

Functional response of suspension feeding anuran larvae to different particle sizes at low concentrations (Amphibia)

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Abstract

The influence of particle size, initial particle concentration and larval stage on the ingestion rate, 'retention efficiency', and filtering rate of anuran larvae with varying filter apparatus anatomy and different life histories was investigated for four species. Larvae of premetamorphic Stages 28 and 32 and prometamorphic Stage 40 were selected for filtering experiments on the basis of their different growth rates. Three different sizes of silica gel particles were offered as mock food. Particle concentration was measured photometrically. The Michaelis-Menten model was used to describe the dependency of ingestion rate, filtering rate, and 'retention efficiency' upon initial particle concentration, and to calculate maximum ingestion rate, threshold concentration, and the half-saturation constant.

(1) The highest ingestion rates, filtering rates and 'retention efficiencies' were achieved by *Xenopus laevis* larvae, followed by *Bufo calamita* larvae. *Bufo bufo* larvae lay at the opposite end of the scale. *Rana temporaria* larvae were placed between *B. calamita* and *B. bufo* larvae. This order is attributed to differences in life histories, especially the different breeding environments in which these larvae occur. (2) The larger the particle size and the older the stage, the greater the tendency toward saturation of the ingestion rate, filtering rate and 'retention efficiency'. These filtration parameters are graded according to particle size. The ingestion rate (number of particles), filtration rate and 'retention efficiency' are greatest for PS3. Ingestion volume is greatest for PS1. The difference between PS3 and PS2 on the one hand, and PS1 on the other, is often great; for Stage 28 *X. laevis* it is very great. This shows that larvae ingest large particles more effectively, and that the most effective ingestion takes place at Stages 28 and 32, owing to the growth function of these stages. The ability of larvae to ingest large particles effectively is possibly a very basic phylogenetic characteristic. (3) The threshold concentration is lowest when the particles are at their largest. In accordance with conclusions drawn by other authors, threshold feeding is attributed to regulation by buccal pumping and mucus production. Considerable importance is attributed to threshold feeding with respect to larval adaptation to oligotrophic environments.

Introduction

Populations of anuran larvae are strongly controlled by nutrient supply and predators. Environmental evaporation also has a catastrophic

effect on larval populations. A high nutrient supply, i.e. a high ingestion of exploitable food, leads to large and rapid growth, rapid development and therefore early metamorphosis (Collins, 1979; Hota & Dash, 1986; Murray, 1990; Wilbur, 1977).

Larger larvae are the subject of predation less often than smaller larvae (Cronin & Travis, 1986; Formanowicz, 1986; Travis, 1983; Semlitsch, 1990; Semlitsch & Gibbons, 1988). At the same time, the preference of predators for smaller larvae means that the latter no longer exist as food competitors, which, in turn, accelerates the growth of larger larvae (DeBenedictis, 1974). Accelerated development allows the larvae to escape more quickly from aquatic predators and environmental evaporation. The supply and indigestibility (and digestibility) of food therefore has a direct influence on the survival rate of larvae and therefore also on the population dynamics of adults.

It is known that macroinvertebrates (i.e. amphipoda, oligochaeta, mysidacea) have a considerable influence on the composition of the bottom community through sediment feeding (Krezoski *et al.*, 1978). This is also true of anuran larvae. Dickman (1968) describes the considerable effect of periphyton scraping by *Rana aurora* larvae on the sessile community. The influence of anuran larval grazing and ingestion on the community structure of their ecosystems is often large: i.e. effect on algal diversity and productivity, nitrogen flux, phosphorus and organic carbon content (Seale, 1980; Weigmann, 1982).

Evidently, feeding strategy is of central importance for the understanding of anuran larval biology.

Anuran larvae are, with few exceptions, suspension feeders (Wassersug, 1972). The filter apparatus enables them to exploit a wide range of food sources: tadpoles filter suspended food particles such as phytoplankton and detritus from the water. Tadpoles with keratinized mouth parts scrape food off the substrate, suspend it, and filter it. Many anuran larvae are also bottom feeders. These ingest periphyton, detritus and interstitial organisms from the sediment, and also large quantities of indigestible sediment of different particle sizes (Diaz-Paniagua, 1985, 1989; Harrison, 1987; Hendricks, 1973; Löschenkohl, 1985; Datta Munshi *et al.*, 1986; Sabnis & Kuthe, 1980; Sahu & Khare, 1988; Viertel, 1978).

Seale & Wassersug (1979) studied functional

response of *Rana sylvatica* and *Xenopus laevis* larvae feeding on *Chlorella pyrenoidosa* (cell diameter 2.7 μm ; initial concentrations 5 10^5 to 10^8 algae ml^{-1} or 5 10^6 to 10^9 $\mu\text{m}^3 \text{ml}^{-1}$) and *Anabaena spherica* (cell diameter 5.1 μm ; each colony had an average of 27.9 cells; initial concentrations 6 10^6 to 1.5 10^8 $\mu\text{m}^3 \text{ml}^{-1}$). They demonstrated a lower and upper limit of initial food concentration for filtering and ingestion, as well as a peak in the filtering rate at a critical concentration (definitions see 'Materials and methods, Statistical analysis'). Seale & Beckvar (1980) investigated the ingestion and filtering of *Anabaena spherica* and *Chlorella pyrenoidosa* by *Rana catesbeiana*, *Hyla crucifer* and *Bufo woodhousei fowleri* larvae. All species regulate food intake as a function of volume and biomass and distinguish between different food sources. Ingestion was maximum and constant over a wide range of initial concentrations (*H. crucifer*: 2 10^7 to 4 10^7 $\mu\text{m}^3 \text{ml}^{-1}$; *B. woodhousei fowleri*: 1.5 10^7 to 4 10^7 $\mu\text{m}^3 \text{ml}^{-1}$; *R. catesbeiana*: 1 10^7 to 4 10^7 $\mu\text{m}^3 \text{ml}^{-1}$), and declined at lower concentrations. Threshold feeding was demonstrated. Seale *et al.* (1982) analysed the threshold feeding of *X. laevis* on yeast cells (diameter 3 to 5 μm , Wassersug, 1972) and described a functional response similar to that of suspension feeding zooplankton (crustaceans).

In *Bufo calamita*, *Rana temporaria*, *Bufo bufo* (Gosner Stages 28, 32, 40) and *X. laevis* (Nieuwkoop and Faber Stages 51, 53 and 57) ingestion of *Chlorella fusca* algae (cell diameter 5.8 μm , cell volume 102.2 μm^3) occurred far below the initial food concentrations tested by Seale and Wassersug (1979) for *Rana sylvatica* (i.e., below 5 10^5 *Chlorella pyrenoidosa* ml^{-1} , or 5 10^6 $\mu\text{m}^3 \text{ml}^{-1}$). Apart from *B. bufo*, the early larval stages attained the highest suspension feeding efficiency, corresponding with the high growth rates of these stages. In *B. bufo* only the older larvae showed ingestion at low initial concentrations. Threshold feeding behaviour (threshold concentration) in younger larvae is probably caused by reduction of buccal pumping and mucus production (Viertel, 1990).

Since food particles that were considerably larger (over 150 μm) than those hitherto used in

suspension feeding experiments were found in the intestine of anuran larvae (algae colonies, bacteriophytes, sedimentary particles; Diaz-Paniagua, 1985, 1989; Datta Munshi *et al.*, 1986; Viertel, 1978), several questions arise: (1) It seems probable that tadpole species which develop in environments that are rich in sediment but also oligotrophic, and/or are subject to high food competition, achieve a higher suspension feeding efficiency with larger particles both in the lowest and in high concentrations than species which inhabit nutrient rich waters. The first species depend on being able to exploit every available source of food, such as large plankton, large periphyton and interstitial organisms. This presupposes ingestion even of indigestible bottom sedimentary particles of all sizes and concentrations (substratum feeders). It may also be supposed that species that develop in oligotrophic environments are capable of exploiting the lowest particle concentrations. (2) What influence does higher particle size, i.e. particle volume, have on functional response? Knowledge of the various filter apparatus morphologies and their function (see Viertel 1985, 1987, 1989, 1991; Wassersug, 1972; Wassersug & Hoff, 1979; Wassersug & Rosenberg, 1979) leads to the conclusion that this occurs in different ways. (3) Is suspension feeding efficiency stage dependent under these circumstances? (4) Is functional response comparable with that of suspension feeding crustaceans.

Materials and methods

Selection of species and stages

R. temporaria, *B. calamita* and *B. bufo* have a similar filter apparatus. They represent Orton's (1953) larval Type IV, are bottom feeders and scrape off periphyton with their horny beaks and the toothlets of their oral discs. They are less frequently observed suspension feeding in the water column (see also Löschenkohl, 1985). *B. calamita* larvae are found in small ephemeral and frequently oligotrophic ponds (Beebee, 1983; Bregulla, 1986, 1988; Strijbosch, 1979; Viertel, 1976). *B. bufo* adults spawn in larger, nutrient-

rich, permanent bodies of water (Heusser, 1958, 1960; Viertel, 1976, 1978). *R. temporaria* spawn in both nutrient-rich, permanent water and in temporary water (Savage, 1961; Strijbosch, 1979). *X. laevis* is a pipid larval Type I (Orton, 1953) whose filter apparatus is quite different to that of the species above. It is a microphagous midwater suspension feeder, lacking a horny beak and oral disc, but can also feed facultatively from the bottom and on deposit (Wassersug, 1972; Wassersug, personal communication). This African species also spawns in small ephemeral ponds (Channing; Fischer & Hinkel, personal communications). Furthermore, *X. laevis* is the species whose suspension feeding and filtering mechanism have been investigated most, and which therefore offers valuable opportunities for comparison.

Larvae of *R. temporaria*, *B. bufo* and *B. calamita* were collected and staged using normal tables (Gosner, 1960). *X. laevis* larvae were staged according to Nieuwkoop & Faber (1956). Only criteria of hindlimb development were used. This character is the only diagnostic criterium common to both larval Type I and IV. Stage 51 of Nieuwkoop and Faber corresponds to Stage 28 of Gosner, Stage 53 to Stage 32 (premetamorphic stages according to Etkin, 1968) and Stage 57 to Stage 40 (prometamorphic stages).

