Rotifer populations in plankton communities: Energetics and life history strategies

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Abstract. Rotifers play an important role in many freshwater plankton communities. The populations are controlled from 'bottom-up' depending on different food quantities and qualities. As threshold food levels for rotifers are higher than for cladocerans they are often outcompeted when food concentrations are lowered by the clearance activity of cladocerans. Rotifers also are controlled from 'top-down' by predators, especially by copepods, by instars of *Chaoborus* and by predatory rotifers. Mechanical interference by daphnids is considered here as a special case of 'predation'. Different defense mechanisms are discussed. At the cost of higher food concentrations (high K_s-food levels) rotifers may exhibit high maximum growth rates (r_{max}) and short times for their population development. This ability increases with rotifer body size. Within this taxonomic unity, therefore, different life history strategies have developed. These strategies may be characterized by the r_{max}/K_s-model presented.

Key words. Food quality; food quantity; competition to cladocerans; predation; body size; r_{max}/K_s-strategy; bottom-up control; top-down control.

I Introduction

Species living in the freshwater plankton are simultaneously in competition for limited resources and are under heavy predation pressure in aquatic environments that are variable in time and space. The success of a species depends on its ability to use the available resources (food that varies in size, nutrient content and concentration) and on its life history strategy to meet the different constraints of resource allocations.

The plankton community is a functional system with its environment. The population densities of the species are dependent on the resources of the environment, but, in the long run, the present activity of the organisms changes the environment itself. The organisms, therefore, are in the centre of regulation control loops with feedbacks between the organisms and their environments, which includes other organisms. The characteristic features of this regulation are based on the metabolism of the organisms exhibiting different life history strategies. A life history strategy is a product of the conflict between metabolic demands and the biotic and abiotic conditions of the environment. Evolution has resulted in different strategies of resource allocation as a mechanism for success in competition with other users of the same or similar resources and in reaction on predators.

Organisms with low energetic demands have advantages in environments with low food concentrations. On the other hand, they easily come under the control of a predator ('top-down'-control). Other organisms with a higher energetic metabolism require a higher specific food supply rate and can be outcompeted at lower food concentrations. They are rather controlled by 'bottom-up' factors (resources). On the other hand, they are able to avoid 'top-down' controls by predators by the high kinetic features of their metabolism, i.e. by high growth rates or by high efforts for defense mechanisms. These types represent the extremes of different strategies selected for high growth rates (r_{max}) or to low utilization of scarce resources (low K_s-values, see below).

This paper concentrates on the response on biotic conditions that affect regulation mechanisms. Abiotic conditions are regarded as boundary limits and were further discussed in Walz[188]. An introduction to basic rotifer ecology was given by Starkweather[157], Wallace and Snell[180], and Nogrady et al.[113].

II Energetics of Rotifer growth

II.1. Rotifer growth dependence on food quality

Impact of food size. According to the competitive exclusion principle[72], animals competing for the same limiting resources – especially food – can not coexist indefinitely. Therefore, a prerequisite for coexistence is that there must be selectivity for different food types. Food types can be classified by size, energetic or biochemical content. Because zooplankton species differ greatly in size, a size selectivity for food was examined first.

The size-efficiency-hypothesis was an attempt to clarify a functional relationship between the body size of the consumer and the size of its food particles[70]. It was argued that smaller species, especially rotifers, should be able to ingest smaller particles and vice versa[55]. For that reason – and because the diet of protozoa was unknown – rotifers were considered to be the main bacteria feeders in the plankton. Also a linear relationship was demonstrated between the length of the cladocerans and food size[16].

Larger crustaceans, however, may not fit this pattern. According to analyses of the distance between their filter-setulae and their ingestion- and growth rates, many cladocerans filter unselectively over a wide size range from bacteria to nanoplankton of about 30 µm. To this group belong *Diaphanosoma*, *Chydorus*, *Ceriodaphnia* and species of the genus *Daphnia* (e.g. *D. pulex*). Another group filters bacteria and picoplankton (<3 µm) very inefficiently, if at all: *Bosmina*, *Simocephalus*, *Sida*, other *Daphnia*-species e.g. *D. pulicaria*[10,15,24,25,42,116]. In those species capable of ingesting bacteria at all, the capacity to ingest bacteria drops with increasing distance between the setulae of the feeding appendages, which is correlated with body size[15,123]. Consequently, cladocerans, especially daphnids, feed unselectively in a broad range of nanoplankton from 3 to 20 µm[165]. This is, however, roughly the same range in which many rotifers feed[128].

By no means are rotifers the dominant bacteria and picoplankton algae feeders in plankton[10,114,117,134,176] as previously assumed, based on their size. Rotifers ingest bacteria very inefficiently so that a very high density of particles of that size is required[147,153]. Only *Keratella cochlearis*, *Kellicottia longispina* and *Conochilus unicornis* were found to consume bacteria and small aflagellate algae efficiently[9,10,46,133]. These species also feed unselectively on larger algae, characterizing them as 'generalists'[46]. Food preference of *Keratella quadrata* is not much different from *K. cochlearis*. *K. quadrata* is a polyphagous species feeding on particles smaller than 10 µm, especially Chlorococcales, Volvocales, Chrysomonadales, *Euglena*, *Rhodomonas* and centric diatoms, but also on detritus, but with a higher portion of nanoplankton[110,128]. Similar feeding preferences are typical for *K. hiemalis*[201].

Rothhaupt[135] studied the particle size spectrum for the particles ingested by three *Brachionus*-species. Clearance rates and incipient limiting levels depended on optimum particle sizes, which were correlated to body size of the rotifers. But the optimal size for the studied *Brachionus*-species were 12 µm and smaller. Ingestion rates of smaller particles at higher concentrations were as high as for optimally sized particles. Larger particles were ingested at a somewhat lower rate; but the rate remained high. In demonstrating the general strategy of rotifers compared with other zooplankton groups, these differences seem to be too narrow for a selective advantage. It may be emphasized, however, that for the seasonal succession of rotifers themselves some species may be favoured by these differences. For these reasons *Brachionus* species belong to the generalists, as well. This corresponds to the general feeding morphology in the family Brachionidae[32,43,54].

Filinia-spp. are an exception to the 'non-bacteria-feeding rule' since they are often found in bacterial horizons of eutrophic stratified lakes[64]. They feed on bacteria and minute detritus particles[110] and are very rare in larger lakes.

Sanders et al.[142] found that *Gastropus* sp., *Hexarthra* sp. and *Filinia longiseta* feed on bacteria-sized microspheres and reported lower ingestion rates for *Anuraeopsis fissa*, *Kellicottia bostonensis* and *Keratella* spp. on these particles. *Conochilus* sp. was called 'bacteriophagous', but not *Polyarthra* sp. and *Trichocerca* sp. The relative bacterial grazing impact of rotifers in eutrophic Lake Oglethorpe (Georgia, USA) accounted for a maximum of 13%, compared with 55–99% for heterotrophic flagellates, 2–45% for phagotrophic phytoflagellates, and 14–80% for ciliates. In a review of rotifer impact in the microbial web, Arndt[2] drew the conclusion that rotifers were not able to control bacterial production from top-down.

The effect of cladocerans on bacteria remains controversial. The above-mentioned Cladocera feeding on bacteria did not have an important grazing effect on the bacteria[12,121] and the nutritional value for the Cladocera is very low[121]. Other species of Cladocera may be significantly involved in bacterial grazing[63], but today it is highly evident that the heterotrophic nano-flagellates (HNF) are the most important bacteria grazers in limnic biotopes[2,6].

