Hydrobiologia 157: 129–141 (1988)

Food and growth relations of the marine microzooplankter, *Synchaeta cecilia* (Rotifera)

David A. Egloff
Department of Biology, Oberlin College, Oberlin OH 44074, USA

Received 30 July 1986; in revised form 6 December 1986: accepted 14 January 1987

Key words: rotifers, food, predators, *Acartia,* marine

Abstract

The trophic interactions of the marine rotifer *Synchaeta cecilia* were investigated by determining its feeding and growth rates on a wide variety of marine phytoplankton and by determining its susceptibility to predation by the calanoid copepod, *Acartia tonsa.* Reproduction of *S. cecilia* was sustained in four-day feeding trails by 13 of 37 algal species tested. Growth-supporting species included species of Cryptophyceae, Dinophyceae, Chlorophyceae and Haptophyceae in sizes from 4 to 47 μm. Within these taxa, other species in the acceptable size range failed to support growth. No species of Cyanophyceae, Bacillariophyceae, or Chrysophyceae supported growth of the rotifer. *S. cecilia* can be maintained on unialgal cultures of Cryptophyceae but growth is enhanced by a combination of two or three species; a mixture of *Chroomonas salina* (Cryptophyceae), *Heterocapsa pygmaea* (Dinophyceae), and *Isochrysis galbana* (Haptophyceae) has sustained laboratory stocks of *S. cecilia* for over four years. The expected response of *S. cecilia* to food quantity was observed: as food concentration was increased from 58 to 1154 μg C l^{-1}, the population growth constant increased from 0.17 to 0.60 d^{-1} at 20 °C. This is equivalent to population doubling times of 4.0 and 1.1 days at *H. pygmaea* densities of 500 and 10^4 cells ml^{-1}, respectively. The susceptibility of *S. cecilia* to predation was investigated by determining its rate of capture by the omnivorous marine copepod *Acartia tonsa.* At prey densities of 5 to 35 μg C l^{-1} (0.3 to 1.9 individuals l^{-1}), *A. tonsa* readily ingested *S. cecilia* at rates up to 3 μg C copepod^{-1} day^{-1}.

Introduction

Among the marine microzooplankton, rotifers have been virtually unstudied. Although rotifers are not as diverse nor as ubiquitous in the oceans as they are in fresh-water environments (Hutchinson, 1967), they do occur in most marine habitats (Berzins, 1952, 1960; Eriksen, 1968; Remane, 1929; Ruttner-Kolisko, 1974; Shih & Figueira, 1971; Sudzuki, 1964). In some marine ecosystems rotifers make up a major fraction of the biomass (Ackefors & Hernroth, 1975; Hernroth & Ackefors, 1979; Johansson, 1983; Schnese, 1973; Snell & Thomsen, 1980) as they do in many freshwater ecosystems (Makarewicz & Likens, 1979; Pace & Orcutt, 1981). Marine rotifers occur not only in coastal ponds and estuaries, but also in neritic (Berzins, 1952; Cassie, 1960) and, although less prominently, in oceanic systems (Berzins, 1960). Intensive sampling in coastal waters has demonstrated periods of high rotifer abundance alternating with periods of low or zero densities (Ackefors & Hernroth, 1975; Snell & Thomsen, 1980; Schnese, 1973). Information on rotifers from oceanic areas is more limited, but this is not surprising given the small size (< 200 μm) of the species most likely to occur there, the failure of the non-loricate species to be preserved

in an easily recognizable form, and their life cycles which result in large temporal and spatial discontinuities in distribution and abundance. The occurrence and significance of rotifers in offshore regions cannot be fully evaluated until frequent water samples are fixed in a way that will preserve rotifers in an expanded condition.

Rotifers of the genus *Synchaeta* occur abundantly in estuaries and coastal areas throughout the world. Species of the genus *Synchaeta* are especially well-adapted to marine environments (Remane, 1929; Ridder, 1981; Zelinka, 1907); of the 32 described species in the genus, approximately 20 may be considered truly marine, without representation in freshwater (Nogrady, 1982). Because of their small size (100–200 μm), these rotifers have not been captured in the large mesh samplers commonly used and therefore may be more abundant than published reports indicate. Despite their wide distribution, however, virtually nothing is known about the role *Synchaeta* spp. play in marine planktonic food chains. In this paper I report on the algal food requirements and growth rates of one marine *Synchaeta* species and on its susceptibility to predation by the omnivorous copepod *Acartia tonsa*. Using this information, I calculate the expected response of natural populations of rotifers to the combined influence of a range of food concentrations and predator densities.

Materials and methods

Synchaeta cecilia was originally isolated from Perch Pond (Falmouth, Massachusetts) in July 1982. Stock cultures of clones of *S. cecilia* were maintained in a sea water-trace metal medium (75% SW+) prepared by diluting 100% sea water with deionized water and by adding 0.1 ml l^{-1} of the trace metal mixture from Guillard's (1975) f/2 formulation. A mixture of three species of algae was used as food: *Chroomonas salina* (strain 3C), *Isochrysis galbana* (strain ISO) and *Heterocapsa pygmaea* (strain GYMNO). These algae and all other species used in the feeding experiments were cultivated in f/2 enriched sea water (Guillard, 1975) in batch cultures at 20 °C at a light intensity of ca. 300 μE m^{-2} s^{-1}. Rotifers were maintained in the same chamber at light intensities of ca. 25 μE m^{-2} s^{-1}. Transfers of rotifers and algae were made weekly in 25 × 150 mm culture tubes or at intervals of 10–21 days for cultures in 125–500 ml flasks.

Experiments to determine the relative food value of algae were performed in 24-well polystyrene tissue culture plates (Falcon 3047). Rotifers were isolated singly or in pairs in each well to which 1 ml of the sea water medium (75% SW+) and the test alga or algae were added at $6-10 \times 10^3$ cells ml^{-1}. The rotifers were incubated at 20 °C in dim light for a total of four days with a transfer of rotifers to fresh medium after two days. At the end of three to four days the number of eggs and rotifers were counted. Four to six replicate wells were established for each of four different experiments, which included different sets and combinations of algae.

Experiments to determine the population growth rates at 20 °C were conducted at varying concentrations of *Heterocapsa pygmaea*. These experiments were conducted in 200 ml of sea water in triplicated 250 ml Erlenmeyer flasks from which 50 ml subsamples were removed on the first, third and fifth day. On the second and fourth days, one-half of the medium of all flasks was replaced with fresh medium. At these times the algal densities were adjusted to return the *H. pygmaea* to the nominal densities of 5×10^2, 10^3, 5×10^3 and 10^4 cells ml^{-1}. Rotifers removed in the 50 ml subsamples were anaesthesized by the addition of 30 ml of carbonated sea water, preserved in acid Lugol's solution (Edmondson, 1959), and enumerated by the Utermöhl method (Hasle, 1978) after settling three 25 ml aliquots for each subsample. Population growth constants (r, day^{-1}) were calculated by the formula $r = {}^{\ln(N}t + x^{-N}x)/x$ (Edmondson, 1960) where N is the number of rotifers at times t and t + x. In the experiments reported here the r-values were calculated for the period beginning on day one (t) and extending for four (x) days. Doublings per day (DT) were calculated from the equation, DT = ln 2/r (Edmondson, 1960), where r is the growth constant as defined above.

