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Ecology

Body size and food size in freshwater zooplankton

(ultraplankton/competition/selective feeding)

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ABSTRACT **We used double-label liquid scintillation techniques to measure the efficiencies with which eight different-sized zooplankton species ingested four cell types relative to a standard cell type (*Chlamydomonas*). Efficiency ratios (ERs: clearance rate on cell type X ÷ clearance rate on *Chlamydomonas*) on the three ultraplankton (<5 μm in diameter) cells (a coccoid bacterium and the algae *Synechococcus* and *Nannochloris*) varied greatly among zooplankton species but were not correlated with zooplankton body length. Variation in ERs on a much larger (17 × 14 μm) algal cell (*Cryptomonas*) was only partly explained by zooplankton body length. The eight zooplankton species were classified into three functional groups: (*i*) species having moderate to high ERs on all ultraplankton (0.4 < ER < 1.6) and ERs on *Cryptomonas* proportional to their body lengths (*Conochilus*, *Diaphanosoma*, and probably *Keratella cochlearis* and *Ceriodaphnia*); (*ii*) species having extremely low ERs on bacteria (mean ER < 0.05), higher but still low ERs on ultraphytoplankton (ER generally < 0.4), and ERs on *Cryptomonas* proportional to their body lengths (*Bosmina*, *Diaptomus* copepodites and adults); (*iii*) species having extremely low ERs on all ultraplankton (mean ER < 0.05) and ERs on *Cryptomonas* much higher than expected given their body lengths (*Keratella crassa*, *Polyarthra*, and *Diaptomus* nauplii). These functional groups follow neither taxonomic nor body-length groupings. We conclude that zooplankton body length may influence the maximal particle size a species can ingest but has little influence on the ingestion of smaller particles. Two frequently used models relating zooplankton body size and food size are unrealistic.**

Data on interspecific variation in the ability of suspension-feeding zooplankton to ingest ultraplankton (bacteria and algae <5 μm in any linear dimension) are scarce but important to aquatic ecology. Ultraplankton are the most numerous cells in lakes and oceans and can make substantial contributions to auto- and heterotrophic production (1, 2). Assumptions about their consumption by zooplankton are critical to models of energy flow and community structure in pelagic ecosystems.

Models of size-dependent competition among zooplankton rely on assumptions relating ultraplankton consumption to body length. The first such model was the size-efficiency hypothesis (3, 4). It assumes that all freshwater zooplankton can utilize cells in the 1- to 15-μm range, that large zooplankton can also eat larger cells, and that there is no relationship between zooplankton size and the minimal size of ingestible cells. Only the second postulate is supported by some evidence. The size-efficiency hypothesis also suggests that large zooplankton can survive and reproduce at lower food levels than small zooplankton. This suggestion is based on the idea that the ability of zooplankton to collect food increases with body size more than per capita respiration costs. Taken together, the assumptions and postulates of this hypothesis indicate that large and small zooplankton should compete for similarly sized foods and that large zooplankton should outcompete small zooplankton when these resources become limiting, both because of their ability to utilize large as well as small cells and because of their ability to exist at lower food levels.

The second model relating ultraplankton consumption to zooplankton body length originated from a study measuring the abilities of different-sized freshwater zooplankton to ingest various size fractions of sand grains (5). This study showed that small zooplankton (rotifers and small cladocerans) generally ate fine (1–5 μm) grains, whereas larger zooplankton (large cladocerans and copepods) generally consumed larger grains. These results have led to the supposition that small zooplankton specialize on small cells that larger zooplankton do not eat. This model clearly is very different from the size-efficiency hypothesis. It suggests that there is a partitioning of food resources among different-sized zooplankton, reducing potential competition between the small zooplankton and the perhaps competitively superior large zooplankton, and that the importance of small zooplankton in freshwaters should increase with the proportion of ultraplankton in the suspended cell fraction.

It is clear that an evaluation of these models depends on a better understanding of the relationship between zooplankton size and food size. The purpose of our study was to use a variety of radioactively labeled tracer cells to determine the efficiencies with which different-sized zooplankton ingest different-sized cells.

