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Suspension feeding of Anuran larvae

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Filtration ist neben der Aufnahme von Teilen höherer Pflanzen, von Aufwuchs und von Bodensubstrat eine wichtige Strategie der Nahrungsaufnahme der mitteleuropäischen Anuren-Larven. Eine Auswirkung auf die planktische Biomasse eines Ökosystems ist daher ebenso anzunehmen wie die des Planktonangebotes auf die Biomasse der Larven. Wie werden die Filtrationsrate und die Ingestionsrate durch unterschiedliche Größe und Konzentration des Planktons bei unterschiedlichen Anurenspecies und ontogenetischen Stadien beeinflußt? Ein Modellversuch wurde zu dieser Fragestellung zusammengestellt: Kieselgel dient als Planktonattrappe. Seine Konzentration wird in suspendiertem Zustand durch eine Photozelle gemessen und registriert. Untersucht wurden zunächst die Konzentrationen 25 000 bis 1 Mill. (bzw. 1.9 Mill.) Partikel pro Liter der Korngröße 75-100 µm. Die Abhängigkeit der Filtrationsraten von der Konzentration gleicht einer Sättigungskurve außer bei *Bombina variegata*, wo sie bis 1.9 Mill. Part./l linear ist. *Alytes obstetricans* und *Bufo viridis* haben im Gegensatz zu *Rana temporaria* bei mittleren und hohen Konzentrationen ihr Optimum. *Hyla arborea* und der typische Filtrierer *Xenopus laevis* liegen dazwischen (Stadien 32 bzw. 36).

Anuran larvae, concentration, filtering rates, ingestion rates, population dynamics, suspension feeding.

1. Introduction

Reproduction and the trophic factor are together with inter- and intraspecific competition the most important parameters influencing population dynamics. Thus it is not surprising that a great number of ecological studies pay attention to this fact.

The following article gives a survey on the beginning of my explorations in feeding strategy of Central European Anuran larvae. Literature tells us that these species are mainly omnivorous. Thus they avoid intraspecific food competition with the carnivorous metamorphosed individuals. For this reason, suspension feeding or filtering are important ways of feeding. Like many other suspension feeders they belong to the first link of the aquatic food chain. The filtered spectrum of food consists mainly of phytoplankton, but also includes detritus, bacteria and zooplankton. Thus the tadpoles are primary consumers, secondary consumers, detritus feeders and consumers of saprotrophs. As a result their influence on energy flow and biomass, for example of the ecosystem 'pond', is obvious. Thus various questions arise: Does this strategy of food intake follow a set pattern? Is there any selectivity relating to the diameter of the suspended particles or organisms? How does a varied concentration of nutrient supply influence filtering rate and ingestion rate? Is the latter influenced by abiotic factors such as oxygen and carbon dioxide? What is the effect of different food concentrations on the biomass and survivorship of the larvae? Do different species and ontogenetic stages react in different ways? Is there any difference between r- and k-selected species or between sympatric and allopatric species? Do different filtering rates or different size range preferences select trophic niches or microhabitats and thus avoid interspecific food competition?

Summarizing: Did the evolution of these larvae effect adaptations to the nutrient supply of the different aquatic ecosystems and to the conditions under which they hatch? And last not least: What parts of the buccalpharynx work as filtering mechanisms and how do they work?