Feeding rates for rotifers were determined directly using the cell count method (Rigler, 1971) in 8 hour experiments. Rotifers were obtained from stock cul-

tures, rinsed twice on 30 μm Nitex mesh, and resuspended in algae-free sea water medium (100% SW+) for one hour. Experiments were performed in 25 × 150 mm culture tubes (2–6 replicates) to which 50 rotifers and 10 ml of medium were added. Before the experiment was started, the rotifers were counted and transferred in Pasteur pipettes to 5 ml of 100% SW+ medium without algae. At each algal concentration, four control tubes containing medium but no rotifers were established. At t_0, 5 ml of additional medium with algae at 2 × the desired concentration of 0.5 to 1 × 10^4 cells ml^{-1} was added to each test tube. Duplicate tubes were fixed immediately after the addition of algae for estimating its initial density. The remaining tubes were incubated in the dark at 20 °C, usually between 10.00 and 18.00 hours. Because all or most (94% or higher) rotifers survived the experiment the initial rotifer density was used to calculate the grazing and ingestion rates. Algal densities were obtained by visual cell counts of 1 ml aliquots in Sedgewick-Rafter cells at a magnification of 210 ×. Over the course of 8 hours, algal concentrations were reduced to less than 30% of initial concentration.

Conversion of densities to equivalent carbon concentrations was based on the following values: *I. galbana* and *Pyramimonas* sp., 5.18 pg C $cell^{-1}$; *C. salina* 45.78 pg C $cell^{-1}$; *H. pygmaea,* 115.37 pg C $cell^{-1}$; *H triquetra,* 340 pg C $cell^{-1}$ and *S. cecilia,* 18.12 ng C $rotifer^{-1}$ (Heinbokel, 1978; Verity & Stoecker, 1982; Stoecker & Egloff, unpublished data).

Feeding rates for copepods (*Acartia tonsa*) on *S. cecilia* in the presence and absence of an alternative food species *H. triquetra* were determined at 20 °C in 500 ml bottles which were rotated at 2 rpm in the dark for 12 hours, usually between the hours of 19.00 and 07.00. Two types of experiments were conducted: one in which the density of the rotifers was varied in the presence of a single concentration of *Heterocapsa,* and another in which the rotifer density was constant and the concentration of *Heterocapsa* was varied. Adult copepods were picked from net samples from Perch Pond 30 hours before the start of the experiment (t_0) and isolated in 6–10 liters of 1 μm filtered sea water. Six hours before t_0, 10 copepods were transferred in wide mouthed pipettes to each of the 500 ml experimental bottles half-filled with sea water. Replicate control flasks without copepods were also set up at this time. At t_0 additional water with the rotifers and/or algae was added to yield initial concentrations of rotifers (0.3–2.0 *S. cecilia* ml^{-1}) and/or algae (0 to 3000 *H. triquetra* ml^{-1}). Duplicate flasks for determining initial values of rotifers and algae were fixed at t_0. After 12 hours, the contents of the experimental and control bottles were fixed with Lugol's solution. Algae and rotifers were enumerated from 50–100 ml settled aliquots.

For all of the feeding experiments the clearance or grazing rate, F (volume swept clear, μl $animal^{-1}$ t^{-1}), the ingestion rate, I (μg C $animal^{-1}$ t^{-1}) and the mean cell concentration, (μg C ml^{-1}) were calculated using Frost's (1972) equations.

Results

In four-day feeding trials, only thirteen of the 37 algal species presented to *S. cecilia* in unialgal cultures were capable of supporting reproduction (Table 1). Algal concentrations (6–10 × 10^3 cells ml^{-1}) used were well within the range in which Stemberger (1985) found positive population growth rates for eight species of fresh-water planktonic rotifers. The thirteen growth-supporting species belong to four major algal taxa (Cryptophyceae, Dinophyceae, Haptophyceae and Chlorophyceae) and span a range in size from *Isochyrsis galbana* (4 × 5 μm) to *Prorocentrum micans* (13 × 47 μm). These results show that size is not a reliable guide to nutritional value. For example, among the Haptophyceae only one of the three tested species of nearly identical size was an adequate food. Furthermore, eleven of the thirteen acceptable species had a maximum dimension equal or less than 14 μm, but two of the nutritionally adequate dinoflagellates, *H. triquetra* and *P. micans,* were larger.

The dietary inadequacy of several species was not the result of failure of these species to be ingested by *S. cecilia.* Examination of the gut contents by epifluorescence microscopy revealed that only two of the nine nutritionally inadequate species presented to *S. cecilia* (Table 1), were not ingested: *Thalassiosira weissflogii* and *Olisthodiscus luteus.*

Table 1. The relative food value of 37 algal monocultures expressed as the maximum numbers of *Synchaeta cecilia* and *S. cecilia* eggs after four days (N_4) relative to the initial number (N_0). Twelve algae were qualitatively tested in separate feeding trials to see whether they were ingested (I) or not ingested (NI).

Species (strain)	Size (μm)	Relative food value	Qualitative feeding test
Cryptophytes			
Chroomonas salina (3C)	6 ×12	+ +	I
cryptomonad sp. (PARA)	6 ×10	+ +	
cryptomonad sp. (M2)	5.2×10.1	+ +	
Cryptomonas obovoidea (VW354)	6.0× 8.5	+ +	
cryptomonad sp. (WH2)	6.1×11.3	+ +	
cryptomonad sp. (F5A)	8.2×12.7	+ +	
Rhodomonas lens (R. lens)	5.5× 9.9	+ +	
Dinoflagellates			
Amphidinium carteri (AMPHI)	10 ×16	−	
Cochlodinium helicoides (COCH)	32 ×35	−	
Gonyaulax tamarensis var. *excavata* (GT429-Ipswich)	35 ×35	−	
Gyrodinium uncatenum (GYRO)	62 ×78	−	
Heterocapsa pygmaea (GYMNO)	7 ×14	+ +	I
Heterocapsa triquetra (HT 984)	16 ×22	+ +	
Prorocentrum mariae-lebouriae (EXUV)	12.6×18.1	−	I
Prorocentrum micans (PRORO)	13 ×47	+ +	I
Scrippsiella trochoideum (PERI)	23 ×30	−	
Thoracosphaera heimii (A1379)	11.5	−	I
Haptophytes			
Emiliana huxleyi (A1168)	3.8	−	I
Isochrysis galbana (ISO)	4 × 5	+ +	
Pavlova lutheri (MONO)	4.5× 4	−	
Chlorophytes			
Chlamydomonas sp. (S.W. CHLAMY)	5 × 8	−	
Chlorella autotrophica (CHL580)	2.6	−	
Dunaliella tertiolectra (DUN)	5.4× 9	−	
Micromonas sp. (DW8)	1.4× 2	−	
Nannochloris sp. (Nanno)	1.9	−	I
Pyramimonas sp. (13 − 10 PYR)	4.5× 5.2	+	
Tetraselmis suecica (TETRA)	8 ×12	+	
Chrysophytes			
Olisthodiscus luteus (OLISTH)	7 ×15	−	NI
Olisthodiscus luteus (OLNB)	-		
Diatoms			
Asterionella glacialis (A1011)	7 ×20	−	
Chaetocerus simplex (A1165)	4.5× 7.3	−	I
Phaeodactylum tricornutum (TFX1)	2 ×27	−	
Skeletonema costatum (A1076)	2.6× 4.2	−	I
Skeletonema costatum (SKEL)	6 × 7	−	
Thalassiosira pseudonana (3H)	7 × 7	−	
Thalassiosira weissflogii (Actin)	9.5×13	−	NI
Cyanophytes			
Synechococcus sp. (DC-2)	1.0	−	I

− $N_4 < N_0$ or no eggs produced
\+ $N_0 < N_4 < 2N_0$
\+ + $N_4 > 2N_0$

Table 2. The relative food value of six algal species that support the reproduction of *Synchaeta cecilia* during four day feeding trials when presented in pairs or as monocultures. The relative food value is expressed as the maximum number of rotifers and eggs after four days (N_4) relative to the initial number (N_0).