Other rotifer species can be considered as 'specialists'[47]. *Polyarthra*-species were unable to feed on bacteria and their ingestion efficiency decreased to small aflagellate algae. They prefer larger flagellate *Cryptomonas*-species[9,10,46] and ingested *Euglena* up to 45 µm[8]. When *Polyarthra vulgaris* was the predominant rotifer a significant decrease in large cryptomonads was observed[144]. Some *Synchaeta* spp., especially *S. pectinata*, are pronounced specialists for larger particles, which suck out large *Cryptomonas*, and *Trichocerca* spp., which feed larger filamentous algae[126]. *Ascomorpha ovalis* and *A. saltans* are specialists on dinoflagellates[92,128] and *Ascomorpha ecaudis* captures green algae and Chrysomonades[125,140]. *A. ecaudis* caught *Cryptomonas erosa* in experiments by means of its gelatinous envelope[162]. Other *Synchaeta* and *Trichocerca* species are carnivorous including the omnivorous *Asplanchna*, which feeds on large algae and rotifers[34,67].

As Cladocera seldom graze on particles larger than 20 µm[56,165], some of these rotifers may be specialists on large algae, the so-called inedible algae. This rotifer group may compete with *Eudiaptomus gracilis* and *Cyclops vicinus*[80,81] and generally with other copepods that prefer larger algal cells. However, copepods show a highly selective feeding behaviour, grasping individual algal cells separately. Physical and chemical characteristics, e.g. taste[26], of the particles play a dominant role. Indeed, in this range of particles, the netplankton, different specialist consumers may find specific niches. The effects of rotifer and cladoceran grazing, however, on phytoplankton is very different. In short-term

enclosure experiments separate macrozooplankton (*Daphnia gale-ata*) suppressed phytoplankton while microzooplankton (*K. cochlearis*) enhanced phytoplankton[74]. In similar treatments[5] small zooplankton (especially rotifers) enhanced smaller phytoplankton and suppressed larger cells, whereas larger zooplankters dominated by *Daphnia* caused declines of smaller algae while larger phytoplankton increased.

Impact of cyanobacteria on food availability. In the presence of cyanobacteria, especially filamentous forms, different strategies in the zooplankton have been observed. Larger cladocerans seem to be more inhibited than smaller cladocerans, copepods or rotifers[29,115,130]. The inhibition may consist of mechanical interference, poor food quality or toxicity of the cyanobacteria. Rotifers, including generalists like *Brachionus* species, are remarkably uninhibited and may profit in such situations. *B. calyciflorus* feeds on filamentous *Aphanizomenon* sp. by nibbling the ends of the filaments[29]. In Lake Nakuru, an East-African soda lake, *B. plicatilis* and *B. dimidiatus* nourished exclusively on the blue-green *Spirulina platensis*[179]. By stomach analysis Infante[84] found that 35% of *B. calyciflorus* individuals had eaten cyanobacteria. Whereas some strains of cyanobacteria are toxic for rotifers (e.g. *Anabaena flos-aquae* for *Asplanchna girodi*[150]), most cladoceran-toxic strains do not affect rotifers. *B. calyciflorus* grew in the presence of toxic strains of *Anabaena flos-aquae*[155,156] and *Microcystis aeruginosa*[38], in contrast to cladocerans. In competition experiments however, blooms of non-toxic *M. aeruginosa* did not improve competitive ability of *B. calyciflorus* as the rotifers were outcompeted by *Daphnia ambigua* at low concentrations of the food algae[39]. The advantage of rotifers seems to lie in resistance to toxicity. *Microcystis aeruginosa* was ingested by *Brachionus rubens*, although it was toxic from endotoxins. Those individuals feeding on *M. aeruginosa* died faster than non-fed individuals. At high concentrations ingestion was stopped. The tough filaments of *Cylindrospermopis* were not ingested[138].

With cyanobacteria-free food, the largest studied *Daphnia*, *D. pulicaria*, exhibited the lowest threshold food concentration and the smallest, *D. cucullata*, the largest. This pattern was reversed in the presence of cyanobacteria. *Cylindrospermopsis raciborski* filaments increased the threshold food concentration for body growth and reproduction[59]. Rotifers may gain competitive superiority as the largest *Daphnia*, with the strongest impact in interference competition (see below), are most adversely affected.

Gilbert[52] studied the effect of *Anabaena affinis* filaments on the growth rate of cladocerans and rotifers. *Anabaena* was toxic only when ingested, i.e. it functions as an endotoxin. The growth rate of *Daphnia*, especially of larger species, was reduced, in contrast to rotifers in which a reduction was not observed. In competition

experiments, *Daphnia* excluded *Synchaeta pectinata*; but when *Anabaena* was present *Daphnia* disappeared and the *Synchaeta* population increased.

B. plicatilis grew better with a mixed diet of *Chlorella* and the blue-green *Schizothrix calcicola* than on either of these algae alone separately[151]. *Anabaena flos-aquae*, together with *Monoraphidium*, was a better food for *B. rubens* than *Monoraphidium* alone. *Anabaena* alone had no food value[138]. *Planktothrix agardhii*, however, when used alone was found to be a poor food resource for *B. calyciflorus*. Likewise, additions of this cyanobacterium increased the growth rates, compared with *Monoraphidium* alone[192].

On the other hand, low concentrations of non-toxic *Anabaena flos-aquae* filaments mechanically interfered with abilities of *D. pulex* and *D. galeata* to feed on *Chlamydomonas*[53]. Clearly the food quality of *A. flos-aquae* could compensate for the lower ingestion rates. In contrast, *K. cochlearis* was inhibited only at high filament concentrations, but these were not eaten efficiently and had no effect on growth rates. In a plankton community, mechanical interference of daphnids by cyanobacteria may reduce the danger for interference on rotifers.

Impact of clay on food quality. Suspended clay and silt particles inhibited cladocerans but not rotifers and may reverse the competitive advantage of the former[89]. The presence of suspended clay decreased ingestion rates of five cladoceran species but not of three rotifer species. Rotifers were more selective for phytoplankton offered simultaneously with clay. Cladocerans ingested more suspended clay particles than did rotifers. Smaller cladocerans were less selective for phytoplankton over clay than were larger cladocerans, and were thus more inhibited by clay. From enclosure experiments with mineral turbidity it was concluded[22] that copepods and rotifers were favoured over cladocerans, except the 'clay-tolerant' genus *Diaphanosoma*.

Impact of biochemical content on food quality. Growth is not only dependent on food quantity but a basic prerequisite is also good food quality. For example, the marine *Synchaeta cecilia* can grow on thirteen algal species of different sizes and taxa but they grow best for the long-term with *Cryptomonas ovoidea*[33]. Twenty four tested algal species did not support rotifer growth although some of them were ingested. When six of the nutritious species were fed in mixture of two species in short-term experiments, reproduction of *Synchaeta* was greatly enhanced by some of the combinations, especially when compared with the cryptophyte *Chroomonas salina*. Similar examples have been shown for freshwater rotifers[125,158]. *Keratella taurocephala* is capable of selective and flexible feeding behavior in Little Rock Lake (Wisconsin, USA) but the algae selected were uncorrelated to the ability of this algae to support rotifer growth[148].

The growth-ingestion efficiency (K_i) of *B. plicatis* depended on the growth rate of the food alga *Brachimonas submarina* in a two-stage chemostat[146]. The proportion of carbohydrates decreased whereas lipid and protein contents of the alga increased with higher algal growth rates. In aquaculture of rotifers it is long known that yeast is inadequate as food and higher population growth rates are obtained with mixed diets of several algae or algae and yeast. This is confirmed by more recent studies on life history characteristics of *B. plicatilis*[91].

Additions of cobalamin (Vitamin B_{12}) to the culture medium enhanced *B. plicatilis* growth with *Chlorella*, which alone produced suppressed growth[78]. On the other hand, rotifers grown on bakers' yeast are deficient in total lipids. In rotifers the fatty acid structure is determined by the diet[98]. Rotifer growth especially depended on the content of highly unsaturated fatty acids (HUFA) in the food[99].

