leaved macrophyte populations. In *The structuring role of submerged macrophytes in lakes*: 227–232. Jepesen, E., Søndergaard, M., Søndergaard, M. & Christofferesen, K. (Eds). New York: Springer.
- Lafferty, K. D. & Page, C. J. (1997). Predation on the endangered tidewater goby, *Eucyclogobius newberryi*, by the introduced African clawed frog, *Xenopus laevis*, with notes on the frog’s parasites. *Copeia* **1997**: 589–592.
- Lannoo, M. J. (1986). Vision is not necessary for size-selective zooplanktivory in aquatic salamanders. *Can. J. Zool.* **64**: 1071–1075.
- Lauder, G. V. & Reilly, S. M. (1994). Amphibian feeding behaviour: comparative biomechanics and evolution. In: *Advances in comparative and environmental physiology*: 163–195. Bels, V. L., Chardon, M. & Vandewalle, P. (Eds). Berlin: Springer Verlag.
- Lechowicz, M. J. (1982). The sampling characteristics of electivity indexes. *Oecologia* **52**: 22–30.
- Legler, J. M. & Sullivan, L. J. (1979). The application of stomach-flushing to lizards and anurans. *Herpetologica* **35**: 107–110.
- McCoid, M. J. & Fritts, T. H. (1980). Notes on the diet of a feral population of *Xenopus laevis* (Pipidae) in California. *SWest. Nat.* **25**: 257–282.
- McWilliams, S. R. & Bachmann, M. (1989). Foraging ecology and prey preference of pond-form larval small-mouthed salamanders *Ambystoma texanum*. *Copeia* **1989**: 948–961.
- Measey, G. J. (1997). *Ecology of feral Xenopus*. PhD dissertation, University of Bristol.
- Measey, G. J. (1998). Terrestrial prey capture in *Xenopus laevis*. *Copeia* **1998**: 787–791.
- Measey, G. J. & Tinsley, R. C. (1997). Mating behaviour of *Xenopus wittei*. *Copeia* **1997**: 601–609.
- Measey, G. J. & Tinsley, R. C. (1998). Feral *Xenopus laevis* in South Wales. *Herpetol. J.* **8**: 23–27.
- Miller, D. J. (1989). Introductions and extinctions of fish in the African Great Lakes. *TREE* **4**: 56–59.
- Northcote, T. G. (1988). Fish in the structure and function of freshwater ecosystems: a “top-down” view. *Can. J. Fish. Aquat. Sci.* **45**: 361–379.
- Nuutinen, V. & Ranta, E. (1986). Size-selective predation on zooplankton by the smooth newt, *Triturus vulgaris*. *Oikos* **47**: 83–91.
- Oliver, D. R. (1971). Life history of the Chironomidae. *Ann. Rev. Ent.* **16**: 211–230.
- Parker, M. S. (1993). Size-selective predation on benthic macro-invertebrates by stream-dwelling salamander larvae. *Arch. Hydrobiol.* **128**: 385–400.
- Parker, M. S. (1994). Feeding ecology of stream-dwelling Pacific giant salamander larvae (*Dicamptodon tenebrosus*). *Copeia* **1994**: 705–718.
- Peckarsky, B. L. & Dodson, S. I. (1980). Do stonefly predators influence benthic distributions? *Ecology* **61**: 1275–1282.
- Power, M. E., Marks, J. C. & Parker, M. S. (1992). Variation in the vulnerability of prey to different predators – community-level consequences. *Ecology* **73**: 2218–2223.
- Schoonbee, H. J., Prinsloo, J. F. & Nxiweni, J. G. (1992). Observations on the feeding habits of larvae, juvenile and adult stages of African clawed frog, *Xenopus laevis*, in impoundments in Transkei. *Wat. S. Afr.* **18**: 227–236.
- Sih, A. (1979). Stability of prey behavioral responses to predator density. *J. Anim. Ecol.* **48**: 79–89.
- Sokol, O. M. (1969). Feeding in the pipid frog *Hymenochirus boettgeri*. *Herpetologica* **25**: 9–24.

- Tejedo, M. (1993). Size-dependent vulnerability and behavioural responses of tadpoles of two anura species to beetle larvae predators. *Herpetologica* **49**: 287–294.
- Tinsley, R. C. & Kobel, H. R. (1996). *The biology of Xenopus*. Oxford: Oxford University Press.
- Tinsley, R. C., Loumont, C. & Kobel, H. R. (1996). Geographical distribution and ecology. In: *The biology of Xenopus*: 35–59. Tinsley, R. C. & Kobel, H. R. (Eds). Oxford: Oxford University Press.
- Tinsley, R. C. & McCoid, M. J. (1996). Feral populations of *Xenopus* outside Africa. In: *The biology of Xenopus*: 81–94. Tinsley, R. C. & Kobel, H. R. (Eds). Oxford: Oxford University Press.
- Vanderploeg, H. A. & Scavia, D. (1979). Calculation and use of selectivity coefficients of feeding: zooplankton grazing. *Ecol. Model.* **7**: 135–149.
- Walde, S. J. & Davies, R. W. (1984). Invertebrate predation and lotic communities: evaluation of in situ enclosure/exclosure experiments. *Ecology* **65**: 1206–1213.
- Werner, E. E. & Hall, D. J. (1974). Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology* **55**: 1042–1052.
- Werner, E. E., Mittelbach, D. J., Hall, D. J. & Gilliam, J. F. (1983). Experimental tests of optimal habitat use in fish: The role of relative habitat profitability. *Ecology* **64**: 1525–1539.
- Zerba, K. E. & Collins, J. P. (1992). Spatial heterogeneity and individual variation in diet of an aquatic top predator. *Ecology* **73**: 268–279.