Species (strain)	*C. salina*	Unidentified cryptophyte	*H. triquetra*	*H. pygmaea*	*I. galbana*	*T. suecica*
Chroomonas salina (3C)	+ +	+	+ + +	+ + +	+ + +	+
Unidentified cryptophyte (PARA)		+ +	+	+ +	+ +	+ +
Heterocapsa triquetra (HT984)			+ +	+ +	+ +	+ +
Heterocapsa pygmaea (GYMNO)				+ +	+ + +	+
Isochyris galbana (ISO)					+ +	+
Tetraselmis suecica (TETRA)						+

\+ = $N_0 < N_4 < 2N_0$
\+ + = $2N_0 < N_4 < 10N_0$
\+ + + = $N_4 > 10N_0$

In long-term unialgal cultures only Cryptophyceae were capable of sustaining growth of *S. cecilia.* For example, *S. cecilia* was maintained on unialgal cultures of *Cryptomonas obovoidea* (strain VW354) or on the unidentified cryptophyte (strain WH2) for over 12 months. In contrast, unialgal cultures of *H. pygmaea* ceased to sustain reproduction after two months; unialgal cultures of the haptophyte *Isochrysis galbana* or the chlorophyte *Pyramimonas* sp. (strain 13-10 PYR) sustained reproduction for only two weeks.

When six of the nutritious species identified in Table 1 were fed in pairs, reproduction of *S. cecilia* was enhanced greatly by some of the combinations (Table 2). Especially notable is the enhanced growth observed with the cryptophyte, *C. salina* when paired with either of the dinoflagellate *Heterocapsa* spp. or with the haptophyte, *I. galbana.* The combination of the *I. galbana* with *H. pygmaea* proved equally stimulating. On the basis of these observations, three of these four species were selected for long-term culture; the fourth alga, *H. triquetra,* was not used because it was not as stimulating in combination with *I. galbana* as was *H. pygmaea.* The combination of the three selected species – *Chroomonas salina, Heterocapsa pygmaea* and *Isochrysis galbana* – has proven capable of maintaining stock cultures of *S. cecilia* without failure for more than four years.

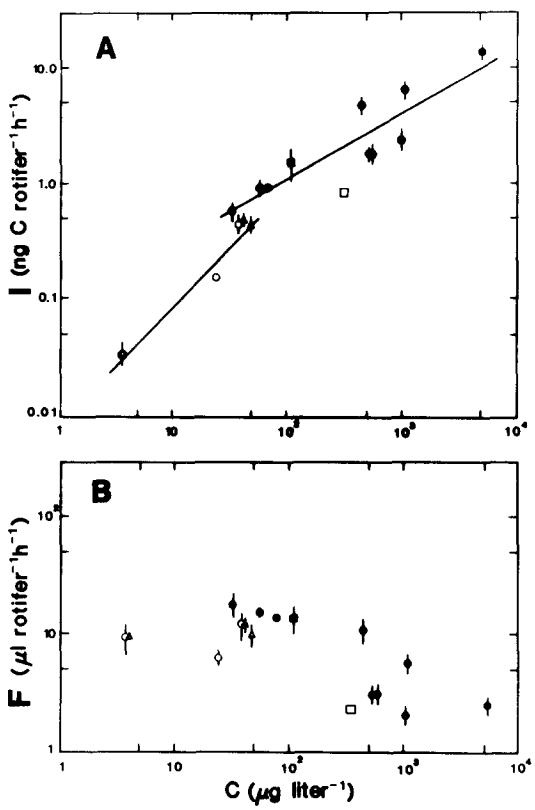

Fig. 1. Ingestion (I) and clearance (F) rates of *Synchaeta cecilia* at 20 °C. The regression equation for the ingestion of the smaller algae (<5 µm), *Isochrysis galbana* (open circles, n = 3) and *Pyraminmonas* sp. (triangles, n = 3), is $I = 0.008\ C^{1.05}$ ($r^2 = 0.97$). For *Heterocapsa pygmaea* (closed circles, n = 9) the regression equation is $I = 0.079\ C^{0.56}$ ($r^2 = 0.84$). Other ingestion and clearance values are given for *Chroomonas salina* (open square, n = 1) and *Heterocapsa triquetra* (closed square, n = 1). The means ± 1 SE are indicated by vertical lines.

Feeding Rates

Ingestion rates for *Synchaeta cecilia* feeding on algal cells (Fig. 1A) ranged over three orders of magnitude from 0.03 to 13.51 ng C rotifer^{-1} h^{-1} as a function of algal concentration (4 to 5440 μg C l^{-1}). This rate is equivalent to the ingestion of 6 to 86 *I. galbana* cells rotifer^{-1} h^{-1} or of 5 to 117 *H. pygmaea* cells rotifer^{-1} h^{-1}. Ingestion rates increase with algal concentration but at a different rate for the small (< 5 μm) and large (> 6 μm) species. For this reason two regression equations were calculated; one for the small species (*I. galbana* and *Pyramimonas* sp.) and another for *H. pygmaea,* the only large species for which sufficient data was obtained. Single data points for *H. triquetra* and *C. salina* are also given in Fig. 1 but are not included in the regression calculations.

Clearance rates (Fig. 1B) range from a maximum of 18 μl rotifer^{-1} hr^{-1} to a minimum of 2 μl rotifer^{-1} hr^{-1}. These rates were constant at the lower food concentrations and associated largely with the small algae. As algal size increased and the concentration exceeded 50 to 100 μg C l^{-1}, the clearance rates decreased.

Growth Rates

Growth rates (Table 3) of *S. cecilia* increase as a function of *H. pygmaea* cell density. A maximum population growth constant (r) of 0.604 day^{-1} was obtained at the highest food density of 10^4 *H. pygmaea* ml^{-1}; this rate corresponds to a population doubling time of 1.1 days. As food density decreased, the growth rate was diminished to a point where population doubling times were more than 3.6 × longer (4.0 days at 500 cells ml^{-1}).