MATERIALS AND METHODS

The aim of our methodology was to determine the efficiencies with which individuals of a number of zooplankton species remove different types of tracer cells from suspension. A measure of this efficiency (E) for a given zooplankton species and tracer-cell type is E = CR/WTR, in which CR is the clearance rate and WTR is the water transport rate. Both of these rates are expressed as $\mu l \cdot individual^{-1} \cdot hr^{-1}$. CR is defined as the volume of water from which an individual removes all tracer cells per unit time. It is calculated from the equation CR = IR/[tracer cell], in which IR is the ingestion rate of tracer cells in $cells \cdot individual^{-1} \cdot hr^{-1}$ and in which the concentration of tracer cells is expressed as $cells \cdot \mu l^{-1}$. WTR is the amount of water that an individual processes or moves past its feeding apparatus per unit time. This rate would be higher than the CR unless the individual were 100% efficient in removing tracer cells from the water. Unfortunately, no one has yet measured, nor is it practical to consider measuring, WTRs for metazoan zooplankton.

However, the efficiency with which an individual can ingest one tracer-cell type relative to another tracer-cell type can be determined if both tracer-cell types are offered simultaneously. This is because the WTR has to be the same for

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Abbreviations: ER, efficiency ratio; CR, clearance rate; WTR, water transport rate.

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both tracer-cell types and therefore cancels out of the equations, leaving the relative efficiency a function only of the CRs on the two tracer-cell types. This is illustrated in the following equations for tracer-cell types 1 and 2:

$$\frac{E_1}{E_2} = \left(\frac{CR_1}{WTR_1}\right) \div \left(\frac{CR_2}{WTR_2}\right)$$

$$WTR_1 = WTR_2$$

$$\frac{E_1}{E_2} = \frac{CR_1}{CR_2}.$$

In our study, we measured the efficiencies with which eight zooplankton species ate four different tracer-cell types relative to a standard tracer-cell type–*Chlamydomonas reinhardtii*. We did this by performing a series of pair-wise comparisons in which the CR on one tracer-cell type was compared to that on *C. reinhardtii*. We call the CR on a tracer cell divided by that on *C. reinhardtii* an efficiency ratio (ER).

We offered natural assemblages of zooplankton four pairs of cell types. Routine methods are detailed elsewhere (6, 7). Here, we present only important modifications. In each pair, one of four cell types—an unidentified coccoid bacterium (0.95 μm in diameter), *Synechococcus cedrorum* (a rod-shaped, blue-green alga 3.5 × 1.5 μm), *Nannochloris oculata* (a spherical, green alga 1.8 μm in diameter), and *Cryptomonas* sp. (an obovate, flagellated alga 17 × 14 μm)—was presented with *C. reinhardtii* (a spherical, green alga 5–6 μm in diameter). *Chlamydomonas* cells (84 μm^3 per cell) were labeled with ^{33}P, and final concentrations of these cells in the incubation chamber were 2.5 cells·μl^{-1}. The other cells were labeled with ^{32}P and were at equivalent biovolume concentrations, final concentrations of these cells being 472, 112, 64, and 1.5 cells·μl^{-1} for the bacterium (0.45 μm^3 per cell), *Synechococcus* (1.9 μm^3 per cell), *Nannochloris* (3.3 μm^3 per cell), and *Cryptomonas* (166 μm^3 per cell), respectively. The bacterium and *Cryptomonas* were recent isolates from nature. The *Synechococcus*, *Nannochloris*, and *Chlamydomonas* were cultures LB1191, LB1998, and 90, respectively, from the University of Texas collection.

All cells were grown in modified MBL medium (8) at 20°C. In the evening before each experiment, logarithmic-phase cells were concentrated by centrifugation and resuspended in PO_4-free MBL medium. ^{32}P or ^{33}P as phosphoric acid was added, and on the following morning the cells were concentrated, washed, and resuspended in MBL medium. The number and volume of cells per unit volume of each stock suspension of radioactively labeled algae were determined with an electronic particle counter.