3. Materials and Methods

Larvae of *Bombina variegata*, *Alytes obstetricans*, *Bufo bufo*, *Bufo viridis* and *Rana temporaria* were collected in the field. *Hyla arborea* and *Xenopus laevis* larvae were reared. Stage 32 of the normal table of LIMBAUGH & VOLPE (1957) was chosen to test growing tadpoles. At stage 36, the curve of growth has already flattened (SAVAGE 1952; VIERTEL 1981). Within the Palaeobatrachiens a comparison of the two stages could be made. 48 hours before the experiments tadpoles from these stages were selected and exposed to a concentrate of proteins, carbohydrates and trace elements for about 6-8 hours. Afterwards the individuals were conditioned to the standard water used for all filtering experiments (ASHWORTH, CROZIER 1972: 73.99 g $CaCl_2$ + 67.76 g $MgCl_2 \cdot 6\, H_2O$ + 1000 ml Aqua dest. ≙ solution A; 56.03 g $NaCO_3$ + 1000 ml. Aqua dest. ≙ solution B; 1.79 ml A + 4 ml B + 1000 ml Aqua dest. = 'standard water'). The exposure to the concentrate was undertaken in order to prevent the formation of faeces and their entrance into the canal of measurement. Each experiment starts with the exposure of a number of larvae with a biomass of about 2 grams over a net. Suspended silica gel of the definite diameter of 75-100 µm was used as planktonic trap. Silica gel is inert and therefore useful for testing the mechanism of filtering without the influence of chemical sense. Measurement and registration of the suspension were made possible by using a photoelectric cell and a recorder with a separate low cut filter. The concentration of oxygen was also measured and registered. After 30 minutes the suspending propeller was switched off. After the sedimentation of silica gel the difference in the number of the remaining particles and the initial number were calculated. The system was adjusted by weighing an amount of silica gel with an analytical balance (accuracy up to 0.001 mg). The number of particles per unit of weight was determined by counting them under the Utermöhl microscope. A coat of water around the testing chamber supplied by a water bath kept the temperature constant at 25.3 °C. At the end of each experiment the tadpoles were weighed.

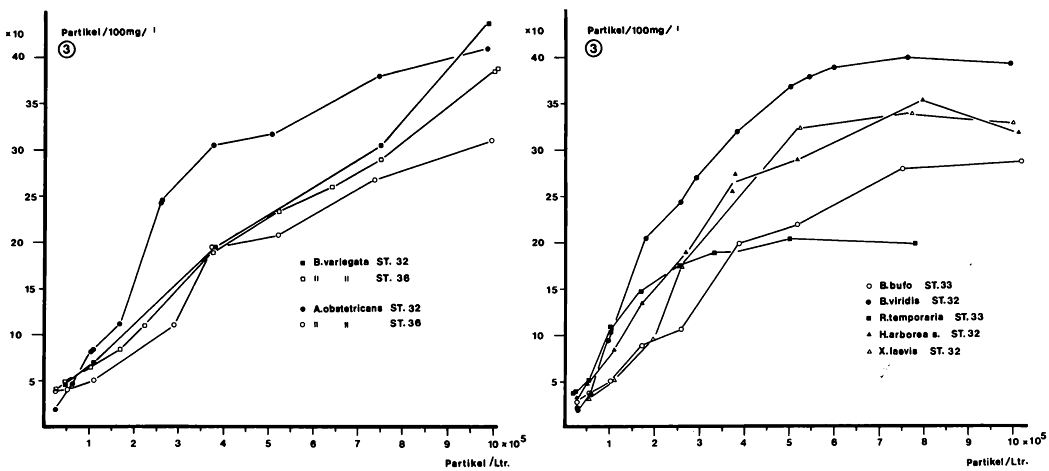

Fig. 1: Filtering rates plotted against the concentration.
a. Palaeobatrachiens (left), b. Neobatrachiens (right).

3. Results and Discussion

Fig. 1a and b show the filtering rates plotted against the concentrations of suspended silica gel. The filtering rates are converted into particles filtered per 100 mg of biomass of the tested larvae per minute.

Both stages of *Alytes obstetricans* show a steep increase of the filtering rate when concentration is raised. Both curves are almost saturation curves with a steep ascent - stage 32 - or a flat trend in stage 36. The higher efficiency unit of stage 32 is obvious. The filtering rates of *Bombina variegata*, however, increase linear to the increasing concentration up to 1.9 million/litre. Stages 32 and 36 differ only slightly.