Table 3. Growth rates (r ± 95% C.L.) and doubling times (DT) for *Synchaeta cecilia* during four days of exponential growth at 20 °C at four concentrations of *Heterocapsa pygmaea.*

	H. pygmaea		r ± 95% C.L. day^{-1}	DT days
	cells ml^{-1}	ng C ml^{-1}		
A	500	57.5	0.172 ± 0.157	4.0
B	1000	115.0	0.245 ± 0.091	2.8
C	5000	575.0	0.507 ± 0.125	1.4
D	10000	1150.0	0.604 ± 0.158	1.1

Synchaeta as Prey

The vulnerability of *S. cecilia* to a coexisting potential predator, the copepod *A. tonsa,* is presented in Fig. 2. Over the tested range of prey densities (5 to 35 μg C l^{-1} which is equivalent to 0.3 to 1.9 rotifers ml^{-1}) *A. tonsa* captured an increasing proportion of the rotifers (Fig. 2A), with no indication of a plateau at the higher concentrations. On the other

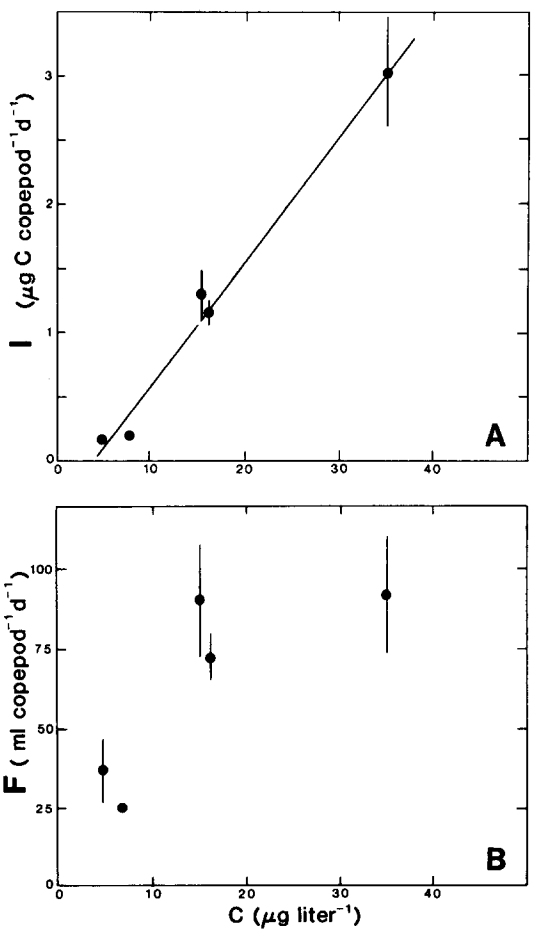

Fig. 2. Ingestion (I) and clearance (F) rates of *Acartia tonsa* adults grazing on *Synchaeta cecilia* at 20 °C. Regression for ingestion rate (μg C copepod^{-1} day^{-1}) vs prey concentration (μg C liter^{-1}) is I = −0.383 + 0.099 C (r^2 = 0.98). Vertical bars indicate the mean ± SE.

Table 4. Ingestion and grazing rates per copepod ± SD for *Acartia tonsa* adults feeding at 20 °C on *Synchaeta cecilia* in the presence of increasing concentrations of *Heterocapsa triquetra*. Density of prey *S. cecilia* was constant in all treatments at 50 ng C ml^{-1} (2.8 rotifers ml^{-1}). Three replications at each concentration.

H. triquetra		Grazing rate ml copepod^{-1} day^{-1}	Ingestion rate μg C copepod^{-1} day^{-1}
cells ml^{-1}	μg C l^{-1}		
0	0	91.5 ± 37.5	3.05 ± 0.86
120	41	70.6 ± 21.5	2.02 ± 0.43
670	230	52.0 ± 10.5	1.97 ± 0.29
1580	537	57.5 ± 24.5	2.14 ± 0.65
2665	906	45.5 ± 13.0	1.90 ± 0.43

hand, the clearance rate (Fig. 2B) increased up to a prey density of one rotifer (= 18.12 μg C l^{-1}), above which it was constant, indicating a threshold for maximal feeding effort.

The effect of an increasing concentration of an alternative algal food on the copepod's predation on the rotifer is given in Table 4. At a constant rotifer density of 50 ng C ml^{-1} (2.8 individuals ml^{-1}) neither ingestion nor clearance rate change significantly over the range of *H. triquetra* concentrations tested, namely from 0 to 906 μg C l^{-1}, which is equivalent to 0 to 2700 *H. triquetra* cells ml^{-1}.

Discussion

Synchaeta cecilia is the smallest of the described species in the genus; its maximum length of 100–130 μm puts it in a size class with many coexisting protozoans and crustacean larvae. As a result, this species should fit into the same food chains in which copepod nauplii (Conover, 1982) and tintinnid ciliates (Stoecker & Govoni, 1984; Stoecker & Sanders, 1985) play a dominant role. My observations confirm that *S. cecilia* is capable of ingesting many commonly occurring size classes and taxa of marine phytoplankton and is vulnerable to predation by copepods. For these reasons *S. cecilia* must play a trophic role in marine food chains similar to other microzooplankton such as nauplii and tintinnids.

This rotifer species is not, however, an indiscriminant grazer of phytoplankton. Many algae which are within the acceptable size range for *S. cecilia* were either not ingested or failed to support reproduction (Table 1). Among the dinoflagellates, *Amphidinium carteri* (10 × 16 μ) was an inadequate diet, while the smaller (*Heterocapsa pygmaea*) and the larger (*Heterocapsa triquetra*) species proved to be excellent food. Among the chlorophytes, *Dunaliella tertiolecta* (5 × 9 μm) was inadequate, while a smaller (*Pyramimonas* sp) and a larger (*Tetraselmis suecica*) species proved nutritionally adequate as food for *S. cecilia.*

Based on present laboratory findings, only a few taxa can support extended reproduction of *Synchaeta* spp. In both freshwater (Pourriot, 1965; Stemberger, 1981) and in marine environments cryptophytes are an especially good food for *Synchaeta* spp. In this study some dinoflagellates also proved nutritious; comparable studies have not been reported for freshwater *Synchaeta*, but dinoflagellates are consumed by *Ascomorpha ovalis* (Ruttner-Kolisko, 1938; Pourriot, 1965) and by *A. saltans,* whose virgate mastax is characteristic also of the Synchaetidae (Hutchinson, 1967, p. 529). Diatoms and chrysophytes, on the other hand, although they may be ingested, cannot support reproduction of either freshwater *Synchaeta* spp. (Pourriot, 1965) or the marine *S. cecilia.* To the algal taxa previously reported to support reproduction in *Synchaeta* can be added two chlorophyte species (*Tetraselmis suecica* and *Pyramimonas* sp.) and a haptophyte species (*Isochrysis galbana*), based on the results reported here.

The failure of 24 of the 37 tested algal species to support growth may result from nutritional deficiencies. Qualitative deficiencies have been demonstrated for many phytoplankton species fed to crustaceans (Provasoli *et al.,* 1970; Lee *et al.,* 1976) and bivalves (Davis & Guillard, 1958). In fact, of the nine nutritionally inadequate species fed to *Synchaeta cecilia* in this study and observed for ingestibility, seven of the species were ingested. These species may lack essential nutrients or, as is the case for some freshwater cyanophytes, they may not be assimilated (Porter, 1977). Of the two species not ingested (*Thalassiosira weissflogii* and *Olisthodiscus luteus*), the former may be protected from ingestion by its

elongated shape, whereas the latter is apparently protected by its ability to produce a mucus coat which entangles the cells on the rotifer's cilia and setae (Egloff, 1986).