Apparatus and adjustment

Grain-sized fractional silica gel (SiO₂, specific gravity 2.6) in three different particle sizes (PS1, PS2, PS3, see Fig. 1) was offered to the larvae as food. Since the larvae under investigation are facultative sediment feeders under natural conditions and generally take in plankton of hard consistency (see above), it may be assumed that this mock food can be used without significantly distorting the results. An experimental chamber of blackened nickel plate was set up with a temperature controlled water-jacket and two cuvette windows for measurement. The total volume of the test chamber was 2000 ml. Measurements using emission spectroscopy revealed that 26 ppb

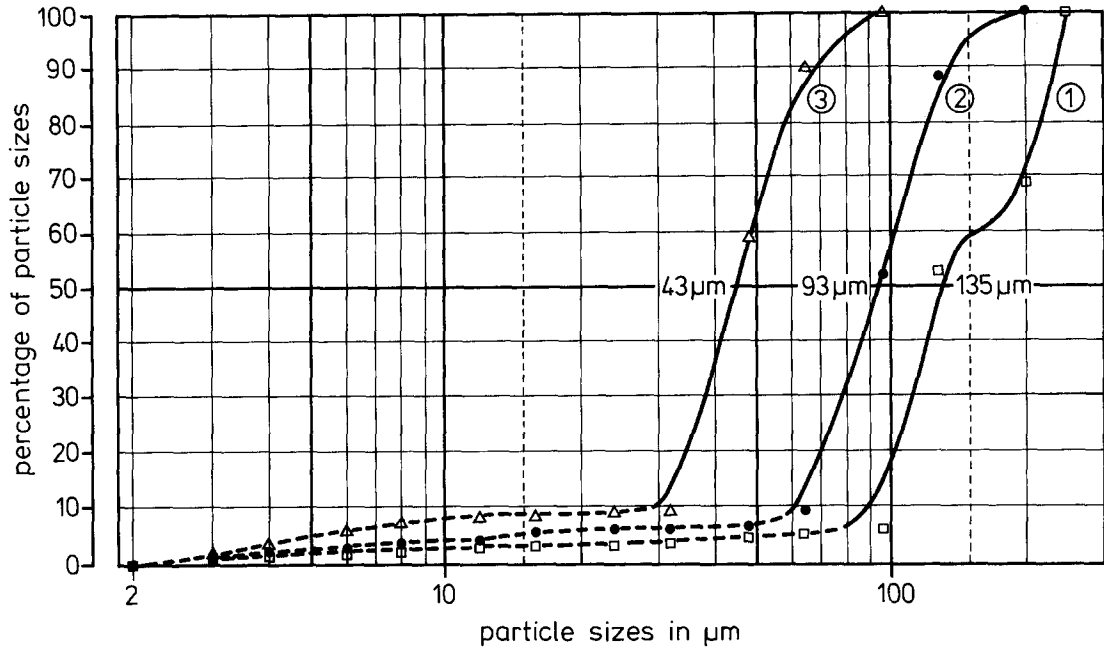


Fig. 1. Percent distribution of particle sizes. Encircled numbers indicate particle sizes PS1, PS2 and PS3. The dashed lines indicate the particles washed away before application. Numbers in μm demonstrate the diameters of 50% of the total sample.

copper, 20 ppb antimony, 60 ppb arsenic and no nickel (precise to 0.1 ppb) was released into the test water in two hours. It is presumed that these quantities had no influence on the tadpoles during the 30 min. experiments (Scheinberg, 1984). Toxic effects were therefore not expected to arise: WHO/FHO recommends maximal concentration of 20–50 ppb arsenic for drinking-water!

A photometric measurement unit was mounted: An electric light bulb (6 V, 0.4 A, 2.4 W, emission spectrum 380–2000 nm) fed by a constant current transformer (Philips PE 1507, 0.15 V, 700 mA) was used as light source. The transmission (Tevini & Häder, 1985) supplied a silicon photocell BPY 47 P (see Siemens Opto-Halbleiter Datenbuch, 1981/82) attached to a compensation recorder. A rejection voltage had to be interposed to compensate for the contrast between low measurement intervals and high open-circuit voltage while taking exact readings in the 0.5–50 mV range. An electronic lowcut-filter (0.1 Hz) eliminated disturbance caused by individual silica gel particles drifting past the silicon photocell.

Owing to its specific gravity, the silica gel sedimented. It was maintained in suspension using a propeller (diameter 45 mm, three vanes, pitch 24 mm) with a rotation speed of ca 200 rev min^{-1} . A net prevented the larvae from mutilation by the propeller. In order to estimate the influence of this current on ingestion, the buccal pump strokes were counted by eye both in turbulent and still particle-free water. The resulting percentage differences in the buccal pump strokes with and without turbulence were included in the ingestion calculations (Fig. 2). Control experiments revealed that a loss of silica gel from suspension nevertheless occurred (PS1 = 25%, PS2 = 25%, PS3 = 20%).

A particle weight-particle number relationship was established by weighing a silica gel sample and counting the particles in this unit of weight under the reversed microscope (Utermöhl, 1958). This allowed the calculation of silica gel weights required to provide particle concentration at $5 \cdot 10^4$, $1 \cdot 10^5$, $2 \cdot 10^5$, $3.3 \cdot 10^5$, $1 \cdot 10^6$, $1.5 \cdot 10^6$ and $2 \cdot 10^6$ per 2 liter test volume. The recording indicated the standard transmission measurement for a

specific concentration of a specific particle size.

All experiments were carried out at 22 ± 0.2 °C. The oxygen concentration was 6.8 ppm (equals 80% saturation, according to Truesdale *et al.*, 1955; cited in Höll, 1979). The oxygen measurements were taken with a Clark electrode (WTW Oxi Digi 88). The carbon dioxide concentration was 2.2 ppm (titration according to Schwörbel, 1966).

Experimental procedure

To prevent photometric disturbance resulting from faeces defecated by the tadpoles, the latter were incubated for 4.5 h in a solution of Vivasorb at a concentration of roughly 80 mOsmol (see also Viertel, 1990). Vivasorb is a clinical food concentrate of essential and non-essential amino acids, essential fatty acids, glucose, oligosaccharides, minerals, vitamins and trace nutrients (Pfrimmer & Co., Pharmazeutische Werke Erlangen). Vivasorb is fully absorbed in the alimentary tract and therefore faeces are not produced. Test feeding with commercially dried fish food and with silica gel showed that the tadpoles resumed ingestion of food and silica gel immediately under these conditions, as was confirmed by examining the alimentary tract. The buccal pump stroke frequency of the larvae incubated in Vivasorb was found to be normal when these were compared with the normally fed larvae. Feeding behaviour is, therefore, assumed to be normal during filtering experiments. Following Vivasorb treatment the tadpoles were introduced into 22 °C AOAC-water (after Ashworth & Crozier, 1972; concentration: 10 mOsmol, hardness: 10 °dH equivalent to 3.57 mval, conductivity: 650 μ S, pH 7.3) for 24 h in order to acclimate them to the water and temperature used in the experiments.

According to the transmission adjustment measurements (standards) the photometric measurement unit was switched on and maintained with the propeller running for about 45 min until temperature and transmission measurement read constant. After reaching constant transmission silica gel was introduced into the experimental chamber according to the standard transmission

measurement (initial concentration of silica gel, C_i). The tadpoles (total mass 1.5–2 g) were introduced into the experimental chamber and ingestion led to a gradual increase in transmission. In order to ensure that the transmission record was running without disturbance, the propeller was switched off 30 min after the start of the experiment causing both silica gel sedimentation and a return to basic transmission (as a control for undisturbed measurement). For the same reason, the whole transmission measurement was repeated: transmission was controlled by resuspending the silica gel with the use of the propeller and allowing it to sediment until basic transmission was reestablished.

To prevent pollution by faeces produced during the experiments by the ingestion of silicagel particles the experimental time was shorter than the clearance time (time for food passing through gut) (Altig & McDearman, 1975; authors' observation).

Critical assessment of methods

In order to discuss the effect of propeller turbulence on buccal pump stroke frequency, particularly for *X. laevis*, it is necessary to verify the results. The effect on the other species was calculated at between 10 and 20%; it was above 20% only at Stage 28 *R. temporaria*. Thus the influence of turbulence may be considered identical for *B. calamita*, *R. temporaria* and *B. bufo*. Although buccal pump stroke frequencies were measured in clear water, they are comparable to rates within the experimental range of particle concentrations. Seale *et al.* (1982) established that Stage 30–34 *X. laevis* adjust their buccal pump stroke frequency and buccal pumping volume to C_i . Continuous pumping with about 117 pump strokes min^{-1} occurs with $C_i = 9 \cdot 10^5$ yeast cells ml^{-1} . The Stage 28 and 32 *X. laevis* buccal pump stroke frequency in particle-free water was calculated at ca 100 and 90 pump strokes min^{-1} , which is not far from the 117 pump strokes min^{-1} counted by Seale *et al.* (1982). Consequently it may be assumed that the low concentrations of silica gel suspension used had no significant effect

