Differential grazing by *Acartia tonsa* on a dinoflagellate and a tintinnid

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Abstract. The calanoid copepod, *Acartia tonsa* Dana, ingests both the dinoflagellate, *Heterocapsa triquetra* (Ehrenberg) Stein, and the tintinnid ciliate, *Favella* sp. In laboratory experiments its ingestion rate increases with increasing dinoflagellate density to a maximum at ~650 cells ml⁻¹, then declines. With *Favella* as the sole food item, ingestion rate increases up to and possibly above prey densities of 3.4 *Favella* ml⁻¹. In mixtures of the two prey, the clearance rate of *Acartia* for *Favella* decreases with increasing concentration of *Heterocapsa*. At a *Favella* concentration of ~1 ml⁻¹ and a *Heterocapsa* concentration of ~40 cells ml⁻¹, *Acartia* ingests the same biomass of each prey type. The copepods preferentially feed on *Favella* even when the dinoflagellate is more abundant in terms of carbon and nitrogen than the tintinnid. If the effect of food density on the growth of *Favella* is considered as well as copepod predation, it is evident that both of these factors, and their interaction, can be important in regulating populations of this ciliate.

Introduction

Planktonic ciliates constitute an important component of the microzooplankton that is available to omnivorous and carnivorous copepods (Beers and Stewart, 1967, 1969, 1971; Smetacek, 1981). Ciliates may be both a trophic link between nanophytoplankton and macrozooplankton (Beers and Stewart, 1967, 1969, 1971; Blackbourn, 1974; Hedin, 1975; Berk et al., 1977; Heinbockel and Beers, 1979) and competitors with macrozooplankton for microplanktonic foods (Smetacek, 1981). The investigations of Berk et al. (1977), Robertson (1983), and Turner and Anderson (1984) have demonstrated that copepods prey on planktonic ciliates but questions remain about the factors which control the relative rates of grazing by copepods on algae and ciliates.

One ecologically important question is whether copepods selectively consume particles which are in the greatest abundance and switch to new food items when these become relatively more abundant (Richman et al., 1977; Landry, 1981). Switching between feeding on phytoplankton and ciliates has not been intensively studied. Schnack (1975; cited in Smetacek, 1981) suggested that copepods may feed selectively on tintinnids in tintinnid-algal assemblages. This may explain how copepods might limit ciliate populations even during periods of phytoplankton abundance (Smetacek, 1981). Robertson (1983) and Turner and Anderson (1984) found that the calanoid copepods, *Acartia tonsa* Dana, and *A. hudsonica* Pinhey
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have higher clearance rates for tintinnids than for some phytoplankton. The effects of phytoplankton density on predation by copepods on tintinnids has not been investigated.

The copepod, *Acartia tonsa* Dana, a dinoflagellate, *Heterocapsa triquetra* (Ehrenberg) Stein and a tintinnid, *Favella* sp. co-occur in small estuaries on Cape Cod, MA. *Heterocapsa* is ~16 × 22 μm in size, and may reach densities of up to 3000 cells ml⁻¹ during blooms, although lower densities, 1000 cells ml⁻¹ or less, are more typical (Stoecker et al., 1983; Stoecker et al., 1984). *Favella* sp. has an oral lorica diameter of 65–75 μm and is 100–200 μm long. This tintinnid is a predator on dinoflagellates and other ciliates and commonly co-occurs with *Heterocapsa* during spring and fall dinoflagellate blooms (Stoecker et al., 1981). *Favella* densities occasionally are as high as 4.0 ml⁻¹, but lower densities, 0.05–1.0 ml⁻¹, are more typical (Stoecker et al., 1983; Stoecker et al., 1984). *Heterocapsa* and *Favella* are potentially important seasonal components of the diet of *A. tonsa*. *Acartia hudsonica*, a closely related species which replaces *A. tonsa* in these estuaries in winter and spring (Conover, 1956; Grice, 1960; Heinle, 1966), may also feed on *Heterocapsa* and *Favella*.

