Oecologia (1990) 85:167–177

Oecologia

Suspension feeding of anuran larvae at low concentrations of *Chlorella* algae (Amphibia, Anura)*

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Received November 27, 1989 / Accepted in revised form August 5, 1990

Summary. Ingestion and filtering rates in larval *Xenopus laevis*, *Bufo calamita*, *Rana temporia* and *Bufo bufo* fed suspensions of *Chlorella fusca* were investigated. Concentrations were measured with a Coulter Counter. (1) For all species, filtration occurred at concentrations far below those reported by other authors for *Rana sylvatica* feeding on *Chlorella pyrenoidosa*. For *Bufo bufo*, only larvae near metamorphosis showed ingestion at low particle concentrations. Since buccopharyngeal ventilation continues even in the absence of food particles, this threshold feeding behaviour in the younger larvae must be due to different mechanisms to those found in *Daphnia* and *Calanus* studied by other authors: probably reduction of the buccal pumping rate and the mucus production of the filter apparatus. (2) For *B. calamita, R. temporaria* and *X. laevis* the highest suspension feeding efficiency was at early tadpole stages, corresponding with the high growth rate of these stages. (3) The life histories of the species provide the basis for understanding their different retention efficiencies and functional responses.

Key words: Anuran larvae – Suspension feeding – Food concentrations – *Chlorella* algae

Anuran larvae are, with few exceptions, suspension feeders. The comparative performance of the tadpole filter apparatus of *Rana sylvatica* and *Xenopus laevis* at biovolume concentrations of over 5×10^6 μm^3 *Chlorella pyrenoidosa* ml^{-1} (5×10^5 *C. pyrenoidosa* cells ml^{-1}) were the primary focus of studies by Seale and Wassersug (1979). Seale et al. (1982) continued the investigations on suspension feeding of *X. laevis*. Seale and Beckvar (1980) studied the ability of *Hyla crucifer, Bufo woodhousei fowleri* and *Rana catesbeiana* larvae to distinguish between different food sources.

The aims of the investigations cited above were to: (1) demonstrate the functional response (Steele 1974; "feeding dynamics" of Seale and Wassersug 1979), and, (2) determine the "critical" concentration (CC) and the threshold concentration (TC) during both ingestion and filtration. The CC is the concentration of suspended nutrient above which ingestion does not increase; thus filtration peaks and then more or less decreases (Frost 1972; McMahon 1965; Rigler 1961). In filter-feeding zooplankton CC is termed "incipient limiting level". The TC is the concentration of suspended nutrient below which ingestion and filtering both cease and above which filtration increases up to CC level (Frost 1974; Muck and Lampert 1980; Seale and Wassersug 1979). Ingestion is the process of capturing suspended particles. 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 most often expressed as the water volume cleared of suspended particles per unit of time, and is the gauge of a suspension feeder's ability to react to a nutrient suspension by increasing or lowering the water current (Jorgensen 1983). The filtering rate is identical with pumping rate if the retention efficiency reaches 100%. Pumping rate is the volume of water flowing per unit of time through the filter apparatus. Retention efficiency (RE) is the percentage of food particles of a defined diameter removed from a given nutrient concentration (see also Randlov and Riisgard 1979: RE = 1 – exhaled concentration/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 algal concentration in the experimental chamber. Therefore it is apostrophized as "retention efficiency" ("RE").

Kenny (1969a, b) and Wassersug (1972) showed that pharyngeal mucus entrapped food particles suspended in the water current similar to the mucus entrapment system of lower chordates. The ability of tadpoles to filter suspended food allows them to exploit a wide spectrum of nutrient supply. By contrast with their macrophagous relatives, the larvae of salamanders and caecilians, filter-feeding anuran larvae are not dependent for prey upon consumers of the third and the fourth trophic level,

* Supported by the Deutsche Forschungsgemeinschaft-DFG

which occur in comparatively low biomass. Instead they feed on planktonic producers, which usually occur in larger biomass and which can, in many cases, supplement this with primary consumers. These detritus and bottom feeders (larval Types III and IV of Orton 1953) use their horny beaks to scrape food off the substrate (Löschenkohl 1985; Viertel 1978). This material is suspended in the water current and is then filtered off and transported down the alimentary tract. In all of these cases, the organisms of the sediment and detritus are exploited. Thus anuran larvae have a favorable position in the food chain: already existing high nutrient-value substance is transformed and incorporated into their own living biomass. The influence of anuran larvae on aquatic ecosystems is thus considerable (Dickman 1968). Seale (1980) proved that, as far as phytoplankton and nitrogen flux are concerned, anuran larvae are regulatory consumers and that they both reduce standing crop and alter specific growth rates of algae.

Several further questions demand experimental clarification: (1) Do ingestion and filtering occur below the particle concentrations tested by Seale and Beckvar (1980) and by Seale and Wassersug (1979) (i.e., below 5×10^5 *Chlorella pyrenoidosa* ml^{-1}, or 5×10^6 μm^3 ml^{-1})?

Even at high trophic levels, the concentrations of phytoplankton occuring in natural waters are typically below the concentrations that have been tested on anuran larvae: 4.57×10^6 μm^3 ml^{-1} is considered eutrophic (Rott 1981); $0.2–2.5 \times 10^6$ μm^3 ml^{-1} is mesotrophic-eutrophic (for Laachersee Scharf et al. 1988). The phytoplankton concentrations occuring in oligotrophic waters are considerably lower: $0.081–0.13 \times 10^6$ μm^3 ml^{-1} (Rott 1981); 1000–6000 cells ml^{-1}, (for Meerfelder Maar, Ehlscheid 1985); 385–22000 cells ml^{-1} and 958–4201 cells ml^{-1} (for Weinfelder Maar Schalkenmehrener Maar, Post 1980). Test concentrations above those of the highest trophic level, "eutrophic", must therefore be considered unrealistic. Furthermore, the extent to which a filter apparatus is capable of transferring sufficient nutrients to the organism – especially at low food concentrations – is a factor determining the growth of larvae and is therefore of great interest.

(2) Are ingestion rates and filtering rates of different larval stages different when the food concentration remains constant?