Daphnia-species have higher P:C values than their food (about 30 µg P/mg C)[77]. Unfortunately only one value has been found for the rotifers with 26 µg P/mg C for *Euchlanis dilatata*[68], which is not very much lower. This shows a high P demand of both groups and, therefore, a high tendency to be limited by P, in contrast to copepods with about 10 µg P/mg C. Hessen[77] concluded that zooplankton suffer from a direct P-limitation. Severe phosphorus limited algae were nutritionally poor for *B. rubens*[139]. It was not clear if the reduced P content per se or different biochemical constituents were limiting. It should be an interesting question to study both elemental (P) and biochemical contents (especially highly unsaturated fatty acids). In contrast, amino acid profiles of rotifers were not different in dependence of different algae, and, therefore, failed to explain the better nutritive value of certain algae[100].

Impact of protozoans as food for rotifers. Many rotifers are able to feed on protozoans. Arndt[2] presented a list of rotifers feeding on heterotrophic and mixotrophic flagellates, among them there are many planktonic genera (*Synchaeta, Asplanchna, Brachionus, Keratella, Kellicottia, Polyarthra*). Autotrophic flagellates are well known as good food for rotifers[128]. The feeding of predatory rotifers, such as *Asplanchna* on ciliates is not surprising[105]: *Paramecium* is a good culture feed[131]. Gilbert and Jack[54] observed *B. calyciflorus*, and particularly *S. pectinata* to feed on ciliates. *S. pectinata* seemed to feed on some ciliates even more efficiently than large cryptomonads that are presumed to be its preferred food. The clearance rates on *Tetrahymena* were twice as high as those on *Strobilidium gyrans* probably because of *Strobilidium*'s saltatory behavior. *B. calyciflorus* had high clearance rates on *Tetrahymena*, higher than those on yeast and algae at low densities. Gilbert and Jack concluded that large rotifers are effective predators on ciliates in the 45–60 µm range[54]. Except for special

cases rotifers should not be able to control the abundance of planktonic protozoans[2], which have high reproductive rates. Cladocerans, on the other side, because of their high clearance capacity can exert a 'top-down' control of nanoplanktonic flagellates and small ciliates[86].

A problem remains for the consumer: is the ingestion of protozoans a subsistence for the growth of the consumer? At least for *Daphnia pulex* it seemed so[194]. Cladoceran growth rate increased up to 50% when ciliates were added to the diet (*Cryptomonas* sp.) but no more than 10% when rotifers were added.

II.2. Rotifer growth dependence on food quantity

Niche separation on the basis of particle size and morphological characteristics of algae cells is perhaps functional only for the rotifer specialists. In contrast, rotifer generalists are in sharp food competition with cladocera. This is the reason why in the 'energetic main stream' of the pelagic zone other principles of niche separation must be operative.

It is obvious that there are not as many food particle classes as consumer species. In contrast, in the plankton there seems to be a broad generalist group, ranging from the rotifers to cladocerans, that compete for the same food sizes, but not with the same success. Some different boundary conditions, e.g. clay, toxins and filament length, have been mentioned, but these mechanisms are confined to special cases only. The decisive factor for any zooplankter is the capacity to which they can adapt to different concentrations of food. This is closely associated with the life history strategies of the species.

Increased niche diversification, therefore, is achieved by different capabilities of animals on food concentration. In aquatic herbivorous animals this relationship may be expressed by different K_s-values in the Monod-equation:

$$r = r_{max} * C/K_s + C$$

r = specific growth rate, C = food concentration, K_s = food concentration for half-maximum growth.

Species with low K_s-values and high k-values ($k = r_{max}/K_s$ = slope at low food concentrations[186]), have higher affinities for food. At low food concentrations their rates of ingestion and growth are higher than those of species with high r_{max} exhibiting lower affinities to food. For example, *Keratella cochlearis* is adapted to lower food concentrations. On the other hand, *Brachionus angularis* is a superior competitor at higher concentrations[184]. Food affinity of *B. rubens* was higher (higher k-values, lower K_s-values) than for *B. calyciflorus*[134]. Food affinity was further dependent on the food-particle size between 2 and 12 µm. The k-values were higher at the optimal food size.
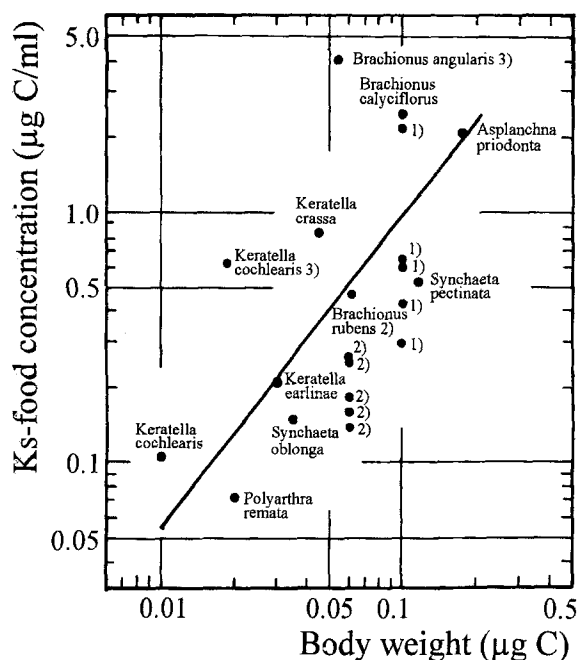
Figure 1. K_s-food concentrations in relation to rotifer body weight. 1) and 2) *B. calyciflorus* and *B. rubens* according to Rothhaupt[134]; 3) *B. angularis* and *K. cochlearis* according to Walz[186]. (After Stemberger and Gilbert[161]).

Figure 2. Threshold food concentrations in relation to body weight. 1) and 2) *B. calyciflorus* and *B. rubens* according to Rothhaupt[134]; 3) *B. angularis* according to Hartmann[73]. (After Stemberger and Gilbert[161]).

These findings correspond well to an interesting relationship between the K_s-food concentration and the body size of the rotifers. The smaller species have a higher food affinity. This relationship was demonstrated[161] in eight rotifer species (fig. 1) with further supplements by four species[134,188]. This generalization also holds within the genus *Asplanchna*[160]. The functional relationship to body size will be further explained.

The concept of K_s in the Monod model[186] has not been widely applied to cladocerans. Nevertheless, other indications for the use of different food concentrations to the cladocerans and to the rotifers exist. From experimental studies the 'incipient limiting levels (ILL)' of the ingestion rate vs. food concentration can be compared. These 'ILL' seem to be in correspondence with K_s. Cladocerans depend less on high food resources than rotifers. Most studies on daphnids indicate that these animals reach maximum ingestion rate is at about $0.3 \, \mu g \, C \, ml^{-1}$ (cf. refs 41, 95, 122). Within the cladocerans, the ILL and the ingestion rates seem to be higher for the larger species, comparing the small *Bosmina longirostris* and the larger *Daphnia rosea*[24].

In contrast, the ILL for rotifers were generally higher. ILL for *Keratella cochlearis* were $> 1.5 \, \mu g \, C \, ml^{-1}$ and $2 \, \mu g \, C \, ml^{-1}$ for *Brachionus angularis* for both *Stichococcus bacillaris* and *Coccomyxa* sp. as food algae[186]. A smaller form of *B. angularis* had an ILL of $1.3 \, \mu g \, C \, ml^{-1}$ with food particle sizes comparable to these algae[30]. The ILL of rotifers seems to depend on particle size. It is relatively lower for optimum sizes but increases especially for smaller particles as a nonlinear
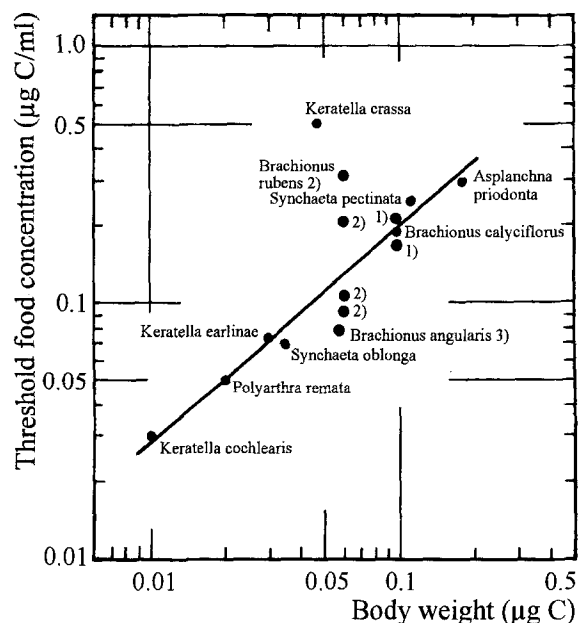
function[134]. Yúfera and Pascual[199] reported ILLs for *B. plicatilis* for different algae that were above $5 \, \mu g \, C \, ml^{-1}$ (if $C = 50\%$ dry wt). Korstadt et al.[91], however, found ILLs of 1.46 and $1.90 \, \mu g \, C \, ml^{-1}$ for this species. The ILL for *B. calyciflorus* was $2.5 \, \mu g \, C \, ml^{-1}$ with the green alga *Euglena gracilis* as food[152] and $1.5 \, \mu g \, C \, ml^{-1}$ with the cyanobacterium, *Anabaena flos-aquae*[155].