We studied the zooplankton from four lakes near Dartmouth College between May and July 1982, one lake at a time. For each lake, the experiments with very small cell types (ultraplankton) were performed during the same afternoon, whereas the experiment with *Cryptomonas* was performed 1–3 days earlier. All experiments were performed in the laboratory between 13:00 and 19:00 hr under room lighting in 10-liter glass carboys filled the morning of the experiment with untreated lakewater collected near the surface of the lake with a 7-liter Van Dorn bottle. These carboys were stored in an incubator that was illuminated (≈300 lux) and kept at the temperature of the lake where the water was collected. Thus, the zooplankton in the carboys had 2–8 hr to equilibrate to their environment before each experiment. One experiment with a pair of cell types (cell X and *Chlamydomonas*) was completed before another one was initiated.

Radioactive cells were added to a carboy by forced ejection from a pipette and then distributed throughout the carboy by stirring very gently for 1 min with a glass rod. After an incubation period of 15 min, the lake water in the carboy was filtered through a 48-μm mesh screen, a filtrate sample was collected, and the concentrated zooplankters were rinsed with 600 ml of filtered lakewater. Immediately thereafter, the zooplankters were narcotized with 4°C carbonated water and partitioned by sieving through a 363-μm mesh screen. The rotifers passed through the screen and were preserved in a 0.5% solution of tannic acid. The crustaceans were retained on the screen and were backwashed into 95% ethanol. Prior experiments (unpublished) showed that such differential preservation prevented significant (>5%) loss of phosphorus label from rotifers and cladocerans.

Within an average of 15 min following fixation, representative individuals from each species were picked from the rotifer and crustacean pools and placed in the well of a spot-plate. After all individuals (generally 5–50 for each of two or three replicates per species) from all species were isolated, the entire contents (zooplankton and fluid) of every well were placed in separate scintillation vials to assure inclusion of any label released from the zooplankton while in the wells.

Many aspects of the methodology described above were designed to prevent errors due to leakage of incorporated label from the zooplankton (see ref. 9). First, the time from preservation to placement into scintillation vials was minimized (≈15 min) by performing the incubations in the laboratory rather than *in situ*. Second, separate preservatives were used for rotifers and crustaceans because no single preservative we tried was good for both groups. Third, two isotopes of phosphorus were employed to minimize any differential loss of label.

RESULTS

CRs varied with zooplankton species, cell type, and lake (Table 1). Rates on each cell type generally increased with zooplankton body length, both within and among species. Variation in the CRs of a given zooplankton species on a given cell type among lakes, and also on *Chlamydomonas* in a given lake, was sometimes considerable and probably due to differences in temperature and especially total food concentration. Such variation in CRs, however, does not affect our analysis of selective feeding, because *Chlamydomonas* was used as an internal standard in each experiment.

Selectivity patterns varied greatly among species (Fig. 1) but only slightly for a given species among lakes. ERs (CR on cell X ÷ CR on *Chlamydomonas*) on the three ultraplankton cell types varied greatly among the eight zooplankton species but were not correlated with zooplankton body length or taxonomic classification (Fig. 1 *A–C*). ERs on *Cryptomonas* cells generally increased with zooplankton body length (Fig. 1*D*); however, *Polyarthra*, and to a lesser extent *K. crassa* and *Diaptomus* nauplii, showed values higher than expected given their body lengths. The ERs for *Polyarthra* and small *Bosmina* from lake 1 on the three pairs of algal cells were not substantially different from conspecifics of similar size from lake 2. Likewise, the ERs of *K. crassa* from lakes 1 and 3 were similar.

DISCUSSION

The maximal CRs we obtained for many of the zooplankton species in this study were higher than those previously obtained from *in situ* studies (6, 7). Thus, we believe that conducting the feeding experiments in carboys in the laboratory, rather than in grazing chambers *in situ*, did not adversely affect the performance of the zooplankton. In fact, *in situ* studies, in which zooplankton are suddenly enclosed within grazing chambers and then analyzed for a short period of time without any equilibration period, may underestimate CRs.