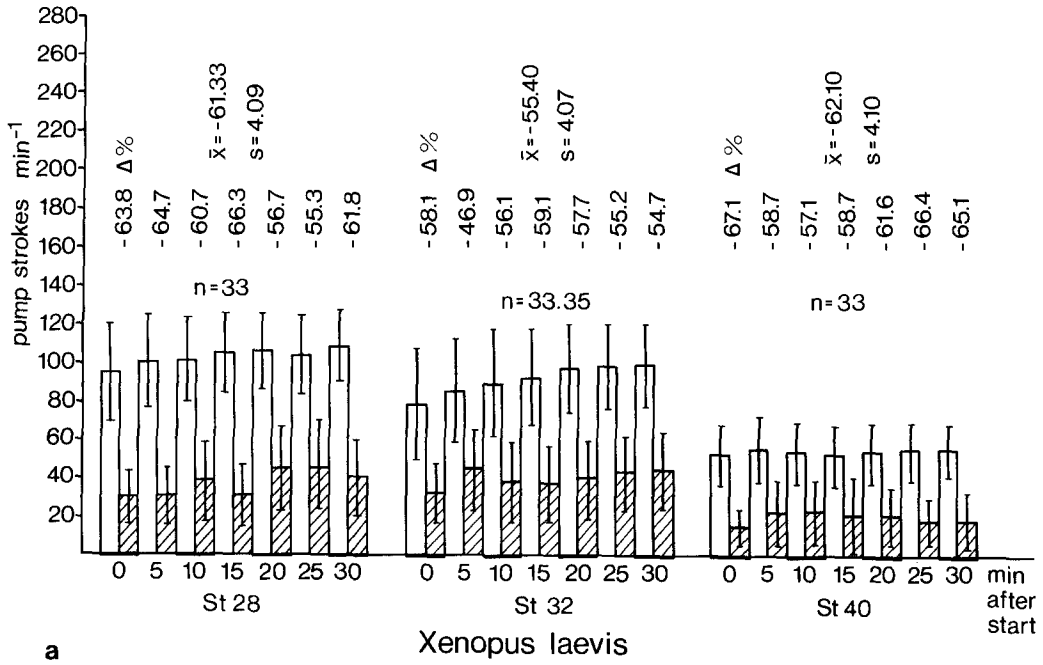


Fig. 2a

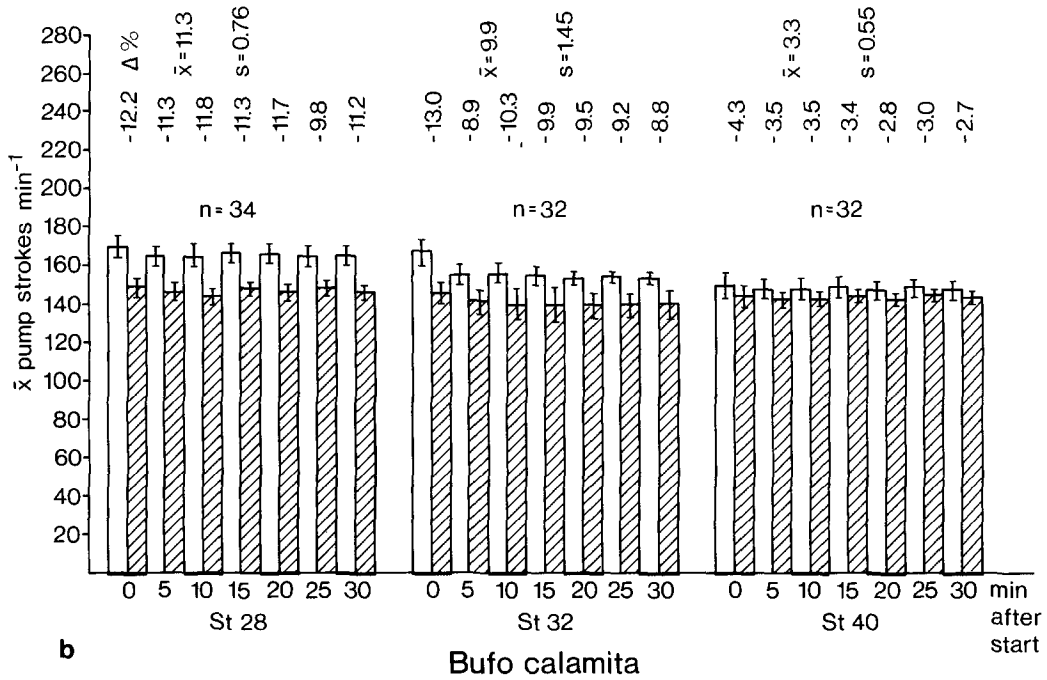
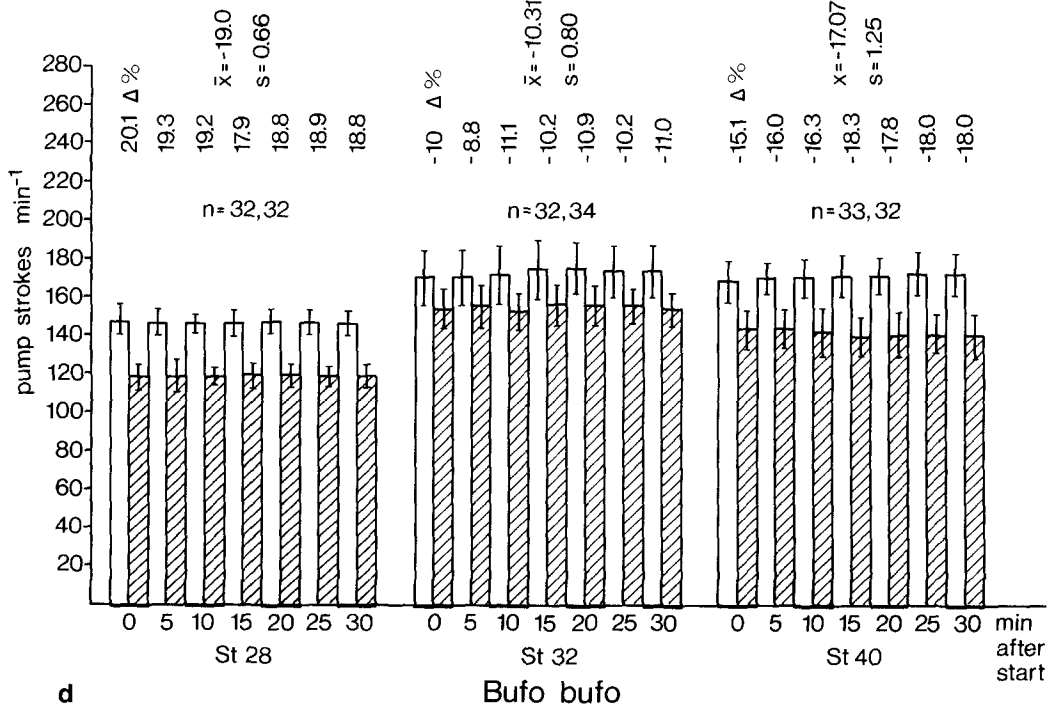
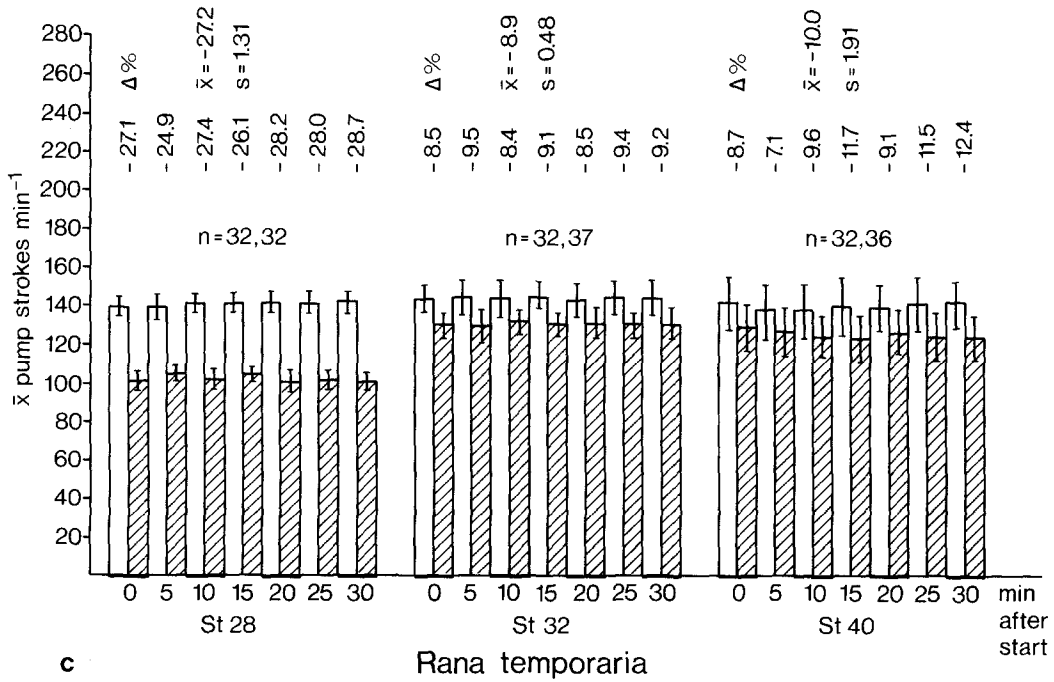


Fig. 2b

Fig. 2a-d. Buccal pump strokes. Open columns = \bar{x} of experiments without turbulence, hatched columns = \bar{x} of experiments with turbulence; significances of \bar{x} differences see Table 3; vertical lines = standard deviations; $\Delta\%$ indicate the differences of tests without and with turbulence; St = stage.



on the buccal pump stroke frequency and therefore did not effect the buccal pumping volume rate of *X. laevis* larvae. The order established here

for suspension feeding efficiency of different species and stages (see 'Results') is identical with that found by Viertel (1990) in filtering experi-

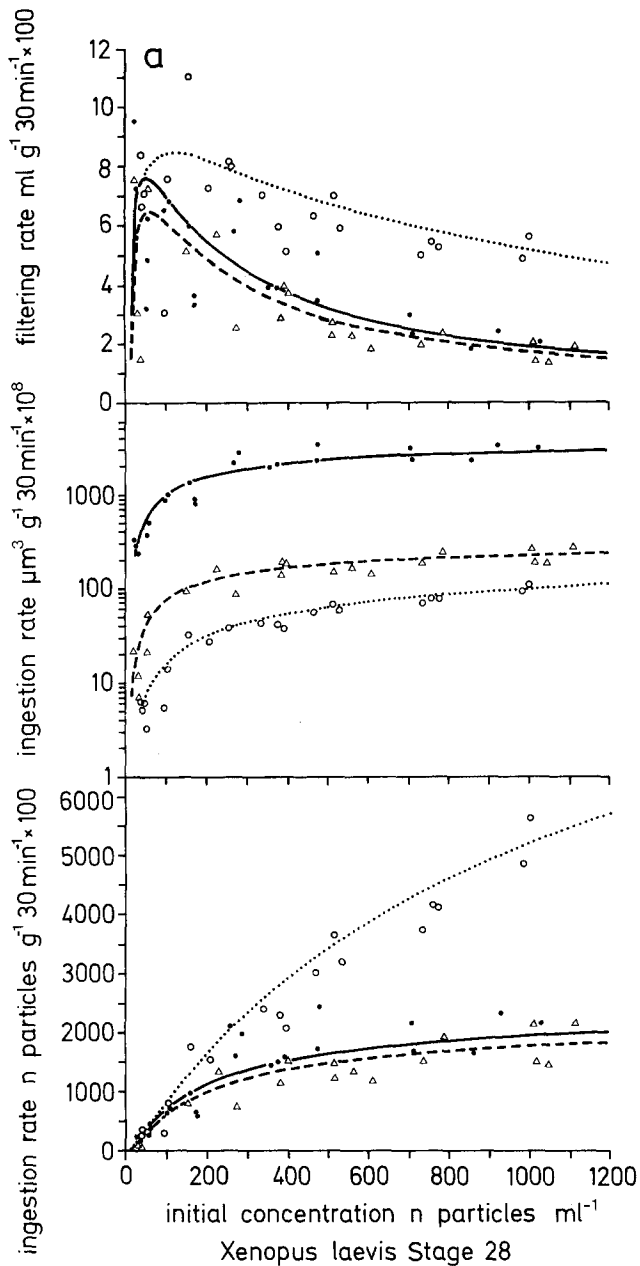


Fig. 3a

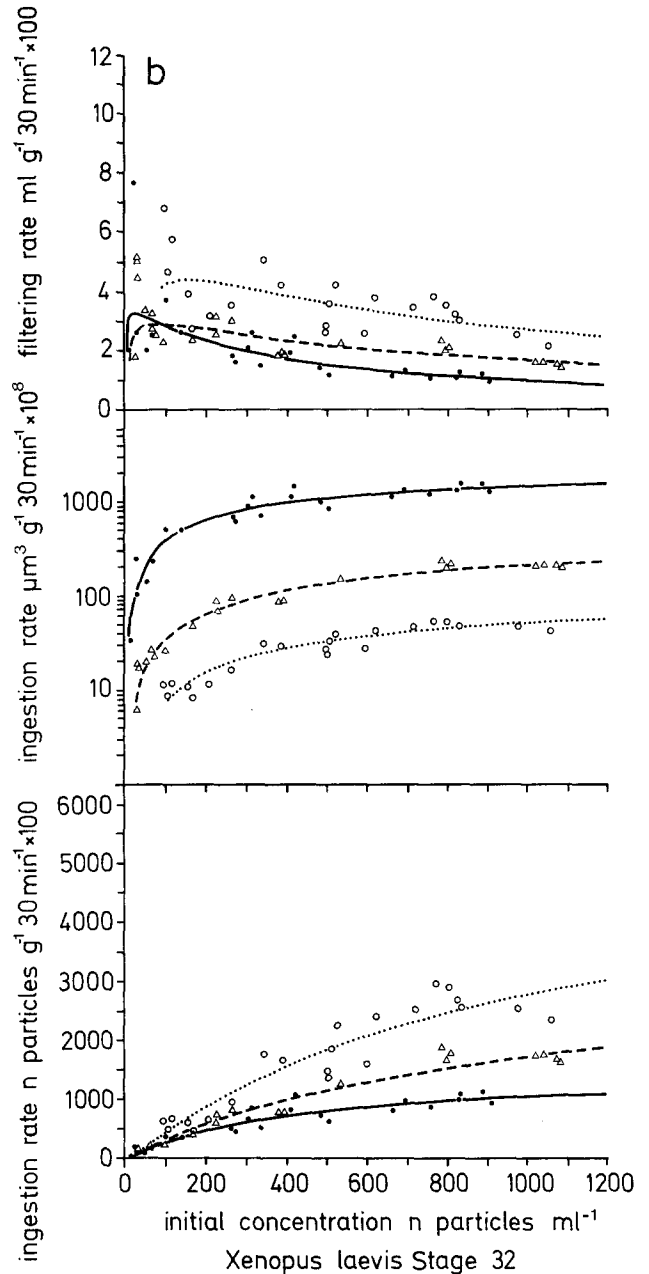


Fig. 3b

Fig. 3a-c. *Xenopus laevis*. Ingestion- and filtering rates plotted against initial concentration. —●— = PS1, —△— = PS2, ...○... = PS3.

ments with *Chlorella fusca*, and *X. laevis*, *B. calamita*, *R. temporaria* and *B. bufo* larvae. The congruence of these results obtained from two entirely different methods (Viertel, 1990; Coulter Counter technology) supports their veracity.