(3) How do points (1) and (2) manifest themselves in species whose larvae (and adults) differ in life histories? *Bufo calamita* larvae develop in small ephemeral and in most cases oligotrophic waters (Beebee 1983; Strijbosch 1979). *X. laevis* larvae are able to grow and metamorphose in ephemeral waters although they are common in permanent environments (Channing; Fischer and Hinkel, personal communications). *Bufo bufo* larvae develop in permanent waters with a rich nutrient supply and large biomass production (Heusser 1958, 1960; Jungfer 1943; Viertel 1978). Additional protective mechanisms enable *B. bufo* larvae to survive the voracity of their predators: schooling behavior simulates a big animal to the predator, a bitter substance makes the larvae inedible for most predators, and the smashed body of a companion leads to immobility of all the other larvae (see Breuer 1984; Eibl-Eibesfeldt 1949; Viertel 1978). The spawning place preference of *Rana temporaria* ranges between those of *B. calamita* and *B. bufo*. The larvae occur in both permanent, nutrient-rich waters and ephemeral waters (Savage 1961; Strijbosch 1979).

(4) Do ingestion and filtering (1 and 2) differ in larvae with differently constructed filter apparatus? For example, the filter apparatus of the Central European species studied here differs greatly from that of *Xenopus* studied so extensively in the past (Viertel 1985, 1987; Wassersug and Rosenberg 1979).

Materials and methods

Preparation of larvae for experiments

Larvae of *R. temporaria B. bufo* and *B. calamita* were collected locally and staged according to Gosner (1960). Only individuals of larval Stages 28 (hindlimb bud length $\geq 1 \times$ diameter), 32 (indentation between toes 5–4) and 40 (subarticular tubercles of hind limb developed) were used. These stages typify both premetamorphosis (Stages 25–35) and prometamorphosis (from Stage 36, Etkin 1968). Laboratory-raised *X. laevis* larvae were also used. They were staged following the normal table of Nieuwkoop and Faber (1956). Since comparison is complicated owing to differences between this species and *Bufo* and *Rana*, hindlimb development and growth were taken as the sole staging criteria. Stages 51 (Stage 28 of Gosner), Stage 53 (Stage 32 of Gosner) and 57 (Stage 40 of Gosner) were selected.

A Coulter Counter (model FN) was used to measure the density of *Chlorella fusca* algae (see below). To avoid faulty measurements by the Coulter Counter system due to defecation, the larvae were incubated for 4.5 h in a solution of essential and non-essential amino acids, essential fatty acids, glucose, oligosaccarides, minerals, vitamins and trace nutrients (Vivasorb, Pfrimmer and Co, Pharmazeutische Werke Erlangen GmbH) at a concentration of 80 mOsm. This is fully absorbed by the alimentary tract and thus faeces are not produced. Following this treatment the larvae were placed in standardized water (see below) at 22° C for 22 h to acclimatize them to the temperature of the subsequent experiments. Test feeding with *Chlorella* algae and dried fish food ("Tetraphyll") showed that the larvae resumed feeding immediately under these conditions, as was confirmed by examining the content of the gut. The buccal pumping rates were normal. Feeding behaviour is therefore taken to be normal during the filtering experiments.

To prevent pollution by faeces produced during the experiments by the ingestion of *Chlorella* algae the experimental time was shorter than the gut passage time.

Algae

Chlorella fusca algae (strain of Bendix and Allen 1962) were grown under sterile conditions in a culture of the inorganic food solution (Strotmann 1966). Daylight and two fluorescent lamps provided illumination. Under these conditions, *C. fusca* reached a diameter of 5.8 µm ($s = 0.33$, $n = 20$) and a cell volume of 102.2 μm^3 (rounded down to 100 μm^3 for presentation of the results; Figs. 3–6).

Setting up and conducting the experiment

AOAC water was used for all experiments following Ashworth and Crozier (1972). Measurements taken were: osmolarity 10 mOsm; hardness 3.57 mval; conductivity 650 µS (at 22° C); pH 7.3. Water temperature was held constant at 22° C ± 0.2.

The experimental chamber, consisting of a double-walled 800 ml glass container connected to a water-bath with silicone

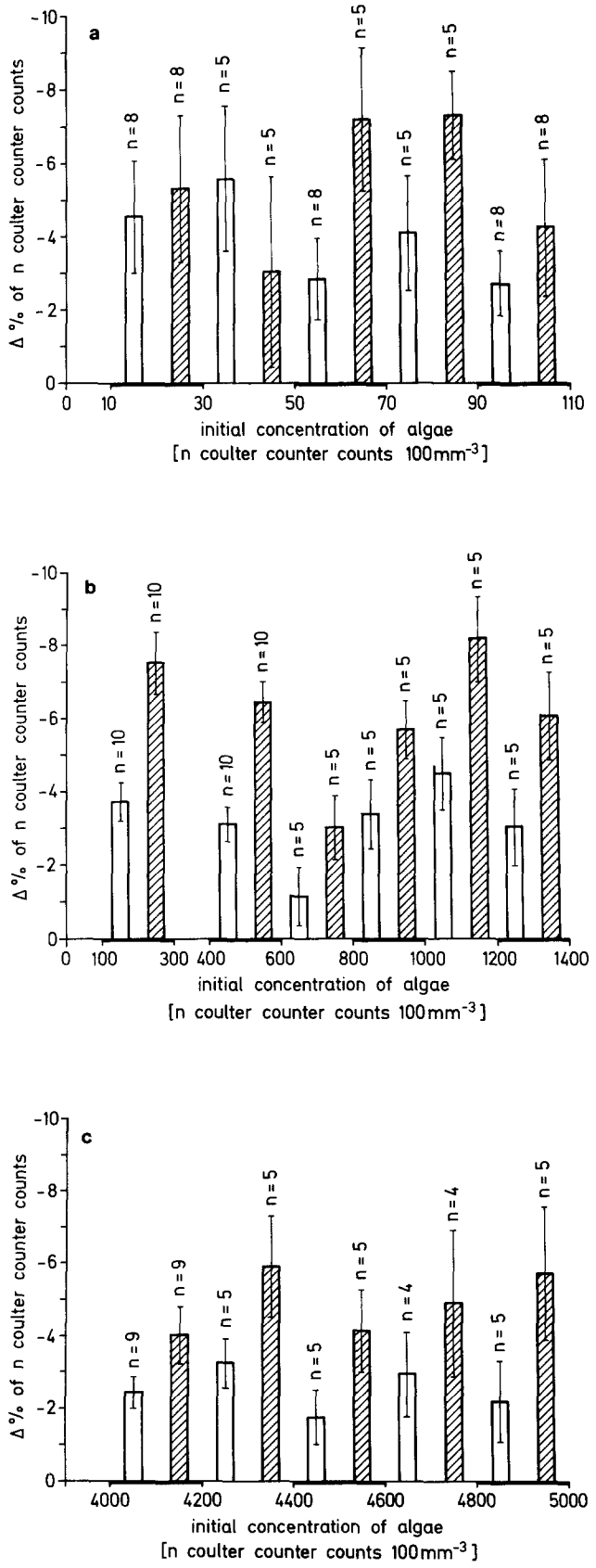


Fig. 1a–c. Systemic loss of *Chlorella fusca* (control experiments); classes of initial concentrations were tested; classes are indicated by sequence of *bold* and *thin lines* of *x* axis; *n* = number of tests per class, *open columns* = 30-min tests, *hatched columns* = 60-min tests, *vertical bars* indicate SE