Table 1. CRs and mean body lengths (BL) of eight zooplankton species simultaneously offered *Chlamydomonas* and one of each of four other cell types (cell X)

Species	BL, μm	Lake	Cell X	CR *Chlamydomonas*	CR Cell X	P
KCT (1)	72	2	S	0.9 ± 0.2	0.7 ± 0.04	0.6
			N	1.7 ± 0.2	0.7 ± 0.05	**
			C	1.6 ± 0.1	0.9 ± 0.1	*
PV (2)	101	3	B	4.0 ± 0.3	0.1 ± 0.05	**
			S	13.4 ± 0.4	0.3 ± 0.02	**
			N	4.9 ± 0.4	0.6 ± 0.5	*
			C	2.3 ± 0.5	21.2 ± 2.0	**
PV (3)	104	2	S	4.0 ± 0.3	0.4 ± 0.1	**
			N	4.3 ± 0.5	0.3 ± 0.02	**
			C	3.9 ± 0.1	9.1 ± 0.8	**
PV (4)	116	1	B	14.5 ± 1.2	1.2 ± 0.1	**
			S	11.4 ± 0.7	0.5 ± 0.02	**
			N	14.0 ± 0.6	0.7 ± 0.2	**
			C	6.0 ± 0.1	12.0 ± 0.4	**
CU (5)	108	4	B	3.7 ± 0.3	3.6 ± 0.4	0.85
			S	9.6 ± 0.5	11.6 ± 2.4	0.50
			N	3.8 ± 0.6	5.3 ± 0.6	0.22
			C	10.4 ± 0.5	4.9 ± 0.5	**
KC (6)	114	3	B	52.7 ± 0.8	0.4 ± 0.1	**
			S	155.4 ± 9.9	2.8 ± 0.1	**
			N	88.8 ± 5.4	3.0 ± 0.5	**
			C	13.4 ± 0.5	15.6 ± 2.0	0.33
KC (7)	117	1	B	25.7 ± 2.1	0.1 ± 0.1	**
			S	22.8 ± 1.1	1.5 ± 0.1	**
			N	21.4 ± 1.6	1.4 ± 0.2	**
			C	8.5 ± 0.5	8.4 ± 0.8	0.91
BL (8)	220	1	B	20.8 ± 8.2	1.8 ± 0.5	+
			S	22.3 ± 0.6	16.9 ± 1.0	**
			N	22.3 ± 0.5	4.3 ± 0.4	**
			C	11.8 ± 2.8	9.0 ± 3.7	0.61
BL (9)	230	2	S	8.8 ± 0.5	6.6 ± 0.3	*
			N	9.0 ± 0.8	3.2 ± 0.7	**
			C	9.1 ± 0.4	8.1 ± 0.7	0.25
BL (10)	270	3	B	108.7 ± 12.3	5.8 ± 0.1	**
			S	124.7 ± 5.0	12.2 ± 0.1	**
			N	98.3 ± 13.6	6.8 ± 0.6	**
			C	47.3 ± 8.1	29.1 ± 4.1	0.11
BL (11)	340	1	B	82.7 ± 4.3	5.3 ± 0.5	**
			S	67.5 ± 2.8	24.8 ± 1.8	**
			N	72.6 ± 9.0	10.3 ± 1.1	**
BL (12)	460	2	S	36.0 ± 8.2	8.1 ± 0.5	*
			N	41.9 ± 5.8	13.5 ± 1.9	**
			C	36.7 ± 4.0	46.2 ± 1.8	+
CQ (13)	540	2	S	105.9 ± 14.8	59.8 ± 2.8	+
			N	86.8 ± 9.2	53.5 ± 3.5	+
			C	65.2 ± 6.1	75.4 ± 6.1	0.58
DL (14)	830	4	B	244.8 ± 33.3	209.1 ± 13.3	0.38
			S	356.7 ± 71.5	387.1 ± 31.8	0.71
			N	205.7 ± 10.6	328.8 ± 33.7	*
			C	209.9 ± 43.9	388.5 ± 88.2	0.14
DMn (15)	210	4	B	113.5 ± 44.2	3.3 ± 0.5	0.13
			S	152.6 ± 7.4	6.1 ± 0.3	**
			N	102.9 ± 5.4	3.7 ± 0.1	**
			C	83.5 ± 4.0	143.3 ± 9.0	**
DMc (16)	500	4	B	266.5 ± 14.9	5.9 ± 0.7	**
			S	306.4 ± 8.9	21.0 ± 0.8	**
			N	304.4 ± 41.9	54.3 ± 5.7	**
			C	212.3 ± 33.7	313.4 ± 17.4	+
DMa (17)	980	4	B	400.4 ± 97.6	4.3 ± 0.9	*
			S	378.7 ± 52.8	31.5 ± 3.1	**
			N	333.6 ± 52.9	69.1 ± 8.1	**
			C	394.3 ± 19.1	804.9 ± 33.2	**