Quantitative deficiencies may also account for some of the failures of the tested species to support rotifer reproduction. Nutritional trials were limited to concentrations of no more than 10^4 cells ml^{-1}. Higher concentrations of algae were not used because higher concentrations are unlikely to be of ecological significance in the marine ecosystems where *Synchaeta* occurs.

If these differences in nutritional adequacy exist in natural populations of phytoplankton, the *relative abundance* of *specific algal taxa* will be more important for the population growth of rotifers than total algal biomass, even if the appropriate size classes are abundant. Moreover, if the greatly enhanced *or* depressed population growth rates of *S. cecilia* which result from combining food species is a general characteristic of other microzooplankton, any attempt to predict growth responses from natural assemblages of food species will be most difficult. On the one hand, certain combinations of algae will enhance reproduction (see Table 2), while other combinations will diminish reproduction because some of the species may be nutritionally inadequate or interfere with ingestion of other, nutritionally adequate species, as is the case for *Olisthodiscus luteus* (Egloff, 1986).

Ingestion of algae by *S. cecilia* increased with increasing algal density with no indication of a plateau at the higher concentrations. A plateau indicating a decrease in feeding efficiency has been observed for many other rotifer species (Starkweather, 1980) but always at a higher food concentration than used in this study. Because higher food concentrations are not ecologically realistic for the marine habitats in which *S. cecilia* occurs (Stoecker, unpublished data; Anderson *et al.*, 1983), they were not tested. The absence of a ingestion plateau indicates that *S. cecilia* is capable of efficiently utilizing food resources at all food concentrations likely to be encountered in the marine ecosystems where it occurs.

Over the range of algal concentrations used (4–5440 μg C l^{-1}) the observed ingestion and clearance rates for *S. cecilia* fall within the range reported for other rotifer species. Exact comparisons are not possible. If, however, carbon is assumed equal to approximately 32% of the dry weight (Peters & Downing, 1984) the published clearance and ingestion rates at 20 °C for *Brachionus calyciflorus* (Starkweather & Gilbert, 1977, Fig. 1) coincide closely to the rates for *S. cecilia* (Fig. 1). Given the great differences in size, morphology, and habitats of the two species, great significance can not be placed on this similarity. The similarity may be only a coincidence resulting from the dissimilarity in the size of food particles used in the two experiments. In the experiments reported here the algae ranged in size from 80 μm^3 for *Isochrysic galbana* to 1595 μm^3 for *Heterocapsa triquetra,* whereas Starkweather and Gilbert (1977) fed a yeast, *Rhodotorula glutinis* (35 μm^3) to *B. calyciflorus.* If clearance rates are a positive function of food size as suggested by Gilbert and Bogdan (1984) for *Synchaeta pectinata, S. cecilia* would be expected to show a relatively higher feeding rate when feeding on larger algal particles.

Growth Rates

The observed increase of population growth rate (Table 3) with increasing food concentration is expected given the demonstrated ability of *S. cecilia* to ingest food in proportion to its availability (Fig. 1 and King 1967). With this ability to capitalize on abundant food resources, *S. cecilia* and congeneric species should be important components of eutrophic marine communities. In fact, maximum densities exceeding 3000 *Synchaeta* spp. l^{-1} have been observed in a shallow, nutrient enriched salt pond (Perch Pond, Cape Cod, Massachusetts) by Egloff and Stoecker (unpublished data). Deevey (1948) reported that *Synchaeta* spp. reached maximum densities of 315 l^{-1} in a similar environment, Tisbury Great Pond on Martha's Vineyard, Massachusetts. In Denmark, Blanner (1982) found populations of *Synchaeta* spp. peaking at a density of 105 rotifers l^{-1} in the Limfjord. In both Tisbury Great Pond and in the Limfjord, where exchange with coastal waters is restricted, the *Synchaeta* peaks were associated with periods of high primary

productivity and salinities of 22–29‰.

Hernroth (1983) has presented additional evidence of *Synchaeta*'s ability to use spring phytoplankton blooms efficiently. He found that in the upper 20 m of the Gullmar Fjord (Sweden) *S. vorax* reached daily production levels of 30 mg C m^{-2}. This rate was equivalent to 2% of the net primary production in the Fjord during a 6 week spring bloom. During this period *S. vorax* had a growth constant (r) of 0.1 d^{-1} and reached a density of 85 l^{-1} (1.7×10^6 m^{-2}). Mean salinity in the Gullmar Fjord is 22.3‰.

In less saline, planktonic communities, other *Synchaeta* spp. have been reported to show similar patterns of abundance, followed by long periods of scarcity, e.g. in the Firth of Forth (Roddie *et al.*, 1984) southern San Francisco Bay (Ambler *et al.*, 1985) and in the Baltic Sea (Ackefors, 1969; Hernroth & Ackefors, 1979; Eriksson *et al.*, 1977). *Synchaeta* spp. can constitute 80% of the total zooplankton biomass during the autumn phytoplankton bloom in the Himmerfjarden (Sweden) where, on an annual basis, *Synchaeta* spp. account for 15–36% of the total zooplankton production (Johansson, 1983). These impressive population sizes and production rates attest to the ability of *Synchaeta* spp. to compete successfully with ciliates, crustacean larvae and other microzooplankton for food resources.

The apparent scarcity of *Synchaeta* in open ocean communities is evidently not the result of an inability of members of this genus to adjust to high salt concentrations. In culture, *S. cecilia* thrives in salinities up to 33.5‰ (Egloff, unpublished data). However, the opportunistic life history pattern of rotifers (Allan, 1976), which allows them to grow very rapidly in the presence of abundant food, makes these organisms less well adapted to the nutritionally dilute open ocean environments. Nonetheless, *Synchaeta atlanticus* has been collected from the mid-Atlantic Ocean (Zelinka, 1907). Further documentation of *Synchaeta* populations in off-shore communities must await a more thorough sampling of microzooplankton populations at short time intervals, especially in productive frontal zones (Pingree *et al.*, 1975).

The role of rotifers in planktonic food webs has been assumed until recently (Makarewicz & Likens, 1979) to be minor (Brooks, 1969; Dumont, 1977), presumably because rotifers are small and appear to occupy a size refuge from visual predators (Banse, 1982). Indeed, predation by many visual predators, e.g. adult fish, on microzooplankton is minuscule or incidental to other feeding behavior (O'Brien, 1979). Fish larvae, on the other hand, are not only adept at the capture of microzooplankton, including rotifers, but depend on them, at least in culture, for normal development (Stoecker & Govoni, 1984; Hirata, 1979; Houde & Schekter, 1980). Among the potential other invertebrate predators of marine rotifers are representatives of a wide variety of taxa, including ciliates, cnidarians, insect larvae and crustaceans. In fresh-water, Anderson (1970) was one of the first to demonstrate that the calanoid *Diaptomus arcticus* (2.2–3.5 mm) not only ingests *Synchaeta pectinata* but prefers them to the spiny *Kellicottia longispina.* With the exception of the recent work by Stemberger (1982, 1985) and Williamson (1980, 1981, 1983, 1984; Williamson and Butler, 1986) on fresh-water copepods, few other studies of copepod predation on rotifers have been published.