tubes, was mounted on a magnetic stirrer. A rust-proof wire net was situated 20 mm above the chamber bottom to prevent larvae from feeding on precipitated algae. The water was aerated through a pipette 30 mm below the surface. Oxygen concentration (8.5 mg $O_2 \cdot l^{-1}$ at 22° C; equals 100% saturation) was reached before the experiment was started. The carbon dioxide concentration was 2.2 mg^{-1}. The standardized water was filtered twice to remove any foreign particles: first through a paper filter and then through a membrane filter of pore size 0.2 µm (Schleicher and Schüll No. 595 1/2 and BA83).

Total larval weight for each test was calculated to be in the range of 1.5–2.0 g biomass (max. $n = 20$). For the Stage 28 *B. calamita* larvae, which were extremely small, measures were based on a larger sample ($n = 50$).

The larvae were introduced into the experimental chamber. After allowing the larvae 30 min acclimatization the algae were introduced into the experimental chamber and stirred. The experiment was started by pipetting out a sample from a constant depth of 30 mm. The sample was measured with a Coulter Counter (Model FN). This was the zero or initial concentration (C_i) of algae. The total duration of the experiment was 60 min. The algae were stirred and a sample was pipetted out and measured (C_{60}). Each sample was measured 10 times. The larvae were then weighed (± 10 mg). For the control experiments samples were taken at zero, after 30 min and after 60 min (Fig. 1).

Adjustment of Coulter Counter and measurement of Chlorella *algae*

The flow-through Coulter Counter was calibrated by comparison with algal cell counts from the microscope and a counting chamber (Neubauer counting chamber, surface area 9 mm^2, volume 0.9 mm^3) and then drawing up a calibration curve.

Control experiments at several known algal concentrations revealed that, in addition to the loss of algae through sedimentation, a systemic loss of *Chlorella* algae of about 8% by sedimentation and adhesion (Fig. 1) is found at each concentration. The fact that this loss increases in direct relation to the duration of the experiment proves that it is systemic and not the result of measurement technique. This variable was held constant during statistical computation of ingestion and filtering rates.

Statistical analysis

The difference between *Chlorella* initial concentrations (C_i) and after 60 min (C_{60}) is the quantity of *Chlorella* ingested by larvae. The ingestion is converted into ingestion rate ($I = n$ algae $\cdot g^{-1}$ larval biomass $\cdot h^{-1}$ duration of experiment or $I = \mu m^3 \cdot$ biovolume $g^{-1} \cdot h^{-1}$). The growth of larvae causes enormous differences in weight of different stages. For this reason, and to enable comparison of different stages and different species, ingestion was related to total biomass and not to individual mass.

The filtration rate (F = ml water filtered $\cdot g^{-1} \cdot h^{-1}$) was calculated from I and C_i ($F = I \cdot C_i^{-1}$, Bergman and Richman 1974; Frost 1972; Seale and Wassersug 1979). F is equivalent to Harvey's (1937) "volume swept clear" with the assumption that retention efficiency is 100%. In this study the filtration rate is simply the mathematical relationship between I and C_i because 100% retention efficiency cannot be assumed. The "retention efficiency" ("RE") is computed from the filtration rates ("RE" $= F \cdot 800^{-1} \cdot 100\%$). This indicates the percentage of particles removed from the 800-ml experimental chamber and enables comparison within this experimental design only.

Ingestion rate was plotted against C_i and the function $y = x^a - b$ fitted to the points by the least-squares method (Press et al. 1988; Table 1, Figs. 2–5). The filtering curve was obtained by transforming the ingestion curve ($y = (x^a - b) \cdot x^{-1}$, Figs. 2–5). Differences in I among species and stages were obtained by substituting C_i, a and b in $y = x^a - b$ and computing y ($= I$) (Fig. 6).

Table 1. Ingestion of *Chlorella* by anuran larvae. Statistical parameters of $y = x^a - b$; r = Pearsons' Correlation Coefficient; SSD = sum of squared deviations; Xl = *Xenopus laevis*, Rt = *Rana temporaria*, Bc = *Bufo calamita*, Bb = *Bufo bufo*

Species	Stage	r	a	b	SSD
$C_i = 1 \times 10^4 - 5 \times 10^4$ algae ml^{-1}					
Xl	28	0.88	0.53	139.38	1.31
	32	0.54	0.37	27.48	5.27
	40	0.77	0.46	70.83	1.42
Bc	32	0.58	0.42	43.15	1.79
	40	0.90	0.44	53.43	0.17
Rt	28	0.51	0.43	50.82	4.24
	32	0.31	0.35	21.82	6.64
	40	0.60	0.73	861.88	7.84
Bb	28	0.35	0.14	3.13	1.51
	32	0.01	0.02	0.58	1.51
	40	0.36	0.49	62.94	6.60
$C_i = 5 \times 10^4 - 1 \times 10^6$ algae ml^{-1}					
Xl	28	0.75	0.56	401.09	293.02
	32	0.73	0.57	635.26	336.40
	40	0.83	0.53	217.82	201.73
Bc	28	0.69	0.52	160.41	102.86
	32	0.74	0.55	472.87	136.36
	40	0.92	0.57	757.55	48.58
Rt	28	0.68	0.66	3,193.65	807.73
	40	0.17	0.28	14.87	178.43
Bb	28	0.26	0.43	103.37	390.98
	32	0.19	0.01	−2.02	307.78
	40	0.37	0.52	456.04	212.79