CRs are expressed as $\mu l \cdot individual^{-1} \cdot hr^{-1}$ (mean ± SEM). SEMs represent variation among replicate vials from one incubation chamber. One-way analysis of variance was used to test for significant differences between the mean CRs on each pair of tracer cells (**, $P < 0.01$; *, $P < 0.05$; +, $P < 0.10$). Experimental treatments averaged 21, 21, 25, and 26°C in lakes 1, 2, 3, and 4, respectively. Species abbreviations: KCT, *Keratella cochlearis* forma *tecta*; PV, *Polyarthra vulgaris*; CU, *Conochilus unicornis*; KC, *Keratella crassa*; BL, *Bosmina longirostris*; CQ, *Ceriodaphnia quadrangula*; DL, *Diaphanosoma leuchtenbergianum*; DMn, DMc, and DMa, late-stage nauplii, early-stage copepodites, and adult *Diaptomus minutus*; B, coccoid bacterium; S, *Synechococcus*; N, *Nannochloris*; C, *Cryptomonas*. Numbers in parentheses next to species abbreviations represent species in Fig. 1.

We believe that the ERs (CR on cell X ÷ CR on *Chlamydomonas*) presented in this study quantify the inherent, relative abilities of the various zooplankton species to collect and ingest the two cell types being compared and will not vary appreciably with environmental factors such as temperature and the amounts and types of food available. In several previous studies on the selective feeding of zooplankton in natural communities (6, 7, 10), as well as in the present one, the CRs of *Keratella* spp., *Polyarthra* spp., and *B. longirostris* on several different cell types relative to those on *Chlamydomonas* remained quite constant for a given consumer species and cell type at different times of the year. More particularly, we believe that the zooplankton species that exhibited very low ERs on the three very small cell types (coccoid bacterium, *Synechococcus*, *Nannochloris*) would not be able to consume these cells any more efficiently in the absence of alternative, more readily ingested cells. A laboratory study on *Brachionus calyciflorus* (11) supports this suggestion. This rotifer had CRs on the bacterium *Aerobacter* that were lower by a factor of 8–15 than those on the larger yeast *Rhodotorula*, whether the two cell types were offered together or separately.

The major result of our study is that there is no general relationship between zooplankton body length and ability to ingest very small bacterial and algal cells. Therefore, the incorporation of ultraplankton production into the pelagic food web cannot be described as a function of zooplankton body length.

In the Crustacea, ERs on ultraplankton appear to be correlated with the structural characteristics of feeding appendages rather than with body size. Observed intersetule distances on thoracic appendages and the sieve theory of filtration were used to predict that *Diaphanosoma brachyurum*, *Ceriodaphnia quadrangula*, and *Bosmina coregoni* would be