In this paper I have demonstrated that *S. cecilia* (100–130 μm) is captured efficiently by the calanoid copepod *Acartia tonsa.* At *Synchaeta* prey concentrations of 1 or 2 rotifers ml^{-1}, ingestion rates by *A. tonsa* ranged from 1.5 and 3.0 μg C copepod^{-1} day^{-1}. This performance, especially the absence of a plateau in the ingestion rate (Fig. 2A), may have been enhanced, however, by using unfed copepods; Frost (1972) found that the ingestion rates by *Calanus pacificus* reached a constant level only if the copepods were fed prior to the experiment. Because the feeding experiments reported here lasted 12 hours, it is unlikely that the initial starved condition of the *Acartia* influenced the observed results beyond the first few hours.

Given a mean body weight of 5.6 μg C copepod^{-1} (Durbin *et al.*, 1983), *A. tonsa* females are clearly capable of attaining a substantial portion of their nutritional needs by predation on *Synchaeta.* In the presence of alternative algal food (Table 4), *A. tonsa* maintains daily ingestion rates of 2 μg C of *Synchaeta* copepod^{-1}; this is equal to 36% of the mean body carbon weight. Even in the presence of an alternative microzooplanktonic prey, the tintin-

nid *Favella* spp. which is similar in size to *S. cecilia, A. tonsa* continues to feed on both (Stoecker & Egloff, submitted). Although the relative preferences for other microzooplankton have not been determined for *A. tonsa,* copepod nauplii are significantly faster and more erratic in their movements and should prove more elusive than either *Favella* or *Synchaeta*. These observations lead to the conclusion that when rotifers are abundant, they can make a significant contribution to higher trophic levels.

The degree of population control exercised by copepods on rotifers will be a function of many factors (Williamson, 1983) including the differential susceptibility of rotifer species to capture and ingestion by predators. Using data from an *in situ* field study, Neill (1984) concluded that rotifer populations were controlled by competitive food limitations rather by predation. However, each of the four species of rotifers which dominated the community studied by Neill had either morphological or behavioral characteristics which make them less vulnerable to predation than *Synchaeta* or other soft bodied rotifers. Two species in Neill's study were *Kellicottia longispina* and *Keratella cochelearis* whose spiny loricas discourage or deter copepod predators (Anderson, 1970; Stemberger, 1982, 1985); a third species, *Conochilus hippocrepis* possesses a soft gelatinous sheath which reduces predation on intact colonies by cyclopoid copepods (Williamson, 1983). Finally the *Polyarthra vulgaris* in Neill's study is adept at avoiding predation by rapid skips or jumps produced by the movement of lateral paddles (Stemberger, 1982; Gilbert & Williamson, 1978; Gilbert, 1985). *Synchaeta* spp., on the other hand, are highly susceptible to predation by calanoid copepods as demonstrated by Williamson and Butler (1986) and by this study.

More studies are required to determine the roles of predation and competition in controlling community structure of rotifers. To estimate the relative impact that each of these factors may have on *Synchaeta* populations, I have combined the experimentally determined growth and predation rates to predict the resulting net rate of increase. The combined influence of these factors is calculated as $\hat{r} = r - g$ where $\hat{r}$ is the net rate of change of rotifers in the presence of predators, r is the instantaneous rate of change in the absence of predators (Table 3) and g is the grazing rate of *Acartia* on *Synchaeta* (Table 4). These values are derived from laboratory data obtained in both instances at 20 °C. Because temperatures in Perch Pond may exceed 19 °C from late June through August or later (Stoecker, unpublished data) the values presented here are representative of the rates that would prevail during the summer months.

The net rate of change for positive values of $\hat{r}$ is presented in Fig. 3 as a function of *Acartia* and *Heterocapsa* densities. The expected increase in $\hat{r}$ values of *Synchaeta* with increasing algal density and decreasing predator density is indicated. Net rates of increase are maximal in the absence of *Acartia* at any given concentration of algae, and these maximal $\hat{r}$ values decline to zero as predator density increases. The impact of predation at any given predator density is diminished as the concentration of an alternative algal food is increased. Because *Acartia* responds to increases in prey density with more egg production (Stoecker & Egloff, submitted) and more prey consumption (Fig. 2), interactions between copepod, rotifer, and alga will be complex. Figure 3 simply illustrates the approximate boundaries with-

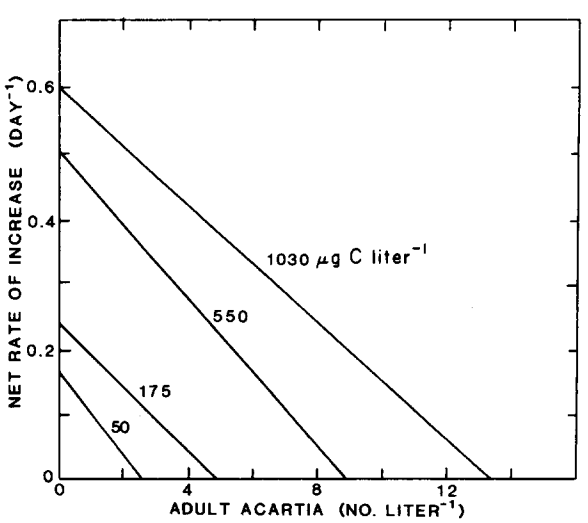

Fig. 3. Calculated net rates of increase for the rotifer *Synchaeta cecilia* as a function of density of the predator *Acartia* and of algal food. Net rates of increase were calculated as the difference between the intrinsic growth rates at 20 °C in the absence of copepods (Table 3) and rate of loss (g) of rotifers to *Acartia* adults at 20 °C at equivalent levels of alternative algal food (Table 4).

in which two members of a trophic triangle affect the growth of the third, *Synchaeta cecilia*, during the summer months.

The important question to ask at this point is whether the predicted rates lie within a realistic combination of food and predators likely to be encountered in natural communities. For Perch Pond, the ecosystem from which *S. cecilia* was originally isolated and from which *Acartia* was collected for these experiments, both dinoflagellate and *Acartia* densities fall well within the predicted ranges.

For example, dinoflagellates are present in Perch Pond throughout the year, with blooms occurring in both the autumn (Stoecker *et al.*, 1986) and spring (Anderson *et al.*, 1983). In the latter study, total dinoflagellate concentrations of 500–800 μg C l^{-1} during spring blooms were recorded. Because not all dinoflagellates are utilized by *S. cecilia* as food (Table 1), usable concentrations of dinoflagellates for *S. cecilia* in Perch Pond must fall below the 550 μg C ml^{-1} food level indicated in Fig. 3. At these food levels, *S. cecilia* would be able to maintain a positive rate of population growth at *Acartia* densities of 8 l^{-1} or less.

Year-round studies of copepod populations in Perch Pond have not been undertaken, but *Acartia hudsonica* and *A. tonsa* are abundant in the region, especially during the spring and summer months. For example, Deevey (1948) found *Acartia* spp. ranging from 0.5 to more than 10 individuals l^{-1} from late-March through mid-August in Tisbury Great Pond. Short term studies by Anderson *et al.* (1983) and Turner and Anderson (1983) have demonstrated bloom densities of *Acartia* spp. of 5–20 individuals l^{-1} during the summer months.