Results

Both *X. laevis* and *B. calamita* larvae ingested algae in the C_i range 1×10^4–1.2×10^4 *Chlorella fusca* ml^{-1} (Figs. 2a, c, e, 3b, d). For all the stages of *X. laevis* and *B. calamita* tadpoles examined ingestion occured below the lowest C_i tested by other authors, namely 5×10^5 *Chlorella pyrenoidosa* ml^{-1}. By contrast, Stage 28 *B. bufo* had the lowest ingestion and filtering rates and showed little suspension feeding below $C_i = 5 \times 10^4$ *Chlorella fusca* ml^{-1}, and only in individual cases. The ingestion rate was only slightly higher at Stage 32 for this species below the same C_i. Only in Stage 40 did *B. bufo* tadpoles show ingestion below $C_i = 5 \times 10^4$ *Chlorella fusca* ml^{-1} (Figs. 5a, c, e, 6d). This indicates that the earlier larval stages of *B. bufo* are unable to exploit the plankton density of oligotrophic-mesotrophic waters. *R. temporaria* larvae ceased to ingest at about 1.2×10^4 *Chlorella fusca* ml^{-1}. Their ingestion rate was consistently lower than that of *X. laevis* and *B. calamita* when the C_i was low, but was higher than that of Stage 28 *B. bufo*. For Stages 32 and 40, the ingestion and filtering rates of *R. temporaria* and *B. bufo* were similar at low C_i (Figs. 4a, c, d, 6c).

X. laevis generally had the highest ingestion and filtering rates. This was particularly evident in the C_i range 1×10^4–5×10^4 *Chlorella fusca* ml^{-1} (Figs. 2a, c, e, 6a; Table 1). At high C_i the ingestion rate of the *B. calamita* larva was only slightly lower than that of *X. laevis*, and even marginally exceeded it at Stage 32. *B. calamita* was an altogether more efficient suspension feeder than the other representatives of larval Type IV tested here (Figs. 3b, c, e, 6b). At high C_i *R. temporaria* Stage 28 achieved almost the same ingestion rates as *X. laevis* and *B. calamita* (Figs. 4b, 6c). A low maximum filtration rate was found only in Stage 28 of *X. laevis* and *B. calamita* and Stage 40 of *R. temporaria* (Figs. 2b, 3a, 4f). Retention efficiency increased in relation to the filtering rates (Figs. 2–5).

As might be expected, there was little correlation between C_i and I (r, Pearsons' Correlation Coefficient for any of the *B. bufo* stages (Table 1). For all other species and stages, r was at least a moderate, and in most cases high, except for Stages 32 (low C_i) and 40 (high C_i) *R. temporaria* (Table 1). This means that, with the exception of *B. bufo* and Stages 32 and 40 *R. temporaria*, the other species and stages all clearly reacted to increases in the supply of suspended food by increasing their ingestion rate.

Generally, the more effectively a species filtered over a certain C_i range, the greater the difference between its premetamorphic (Etkin 1968) Stage 28 and prometamorphic Stage 40: Stage 28 *X. laevis* exceeded Stage 32 (Fig. 6a). Stage 28 of *B. calamita* and *R. temporaria* only exceeded Stage 40 in the C_i range 8×10^4–1×10^6 *Chlorella fusca* ml^{-1} (Figs. 3, 4). Once again *B. bufo* larvae prooved to be the exception: Stage 40 was the most effective compared to the Stages 28 and 32 at a low C_i (Fig. 6d).