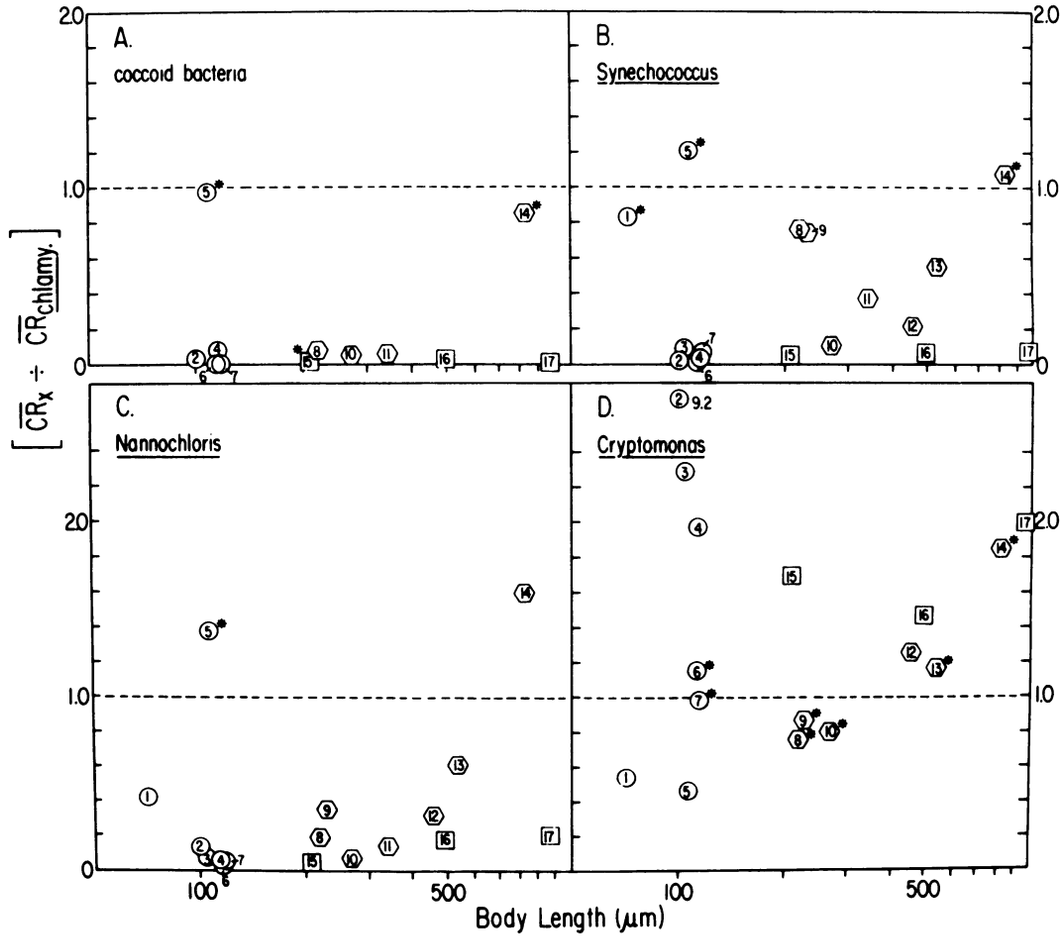

FIG. 1. Relationship between the body lengths of eight zooplankton species and their ERs on each of four cell types simultaneously offered with *Chlamydomonas*. ERs equal mean CRs on cell X divided by mean CRs on *Chlamydomonas*. Actual values are plotted, but those based on CRs that are not significantly different at the 0.10 *P* level (to minimize type II error given low degrees of freedom) are noted with an asterisk. Dashed lines represent a ratio of 1—the case of equal filtration efficiencies. Species notation as in Table 1: ○, rotifers; ⬭, cladocerans; □, developmental stages of *Diaptomus*.

progressively less effective in collecting ultraplankton (12). Our independent ranking of *D. leuchtenbergianum*, *C. quadrangula*, and *B. longirostris* based on the actual ingestion of ultraplankton was identical. This correlation between structure and function suggests that sieve theory may adequately describe the ability of some cladocerans to ingest ultraplankton.

It has been argued that the setules on the setae of the thoracic appendages of cladocerans cannot serve as sieves, because under the viscous conditions of low Reynolds numbers the mesh of the setules would function as a solid wall (13). However, it seems possible to us that water could be forced through the setules by hydrostatic pressure created by appendage movements.