Statistical analysis

To understand functional response, dependence of feeding parameters on particle size and particle concentration must be analyzed. The para-

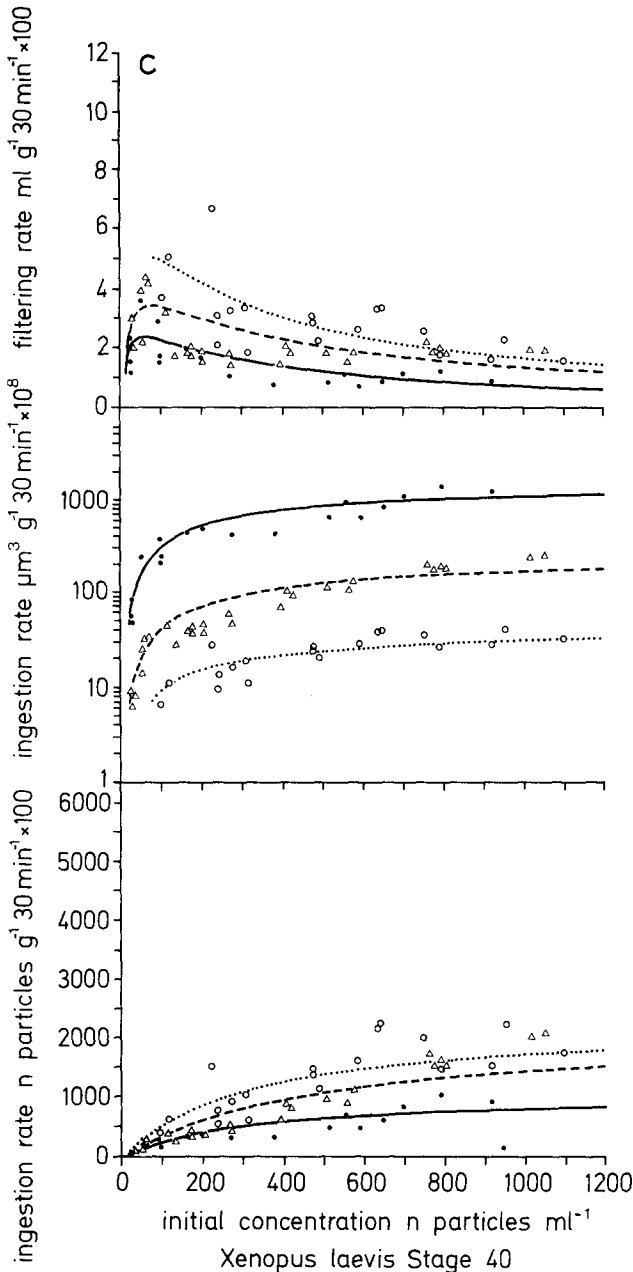


Fig. 3c

meters are: the maximum ingestion rate (I_{\max}), the maximal filtering rate (F_{\max}), the threshold concentration (TC) at which ingestion begins, the retention efficiency (RE), and the critical concentration (CC) at which F_{\max} occurs. CC is synonymous with the term 'incipient limiting level' in zooplankton filter feeders. Ingestion rate is the

number of particles captured per individual or per unit of biomass and time and is the gauge of actual nutrient exploitation by a suspension feeder. Filtering is the water volume cleared of suspended particles (Harvey, 1937; Jorgensen, 1966). The filtering rate characterizes the ability of a suspension feeder to react to a nutrient suspension by increasing or lowering the water current (Jorgensen, 1983). The filtering rate is identical with pumping rate if retention efficiency reaches 100%. The volume of water pumped per unit of time through the filter apparatus is the pumping rate. Retention efficiency is the percentage of food particles of a defined diameter removed from a given nutrient concentration (see Randlov & Riisgard, 1979: $RE = 1 - \text{exhaled concentration} / \text{inhaled concentration}$). It is the gauge of the filtering efficiency of a filter apparatus. In the present study RE is only the percentage of particles removed from the initial concentration of silicagel particles in the experimental chamber. It is therefore apostrophized as 'retention efficiency' ('RE').

The difference between initial transmission measurement of silica gel and final transmission was converted to number of particles according to the adjustment. The silica gel loss by sedimentation was subtracted from this, leaving the number of particles ingested by the tadpoles. The percentage reduction in buccal pump stroke frequency due to propeller turbulence was added (see Fig. 2). The weight of a defined silica gel particle number was known (see above in 'Apparatus and adjustment'). The number of particles was converted to particle volume (weight per particle divided by the specific gravity 2.6). This allowed the calculation of the particle diameter. Although the silica gel particles are in fact polygonal, they were taken to be round for the purposes of this experiment (radius = $\sqrt[3]{\text{particle volume} / (4/3 \pi)}$). Ingestion rates, as number of particles (I_n) and volume of particles (I_v), were calculated based on 1 g larval biomass (live weight) and 30 min experimental duration ($I_n = n \text{ particles g}^{-1} 30 \text{ min}^{-1}$ or $I_v = \mu\text{m}^3 \text{ particle volume g}^{-1} 30 \text{ min}^{-1}$). For purposes of comparison of the different stages and

species, it was necessary to relate ingestion to biomass rather than to larval individuals, since it is not possible to maintain constant larval growth. This also fails in cultures. Therefore larval growth leads to differences in weight not only of different species but also of identical stages of the same species.

Filtering rate (F), as ml water filtered $g^{-1} 30 \text{ min}^{-1}$, was calculated from I_n ($F = I_n C_i^{-1}$, see Bergman & Richman, 1974; Frost, 1972). In this study the filtering rate is the mere mathematical relationship between I and C_i because 100% retention efficiency cannot be assumed. The 'retention efficiency' ('RE') was calculated from F ('RE' = $F 1000 \text{ ml}^{-1} 100\%$). This expresses the percentage of particles removed from 1000 ml of water. It is calculated to enable comparison of ingestion of different particle sizes within this study.

The Michaelis-Menten equation was used to fit a curve to the data (one point in diagrams (Figs 3–6) represents one feeding trial) and thus also to express the dependence of I and F on C_i and to characterize the expected saturations. Mullin *et al.* (1975) modified this equation to include threshold concentration in the description of feeding dynamics. They used the expression C_i -TC from the Ivlev-Parsons-LeBrasseur-Fulton equation ($I = I_{\max} (1 - e^{-\delta(C_i - TC)})$) thereby mathematically modifying C_i ($I = I_{\max} (C_i - TC) (K_{\frac{1}{2}} + (C_i - TC))^{-1}$). I is I_n , I_{\max} is the maximum I_n and $K_{\frac{1}{2}}$, as the half-saturation constant, is the C_i in which half of I_{\max} is reached.

In order to compare the 'retention efficiencies' of the different species and stages in relation to different particle sizes, the computed values for I_{\max} , $K_{\frac{1}{2}}$ and TC and the same C_i 's in each case were inserted into the Michaelis-Menten equation and I_n calculated (Fig. 7).

Mathematical models used to describe the dependence of I and F on C_i have often been the subject of discussion. The simplest method is the rectilinear model (Frost, 1972), following the least squares method. Its main disadvantage is that the alignment of points must be divided fairly arbitrarily when fitting the curve into ascent and plateau. The Ivlev equation was modified by Parsons

et al. (1967) for the description of ingestion and filtering rates ($I = I_{\max} (1 - e^{-\delta(C_i - TC)})$; $-\delta$ is a constant). The modified Ivlev equation was equated by Mullin *et al.* (1975) and Muck & Lampert (1980) with the Michaelis-Menten model and the rectilinear model. These authors are of the opinion that none of these models suitably describes the relationships of I to C_i and of F to C_i . My opinion of that I_{\max} and TC should be computed by fitting the saturation curves. It is also worth knowing $K_{\frac{1}{2}}$ for control purposes. Thus, I have chosen the Michaelis-Menten model.

In considering absolute test values and size ranges, recall that F and F_{\max} were calculated from I and C_i , and were not the result of direct measurement. If the regulative factors in anuran suspension feeding are as effective as the discussion below suggests, then F is directly influenced by buccal pump stroke frequency and buccal pump stroke volume. However, increased mucous extrusions at moderately high C_i and reduced mucous extrusions at very high C_i , and possibly at low C_i , would influence I directly, thereby falsifying the mathematically derived F and CC. At very low C_i , on the other hand, a high F and low CC are calculated despite low I . This must be understood as a mere mathematical effect of the low C_i and does not indicate high F and low CC in the experiment. As far as anuran larvae are concerned, therefore, CC cannot be seen as a 'turning point' of the kind Rigler (1961) posits for *Daphnia magna* before which F increases in proportion to C_i and after which F remains constant regardless of C_i .

Results

The smaller the particle size, the higher was the I_n , I_{\max} , F , the maximal filtering rate F_{\max} and 'RE' for all tadpole species and stages (Figs 3–7, Table 1): The only exception was Stage 28 *X. laevis* larvae, which showed a slightly higher I_n , I_{\max} , F_{\max} and 'RE' with PS1 than with PS2 (Fig. 3a, Table 1). I_v of the larger PS1 was ten times higher than the smaller PS3. The tendency toward saturation indicated by I_n , I_v , F and 'RE' increased

Table 1. Parameters of Michaelis-Menten equation and by C_i^{-1} transformed Michaelis-Menten equation (F_{\max} , CC).

Stage	PS	I_{\max} particles $g^{-1} 30 \text{ min}^{-1}$	$K_{\frac{1}{2}}$ particles ml^{-1}	TC particles ml^{-1}	F_{\max} ml $g^{-1} 30 \text{ min}^{-1}$	CC particles ml^{-1}
<i>Xenopus laevis</i>						
28	1	2302.3	199.92	9.66	770	50
28	2	2122.5	213.82	11.08	650	60
28	3	10386.0	995.67	10.98	850	100
32	1	1461.5	387.30	1.23	330	20
32	2	3489.4	1004.80	5.09	290	60
32	3	5303.1	883.02	21.08	440	120
40	1	1043.9	303.31	8.93	240	50
40	2	2080.9	455.91	9.49	340	70
40	3	2230.8	300.03	12.38	510	80
<i>Bufo calamita</i>						
28	2	6128.7	1206.00	54.13	330	300
28	3	6850.5	1346.50	61.53	330	300
32	2	2097.5	417.25	20.50	330	110
40	1	947.3	511.97	9.88	130	60
40	2	1768.0	405.79	9.48	320	70
40	3	3703.0	401.60	19.51	610	110
<i>Rana temporaria</i>						
28	1	1683.5	358.90	9.16	340	60
28	2	3280.7	650.05	35.84	320	170
32	1	645.3	300.58	9.73	140	60
32	2	1363.8	507.90	11.49	190	80
32	3	2461.9	504.58	7.54	370	70
40	1	400.2	208.63	9.00	110	50
40	2	752.7	311.80	10.19	160	60
40	3	1571.5	313.31	27.22	290	110
<i>Bufo bufo</i>						
28	2	1257.1	356.76	17.30	220	90
32	2	1178.1	418.52	9.13	210	70
32	3	2308.1	250.48	8.72	640	70
40	1	965.4	366.40	15.35	170	80
40	2	1532.9	385.87	16.13	260	80
40	3	2015.5	398.02	10.45	360	80

with increasing particle size and age of the larvae (Figs 3–7, Tables 1 and 2). The filtering rate rose steeply to CC in each experiment and then fell again gradually at a C_i that was only slightly higher. The smaller the particle size, the higher was the CC (Table 1). The TC tended to be lower with large PS1 than with small PS3, and in some cases also lower than with PS2 (Table 1). All the species (apart from *B. calamita* at low C_i and *B. bufo* with PS2) showed a tendency toward a

much larger I_n , I_v , F , F_{\max} and 'RE' in Stage 28 than in the later stages (Figs 3–7, Table 1). In most cases, Stage 32 also showed higher values than Stage 40. This was consistent with results of the control experiments on the effect of turbulence (Fig. 2). *X. laevis* larvae in particular showed their highest buccal pump stroke frequency in Stage 28 and 32 (Fig. 2a, Table 3). Stage 28 *B. calamita* showed the highest buccal pump stroke frequency, and Stage 32 higher buccal

Table 2. 'Retention efficiency'. Comparison of stages and particle sizes.