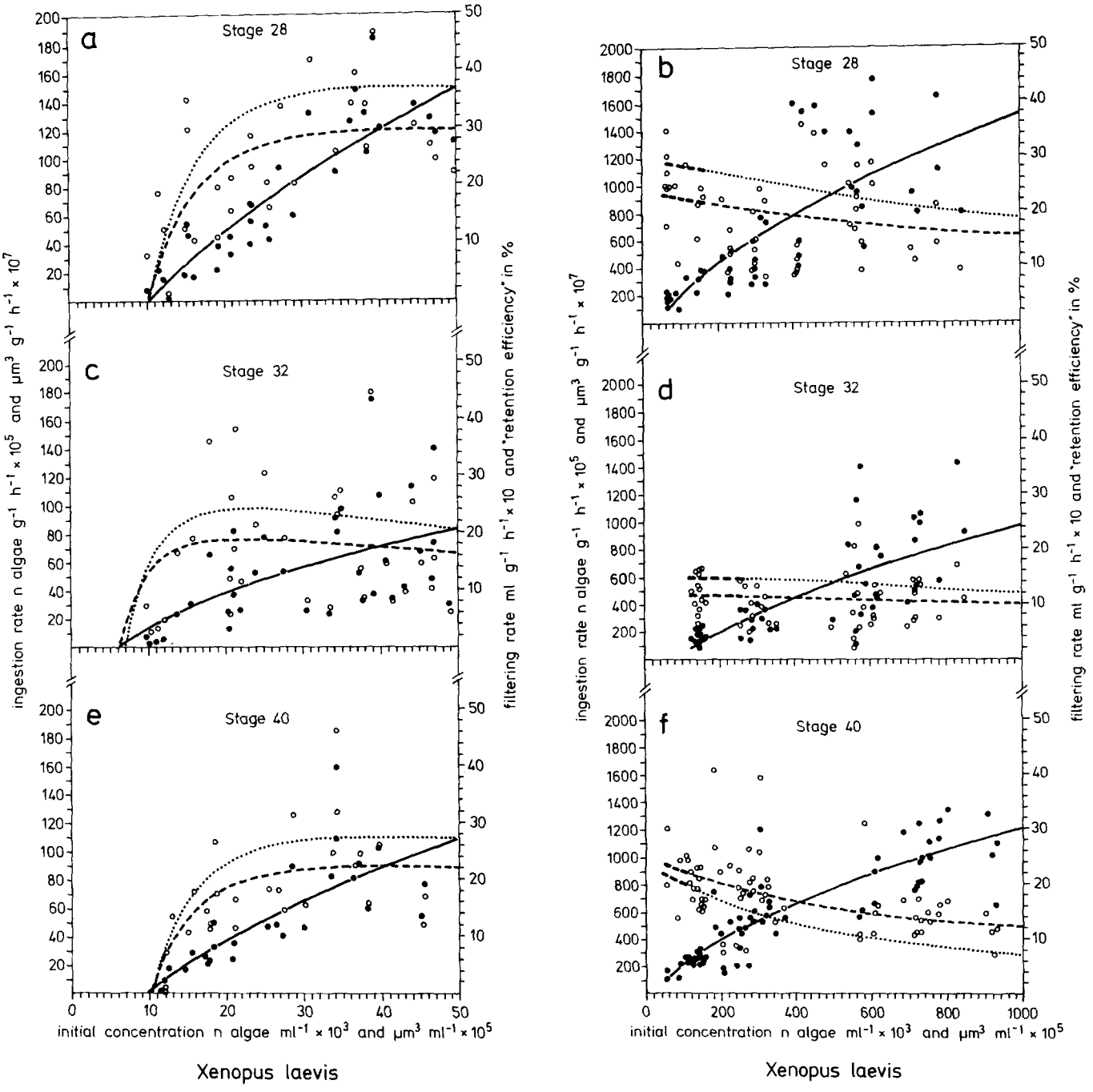
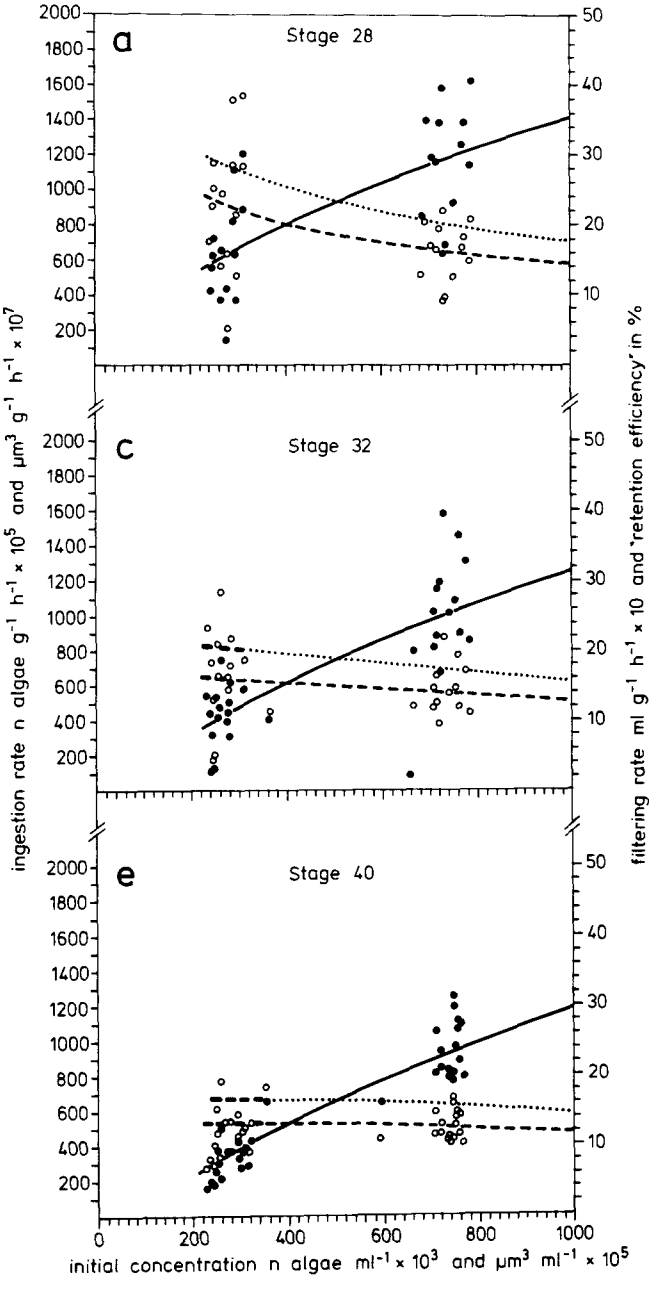


Fig. 2a–f. *Xenopus laevis*. Ingestion rate, filtering rate and "retention efficiency" plotted against initial concentration. ●, – = ingestion; ○, – – = filtering;.... = "retention efficiency"; —— = short sections of filtering and "retention efficiency" curves fitted by eye

Discussion

The question of what model best describes the correlation between I (or F) and C_i has often been the subject of discussion. Beside linear regression, following the least square method which results in a rectilinear x-y correlation (Frost 1972), the Ivlev equation was specially modified by Parsons et al. (1967) in order to express ingestion and filtering results ($I = I_{max} \cdot (1 - e^{-\delta(C_i - TC)})$. I_{max} is the maximum ingestion rate, TC the threshold concentration where ingestion ceases and δ is a constant. Mullin et al. (1975) modified the Michaelis-Menten equation to include TC in the description of feeding dynamics ($I = I_{max} \cdot (C_i - TC)) \cdot (K_{1/2} + (C_i - TC))^{-1}$). The half-saturation constant $K_{1/2}$ is the C_i at which half of the I_{max} is reached. As the anurans did not reach I_{max}, and thus also not $K_{1/2}$ in the C_i ranges tested, neither the modified Michaelis-Menten equation nor the modified Ivlev equation are applicable. The simplest fit, a nonlinear function $y = x^a - b$ describes the alignment of points but provides little insight into the underlying biological regulation of the tadpoles' functional responses.