We investigated feeding by *Acartia tonsa* on *Heterocapsa triquetra* and *Favella* sp. We report here experiments which quantify the relationships between food concentrations and feeding rates, show the influence of *H. triquetra* density on the feeding rate of *A. tonsa* on *Favella*, and indicate that *Acartia* differentially grazes on *Favella* in ciliate-algal assemblages. These data were used to estimate the potential contribution of *Favella* and *Heterocapsa* to *Acartia's* diet and to predict the conditions under which grazing by *Acartia* could limit the growth of *Favella* populations.

**Methods**

Cultures of a dinoflagellate and a tintinnid, isolated from Perch Pond, Falmouth, Massachusetts, were used as prey in the feeding experiments. The dinoflagellate, *Heterocapsa triquetra* (strain A984), was grown in enriched seawater medium f/2 (Guillard, 1975) with silicic acid omitted, on a 14:10 h light:dark cycle at 20°C. *Favella* sp. (strains P081 and P082) was cultured at 20°C in a seawater medium (Stoecker et al., 1981) with ~1000 cells ml⁻¹ of *Heterocapsa* as food.

*Acartia tonsa* was used in the six feeding experiments, which are outlined in Table I. Feeding by *Acartia* on *Heterocapsa* at varying food concentrations was investigated in Experiment 1. Experiment 2 was designed to investigate its feeding on *Favella* at varying prey concentrations. The effect of *Heterocapsa* density on the feeding rate of *Acartia* on *Favella* was determined in Experiments 3–5. Experiment 6 was designed to determine if *Acartia* has a different clearance rate for the two prey types when they are present simultaneously. In order to estimate the feeding rate of *Acartia* on *Heterocapsa* in the presence of *Favella* it was necessary to determine the grazing rate of *Favella* as part of this experiment (Table I).

The first five experiments were run between 24 June and 26 July 1982 and the same methods were used in all five. Copepods were collected with a plankton net
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(300 μm mesh) from Perch Pond. Adult female *Acartia tonsa* were sorted under a dissecting microscope. Ten females were added to 500 ml of filtered seawater (Whatman GF/C) in a glass jar (946 ml). They were then allowed to acclimatize on a 14:10 h light:dark cycle at 20°C (ambient water temperatures in Perch Pond ranged from 20 to 28°C) for 15 to 20 h. At midnight, three experimental and four control (no copepods) jars were inoculated with each prey treatment (Table I). *Heterocapsa*, from exponentially growing cultures, were added to the jars with a pipette. *Favella* were individually picked from cultures with a Pasteur pipette and added to the jars to achieve the specified densities (Table I) in Experiments 2, 3 and 4. For Experiment 5, in which much higher *Favella* densities were used, the *Favella* were concentrated from a culture above a 41 μm mesh net and then small volumes of this concentrate were added to the jars with a pipette to get the required density. At time zero, one control jar from each treatment was preserved with acid Lugol's solution so that actual initial prey densities could be determined. The experimental and remaining control jars were then placed in the dark at 20°C. The jars were not rotated on a wheel. Preliminary experiments showed that ingestion rates were similar in stationary and rotated jars when the two prey types were used singly. However, if the two prey distributed themselves differently in jars in which both were present, this could have produced a bias. After eight hours the contents of each jar were filtered through a 200 μm Nitex mesh to remove the copepods. Microscopic inspection of the mesh showed that no *Favella* or *Heterocapsa* were retained. The filtrate was preserved with acid Lugol's solution for later enumeration.

The inverted microscope method (Utermöhl, 1931; Hasle, 1978) was used to count the *Favella* in 100 ml volumes. The estimate of *Favella* density was always based on counts of 100 cells or more and it was necessary to count several 100 ml subsamples at low *Favella* densities. Triplicate, 1 ml, subsamples from each jar were counted for *Heterocapsa*.