Stage	C_i particles ml ⁻¹	PS1-PS2 (%)	PS1-PS3 (%)	PS-PS3 (%)
<i>Xenopus laevis</i>				
28	100	-4.6	6.8	11.4
32	100	0.2	6.9	6.7
40	100	5.2	13.2	7.0
28	300	-2.4	16.2	18.6
32	300	2.6	10.6	8.0
40	300	5.0	9.7	4.7
28	500	-1.5	17.9	19.4
32	500	3.3	10.5	7.2
40	500	4.2	7.4	3.1
28	1000	-0.9	16.3	17.2
32	1000	3.4	8.7	5.3
40	1000	3.2	4.6	1.6
<i>Bufo calamita</i>				
28	100	-	-	-1.7
40	100	9.1	23.9	14.8
28	300	-	-	-0.1
40	300	6.6	20.0	13.1
28	500	-	-	0.3
40	500	5.0	15.6	10.5
28	1000	-	-	0.6
40	1000	3.2	10.0	5.8
<i>Rana temporaria</i>				
28	100	-2.3	-	-
32	100	2.7	11.6	9.0
40	100	2.3	8.8	6.4
28	300	3.2	-	-
32	300	3.0	9.8	6.8
40	300	2.2	8.3	6.2
28	500	3.9	-	-
32	500	2.7	8.2	5.5
40	500	1.8	6.7	4.9
28	1000	3.6	-	-
32	1000	2.0	5.7	3.7
40	1000	1.2	4.2	3.1
<i>Bufo bufo</i>				
32	100	-	-	20.3
40	100	4.7	4.8	9.5
32	300	-	-	12.7
40	300	3.8	3.3	7.1
32	500	-	-	8.9
40	500	3.0	2.6	5.6
32	1000	-	-	5.1
40	1000	2.0	1.6	3.7

pump stroke frequency than Stage 40 (Fig. 2b, Table 3). In *R. temporaria* stage dependent differences of buccal pump stroke frequency are not

confirmed (Fig. 2c, Table 3). By contrast, *B. bufo* larvae had their lowest buccal pump stroke frequencies in Stage 28 (Fig. 2d, Table 3).

Table 3. Buccal pump strokes. Comparison of stages; *t*-test values.

Comparison of stages	Min after begin of experiment	<i>t</i>	$n_1 + n_2 - 2$	<i>P</i> <
<i>Xenopus laevis</i>				
28-32	0	2.31	63	0.025
28-32	15	1.97	63	0.10
28-32	30	1.44	63	0.20
28-40	0	7.86	64	0.001
28-40	15	11.69	64	0.001
28-40	30	12.59	64	0.001
32-40	0	4.23	63	0.001
32-40	15	7.46	63	0.001
32-40	30	9.76	63	0.001
<i>Bufo calamita</i>				
28-32	0	1.25	64	0.25
28-32	15	10.52	64	0.001
28-32	30	9.90	64	0.001
28-40	0	11.96	64	0.001
28-40	15	13.90	64	0.001
28-40	30	14.33	64	0.001
32-40	0	8.45	62	0.001
32-40	15	4.14	62	0.001
32-40	30	4.69	62	0.001
<i>Rana temporaria</i>				
28-32	0	2.68	63	0.01
28-32	15	1.83	63	0.10
28-32	30	1.56	63	0.10
28-40	0	1.29	62	0.20
28-40	15	0.28	62	0.80
28-40	30	0.48	62	0.70
32-40	0	0.19	63	0.90
32-40	15	1.44	63	0.10
32-40	30	0.38	63	0.70
<i>Bufo bufo</i>				
28-32	0	7.68	62	0.001
28-32	15	9.45	62	0.001
28-32	30	9.69	62	0.001
28-40	0	8.76	63	0.001
28-40	15	10.86	63	0.001
28-40	30	11.48	63	0.001
32-40	0	0.50	63	0.70
32-40	15	1.03	63	0.30
32-40	30	0.49	63	0.70

To summarize, *X. laevis* larvae had the highest suspension feeding efficiency, followed by *B. calamita* larvae. The efficiency of *B. bufo* larvae was

clearly lower. *R. temporaria* larvae were intermediate between *B. calamita* and *B. bufo* larvae.

A comparison of the ingestion of different particle sizes showed a characteristic 'RE' picture (Figs 7a,b,c,d, Table 2). The only species-specific reaction to particle size was suggested by small differences between *B. bufo* and *B. calamita* at Stage 40, with PS1 and PS3. For all the species examined, however, there was only a small 'RE' difference between PS1 and PS2. The earlier the stage, the greater was the PS1-PS3 and PS2-PS3 difference (with the exception of *X. laevis* $C_i = 100$, PS1-PS3 and *B. calamita* Stage 28, PS2-PS3). The difference in 'RE' tended to be smaller when the C_i was high.

Discussion

Comparison with the results of other authors

The tadpoles investigated here, apart from *X. laevis*, ingest PS3 in similar quantities to the *Chlorella pyrenoidosa* and *Anabaena sphaerica* ingested by other anuran species. The smallest maximum I_v of PS3 (Fig. 5c, *R. temporaria*, Stage 40; Fig. 6c, *B. bufo*, Stage 40) of $0.2-1 \cdot 10^9 \mu\text{m}^3 \text{larva}^{-1} \cdot 30 \text{min}^{-1}$ ($= 1-2 \cdot 10^9 \mu\text{m}^3 \text{g}^{-1} \cdot 30 \text{min}^{-1}$) is within the same range as that calculated by Seale and Wassersug (1979) for *R. sylvatica* (maximum I_v ca $10^9 \mu\text{m}^3 \text{Chlorella pyrenoidosa larva}^{-1} \text{h}^{-1}$ at a C_i of $10^8 \mu\text{m}^3 \text{ml}^{-1}$). Seale & Beckvar (1980) measured ingestion rates of an almost identical range during experiments in which *Anabaena sphaerica* (cell diameter $5.1 \mu\text{m}$, colony 27.9 cells in average) was fed to *H. crucifer* (maximum $I_v = 2.52 \cdot 10^9 \mu\text{m}^3 \text{g}^{-1} \text{h}^{-1}$ at a C_i of $4.12 \cdot 10^7 \mu\text{m}^3 \text{ml}^{-1}$) and to *B. woodhousei fowleri* (maximum $I_v = 2.3 \cdot 10^9 \mu\text{m}^3 \text{g}^{-1} \text{h}^{-1}$ at a C_i of $4.7 \cdot 10^7 \mu\text{m}^3 \text{ml}^{-1}$). In the same study (Seale & Beckvar, 1980) *R. catesbeiana* had a much lower maximum I_v than the other species ($7.76 \cdot 10^8 \mu\text{m}^3 \text{g}^{-1} \text{h}^{-1}$ at a C_i of $1.33 \cdot 10^7 \mu\text{m}^3 \text{ml}^{-1}$). This means that particle sizes from ca 5 to $40 \mu\text{m}$ are ingested more or less equally effectively by these species, although differences in effectivity do arise from species to species. These differ-

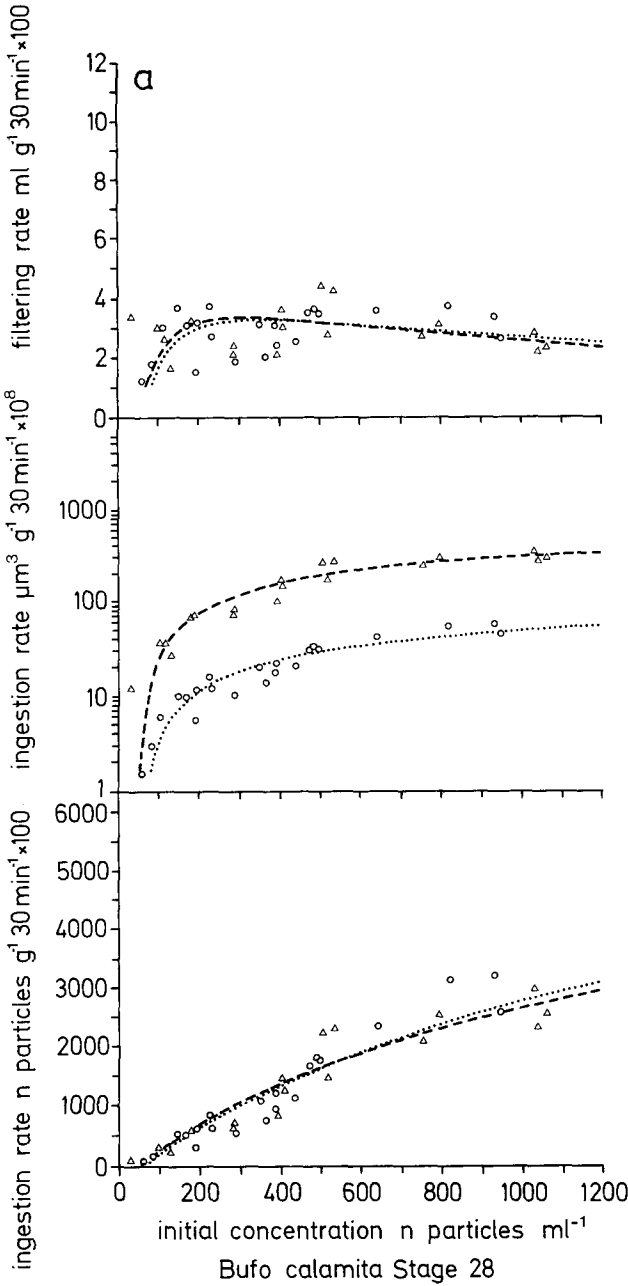


Fig. 4a

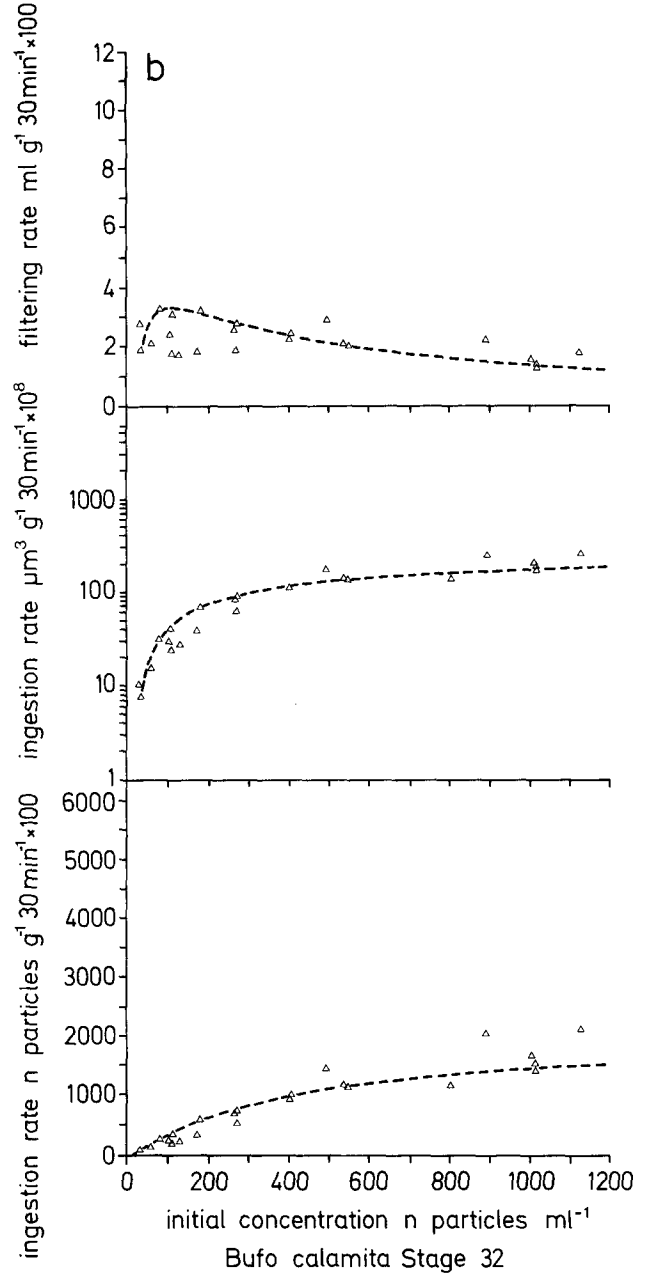


Fig. 4b

Fig. 4a-c. *Bufo calamita*. Ingestion- and filtering rates plotted against initial concentration. ● = PS1, △ = PS2, ○ = PS3.

ences are found in the I_{max} , and especially in the TC (see below). Adaptation to oligotrophic environmental conditions is therefore actually determined by whether larvae are able to ingest low food concentration.