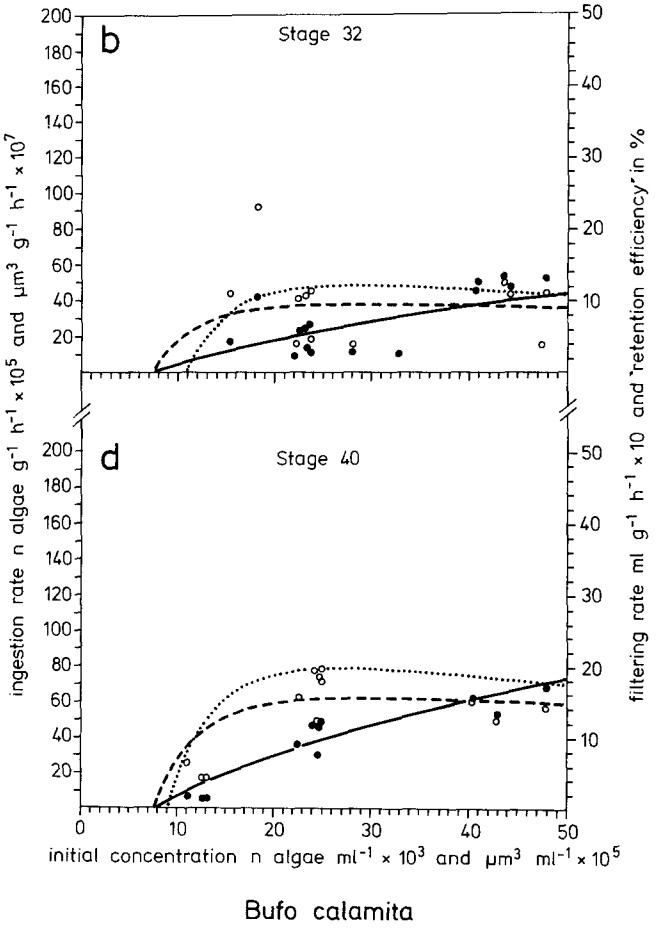
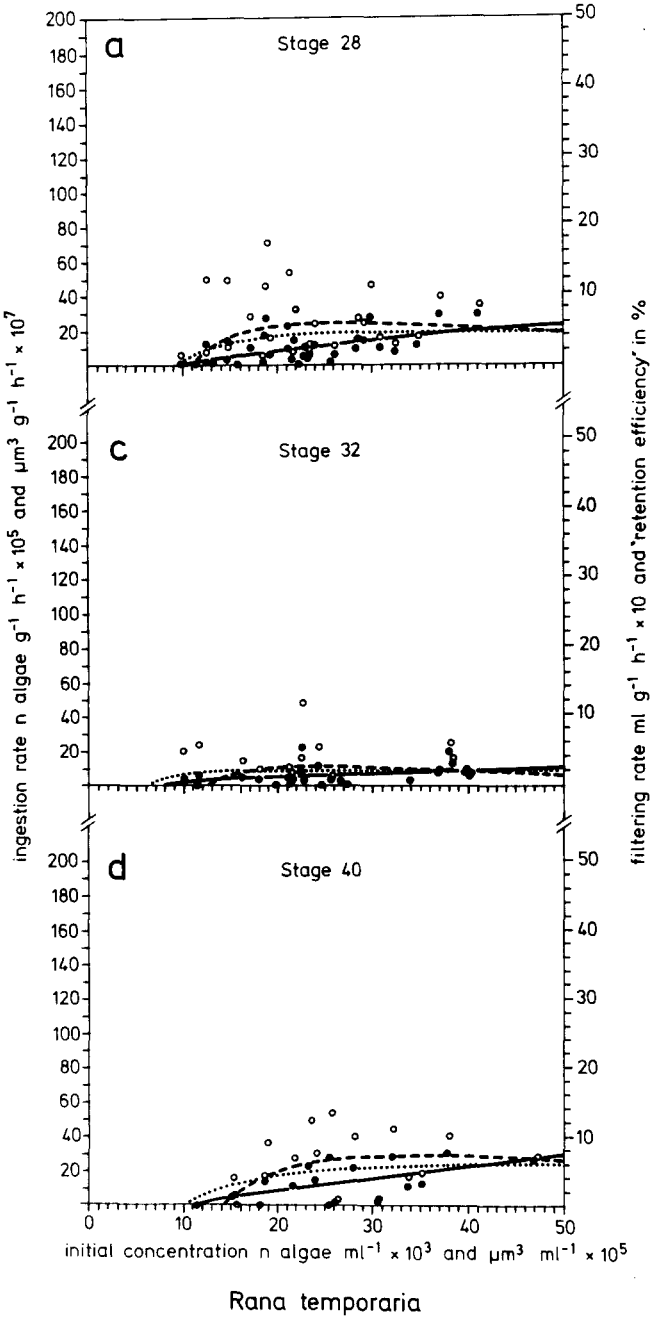


Fig. 3a–e. *Bufo calamita.* Ingestion rate, filtering rate and "retention efficiency" plotted against initial concentration. ●– = ingestion; ○, – – = filtering;... = "retention efficiency"; —— = short sections of filtering- and "retention efficiency" curves fitted by eye

The phenomenon displayed in particular by Stage 28 and 32 *B. bufo* tadpoles, which are unable, or barely able, to exploit a C_i of 1×10^4–5×10^4 *Chlorella fusca* algae ml^{-1} is reminiscent of the threshold feeding behaviour of *Daphnia* and *Calanus*. Many authors have stated that these species actively reduce their filtering rates to avoid a negative energy balance (Frost 1974, 1975a, b; Lam and Frost 1976; Lehman 1976). By contrast, anuran larvae maintain water currents for purposes of respiration even when food particles are not, present (Feder et al. 1984; Gradwell 1970). They therefore constantly invest energy in ventilating the pharynx. The fact that they ingest nothing, or very little, despite both a low nutrient supply and continued ventilation of the bucco-pharynx, can only be explained by looking at the filtering mechanism itself. According to Seale et al. (1982) the *Xenopus* larva drastically reduces its buccal pumping rate below a C_i of 5×10^{-2} mg yeast l^{-1} (equals ca. 1.5×10^9 yeast cells l^{-1}) and above 50 mg yeast l^{-1} (equals ca. 1.5×10^{12} yeast cells l^{-1}). *R. sylvatica* larvae reduce their buccal pumping rate continuously over the whole range of C_i tested by Seale and Wassersug (1979) from 4×10^6 to 10^8 μm^3 *Chlorella pyrenoidosa* ml^{-1} algae (equals ca. 3.8×10^5 to 9.6×10^6 *Chlorella pyrenoidosa* cells ml^{-1}). A further reaction to C_i may be the regulation of filter apparatus mucus production, although Seale and Wassersug (1979) and Feder et al. (1984) assume this to be a reaction to high C_i. Possibly both factors have a regulatory function at low C_i.

The feeding behavior of these anuran larvae explains why they are able to survive in waters whose plankton density lies below the threshold concentration despite the low filtering efficiency some of them demonstrate. *R. temporaria, B. calamita* and *B. bufo* larvae scrape periphyton off surfaces with the horny beaks on their oral disc and are deposit and bottom feeders (see also Savage