The sixth experiment was done on 2 November 1983. The methods used in this experiment were slightly different from those used in the earlier experiments. Copepods were collected from Woods Hole Harbor and the adult *Acartia tonsa* were picked from the sample under a dissecting microscope. They were acclimated in the laboratory in filtered seawater containing initial prey densities of one *Favella* ml⁻¹ and 100 *Heterocapsa* cells ml⁻¹ at 15°C, the harbor water temperature, on a 14:10 h light:dark cycle. Triplicate experimental and control jars containing 600 ml of filtered seawater were inoculated with each prey treatment (Table I). Small volumes of *Heterocapsa* culture and concentrated *Favella* were added with pipettes to achieve the desired prey densities. The jars were mixed and 100 ml volumes removed from each jar and fixed for the time zero counts. Ten adult *Acartia* were then added to each experimental jar. The sex ratio was ~50:50. We used a mixture of males and females so that the results could be used to estimate the grazing impact of natural populations which contain a mixture of the sexes. The jars were incubated, without rotation, in the dark at 15°C beginning at midnight. After 8 h of incubation, the copepods were removed on a mesh and the contents of the jars fixed with acid Lugol's solution. A 100 ml subsample from each jar was counted for *Favella* using the inverted microscope method.
Table I. Experimental designs for grazing experiments

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Initial prey densities (ml⁻¹)</th>
<th>Treatments*</th>
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<tr>
<td></td>
<td>Favella</td>
<td>Heterocapsa</td>
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*H = Heterocapsa only; HF = Heterocapsa and Favella; HC = Heterocapsa and Acartia; F = Favella only; FC = Favella and Acartia; HFC = Heterocapsa, Favella and Acartia.

Subsamples were counted for Heterocapsa using the inverted microscope method for low cell densities and a Sedgewick-Rafter cell for high densities; 400 – 600 cells were counted in all cases.

With light and scanning electron microscopy (SEM), observations were made of the condition of the Favella and their loricae in control and grazed treatments. Specimens fixed in acid Lugol's solution were examined using transmitted light and the inverted microscope. For SEM, loricae, which had been initially fixed in acid Lugol's solution, were subsequently fixed in 1% osmium in 0.2 M sodium cacodylate buffer, dehydrated in ethanol, critical point (Tousimus) dried, and...
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Table II. Volumes and mean carbon and nitrogen contents of *Heterocapsa triquetra* and *Favella* sp.

<table>
<thead>
<tr>
<th></th>
<th>μm³</th>
<th>Mean ± S.D.</th>
<th>ngC cell⁻¹</th>
<th>ngN cell⁻¹</th>
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<tbody>
<tr>
<td><em>H. triquetra</em></td>
<td>2500</td>
<td>0.34 ± 0.01</td>
<td>0.067 ± 0.0002</td>
<td></td>
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<tr>
<td><em>Favella</em></td>
<td>195 000</td>
<td>20 ± 1</td>
<td>5 ± 0</td>
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coated with gold-palladium. Specimens were examined using a JEOL model JSMT 300 scanning electron microscope.

The mean carbon and nitrogen contents of *Heterocapsa* and *Favella* cells were determined so that densities and ingestion rates for these prey items could be compared on a biomass basis as well as by cell number (Table II). CHN analyses of late log phase cultures, similar to those used in the feeding experiments, were done in triplicate using a model 240 Perkin-Elmer CHN analyzer. The *Favella* were first concentrated on a 64 μm mesh net and washed free of *Heterocapsa* cells with media before being filtered onto glass fiber filters (precombusted Whatman GF/C). For *Heterocapsa*, cultures were directly filtered onto the glass fiber filters. The filters were not rinsed because this can lyse the cells and cause loss of carbon. A blank filter, which was placed under the sample filter, was used to correct for adsorbed carbon (Menzel and Dunstan, 1973).