X. laevis in the present study had an I_v of $10^{10} \mu\text{m}^3 \text{g}^{-1} 30 \text{min}^{-1}$ with PS3 and therefore was well above the maximum I_v of the other species discussed. This shows that PS3 lies within the size range exploited by this microphagous

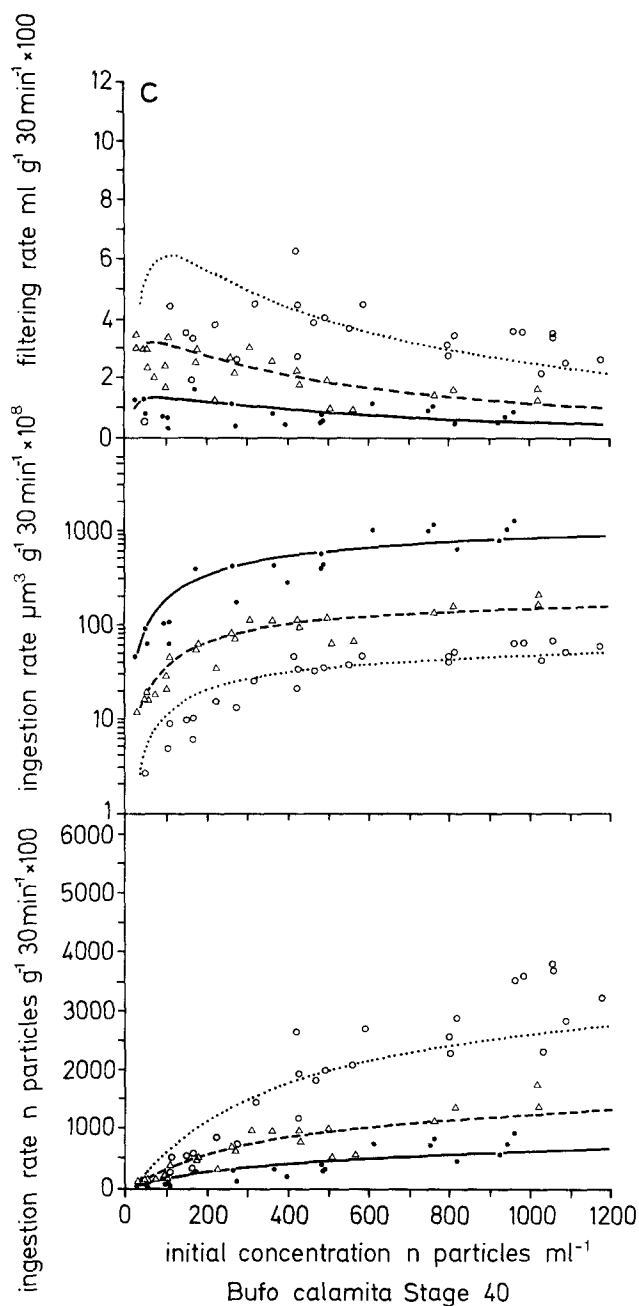


Fig. 4c

suspension feeder (particle sizes under $1\ \mu\text{m}$, Wassersug, 1972; see also Wassersug & Hoff, 1979; Wassersug & Rosenberg, 1979) and mid-water feeder, i.e. that the morphology and feeding mechanism of the pipid filter apparatus are wholly able to ingest these particle sizes. This is

hardly surprising, since some algal plankton (several Chrysophyceae, Pyrrophyta, Pennales, Chlorophyta, Conjugatophyceae) belong within this size range (Huber-Pestalozzi, 1938; Viertel, 1978).

Threshold concentration

The species investigated here were able to filter particles of the size range PS1–PS3 at a TC of well under $100\ \text{particles ml}^{-1}$, indeed in most cases with as few as $10\ \text{particles ml}^{-1}$. As discussed above, this constitutes actual adaptive ability to the nutritive conditions of the environment. This is further explained by the fact that adaptation to shortcomings allows some anuran larvae access to environments which are more favourable to their survival, i.e. avoidance of predators, than would be the case if they had merely adapted to nutrient superabundance (see below 'Suspension feeding and life history').

Larger particles clearly have a greater chance of entrapment by the mucous entrapment, and of being sieved off by the bucco-pharyngeal structures (see below). This explains why particles are ingested at all at such low C_i . *Chlorella fusca*, which are only $5.8\ \mu\text{m}$ in diameter, were not ingested under a TC of $1\ 10^4$ – $1.2\ 10^4\ \text{cells ml}^{-1}$ (*X. laevis*, *B. calamita*), $1.2\ 10^4\ \text{cells ml}^{-1}$ (*R. temporaria*) and $5\ 10^4\ \text{cells ml}^{-1}$ (*B. bufo*) (Viertel, 1990). TC as it is demonstrated by Lehman (1976), Frost (1974, 1975a, b) and Lam & Frost (1976) for *Calanus pacificus*, by Rigler (1961) for *Daphnia magna* and by McMahon (1965) suggests these crustaceans use threshold feeding as a means of regulating their energy balance. Here, the filter feeders are understood to actively reduce their filtering rate at low food concentrations to avoid a negative energy balance. Buccal pump strokes are also observed in anuran larvae in water entirely free of particles (see Fig. 2). In the absence of food, energy is invested in ventilation of the bucco-pharynx for respiration purposes (see also Feder *et al.*, 1984, Gradwell, 1970). Seale *et al.* (1982) and Seale & Wassersug (1979) explain zero ingestion or low ingestion at extreme

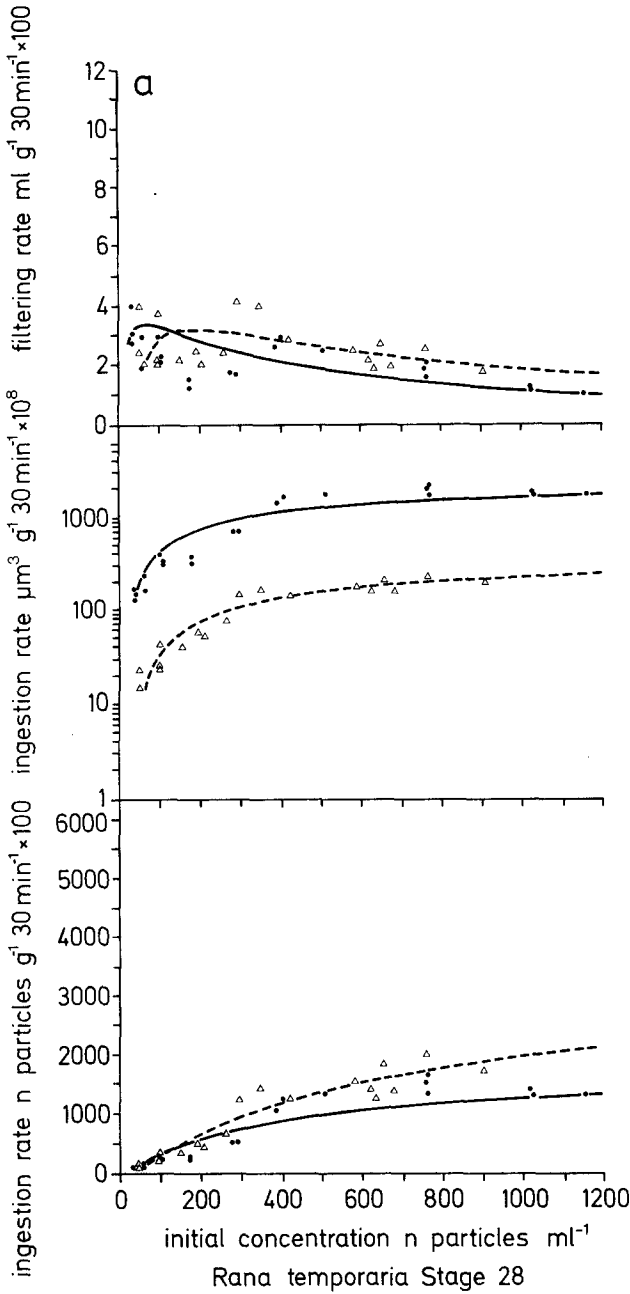


Fig. 5a

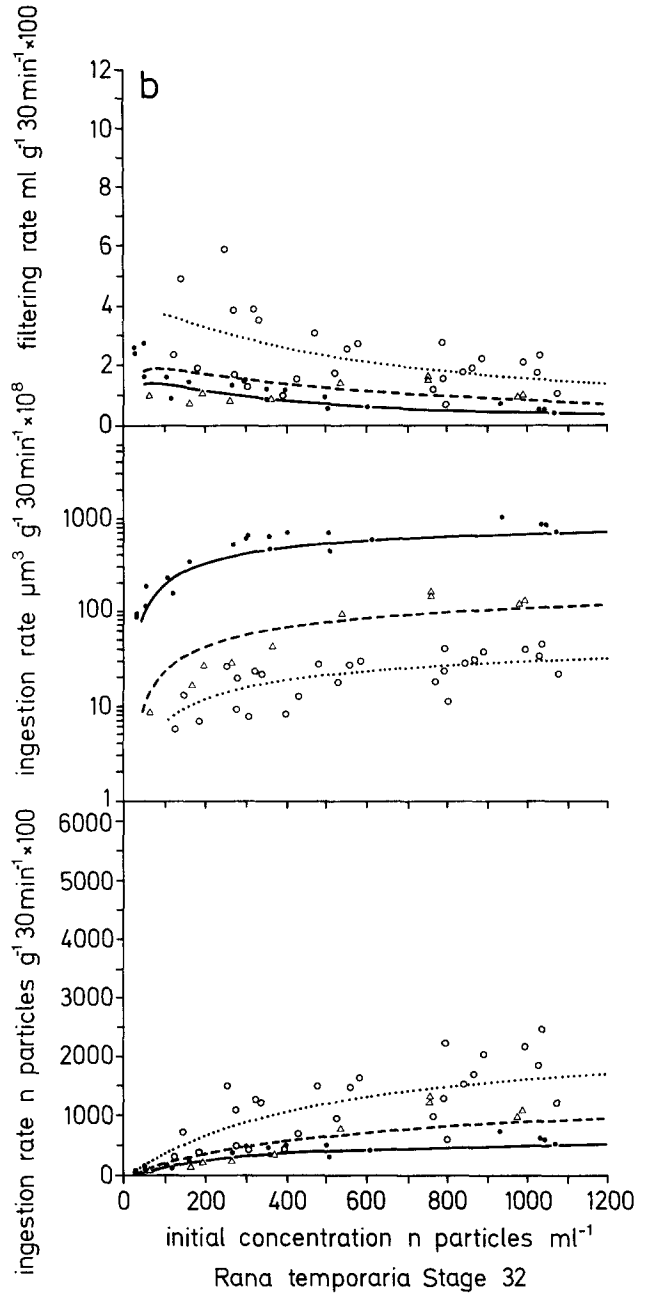


Fig. 5b

Fig. 5a-c. *Rana temporaria*. Ingestion- and filtering rates plotted against initial concentration. ● = PS1, △ = PS2, ○ = PS3.