The metamorphosis of all copepods involves alterations in the structure of their feeding appendages. Such alterations, documented in *Diaptomus siciloides* (14), are increases in the number, length, segmentation, and setulation of these appendages as development proceeds from nauplius to adult. Our results on ultraplankton show that the nauplii of *D. minutus* are much less effective than adults in collecting cells smaller than *Chlamydomonas*. These differences probably are related to structural differences in the feeding appendages. Thus, abundant small cells are less available to nauplii than adults—a factor that has not been fully appreciated in recent hypotheses concerning naupliar mortality (15). The differential impacts that naupliar and adult grazing have on numerous ecological processes in freshwater zooplankton communities, such as nutrient recycling and competitive interactions, constitute a largely unexplored aspect of copepod ecology.

Closely related rotifer species may partition different-sized foods by body size. The smaller *Keratella*, *K. cochlearis* forma *tecta*, had much higher ERs on the small *Synechococcus* and *Nannochloris* cells than did the larger, *K. crassa*, whereas the reverse occurred on the relatively large *Cryptomonas* cells (Fig. 1). We have described elsewhere similar patterns, both in these two *Keratella* species and in two different-sized species of *Polyarthra* (6). Such size-dependent partitioning of resources in zooplankton, however, is probably restricted to congenerics with similar morphologies (16, 17).

Rotifers as a group cannot be considered specialists on extremely small cells, as has been suggested (5). The ERs of *Polyarthra* and *K. crassa* on ultraplankton were close to zero and were much lower than those of any of the much larger cladocerans on these cells (Fig. 1 *A–C*). While these rotifers specialized on cells larger than ultraplankton, those rotifers that did eat the ultraplankton efficiently (*K. cochlearis* forma *tecta*, *C. unicornis*) also ate larger cells quite efficiently.

Polyarthra has long been considered by rotiferologists to be a specialist on large cryptomonad cells (18, 19). Our data support this suggestion. The occurrence of food specialists in the zooplankton has been considered unlikely (20), and models of inclusive food niche overlap (21) state that a spe-

cialist can coexist with a generalist only if the specialist is the more effective competitor on the shared resources. In the three lakes in our study where *Polyarthra* coexisted with *Bosmina*, *Polyarthra* collected *Cryptomonas* cells at rates similar to those of *Bosmina*, which is much larger in size and more catholic in diet. The frequent occurrence of food specialists, such as *Polyarthra* and *Synchaeta* (22), in zooplankton communities poses interesting evolutionary questions and should stimulate new models of competition.

Our results can be used to classify the eight species of zooplankton we studied into three functional groups: (*i*) species having moderate to high ERs on all ultraplankton ($0.4 < ER < 1.6$) and ERs on *Cryptomonas* proportional to their body lengths (*Conochilus*, *Diaphanosoma*, and probably *K. cochlearis* and *Ceriodaphnia*); (*ii*) species having extremely low ERs on bacteria (mean $ER < 0.05$), higher but still low ERs on ultraphytoplankton (ER generally < 0.4), and ERs on *Cryptomonas* proportional to their body lengths (*Bosmina*, *Diaptomus* copepodites and adults); (*iii*) species having extremely low ERs on all ultraplankton (mean $ER < 0.05$) and ERs on *Cryptomonas* much higher than expected given their body lengths (*K. crassa*, *Polyarthra*, and *Diaptomus* nauplii). These groups follow neither taxonomic nor body-length groupings. Body length certainly influences the maximal particle size a species can ingest, but our results show it has little influence on the ingestion of smaller particles. Structural and neurosensory characteristics intimately involved with the feeding process are undoubtedly more important than body length *per se* in determining the ability of a zooplankton species to ingest ultraplankton.

We believe that the efficiencies with which the zooplankton in our study ingested the bacterial, *Synechococcus*, and *Nannochloris* cells indicate the efficiencies with which they would ingest other similarly sized ultraplanktonic cells. However, we do not want to imply that the size of a cell is the only determinant of its tendency to be ingested by a zooplankton species. It is certainly possible that factors such as texture, surface chemistry, and surface charge (see ref. 13) may influence the efficiencies with which some zooplankton species ingest different cells of a given size.