Ingestion rates (cells or ngC copepod⁻¹ h⁻¹) and clearance rates (ml copepod⁻¹ h⁻¹) were calculated for each experimental jar using the equations of Frost (1972). All prey concentrations were calculated as Frost's <C> and, unless otherwise noted, are of average prey concentrations, expressed as cells ml⁻¹ or ngC ml⁻¹. In Experiment 6, the calculation of *Acartia*’s feeding rate on *Heterocapsa* in the presence of *Favella* is complicated by *Favella* grazing on *Heterocapsa*. A maximum estimate of *Acartia*’s grazing on *Heterocapsa* was obtained by assuming that the *Favella* did not graze in the presence of the copepods. A minimum estimate of *Acartia*’s grazing was obtained by assuming that *Favella* grazed at normal rates in the presence of the copepods and calculating a corrected clearance rate for the copepods, \( F_c \), using the formula:

\[
F_c = \left( \frac{g - (F_f <N_f>)}{V} \right) \frac{V}{N_c}
\]

where \( g \) = Frost’s grazing coefficient for the combined grazing due to copepods and *Favella*, \( F_f \) = the clearance rate of *Favella* for *Heterocapsa* (this is estimated from the control treatments without copepods but with *Heterocapsa* alone or *Heterocapsa* and *Favella*, Table I), and \( <N_f> \) the average concentration of *Favella*, calculated similarly to Frost’s \(<C>\), \( V \) = the volume and \( N_c \) = the number of copepods.

Results

Both the dinoflagellate, *Heterocapsa triquetra*, and the tintinnid, *Favella* sp., are eaten by adult *Acartia tonsa* (Figures 1 and 2). When *Heterocapsa* is the only
prey, Acartia’s ingestion rate increases with increasing dinoflagellate density up to densities of 648 cells ml⁻¹ (220 ngC ml⁻¹). Ingestion decreases at higher prey densities. The maximum ingestion rate of Acartia for Heterocapsa was ~700 ngC copepod⁻¹ h⁻¹ (Figure 1). When Favella was the sole prey, Acartia’s ingestion rate also increased with increasing prey density (Figure 2). At the highest Favella density tested, Acartia ate about 11 Favella (215 ngC) copepod⁻¹ h⁻¹ (Figure 2).

In Experiments 3—6, both prey items were available and Heterocapsa densities were varied to determine if the abundance of the dinoflagellate influenced grazing by Acartia on the tintinnid. In Experiments 4 and 6, ingestion of Favella decreas-
Differentiation grazing by *Acartia*

Fig. 3. Ingestion rate of *Acartia* for *Favella* as a function of *Heterocapsa* density. Means ± S.D. for Experiments 3 (△), 4 (●), 5 (∇) and 6 (★).

Fig. 4. Clearance rate of *Acartia* for *Heterocapsa* as a function of *Heterocapsa* density; *Heterocapsa* the sole prey. Means ± S.D. for Experiments 1 (○) and 6 (★).

ed slightly with increasing *Heterocapsa* density (Figure 3) but in Experiments 3 and 5 this trend was not evident (Figure 3).

The clearance rate of *Acartia* for *Heterocapsa* in the absence of *Favella* decreased with increasing cell density (Figure 4). In Experiment 2, the clearance rate of *Acartia* for *Favella* was quite variable (Figure 5). At the lowest density of *Favella*, 0.01 ml⁻¹, the clearance rate of *Acartia* was low but it increased at a *Favella* density of 0.1 ml⁻¹. This suggests a threshold response. At *Favella* densities of 1–4 cells ml⁻¹, the clearance rate of *Acartia* was ~3 ml copepod⁻¹ h⁻¹.

In the treatment in Experiment 6 in which both prey types were available, the clearance rate of *Acartia* for *Favella* decreased with increasing dinoflagellate density (Figure 6). The maximum and minimum estimated clearance rates of *Acartia* for *Heterocapsa* in the presence of *Favella* are also shown in Figure 6. Maximum clearance rate decreases with dinoflagellate density. The relationship is similar to the relationship between clearance rate and food density when the dinoflagellate is the only prey (Figure 4). The minimum estimate of *Acartia* grazing on *Heterocapsa* was in most cases zero (Figure 6). Although *Heterocapsa*, when present, was always more abundant by number and biomass than *Favella* in Experiment 6, the clearance rate of the copepods for *Favella* was always higher.
than for dinoflagellates (Figure 6). There was no evidence for switching (Murdoch, 1969). In our experiments *Acartia* preferentially fed on *Favella* even when the dinoflagellates were much more abundant.