The threshold concept also demonstrates that rotifers depend on high food concentrations. There are different thresholds for the metabolism of individuals and populations[187]. The population-based threshold includes the effort to offset the losses due to mortality $(r = 0)$. From combined experiments of several authors[73,134,185] it is evident that threshold concentrations increased with the body size of rotifers (fig. 2) and are higher than for cladocerans[31,58,94] which again tended to surpass those of calanoid copepods[97]. A similar relationship to body weight was obvious within the genus *Asplanchna*[160]. The ranges between the groups, however, overlap and depend on the specific species and on resource fluctuations[104].

This positive correlation was not found within other zooplankton groups. Thresholds in cladocerans decreased with increasing body size[58,59]. Thresholds for the large *Daphnia magna* were about $0.015 \, \mu g \, C \, ml^{-1}$, and, for the smallest tested cladoceran, *Ceriodaphnia reticulata*, was about $0.04 \, \mu g \, C \, ml^{-1}$. Schiemer[145] arranged aquatic pelagic animals according to increasing theshold concentrations, with cladocerans having $0.04–0.12 \, \mu g \, C \, ml^{-1}$, calanoids with $0.007–0.11 \, \mu g \, C \, ml^{-1}$, and ciliates with $0.6–4.0 \, \mu g \, C \, ml^{-1}$. According to Frost[37] the thresholds of copepods were about
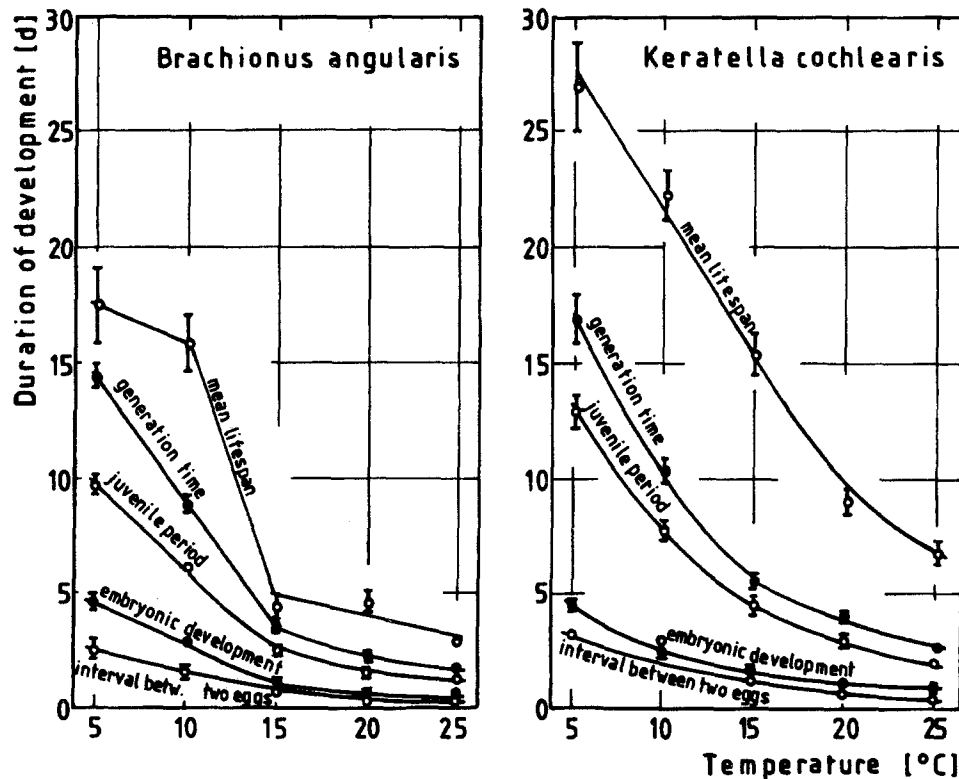
Figure 3. Duration of different life periods and times of developments of *B. angularis* and *K. cochlearis* at different temperatures. (After Walz[188]).

0.05 μg C ml^{-1} for the larger *Calanus finnmarchicus* and 0.01 μg C ml^{-1} for the smaller *Pseudocalanus* sp.[37]. An overall trend based on different taxonomical groups indicates an inverse relationship with body size[31].

Below the metabolism based threshold concentrations individuals consume the reserves, starve and die. At low food concentrations cladocera are superior in two respects: first by having lower thresholds and second by possessing higher energy reserves. Resistance to starvation in cladocerans depends on age and lipid reserves[62,171]. *Daphnia* can withstand significantly larger periods of food shortage than *K. cholearis*[103]. These rotifers had little ability to survive scarce food conditions. For *K. cochlearis* the 'LT$_{50}$' (lethal time 50%, i.e. time when 50% of the individuals are dead) is between 2 days[48] and 4 days[104], much less than for *Daphnia ambigua* (more than 8 days).

III Kinetics of rotifer growth

Energetic and quality preconditions of food are basic for species success in the plankton community. In the long run, species with higher demands on food are outcompeted in favour of species which can graze down the food concentrations below the threshold levels of their competitors. This, however, is an 'equilibrium view' of ecological interactions. This hypothesis assumes that population densities are in equilibrium with

their resources, i.e. they are food-limited and population densities fluctuate around mean values as long as the resources do not vary[196]. Therefore, a strong exclusion principle must be accepted. This equilibrium view, however, does not consider any temporal aspect of the interactions between species. Non-equilibrium models, on the other hand, presume just changing conditions as stabilizing elements for the coexistence of different species[23]. Environmental fluctuations and interactions with predators and competition may be responsible for species succession[27]. It is the speed with which species are able to respond to environmental changes that allows an advantage over competitors. For this purpose, a species should maximize the kinetic features of its growth. This, however, is rather energy consuming. The intermediate disturbance hypothesis[21] argues that the frequency and intensity of a perturbation are deciding factors[129]. This approach may be brought into agreement with the kinetic considerations of the different species.

In any case, there is a resource allocation problem[19], as the species cannot maximize reproduction and survival simultaneously[149]. To maximize growth rate, birth rate must be high and population development time must be short. Both are variables and depend on food conditions and temperature as well as on body size and on egg size.