C_i in terms of the filtering mechanism: *X. laevis* reduces its buccal pumping rate considerably at C_i under $5 \cdot 10^{-2} \text{ mg yeast l}^{-1}$ (equals ca $1.5 \cdot 10^6 \text{ yeast cells ml}^{-1}$) and over $50 \text{ mg yeast l}^{-1}$ (equals

$1.5 \cdot 10^9 \text{ yeast cells ml}^{-1}$). *R. sylvatica* larvae reduced their buccal pump rate continually over the whole range of C_i tested ($4 \cdot 10^6$ to $1 \cdot 10^8 \text{ } \mu\text{m}^3 \text{ ml}^{-1}$ *Chlorella pyrenoidosa*, equals ca $3.8 \cdot 10^5$ to $9.6 \cdot 10^6$

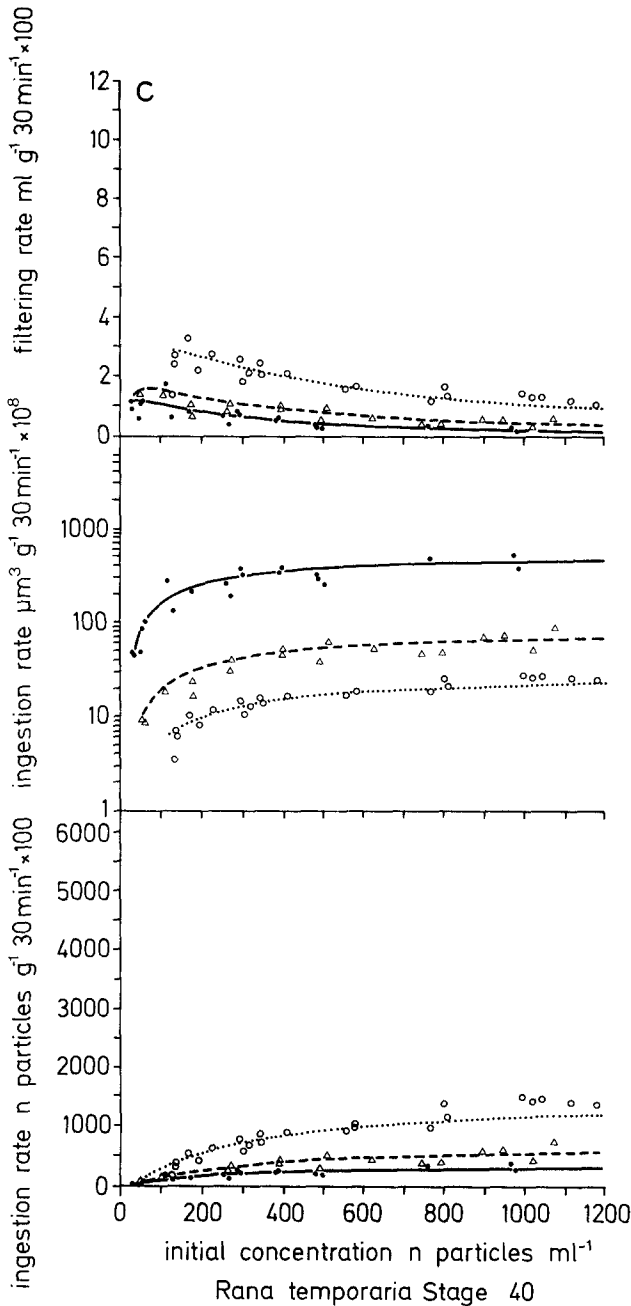


Fig. 5c

Chlorella pyrenoidosa cells ml^{-1}). Mucus production may also be regulatory. Seale & Wassersug (1979) and Feder *et al.* (1984) suppose this to be the case at high C_i . It is possible that both pumping rate and mucus production have a regulatory function at low C_i . As mentioned above, thresh-

old feeding of anuran larvae is influenced not only by C_i but also by particle size. Frost's (1972) assertion that *Calanus pacificus* achieves maximal ingestion at low C_i with larger particles (3.8–87 μm) would appear to confirm this for crustaceans, as would Doyle's (1979) results with the amphipod *Corophium volutator* and particles from 10–60 μm . Seale assumed, cited by Seale *et al.* (1982), that the TC of smaller (younger) anuran larvae is higher than that of larger (older) anuran larvae. This can be entirely confirmed for the developmental stages of *B. calamita*, and partly for *X. laevis* and *R. temporaria*.

Suspension feeding and life history

Viertel (1990) explains the high I and 'RE' in Stages 28 and 32 in terms of the rapid growth of premetamorphic stages (see Breuer, 1984; Funke, 1989; Kadel, 1975; Mittmann, 1989; Viertel, 1981; Waringer-Löschenkohl, 1988). The dependence of buccal pump stroke frequency on stage makes it probable that pump stroke frequency causes a stage-related change in suspension feeding efficiency. Polls Pelaz & Pourriot's (1988) findings that Stages 30–35 *Rana ridibunda* ingest very little, or possibly nothing at all, cannot be confirmed for the species investigated here.

The different suspension feeding efficiency (I_{max} , F_{max} , TC and 'RE') of different species at low *Chlorella fusca* concentrations is explained by Viertel (1990) in terms of the life history of the species. *X. laevis* and *B. calamita* larvae develop in ephemeral and sometimes oligotrophic waters. A high ingestion rate also at low initial concentrations, i.e. a low TC, lead to fast growth and early metamorphosis, increasing the probability that tadpoles will survive the drying up of their larval habitat. *B. bufo* larvae, in contrast, usually inhabit permanent waters with a rich nutrient supply. These tadpoles have not been selected to escape drying ponds, therefore high ingestion rates and efficient exploitation of meagre food supplies have been less vital for them. In addition protective mechanisms enable the *B. bufo* larvae to outfox their predators: schooling behavior sim-

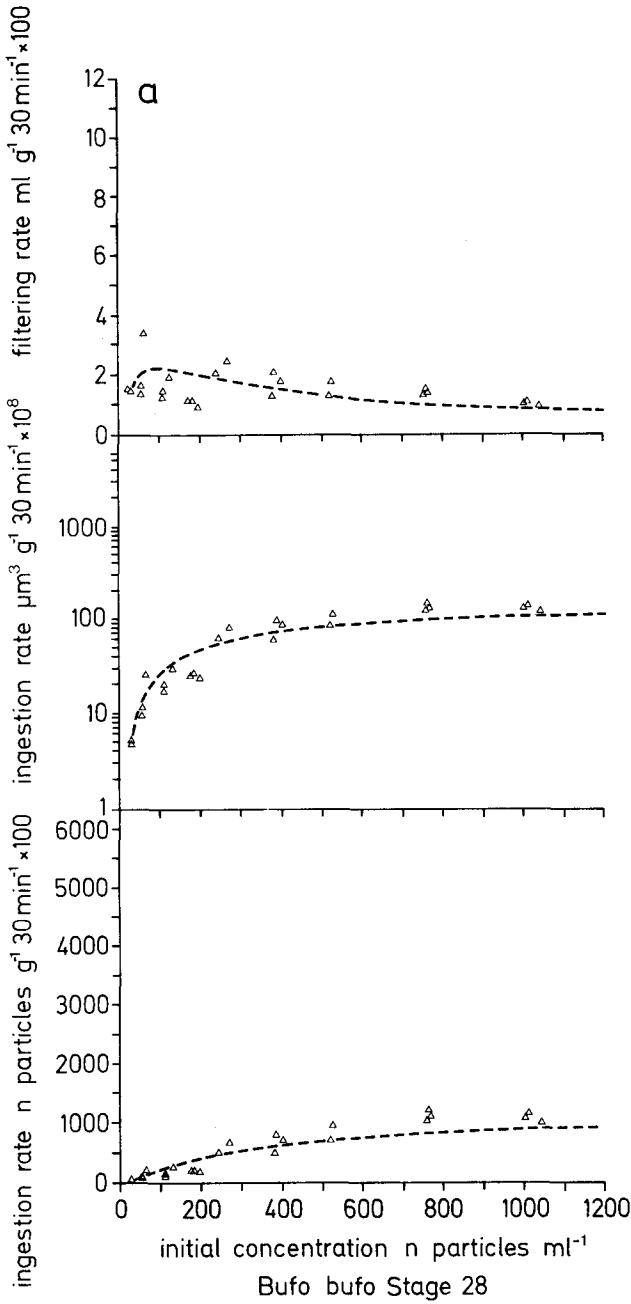


Fig. 6a

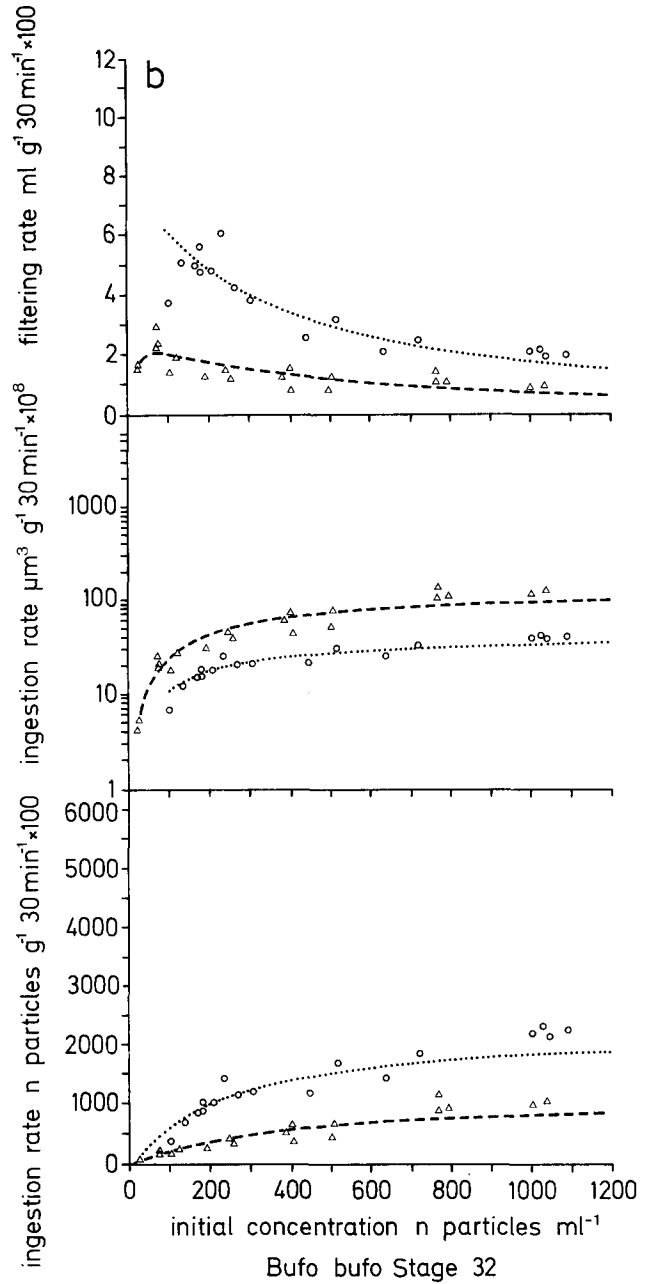


Fig. 6b

Fig. 6a-c. *Bufo bufo*. Ingestion- and filtering rates plotted against initial concentration. ● = PS1, △ = PS2, ○ = PS3.

ulates a big animal, bitter substances in their skin make the larvae inedible for most predators (Voriss & Bacon, 1966) and the smashed body of an injured conspecific leads to immobility of all the other larvae (Breuer & Viertel, 1990; Eib-

Eibesfeldt, 1949; Kulzer, 1954; Pfeiffer, 1966; Viertel, 1978). This explains the lack of pressure on *B. bufo* larvae to accelerate their development and leave their waters quickly. *R. temporaria* tadpoles lie between *B. calamita* and *B. bufo* in terms of