At a *Favella* density of 1.2 cells ml$^{-1}$, adult *Acartia* would derive a greater ration from *Favella* than from *Heterocapsa* when densities of the dinoflagellate were less than 380 cells ml$^{-1}$ (Figure 7). This estimate of *Favella*’s contribution to *Acartia*’s diet is conservative because the maximum ingestion rates of *Acartia* for *Heterocapsa* were used in the comparison. Under these conditions, the highest ingestion rate (total biomass of combined prey items) should be at *Heterocapsa* densities of ~600 cells ml$^{-1}$ (Figure 7).
Fig. 7. A comparison of calculated ingestion of *Favella* (●) and *Heterocapsa* (◇) by *Acartia* at an average *Favella* concentration of 1.2 cells ml⁻¹ (24 ngC ml⁻¹) and varying concentrations of *Heterocapsa*. Data derived from Figure 6; max. estimates of *Acartia*’s clearance rate for *Heterocapsa* were used in the calculations.

Table III. Occurrence of empty and crumpled loricae in control and grazed treatments

<table>
<thead>
<tr>
<th>Loricae containing a tintinnid</th>
<th>Mean No. 100 ml⁻¹ ± S.D.</th>
<th>Grazed by <em>Acartia</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Normal</td>
<td>129 ± 10</td>
<td>45 ± 13</td>
</tr>
<tr>
<td>Crumpled</td>
<td>0</td>
<td>2 ± 3</td>
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</tbody>
</table>

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<tr>
<th>Empty loricae</th>
<th>Mean No. 100 ml⁻¹ ± S.D.</th>
<th>Grazed by <em>Acartia</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Normal</td>
<td>3 ± 3</td>
<td>25 ± 12</td>
</tr>
<tr>
<td>Crumpled</td>
<td>0</td>
<td>47 ± 21</td>
</tr>
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</table>

In the jars exposed to grazing by *Acartia*, there were more empty loricae than in the control jars (Table III). Fifty to 75% of the empty loricae in the grazed jars were crumpled (Table III). Some of these crumpled loricae had clearly been part of copepod fecal pellets but many of them appeared never to have been ingested. In Figure 8, a scanning electron micrograph of a crumpled lorica is compared with one of a normal lorica. Naked tintinnids and tintinnids with Coxiella-form loricae, which are replacement loricae (Laval-Peuto, 1981), were sometimes common in the grazed treatments. We also observed some live tintinnids with crumpled loricae in the grazed treatments (Figure 9).

Discussion and Conclusions

In our laboratory experiments, grazing by *Acartia tonsa* on *Heterocapsa* decreased at cell densities above 1000 cells ml⁻¹ (340 ngC ml⁻¹). It is conceivable that if the copepods had become acclimated for longer to *Heterocapsa*, their
Fig. 8. Scanning electron micrographs of loricae from control (a) and grazed (b) treatments. Note that in (b) the lorica is crumpled. Scale bar = 10 μm.
feeding would not have saturated at this food level (Conover, 1978). During spring dinoflagellate blooms, *Heterocapsa* densities often exceed 1000 cells ml$^{-1}$ (340 ngC ml$^{-1}$) and thus copepod feeding on this dinoflagellate in nature may be depressed. Huntley (1982) and Fiedler (1982) have also observed inhibition of copepod feeding at high dinoflagellate densities *in situ* and have suggested that
this may reduce the grazing pressure on some dinoflagellate blooms.