Kinetic implications of temperature. A pairwise species comparison showed *Brachionus angularis* appears to be
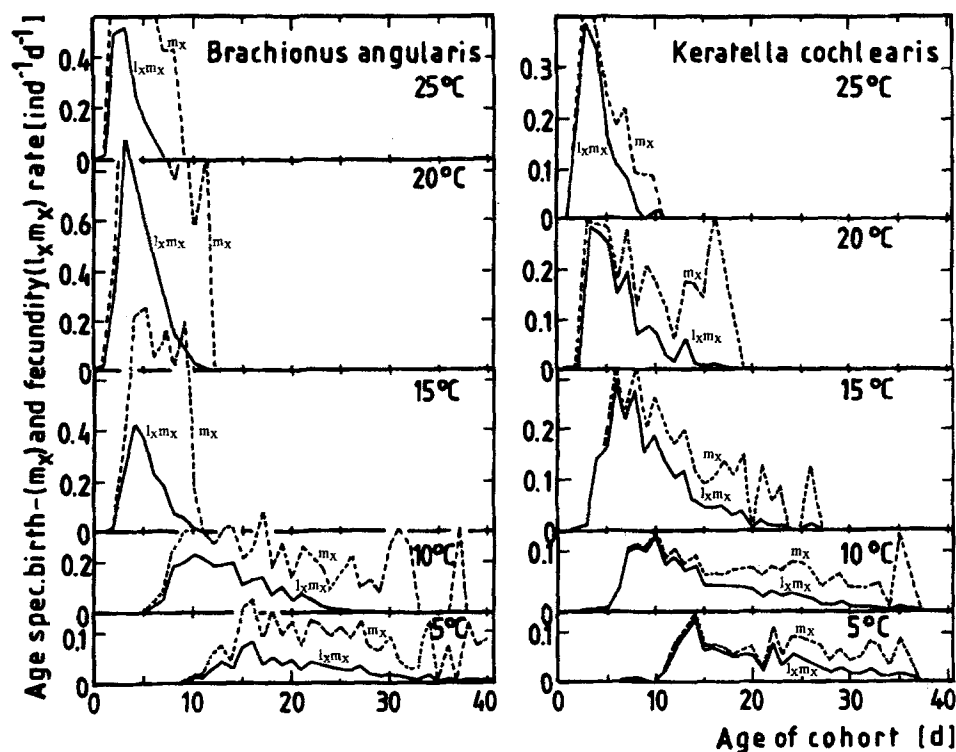
Figure 4. Age-specific birth (m_x) and fertility rates ($l_x m_x$) at different temperatures of *B. angularis* and *K. cochlearis*. (After Walz[188]).

a r_{max}-strategist[184]. Durations of all life history periods were shorter than for the K_s-strategist *Keratella cochlearis* (fig. 3). But as in all other rotifers[76], durations of those periods decreased in both species with increasing temperature[182,184].

Life span is especially important for all other rates of development. The two species do not differ significantly between the number of eggs/female produced in a lifetime[184]. The same is true for the number of hatched young. But on a daily basis egg-laying and hatching rates per female were higher for *B. angularis*. This is also shown by the age-specific birth rates (m_x) and fecundity rates (offspring per surviving female per day, $l_x m_x$) (fig. 4). Throughout, but to a lesser extent at lower temperatures, m_x was higher for *B. angularis*. On the other hand, in *K. cochlearis* life span is longer and survival is better; therefore, its l_x is higher. In this species 50% of a cohort is dead after 15 days, whereas at *B. angularis* this percentage was reached in only 4 days. The product, $l_x m_x$ (R_0) was, however, the deciding factor determining growth rate. This product was higher for *B. angularis*.

Kinetic implications of food concentration. With increasing food concentration, the duration of juvenile phase (D_p, pre-reproductive period between hatching and laying of the first egg) diminishes. In figure 5 the rate of juvenile development ($1/D_p$) is shown to increase with food concentration[185]. This shortening of the pre-reproductive phase with higher food concentrations has been established for many rotifers[88,120] and planktonic crus-
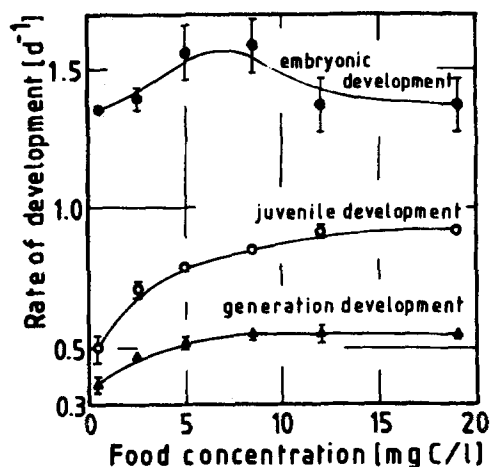

Figure 5. Relationship between the food concentration and the rate of embryonic development ($1/D_e$), rate of juvenile development ($1/D_p$), and rate of generation development ($1/D_g$) of *B. angularis*. (After Walz and Rothbucher[185]).

taceans[191]. For *B. angularis*, the rate of embryonic development ($1/D_e$) is highest in medium range food concentrations, where relative egg size is smallest[185]. But increasing juvenile development rate compensates for the prolongation of the time of embryonic development (D_e). The rate of generation development ($1/D_g = 1/D_e + 1/D_p$), as an analogue to the population growth rate, therefore, reaches a plateau according to a saturation function of the Monod model. The kinetics of rates of development resembles those of the more general
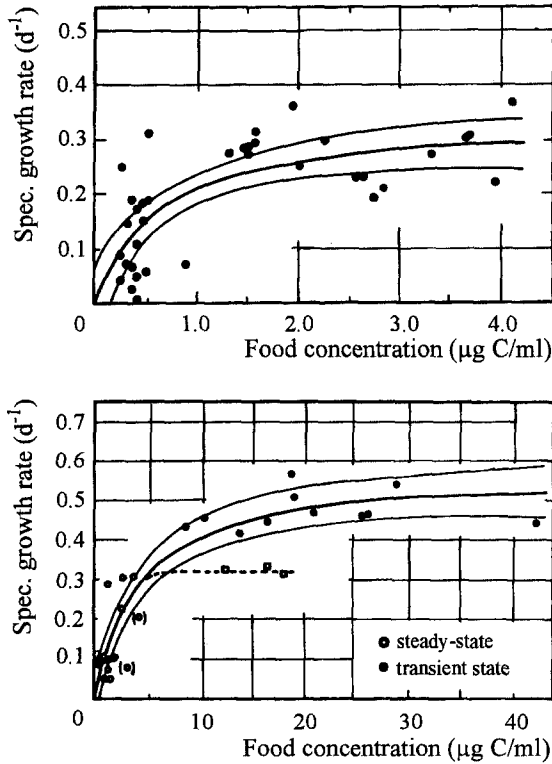
Figure 6. Specific growth rates of rotifers as related to food concentration. Upper panel: *Keratella cochlearis*; lower panel: *Brachionus angularis*. (After Walz[186]).
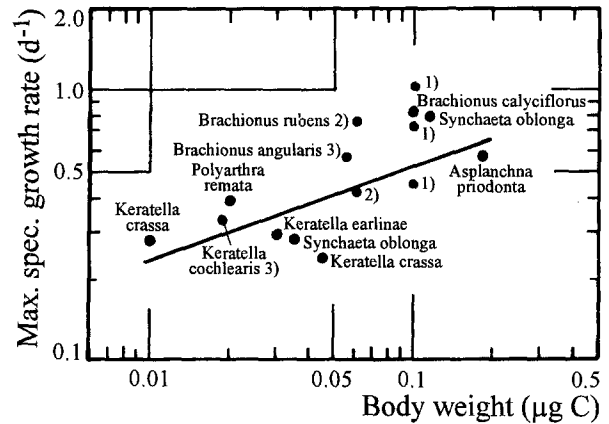

Figure 7. Maximum specific growth rates of rotifers in relation to body weight. 1) and 2) *B. calyciflorus* and *B. rubens* according to Rothhaupt[134]; 3) *B. angularis* and *K. cochlearis* according to Walz[186]. (After Stemberger and Gilbert[161]).
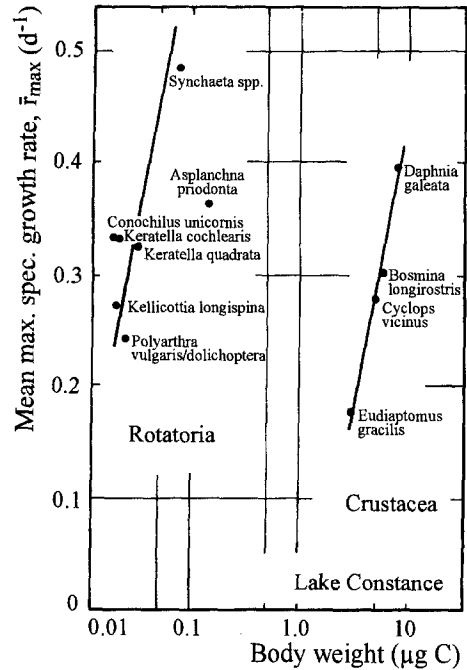

Figure 8. Maximum specific growth rates of rotifers and crustaceans in Lake Constance 1977/1978 in relation to body weight. (After Walz[188]).