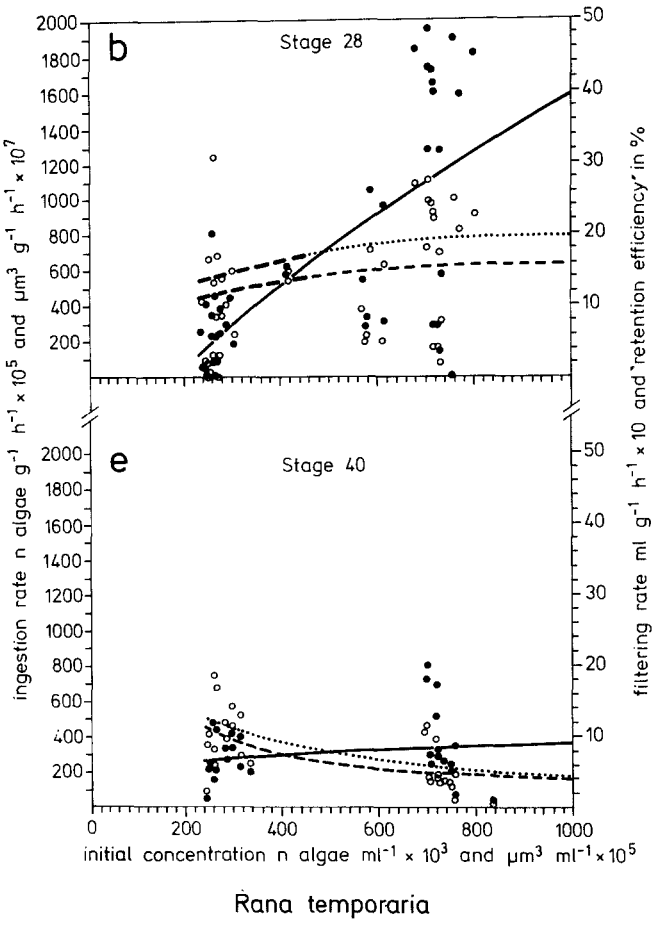


Fig. 4a–e. *Rana temporaria.* Ingestion rate, filtering rate and "retention efficiency" plotted against initial concentration. ●, – = ingestion; ○, – – = filtering;.... = "retention efficiency"; —— = short sections of filtering and "retention efficiency" curves fitted by eye

1937, 1952). *X. laevis* larvae are also able to feed by pressing water out through their mouths and stirring up particles from the bottom into a food-cloud which they then filter (Gradwell 1975). Wassersug (personal communication) observed *Xenopus* larvae stirring up particles using their tentacles. In each of these cases anuran larvae increase the food concentration to the range within which they demonstrate high efficiency (see Seale and Wassersug 1979; Seale and Beckvar 1980; Seale et al. 1982).

The high ingestion rates of the Stages 28 and 32 in contrast to Stage 40 *X. laevis, R. temporaria* and *B. calamita* larvae can be explained as causing the rapid growth of the premetamorphic stages (Breuer 1984; Kadel 1975; Viertel 1978; Waringer-Löschenkohl 1988). Polls Pelaz and Pourriot (1988) state that the Stages 30–35 *Rana ridibunda* ingest very little, if at all. The opposite is the case in *X. laevis, R. temporaria* and *B. calamita* in the present study. The tendency to low ingestion and filtering rates in Stages 28 and 32 *B. bufo* below $C_i = 5 \times 10^4$ *Chlorella fusca* ml^{-1}, however, is the same as in *R. ridibunda.*

Typical differences in ingestion efficiency are closely related to the different life histories of the species tested. High growth and development rates are necessary for *X. laevis* (6–8 weeks) and *B. calamita* (4–6 weeks) larvae living in small, ephemeral environments to avoid the threat of habitat drying. Besides temperature and tadpole density, a major factor influencing growth and development is the ability to ingest large food quantities. Another point is that larger metamorphs achieve a higher survival rate (Heusser 1968; see also Smith 1987). This is only possible in the often oligotrophic larval waters of *B. calamita* (Bregulla 1986) when highly efficient suspension feeding is combined with the feeding behaviour described above at low plankton density. In some cases *X. laevis* larvae also have the same problem (Fischer and Hinkel, personal communication).