The tested Neobatrachiens reach their optima at different concentrations. The curves of the allopatric species *Bufo viridis* and *Rana temporaria* have the same steep ascent up to a concentration of 100 000. At this point the r-selected *Bufo viridis* separates from the others and reaches the double filtering rate. But at low concentrations *Rana temporaria* reaches the highest filtering efficiency of all forms tested. *Bufo bufo*, occurring sympatric with *Rana temporaria* and representing a typical k-selected species has a very flat ascent and never reaches the level of the other *Bufonidae*. At lower concentrations up to 400 000 this curve deviates considerably from the *Rana temporaria* curve, as is once again the case at the higher concentrations. The curve of *Hyla arborea* is close to that of *Bufo viridis* but with a higher efficiency at lower concentrations. *Xenopus laevis* was tested for reasons of comparison. The pharyngeal organs of the *Xenopus laevis* larvae are totally transformed (WEISZ 1945; WASSERSUG 1972; WASSERSUG, HOFF 1979; WASSERSUG, ROSENBERG 1979). The gills are solely filtering organs. From this point of view they are the typical suspension feeders among the Anurans. But it seems not to be surprising, that they do not reach the filtering rate of *Bufo viridis* for the particle size tested. DODD (1950) says that *Xenopus laevis* larvae are able to remove suspended particles within the range of 0.2 - 2 µm. WASSERSUG (1972) terms these filter an ultraplanctonic entrapment in the range of 0.1 µm. Does the fine microfilter prevent the efficient removal of the larger particles? Are they clogged by them? Further investigations with other size ranges of particles will shed light upon these questions.

In the diagrams fig. 2a and b the filtering rates are plotted against the Briggsian logarithm of concentration. The situation at the lower and the highest concentration is impressive. The efficiency of *Rana temporaria* larvae at low concentrations is definite. The sloping down of the saturation curves (except *Rana temporaria*) at the highest concentration proves the decreasing efficiency of the filtering organs under these conditions. The two Palaeobatrachien species, however, do not reach their optimum at 1 million particles per litre.

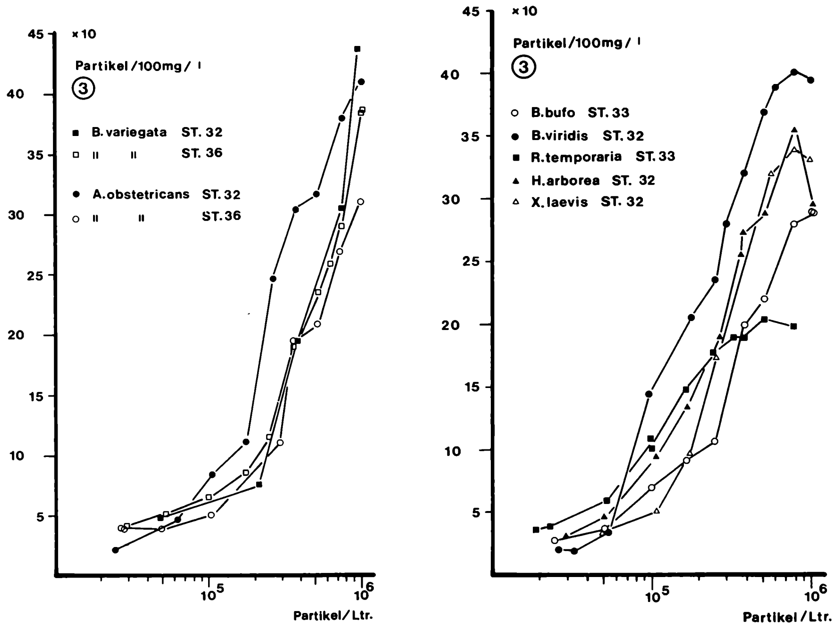

Fig. 2: Filtering rates plotted against the common logarithm of concentration.
a. Palaeobatrachiens (left), b. Neobatrachiens (right).