Quantitative, long term samples of rotifer populations in Perch Pond are also unavailable, but Stoecker (unpublished data) has recorded the presence of rotifers, largely *Synchaeta* spp. in all but 4 of 50 weekly samples taken between September 1981 to September 1982. Periods of especially high abundance were recorded in February, March, May and June.

These data, albeit fragmentary, support the validity of the predicted relationships depicted in Fig. 3, at least for the summer months. As indicated in Fig. 3, copepods at densities of 5 or fewer per ml could cause a net decrease in *Synchaeta cecilia* populations at food concentrations of 175 μg C ml^{-1} or less. Because of the diversity of food species and potential predators in natural ecosystems, these predicted relationships can only roughly approximate the actual situation. To improve our understanding of the dynamics of these planktonic communities and to delineate more completely the niche realized by *Synchaeta cecilia,* intensive field work must be undertaken to test the relationships predicted here.

Acknowledgements

Support for this work was provided by NSF Grant OCE-8206879 to the author and by NOAA Grant No. NA-81RA0014, NSF Grant No. OCE-8200030 and OCE-8315370 to Diane Stoecker, Woods Hole Oceanographic Institution. The invariably generous and skilled assistance of all Woods Hole personnel is most gratefully acknowledged. Peter Starkweather, P. Pourriot, and an unidentified reviewer provided extremely thoughtful and helpful comments on earlier drafts of the manuscript.

References

Ackefors, H., 1969. Ecological zooplankton investigations in the Baltic proper 1963–1965. Inst. Mar. Res. Lysekill, Ser. Biol. Rep., 18: 139 pp.

Ackefors, H. & L. Hernroth, 1975. The distribution and biomass of zooplankton off the coast in the Baltic proper in 1972. Medd. Havsfiskelab. Lysekil 184: 1–16.

Allan, J. D., 1976. Life history patterns in zooplankton. Am. Nat. 110: 165–180.

Ambler, J. W., J. E. Cloern & A. Hutchinson, 1985. Seasonal cycles of zooplankton from San Francisco Bay. Hydrobiologia 129: 177–197.

Anderson, D. M., S. W. Chisholm & C. J. Watras, 1983. The importance of life cycle events in the population dynamics of *Gonyaulax tamarensis*. Mar. Biol. (Berl.) 76: 179–189.

Anderson, R. S., 1970. Predator-prey relationships and predation rates for crustacean zooplankters from some lakes in western Canada. Can. J. Zool. 48: 1229–1240.

Banse, K., 1982. Cell volumes, maximal growth rates of unicellular algae and ciliates, and the role of ciliates in the marine pelagial. Limnol. Oceanogr. 27: 1059–1071.

Berzins, B., 1952. Contributions to the knowledge of the marine Rotatoria of Norway. Univ. Bergen Arb., nat. rekke, 6: 1–11.

Berzins, B., 1960. Rotatoria. I–VI. Fich. Ident. Zooplankton. Cons. int. Explor. Mer.: 84–89.

Blanner, P., 1982. Composition and seasonal variation of the zooplankton in the Limfjord (Denmark) during 1973–1974. Ophelia 21: 1–40.

Brooks, J. W., 1969. Eutrophication and changes in the composition of the zooplankton. In: Eutrophication: causes, consequences, correctives. Nat. Acad. Sci., U.S.: 236–255.

Cassie, V., 1960. A red water bloom of rotifers in Cook Strait, New Zealand. Nature 186: 328–329.

Conover, R. J., 1982. Interrelations between microzooplankton and other plankton organisms. Ann. Inst. océanogr., Paris, 58: 31–46.

Davis, H. C. & R. Guillard, 1958. Relative value of ten genera of micro-organisms as foods for oyster and clam larvae. Fishery Bull. Fish. Wildl. Serv. U.S. 58: 293–304.

Deevey, G. B., 1948. The zooplankton of Tisbury Great Pond. Bull. Bingham Oceanogr. Coll. 12: 1–44.

Dumont, H. J., 1977. Biotic factors in the population dynamics of rotifers. Arch. Hydrobiol. Beih. Ergebn. Limnol. 8: 98–122.

Durbin, E. G., A. G. Durbin, T. J. Smayda & P. G. Verity, 1983. Food limitation of production by adult *Acartia tonsa* in Narragansett Bay, Rhode Island. Limnol. Oceanogr. 28: 1199–1213.

Edmondson, W. T., 1959. Freshwater Biology. John Wiley & Sons, New York. 1248 pp.

Edmondson, W. T., 1960. Reproductive rates of rotifers in natural populations. Mem. Ist. Ital. Idrobiol. 12: 21–77.

Egloff, D., 1986. Effects of *Olisthodiscus luteus* on the feeding and reproduction of the marine rotifer *Synchaeta cecilia.* J. Plankton Res. 8: 263–274.

Eriksen, B. G., 1968. Marine rotifers found in Norway, with descriptions of two new and one little known species. Sarsia 33: 23–34.

Eriksson, S., C. Sellei & K. Wallström, 1977. The structure of the plankton community of the Öregrundsgrepen (southwest Bothnian Sea). Helgoländer wiss. Meersunters. 30: 582–597.

Frost, B. W., 1972. Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus.* Limnol. Oceanogr. 17: 805–815.

Gilbert, J. J., 1985. Escape response of the rotifer *Polyarthra:* a high speed cinematographic analysis. Oecologia 66: 322–331.

Gilbert, J. J. & K. G. Bogdan, 1984. Rotifer grazing: *in situ* studies on selectivity and rates. In Meyers, D. G. & Strickler, J. R. (eds) Trophic Interactions within Aquatic Ecosystems. Westview Press. Boulder: 97–133.

Gilbert, J. J. & C. E. Williamson, 1978. Predator-prey behavior and its effect on rotifer survival in associations of *Mesocyclops edax, Asplanchna girodi, Polyarthra vulgaris* and *Keratella cochlearis.* Oecologia 37: 13–22.

Guillard, R. R. L., 1975. Culture of phytoplankton for feeding marine invertebrates. In Smith, W. L. & Chanley, M. H. (eds) Culture of Marine Invertebrate Animals. Plenum Press, New York: 29–60.

Hasle, G. R., 1978. The inverted-microscope method. In Sournia, A. (ed.) Phytoplankton Manual. UNESCO, Paris: 88–96.

Heinbokel, J. F., 1978. Studies on the functional role of tintinnids in the southern California bight. I. Grazing and growth rates in laboratory cultures. Mar. Biol. (Berl.) 47: 177–189.

Hernroth, L., 1983. Marine pelagic rotifers and tintinnids – important trophic links in the spring plankton community of the Gullmar Fjord, Sweden. J. Plankton Res. 5: 835–846.

Hernroth, L. & H. Ackefors, 1979. The zooplankton of the Baltic Proper – a long-term investigation of the fauna, its biology and ecology. Rep. Fish. Bd. Sweden, Inst. Mar. Res. 2, 60 pp.

Hirata, H., 1979. Rotifer culture in Japan. Spec. Publ. No. 4, European Mariculture Soc: 361–375.

Houde, E. D. & R. C. Schekter, 1980. Feeding by marine fish larvae: developmental and functional responses. Env. Biol. Fish. 5: 315–334.