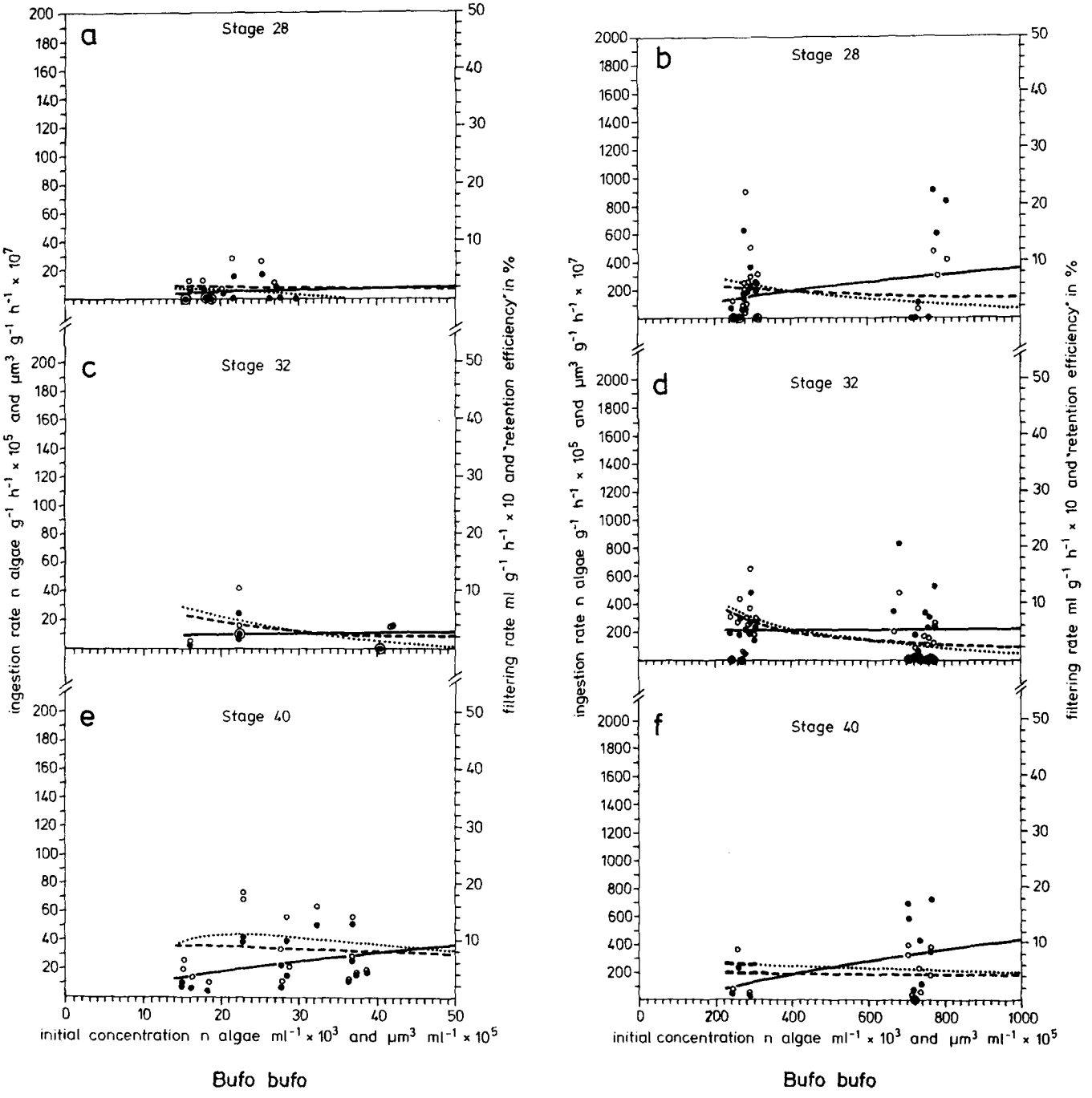


Fig. 5a–f. *Bufo bufo.* Ingestion rate, filtering rate and "retention efficiency" plotted against initial concentration. ●, – = ingestion ⊙ = two points; ○– – = filtering;.... = "retention efficiency"; —— = short sections of filtering and "retention efficiency" curves fitted by eye

B. bufo clearly does not fit into this category. Its low suspension feeding efficiency fits in with this species' well-known ecological characteristics. A rich nutrient supply is present during appearance of the *B. bufo* larvae. Thus this species does not have to achieve fast growth and development (3–4 months) to survive the drying up of its waters. *R. temporaria's* position as a suspension feeder, whose efficiency ranges somewhere between those of *B. calamita* and *B. bufo*, is in keeping with a tadpole that inhabits both permanent and ephemeral waters in most cases of a high trophic level.

Acknowledgements. I am grateful to C. Lissner for technical assistance during the filtering experiments. I should like to thank S. Pätz-Wenzel, H. Golle and P. Breuer for supplying the tadpoles, and Professor A. Wild and B. Schreiner for the *Chlorella fusca* cultures. Professor E. Schleiermacher (Mainz) made a Coulter Counter available for this study. S. Zok, K. Honomichl, R. Nagel and W. Ensenbach kindly introduced me to statistics software. I am

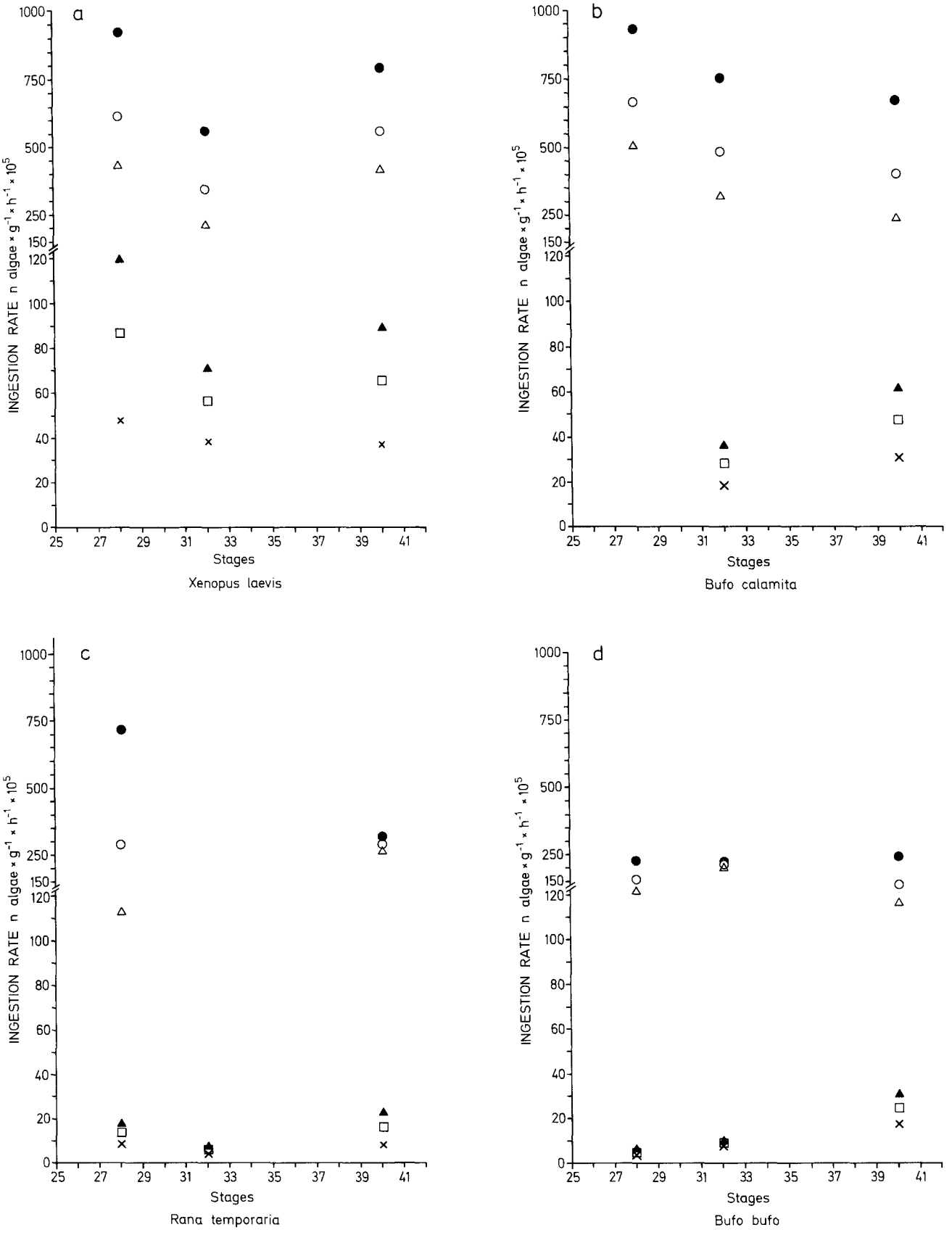


Fig. 6a–d. Comparison of ingestion rates of species and stages at different initial concentrations: $x = 2 \times 10^4$, $\square = 3 \times 10^4$, $\blacktriangle = 4 \times 10^4$, $\triangle = 2 \times 10^5$, $\circ = 3 \times 10^5$, $\bullet = 5 \times 10^5$ *Chlorella fusca* ml^{-1}

indebted to Professors A. Seitz (Mainz) and R. Wassersug (Halifax), and to Dr. H. Brendelberger (Köln) for their critical readings and discussion of the manuscript.

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