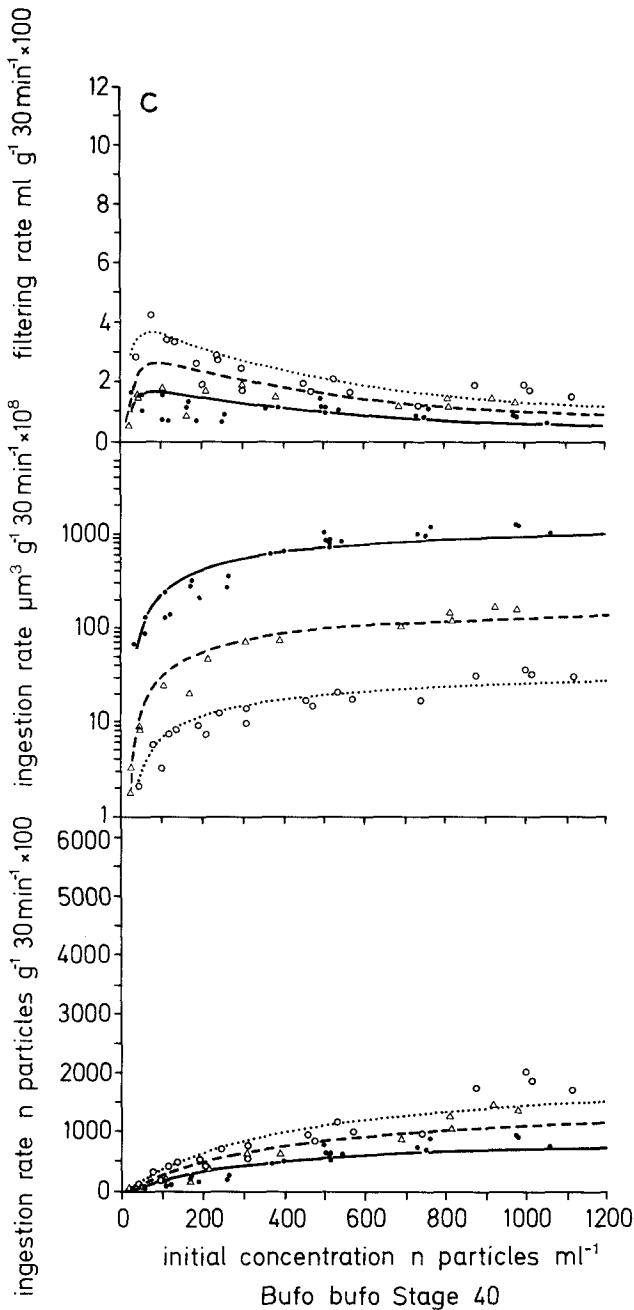


Fig. 6c

feeding efficiency and larval habitat. This species spawns both in small ephemeral ponds and in permanent, nutrient-rich water.

Our picture of the relationship between life history and suspension feeding efficiency can be refined with the help of the present results. Plank-

ton is normally smaller than sessile organisms (see also Huber-Pestalozzi, 1938). The plankton found in the alimentary tract of anuran larvae (*B. bufo*, *Rana dalmatina*, *R. ridibunda*, *Rana perezi*, *Hyla arborea*, *Hyla meridionalis*, *B. calamita*, *Pelobates fuscus*, *Pelobates cultripes*, *Discoglossus pictus*) by Diaz-Paniagua (1985, 1989), Löschenkohl (1985) and Viertel (1978) was mostly smaller than PS1. The exceptions were: several Chrysophyceae, Pyrrophyta, Pennales, *Ankistrodemus* (Chlorophyta), *Netrium*, *Spirotaenia*, *Penium*, *Closterium*, *Micrasterias* (Conjugatophyceae). If we assume that *X. laevis* is more likely to represent derived features from the evolutionary point of view (Inger, 1967; Viertel, 1986), then mid-water feeding (see Wassersug & Hoff, 1979), i.e. feeding on plankton, is a derived feeding strategy within anuran larvae. This enabled the pipid larval type to gain access to new forms of nutrient supply. Observations indicating that *X. laevis* feeds facultatively on bottom and deposit (Wassersug, personal communication) do not contradict this. For *B. calamita*, *R. temporaria* and *B. bufo* feeding on periphyton and on bottom particles is the consequence of their basal anatomy (horny beaks, oral disc toothlets and filter apparatus) (see Inger, 1967). Bottom feeding seems to be the basal feeding strategy. Therefore it seems probable that the ability to filter large particles (e.g. PS1) is primarily linked to bottom feeding. Seale (1980) and Seale & Beckvar (1980) observed that *Rana* larvae begin to feed on the periphyton when the C_i falls below CC.

Zusammenfassung

Untersucht wurde der Einfluß von Partikelgröße, Ausgangskonzentration und Larvalstadium auf die Ingestionsrate, die 'Retentions-effizienz' und die Filtrationsrate von Anurenlarven mit unterschiedlich gebautem Filterapparat und unterschiedlicher Lebensweise. Die Praemetamorphosestadien 28 und 32 und das Prometamorphosestadium 40 wurden wegen ihrer unterschiedlichen Wachstumsraten für die Experimente gewählt. Drei unterschiedlich große Klassen von Silicagelpartikel wurden als

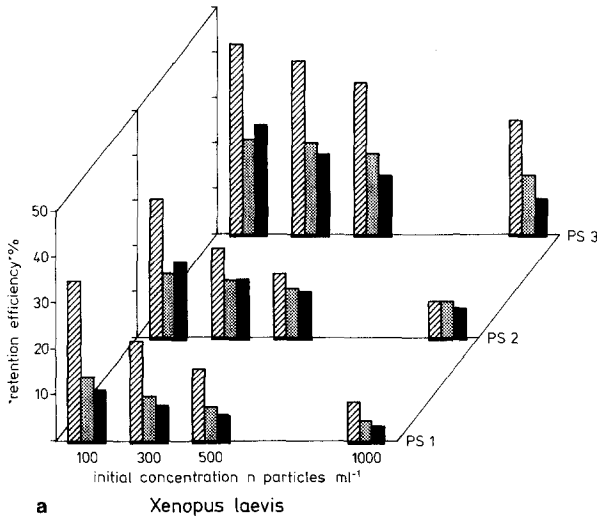


Fig. 7a

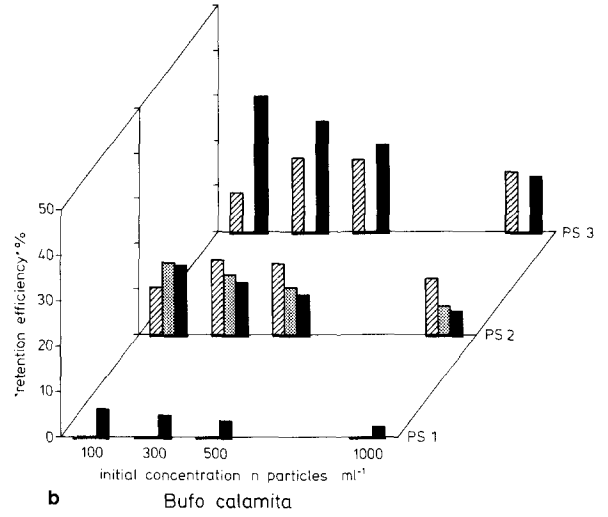


Fig. 7b

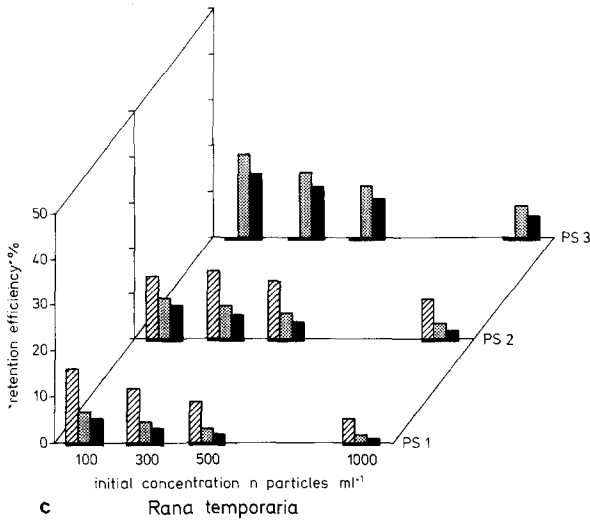


Fig. 7c

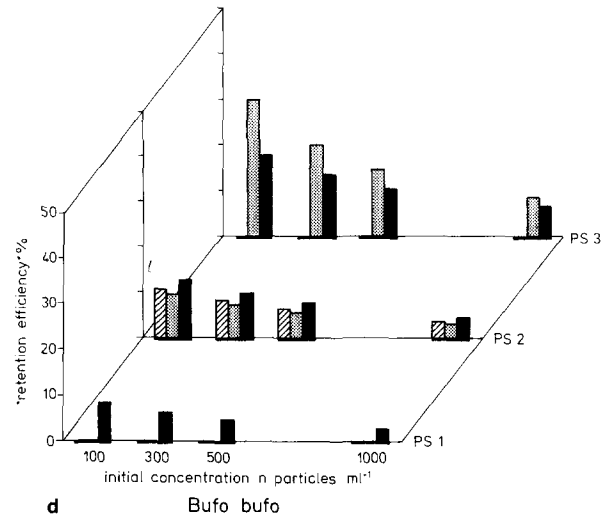


Fig. 7d

Fig. 7a-d. 'Retention efficiency'. Comparison of stages and particle sizes (PS); calculated by inserting the computed I_{max} , $K \frac{1}{2}$ and TC and the same C_i in each case into the Michaelis-Menten equation (see Table 2). Hatched columns = Stage 28, dotted columns = Stage 32, black columns = Stage 40.

Nahrungsattrappe angeboten. Die Partikelkonzentration wurde fotometrisch gemessen. Das Michaelis-Menten Modell wurde verwendet, um die Abhängigkeit der Ingestionsrate, der Filtrationsrate und der 'Retentionseffizienz' von der Ausgangskonzentration zu beschreiben und um die maximale Ingestionsrate, die Threshold-

konzentration und die halbe Sättigungskonstante zu ermitteln.

(1) Die größten Ingestionsraten, Filtrationsraten und 'Retentionseffizienzen' wurden von den *X. laevis* Larven gefolgt von den *B. calamita* Larven erreicht. Hingegen lagen die *B. bufo* Larven am entgegengesetzten Ende der Skala. Die

R. temporaria Larven lagen zwischen *B. calamita* und *B. bufo*. Diese Reihenfolge wird auf die unterschiedlichen Lebensweisen der Larven in Verbindung mit der unterschiedlichen Ökologie der Larvengewässer zurückgeführt. (2) Je größer die Partikelgröße und je älter das Larvenstadium ist, desto größer ist die Tendenz zur Sättigung von Ingestionsraten, Filtrationsraten und der 'Retentionseffizienz'. Diese Parameter der Filtration sind nach der Partikelgröße gestaffelt. Ingestionsrate (Partikelzahl), Filtrationsrate, and 'Retentionseffizienz' sind bei PS3 am größten. Das Ingestionsvolumen ist bei PS1 am größten. Der Unterschied zwischen PS3 und PS2 zu PS1 ist in vielen Fällen groß, bei *X. laevis* Stadium 28 sehr groß. Dies zeigt, daß große Partikel von den Larven am effektivsten aufgenommen werden können und dies in den Stadien 28 und 32 am effektivsten, was mit der Wachstumsfunktion dieser Stadien zusammenhängt. Möglicherweise ist die effektive Ingestion großer Partikel eine phylogenetisch sehr ursprüngliche Fähigkeit. (3) Die Thresholdkonzentration ist bei großen Partikeln am kleinsten. In Anlehnung an andere Autoren wird das Thresholdfeeding auf die Regulation des vom Buccopharynx gepumpten Wasservolumens und der Schleimproduktion zurückgeführt. Dem Thresholdfeeding wird eine große Bedeutung hinsichtlich der Anpassung an oligotrophe Biotope beigemessen.

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