The diagrams fig. 3a and b represent the ingestion rate in milliliters per 100 mg of biomass per minute plotted against the concentration. Ingestion or ingestion rate is calculated from filtering rates and concentration. The two *Bombina variegata* stages start with a high ingestion rate and approach the x-axis at low concentrations, ascending slightly at high concentrations. *Alytes obstetricans* - stage 32 - follows a continuous curve up to its highest rate at c. 250 000 and then slopes down to *Bombina*. Stage 36 acts like *Bombina variegata*, but analogous to stage 32 there is an ascent at around 350 000. The Neobatrachien ingestion curves proceed similarly to *Alytes obstetricans* stage 32. *Xenopus laevis* acts alike. The logarithmic curves reflect these connections very distinctly. The interpretation of the ingestion curves is based partly on the findings of SEALE & WASSERSUG (1979). They mention a critical concentration under which the tadpoles do not have an intake of suspended food. The peaks at 120 000 to 400 000 particles per litre characterize the end of this critical concentration and the beginning of effective filtering (cf. SEALE, WASSERSUG 1979). The peaks at around 50 000 particles per litre are in my opinion not the results of effective filtering. On the contrary they are the effect of mere ventilation.

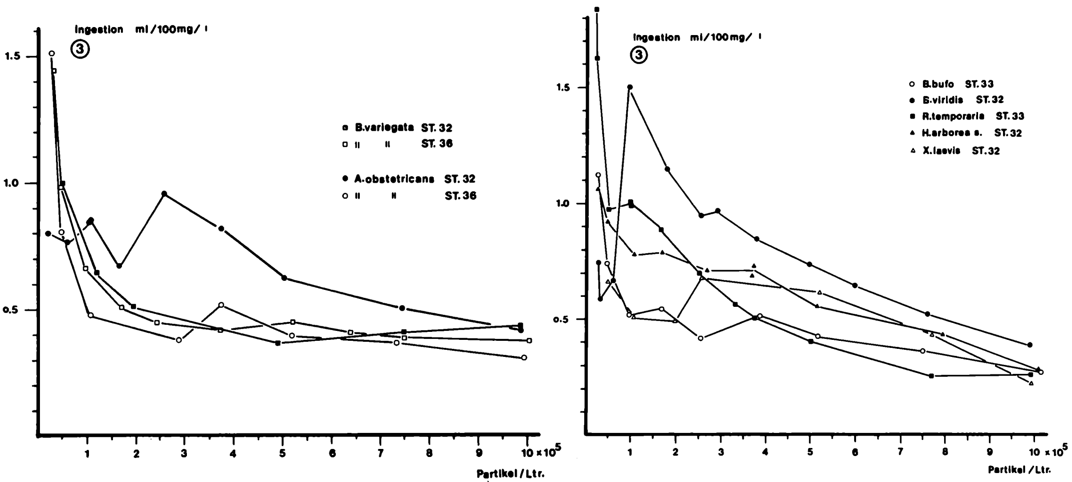

Fig. 3: Ingestion rates plotted against the concentration.
a. Palaeobatrachiens (left), b. Neobatrachiens (right).

4. <u>Summary</u>

- The filtering rates of the species are quite different: *Alytes obstetricans* and *Bufo viridis* are excellent suspension feeders at medium and higher concentrations of 75-100 µm particles. *Bombina variegata*, as an exception, does not reach the optimum within the range of 1.9 million particles per litre.
- *Hyla arborea* and *Xenopus laevis* are intermediate filterers.
- *Rana temporaria* is very effective at low concentrations (below 100 000).
- Stage 36 of *Alytes obstetricans* never reaches the efficiency of stage 32.
- Ingestion rates proceed as saturation curves, except for *Bombina variegata* which shows linearity up to 1.9 million particles per litre.
- The curves of the ingestion rate mark with a peak the end of the critical concentration and the beginning of effective filtering.
- The peak at low concentrations is merely based on the effect of ventilation.
- At this stage of my experiments I do not wish to draw ecological conclusions. Further investigations will throw light upon these matters.

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