Neither of the two frequently used models relating zooplankton body length and food size are realistic. The assumption of the size-efficiency hypothesis that all zooplankton eat cells in the 1- to 15-μm size range cannot be accepted. Our study clearly shows that some zooplankters (*P. vulgaris*, *K. crassa*, *D. minutus*) were unable to efficiently collect cells in the 1- to 4-μm range and probably would be unable to do so even if food resources were extremely limiting. The efficiency with which a species eats different-sized cells within this size range varies tremendously and cannot be predicted by body length. The model suggesting that small zooplankton eat small cells and large zooplankton eat large cells is also incorrect. Some small rotifers (*K. crassa*, *Polyarthra*, *Synchaeta*) eat ultraplankton very inefficiently or not at all, whereas some large cladocerans (*Diaphanosoma*) eat it very efficiently. The sand-grain experiments used as the basis for this model were very misleading. *K. cochlearis* may not eat sand grains >1–2 μm in diameter, but it can easily eat cryptomonad cells 17 μm in length.

In conclusion, our study shows that the assumptions many ecologists have made regarding the ability of various zooplankton to eat small suspended cells are much too simplistic and often erroneous. Attempts to categorize or predict the diet of a zooplankton species by its size or major taxonomic group clearly are unlikely to be realistic. Rather, each zooplankton species must be considered as a separate entity. Theories of zooplankton community structure and function based on zooplankton body size need to be re-evaluated.

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1. Cronberg, G. & Weibull, C. (1981) *Arch. Hydrobiol. Suppl.* **60**, 101–110.
2. Li, W. K. W., Subba Rao, P. V., Harrison, W. G., Smith, J. C., Cullen, J. J., Irwin, B. & Platt, T. (1983) *Science* **219**, 292–295.
3. Brooks, J. L. & Dodson, S. I. (1965) *Science* **150**, 28–35.
4. Hall, D. J., Threlkeld, S. T., Burns, C. W. & Crowley, P. H. (1976) *Annu. Rev. Ecol. Syst.* **7**, 177–208.
5. Gliwicz, Z. M. (1969) *Ekol. Pol. Ser. A* **17**, 663–708.
6. Bogdan, K. G., Gilbert, J. J. & Starkweather, P. L. (1980) *Hydrobiologia* **73**, 73–77.
7. Bogdan, K. G. & Gilbert, J. J. (1982) *Limnol. Oceanogr.* **27**, 918–934.
8. Stemberger, R. S. (1982) *Can. J. Fish. Aquat. Sci.* **38**, 721–724.
9. Holtby, L. H. & Knoechel, R. (1981) *Limnol. Oceanogr.* **26**, 774–780.
10. Gilbert, J. J. & Bogdan, K. G. (1981) *Verh. Int. Ver. Theor. Angew. Limnol.* **21**, 1515–1521.
11. Starkweather, P. L., Gilbert, J. J. & Frost, T. M. (1979) *Oecologia* **44**, 16–30.
12. Geller, W. & Muller, H. (1981) *Oecologia* **49**, 316–321.
13. Gerritsen, J. & Porter, K. G. (1982) *Science* **216**, 1325–1327.
14. Comita, G. W. & Tommerdahl, D. M. (1960) *J. Morphol.* **107**, 297–355.
15. Confer, J. L. & Cooley, J. M. (1977) *J. Fish. Res. Board Can.* **34**, 703–706.
16. Pejler, B. (1957) *K. Sven. Vetenskapsakad. Handl.* **6** (5), 1–68.
17. Hutchinson, G. E. (1967) *A Treatise on Limnology* (Wiley, New York), Vol. 2, pp. 530, 679–684.
18. Dumont, H. J. (1977) *Arch. Hydrobiol. Beiheft* **8**, 98–122.
19. Pourriot, R. (1977) *Arch. Hydrobiol. Beiheft* **8**, 243–260.
20. Levington, J. (1972) *Am. Nat.* **106**, 472–486.
21. Miller, R. S. (1967) *Adv. Ecol. Res.* **4**, 1–74.
22. Gilbert, J. J. & Bogdan, K. G. (1984) in *Trophic Interactions Within Aquatic Ecosystems*, AAAS Selected Symposium 85, eds. Meyers, D. G. & Strickler, J. R. (Westview, Boulder, CO), pp. 97–133.