Monod-saturation functions of population growth rates (fig. 6).

These relationships differ for rotifer species with different life strategies: *K. cochlearis* reached lower maximum growth rates at relatively much lower food concentrations than *B. angularis* which attained growth at much higher food concentrations (fig. 6). *Synchaeta* sp., in the estuarine Potomac River (USA), showed similar growth kinetics[75]. The maximum growth rate ($r_{max} = 0.36\ d^{-1}$) was found only at very high chlorophyll concentrations (expressed as carbon: $> 1.0\ \mu g\ C\ ml^{-1}$).

Kinetic implications of body size. The *Brachionus–Keratella* relationship[184] is only an example of a general trend. A positive interspecific relationship exists between maximum growth rate (r_{max}) and body size. Thus, smaller rotifers are not able to grow as fast as larger species (fig. 7). The values depicted in this figure were obtained from laboratory cultures of different authors[134,161,187]. A further positive relationship is demonstrated between r_{max} and body weight for the rotifers and planktonic crustaceans of Lake Constance (Germany)[188] (fig. 8). For every population, the mean r_{max}-values of the five maximum growth rates of the growing season were calculated. Both rotifers and crustaceans had higher maximum growth rates with increasing body size. Rotifers at the lower end of this size spectrum (*Polyarthra dolichoptera/vulgaris, Kellicottia longispina, Keratella cochlearis* and *K. quadrata*) are more limited

by their kinetic constraints than *Synchaeta* spp. and *Asplanchna priodonta*, which are limited by energetic requirements. It is interesting to see that rotifers with the most pronounced r_{max} are viviparous (*Asplanchna*) or do not carry their eggs (*Synchaeta*), whereas all K_s-strategists bear their eggs until hatching.

Kinetic implications of egg size. Figure 9 shows an inverse relationship between body volume and relative egg size in forty three rotifers species[189]. Larger rotifers had relatively smaller eggs. This corresponds to a functional relationship (fig. 10): species with relatively smaller eggs had higher rates of embryonic development, shorter
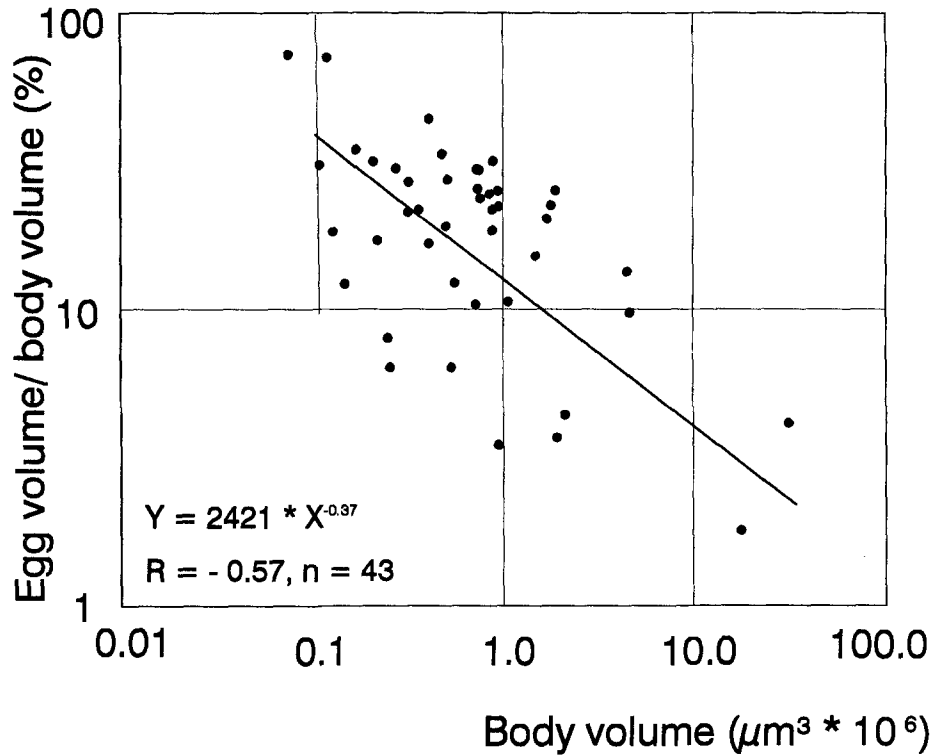
Figure 9. Relationship between body volumes and relative egg volume in rotifer species. (After Walz et al.[189]).
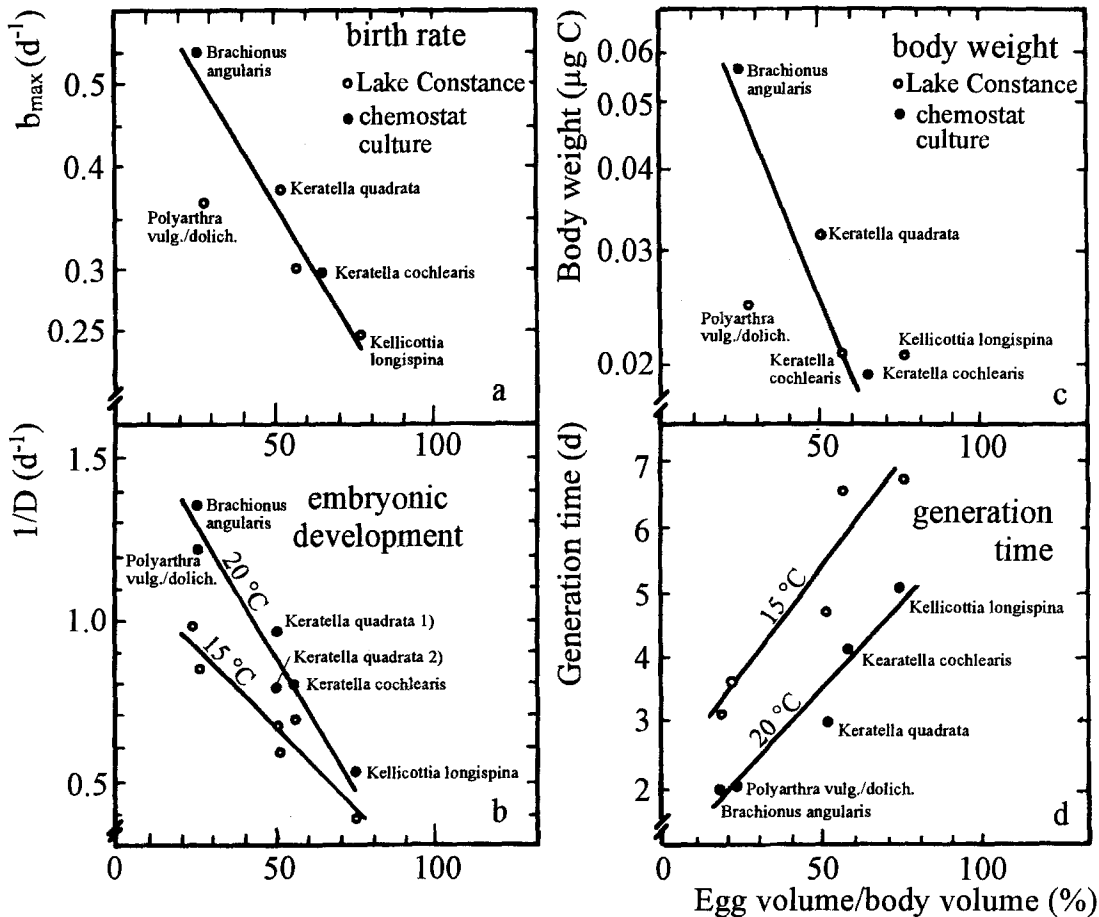

Figure 10. Relationships of different rotifer population dynamic parameters to the relative egg size: *a* maximum birth rate; *b* rate of embryonic development; *c* rotifer body weight; *d* generation time. (After Walz[188]).

generation times and higher maximum birth rates (r_{max}-strategy). Similar trade-offs between relative egg size and body weight, maximum birth rate and rate of juvenile growth as in rotifers hold for cladocerans[132]. Large cladocerans have, as in rotifers, relatively smaller eggs[101].