Hutchinson, G. E., 1967. A Treatise on Limnology. 2. Introduction to lake biology and the limnoplankton. John Wiley & Sons, New York. 1115 pp.

Johansson, S., 1983. Annual dynamics and production of rotifers in an eutrophication gradient in the Baltic Sea. Hydrobiologia 104: 335–340.

King, C. E., 1967. Food, age, and the dynamics of a laboratory population of rotifers. Ecology 48: 111–128.

Lee, J. J., J. H. Tietjen & J. R. Garrison, 1976. Seasonal switching in the nutritional requirements of *Nitocra typica,* a harpacticoid copepod from salt marsh aufwuchs communities. Trans. Amer. micros. Soc. 95: 628–637.

Makarewicz, J. C. & G. E. Likens, 1979. Structure and function of the zooplankton community of Mirror Lake. New Hampshire. Ecol. Monogr. 49: 109–127.

Neill, W. E., 1984. Regulation of rotifer densities by crustacean zooplankton in an oligotrophic montane lake in British Columbia. Oecologia 61: 175–181.

Nogrady, T., 1982. Rotifera. pp. 865–872. In: Parker, S. P. (ed.) Synopsis and Classification of Living Organisms. McGraw-Hill, New York: 865–872.

O'Brien, W. J., 1979. The predator-prey interaction of planktivorous fish and zooplankton. Am. Sci. 67: 572–581.

Pace, M. L. & J. D. Orcutt, 1981. The relative importance of protozoans, rotifers, and crustaceans in a freshwater zooplankton community. Limnol. Oceanogr. 26: 822–830.

Peters, R. H. & J. A. Downing, 1984. Empirical analysis of zooplankton filtering and feeding rates. Limnol. Oceanogr. 29: 763–784.

Pingree, R. D., P. R. Pugh, P. M. Holligan & G. R. Forster, 1975. Summer phytoplankton blooms and red tides along tidal fronts in the approaches to the English channel. Nature 258: 672–677.

Porter, K. G., 1977. The plant-animal interface in freshwater ecosystems. Am. Sci. 65: 159–170.

Pourriot, R., 1965. Recherches sur l'écologie des Rotifères. Vie Milieu, Suppl. 21: 1–224.

Provasoli L., D. E. Conklin & A. S. D'Agostino, 1970. Factors inducing fertility in aseptic Crustacea. Helogländer wiss. Meersunters. 20: 443–454.

Remane, A., 1929. Rotatoria. In: Grimpe, G. & E. Wagler (eds) Die Tierwelt der Nord- und Ostsee. Akad. Verlags. Leipzig. Lief. 16(7e): 156 pp.

Ridder, M. de, 1981. Some considerations on the geographical distribution of rotifers. Hydrobiologia 85: 209–225.

Rigler, F. H., 1971. Zooplankton. In Edmondson, W. T. & Winberg, G. G. (eds.) Secondary Productivity in Fresh Waters. Blackwell Scientific Publication. Oxford: 228–256.

Roddie, B. D., R. J. G. Leakey & A. J. Berry, 1984. Salinity-temperature tolerance and osmoregulation in *Eurytemora affinis* (Poppe) (Copepoda: Calanoidea) in relation to its distribution in the zooplankton of the upper reaches of the Forth estuary. J. Exp. Mar. Biol. Ecol. 79: 191–211.

Ruttner-Kolisko, A., 1938. Die Nahrungsaufnahme bei *Anapus testudo*. Internat. Rev. Hydrobiol. 37: 296–305.

Ruttner-Kolisko, A., 1974. Plankton rotifers: biology and taxonomy. Binnengewässer 26 Suppl: 1–146.

Schnese, W., 1973. Relations between phytoplankton and zooplankton in brackish coastal water. Oikos (Suppl) 15: 28–33.

Shih, C.-T. & A. J. G. Figueira, 1971. A synopsis of Canadian marine zooplankton. Fish. Res. Bd. Can. Bull. 176.

Snell, T. W. & G. H. Thomsen, 1980. Tampa by-pass canal, salinity and rotifer population dynamics in McKay Bay estuary. Flor. Sci. 43 (Suppl.): 24 (abs).

Starkweather, P. L., 1980. Aspects of the feeding behavior and trophic ecology of suspension-feeding rotifers. Hydrobiologia 73: 63–72.

Starkweather, P. L. & J. J. Gilbert, 1977. Feeding in the rotifer *Brachionus calyciflorus*. II. Effect of food density on feeding rates using *Euglena gracilis* and *Rhodotorula glutinis*. Oecologia 28: 133–139.

Stemberger, R. S., 1981. A general approach to the culture of planktonic rotifers. Can. J. Fish. Aquat. Sci. 38: 721–724.

Stemberger, R. S., 1982. Mechanism controlling selection and rates of predation on rotifers in *Cyclops bicuspidatus thomasi*. Ph.D. Thesis Univ. Mich. 95 pp.

Stemberger, R. S., 1985. Prey selection by the copepod *Diacyclops thomasi*. Oecologia 65: 492–497.

Stoecker, D. K., T. L. Cucci, E. M. Hulburt & C. M. Yentsch, 1986. Selective feeding by *Balanion* sp. (Ciliata: Balanionidae) on phytoplankton that best support its growth. J. Exp. Mar. Biol. Ecol. 95: 113–130.

Stoecker, D. K. & J. J. Govoni, 1984. Food selection by young larval Gulf menhaden (*Brevoortia patronus*) Mar. Biol. (Berl.) 80: 299–306.

Stoecker, D. K. & N. K. Sanders, 1985. Differential grazing by *Acartia tonsa* on a dinoflagellate and a tintinnid. J. Plankton Res. 7: 85–100.

Sudzuki, M., 1964. New systematical approach to the Japanese planktonic Rotatoria. Hydrobiologia 23: 1–124.

Turner, J. T. & D. M. Anderson, 1983. Zooplankton grazing during dinoflagellate blooms in a Cape Cod embayment, with observations of predation upon tintinnids by copepods. P. S. Z. N. I.: Marine Ecology 4: 359–374.

Verity, P. G. & D. Stoecker, 1982. Effects of *Olisthodiscus luteus* on the growth and abundance of tintinnids. Mar. Biol. (Berl.) 72: 79–87.

Williamson, C. E., 1980. The predatory behavior of *Mesocyclops edax*: predator preferences, prey defenses, and starvation-induced changes. Limnol Oceanogr. 25: 903–909.

Williamson, C. E., 1981. Foraging behavior of a freshwater copepod: frequency changes in looping behavior at high and low prey densities. Oecologia 50: 332–336.

Williamson, C. E., 1983. Invertebrate predation on planktonic rotifers. Hydrobiologia 104: 385–396.

Williamson, C. E., 1984. Laboratory and field experiments on the feeding ecology of the cyclopoid copepod. *Mesocyclops edax*. Freshwat. Biol. 14: 575–585.

Williamson, C. E. & N. M. Butler, 1986. Predation on rotifers by the suspension-feeding calanoid copepod *Diaptomus pallidus*. Limnol. Oceanogr. 31: 393–402.

Zelinka, C., 1907. Die marinen Rotatorien der Plankton-Expedition. Ergebnisse. Plankton Exped. 2a: 82 pp.