In contrast to *K. cochlearis*[166,188], *K. quadrata*[40] and *Asplanchna girodi*[131], for which constant relative egg sizes have been reported, other species seem to have variable relative egg sizes[190]. It is supposed that those species could switch between reproductive strategies adapted to low or high food concentrations. Relative egg sizes decreased with increasing food concentrations, whereas absolute egg sizes increased continuously (e.g. *B. rubens, B. angularis*) or had a maximum at intermediate concentrations (*B. calyciflorus*)[40,65,66,190]. The reductions in relative egg size, however, were not so much a product of smaller egg size but more of larger body size. Simultaneously carrying of more eggs was reported. The larger body size, therefore, seems to be a prerequisite to carry more eggs.

Egg volumes seem to have an influence on the duration of embryonic development (D_e). In *B. calyciflorus* and *B. caudatus* embryonic development prolonged with increase in egg size[30,127]. But Bennett and Boraas[4] found that a 70% reduction in egg volume had little effect on egg development time in *B. calyciflorus*. In *B. angularis*, no continuous relationship between absolute egg volume and D_e was found, but D_e shortened with higher relative egg size[185].

Species with relatively larger eggs, which should warrant a higher individual fitness of the offspring, should have a higher survival for the younger age classes. This was shown in a comparison between *B. angularis* and *K. cochlearis*[183]. Within a species a higher survival ratio of larger offspring was shown in *B. calyciflorus*[40].

IV Impact of predators on rotifer communities

The abundance of rotifers is not only controlled by food and competition (bottom-up mechanism) but also by predators 'from top-down'. This chapter illustrates the high impact of rotifers in predator-prey relationships in the plankton community. There are two strategies to respond to this threat for extinction. The first is to evolve high kinetic capacities (high r_{max}) resulting in a positive or, at least, a zero net growth rate. Birth rates must be higher than the predation rates by the predator. The other possibility is to evolve defense mechanisms (see below). Both strategies are energy consuming, especially the first one.

The interference between invertebrate predators and rotifers is relatively well known. Many species, especially the crustacean plankton are predators. The copepod *Cyclops vicinus* (older copepodite stages > stage 4 and adults) prefers *Polyarthra* spp., *Keratella quadrata*,

K. cochlearis, Synchaeta spp. and *Asplanchna* spp. with the highest coefficient of selection for *Asplanchna*[13]. On the other hand, Zankai[200] showed that *C. vicinus* did not select rotifers positively, but consumed them in large quantities. Recently it has become clear that adults of *C. vicinus* are omnivorous and feed at least 50% on algae[173,174]. They could reproduce even if fed on the alga diet alone[143].

In Lake Constance, *Cyclops vicinus* represents the key factor for the rotifer development at the end of the spring phytoplankton development[183]. The abundance of rotifers began to increase only after *C. vicinus* has gone into dormancy and disappeared. Then populations of *Polyarthra vulgaris/dolichoptera, Asplanchna priodonta, Keratella cochlearis* and *K. quadrata* start their development. Even though when *C. vicinus* is present their birth rates are high. Additionally, at that time *Synchaeta* populations were totally depressed. Similar observations were reported between *Cyclops bicuspidatus* and *Synchaeta* sp. in Lake Michigan (USA)[159]. This copepod preferred soft-bodied rotifers like *Synchaeta* spec. and *Polyarthra major*. But *Polyarthra vulgaris* (perhaps because of its escape behaviour) and loricate rotifers like *Keratella cochlearis* and *Kellicottia longispina* were avoided.

Mesocyclops leuckarti fed on *Asplanchna* sp. and *Synchaeta pectinata*[60], but preferred *Polyarthra dolichoptera* and *Synchaeta oblonga* and avoided *Keratella cochlearis*[87]. In Lake Constance the contrary course of rotifer[183] and of *Mesocyclops leuckarti*[167] numbers led to the hypothesis that this copepod controlled the population of *Polyarthra vulgaris/dolichoptera* in autumn[183]. *Mesocyclops edax* preyed upon *Asplanchna girodi* and *Polyarthra vulgaris* but not on *K. cochlearis*[44].

Recently, cyclopoid copepods, formerly considered to be obligate predators, were found to be actually omnivorous (see above), and calanoid copepods, before believed to be filter feeders, were observed to be raptors. For example *Diaptomus pallidus* has been reported to prey upon rotifers. Ingestion of rotifers improves survival and reproduction of this calanoid copepod. It was supported by *Synchaeta oblonga*, which is defenseless, less by *Polyarthra ramata*, which escaped by jumping response, and not at all by the hard loricate *Keratella cochlearis*[198].

The predatory rotifers *Asplanchna priodonta* preyed upon *Polyarthra* spp., *Keratella* sp., *Synchaeta* spp. but also on large algae[141]. It preferred *K. cochlearis* and *K. quadrata*[34,67]. According to Gilbert and Williamson[44], *A. priodonta* selected *Keratella cochlearis*, but avoided *Polyarthra vulgaris*. Further experiments with *Asplanchna girodi* demonstrated the easy capture of individuals of *Synchaeta pectinata, K. cochlearis* and *Conochilus* spp.[45]. It rarely captured *Kellicottia bostonensis* and intact *Conochilus* colonies and rejected the peritrich ciliate *Rhabdostylis* sp. and the dinoflagellate *Peridinium*.

In Lake Constance, after the reduction of *Cyclops vicinus* in late spring, a second predator on rotifers appeared: *Asplanchna priodonta*[183]. It executed a strong predatory pressure on *Keratella cochlearis*, which developed only after the complete disappearance of *Asplanchna*. *K. quadrata* was not so much affected and appeared in the presence of *Asplanchna*. A similar situation, but on a spatial scale, was observed in a small oligo-mesotrophic pre-Alpine lake, where *Asplanchna* and *K. quadrata/hiemalis* lived at different depths[79]. In the Lake Fasaneriesee, a eutrophic gravel pit lake near Munich (Germany), *K. cochlearis* evaded the predators *Asplanchna girodi* and *A. priodonta*, by moving to deeper areas[83], from which *Asplanchna* spp. were prevented to follow because their higher demand in oxygen contents[107]. In a man-made lake in the Netherlands high death rates of *K. cochlearis* were reported in the presence of high *Asplanchna* densities[177].

In Japan, in a shallow lake, *B. angularis*, *B. forficularis* and *Keratella* sp. decreased or remained at low densities regardless of egg-ratio when the predator *Asplanchna brightwelli* developed[175]. These prey species were encountered frequently in the stomach of *A. brightwelli*. Other rotifer species, *Polyarthra vulgaris*, *Brachionus calyciflorus* and *Hexarthra intermedia*, which were not found in the stomach, became abundant in the plankton.

Synchaeta species possess a 'virgate' mastax and several species are carnivorous[93,109,110]. Similar conditions are found in the *Trichocerca* species. They sucked out large algae, but the same species are carnivorous on other rotifers[109,110,197]. *Trichocerca capucina* is known to suck out the eggs of other rotifers[126,128], especially *Keratella* spp.[109,110].

Chaoborus larval instars live as predators on zooplankton species. They preferred smaller prey sizes[169]. Therefore, rotifers are the main prey of early instars[108], but *Chaoborus* does not prefer any particular species[29]. According to Williamson[197], *Chaoborus* preys on *Asplanchna*. The first two instars of *C. trivittatus* fed to a high degree on *Keratella cochlearis* and *Kellicottia longispina* when this prey was present in high numbers after the elimination of *Daphnia rosea*[112]. As *Chaoborus* is mostly active in the pelagial at night, being near the sediment at daytime, its influence might have been often neglected.

Because of their optical orientation, fishes do not directly predate on rotifers, whose body sizes are too small to be detected optically. At the most, large *Asplanchna* and colonies of *Conochilus unicornis* have been found in stomachs of pelagial fishes[164]. The influence of fishes is indirect as they feed on the competitors of rotifers[57,111]. On the other hand, fish larvae, after having consumed their egg-yolk, switch to feed on rotifers as their first food. This was shown for perch, carp and roach[36,69,71]. But this predatory activity is only of small ecological importance in the pelagial as the young fishes live in the littoral or near the benthos of the lakes. In freshwater aquaculture, *Brachionus calyciflorus* is used as the first food of carp larvae[195]. Marine aquaculture relies on *B. plicatilis* as food for marine fish, shrimps and crab larvae[35,100,168].

Mechanical interference as 'predation' by cladocerans. Of particular interest is the interference of rotifers with cladocerans. The alternate appearance of *Daphnia* to *Keratella cochlearis* in the plankton is known for a long time[28]. Suppression takes place by the high grazing rates of *Daphnia* lowering phytoplankton densities under the threshold levels of rotifers. Beneath this 'exploitative competition'[178], *Daphnia* species are able to sweep in the rotifers into their grazing chambers and kill them (mechanical interference competition)[48]. Rotifers, especially *Keratella cochlearis* and *Brachionus calyciflorus*, were damaged when swept into the filtering apparatus of *Daphnia*[17,18]. Rotifers had even been found in the intestine of *Daphnia*.

A question is, if this mechanism observed in laboratory experiments, plays an important role in natural communities. In semi-natural enclosures *K. cochlearis* was only suppressed by resource exploitation of *Daphnia*[172]. But the studies that have shown interference in the field are increasing in number. Even at low *Daphnia* densities (1–5 individuals per liter), mechanical interference has been reported to play a role in natural communities[49]. In Loch Leven, Scotland, a case of interference was reported[103] which was earlier considered as unlikely[106]. MacIsaac and Gilbert[103] argued that correlations between *Keratella cochlearis* birth rates and chlorophyll-a showed that rotifers were not limited by low food concentrations.

In a shallow North German lake, rotifers and *Daphnia magna* also demonstrated these known alternate population fluctuations[96]. *Daphnia* reduced the seston concentrations. Rotifers were negatively correlated with *Daphnia* and positively with seston. The inverse correlations, therefore, are sufficiently explained by exploitative competition, but they neglected, as the authors argued, that the rotifer abundance was an order of magnitude higher before *Daphnia* was present. Another field observation on interference competition was made in a shallow lake in Japan[175]. In early July, *Daphnia similis*, a large cladoceran, was present and the *Keratella valga* population was at low densities although food was abundant and the rotifers showed high egg ratios. Other predators were not found.

Because they are of small size (*Keratella cochlearis*, *Synchaeta oblonga*) or delicate (*Ascomorpha ecaudis*), many rotifers are especially vulnerable to *Daphnia* damage. Others, equipped with escape behavior (*Polyarthra*) or with larger size (colonies of *Conochilus unicornis*) are better protected[50]. In contrast to large *Daphnia*, smaller cladocerans (<1.2 mm) did not seem to inhibit rotifers. They often co-occurred at high densities and

did not mechanically interfere with the latter[49]. Ciliates were much more depressed by *Daphnia*-interference than rotifers[193].

Interference and exploitative competition can operate simultaneously at low food concentrations[103], but at high food concentrations the daphnids can eliminate the rotifers only by mechanical interference. Therefore, mechanical interference is a much more rapid method for the cladocerans to eliminate competing rotifers with an even higher efficiency than by resource competition.

Defense mechanisms. Rotifers evolved many defense mechanisms against invertebrate predators such as quick escape responses (e.g. *Polyarthra, Filinia*), hard lorica (e.g. *Keratella*), spines (e.g. *Filinia, Kellicottia, Brachionus*) and other features[163].

In a Spanish reservoir, *Asplanchna girodi* positively selected only *Keratella cochlearis* with spine length less than 15 μm and showed negative selection for individuals with larger spines[20]. Opposed to this gain under predation pressure are the costs of production and operation of spines. Maximum population growth rates of spined *K. testudo* ($0.15 \, d^{-1}$) were less than half of those of the spined forms ($0.39 \, d^{-1}$) at high food concentrations. At lower concentrations spined *K. testudo* had a lower survivorship and fecundity rate[20].

V The ecological role of pelagic rotifers in the plankton

In the preceding chapters it has been shown that rotifers with a low demand for food (low K_s-values, low threshold food levels and low incipient limiting levels) have low maximum growth rates and those with higher growth rates require more food. The energetic and kinetic features of population developments allow a continuum of life history strategies in rotifers that can be expressed as r_{max}/K_s-strategy. This concept is analogous to the well known r/K-strategy theory[102,119], which was founded in terms of the logistic equation. K-strategists are selected 'in equilibrium' by 'density dependent' factors, r-strategists, as opportunistic species, by density-independent factors.

In contrast, this r_{max}/K_s model presented here is derived from the Monod model with kinetic (r_{max}) and energetic (K_s) selection factors. In many cases, both models describe similar phenomena and relationships, particularly those that do not require the strict derivation of a specific model[118]. The r_{max}-strategists are distinguished by the kinetic aspects of growth- and birth-rates. Deciding factors are the higher growth-rates or the lower age at the first reproduction. Since this is coupled with a high K_s-value, r_{max}-strategists are energy-limited and likely controlled from 'bottom-up' in the food-chain.

The kinetic aspect of the K_s-strategy depends on the age-dependent survival rate, l_x. As a lower effort of energy is required for reproduction, reproductive activity begins relatively late in life because more energy is used for the maintenance of body structure. Since survival is more secure, mortality is lower and reproduction may be distributed over a longer period and is, therefore, at a lower rate. This strategy does not demand a high food concentration. As populations of K_s-strategists never attain high r_{max}-values, they are likely to suffer from predator pressure and become controlled from the 'top-down'[188].

The r_{max}/K_s-hypothesis also gives a model for the niche separation between rotifers and their main competitors, the cladocerans. Using food size as the only criterion has not been successful as far as the rotifer generalists are concerned. Only rotifer specialists avoid competition by feeding on larger food particles. A pairwise comparison allows a classification also in a continuum: rotifers, in general, are r_{max}-strategists and cladocerans are K_s-strategists.

The facts, however, are not so simple. It becomes evident that maximum rotifer growth rates are only higher for specialists such as *Asplanchna* and *Synchaeta* (fig. 7) than for cladocerans, especially for *Daphnia*. Also Banse and Mosher[3] found, contrary to Allan[1], that rotifers do not have growth rates as high as expected from interspecific allometric regressions. It is only their short development time that gives rotifers the decisive time advantage, when the food conditions for development are favorable, not the ultimately reached growth rates. Short time delay is a second criterion for r_{max}-strategy; in the words of Gould[61]: "being first is often a better strategy than trying often" and "precocious maturation may play an equally important role as fecundity".

Rotifers as r_{max}-strategists need higher food concentrations. This shows that they depend on 'pioneer' conditions when the Cladocera with their greater filtering efficiency are not present. In such situations they use their advantage: particularly their short juvenile and embryonic periods, and in general, their rapid generation times. Compared with cladocerans, rotifer populations are present earlier and reach high numbers very quickly.

Cladocerans react with a longer time delay even if they finally reach similar or higher actual growth rates than rotifers. Cladocerans attain higher population densities only after a longer time delay of 8 to 14 days[85,124]. Because their kinetic features are lower, they are more likely to be controlled from 'top-down' by fish predation[82].

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