In contrast, *Acartia's* ingestion of *Favella* was high up to the greatest average density, 3.4 cells ml$^{-1}$ (68 ng ml$^{-1}$), used in our experiments. During dinoflagellate blooms in Perch Pond, *Favella* densities often reach 0.1 – 1.0 cells ml$^{-1}$ but only rarely exceed 3.4 cells ml$^{-1}$ (Stoecker et al., 1983; Stoecker et al., 1984).

The clearance rate of *Acartia* for *Favella* ranged from 2.5 to 8.7 ml copepod$^{-1}$ h$^{-1}$ (Figures 5 and 6) and was higher for *Favella* than for the dinoflagellate (Figure 6). *Acartia hudsonica* has a higher clearance rate for the tintinnid, *Eutintinnuspectinus*, than for dinoflagellates (Turner and Anderson, 1984). Robertson (1983) found that *Acartia tonsa* had a higher clearance rate for *Favella pannemensis* than for small flagellates (300 $\mu$m$^3$ or less in cell volume) but not for a large (2250 $\mu$m$^3$ in cell volume) diatom. Differences between the preferences of *Acartia* for dinoflagellates and diatoms (Conover, 1978 and 1980) and preconditioning (Donaghay and Small, 1979) may account for the difference between our results and those of Robertson (1983).

In Experiments 4 and 6, ingestion and clearance rates for *Favella* decreased with increasing *Heterocapsa* density. These trends were absent or not significant in two other experiments (Figure 3). Anraku and Omori (1963) found that the presence of the centric diatom, *Thalassiosira weissflogii* (ex T. fluviatilis), reduced predation by *A. tonsa* on *Artemia* nauplii, and Landry (1981) found that *Calanus pacificus* fed disproportionately on the prey in greatest relative abundance when given mixtures of *T. weissflogii* and conspecific copepod nauplii. On observing that *A. tonsa*’s predation on copepod nauplii was not affected by algal density, Lonsdale et al. (1979) suggested that the finding of Anraku and Omori (1963) may be a function of the size of the algae. *T. weissflogii* is 12.5 – 17 $\mu$m diameter whereas Lonsdale et al. used smaller, 5 $\mu$m diameter cells (*Pseudoiso-chrysis* sp.) which did not reduce the feeding rate on nauplii. *H. triquetra* is comparable in size (16 $\mu$m X 22 $\mu$m) to *T. weissflogii*. Only in some experiments did its presence reduce the ingestion rate of *Favella* by *A. tonsa*. Paffenhofer and Knowles (1980) found that predation by adult copepods, *Centropages furcatus* and *Temora stylifera*, on copepod nauplii was not affected by the presence of diatoms.

Richman et al. (1977) suggested that copepods preferentially feed on the most abundant particles. This selectivity would be an important mechanism by which copepod grazing could reduce the growth of an abundant prey species. Our data (Figure 6) are not consistent with this hypothesis. Although *Heterocapsa* was numerically, and in terms of carbon and nitrogen ml$^{-1}$, more abundant than *Favella*, the clearance rate of *Acartia* for *Favella* was always higher than for *Heterocapsa*. There was no evidence for switching (Murdoch, 1969).

The role of ciliates in the diets of copepods and other macrozooplankton is poorly known (Poulet, 1983). Robertson’s (1983) and our data (Figure 7) indicate that tintinnids can be of quantitative importance in the diet of *Acartia tonsa* under certain circumstances. Even when tintinnids and other ciliates are not major constituents of the diets of copepods in terms of carbon, their presence may enhance the survival and growth rates of copepods (Heinle et al., 1977).

We observed empty, crumpled loricae in fecal pellets and free in the jars
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**Fig. 10.** Estimated net rate of increase of *Favella* as a function of *Acartia* density at three *Heterocapsa* densities, 100, 500 and 1000 cells ml$^{-1}$. The equation, $r = K_e - g$, was used to calculate the net rate of increase ($r$) as a function of the specific growth constant ($K_e$) of *Favella* and the grazing coefficient ($g$) of *Acartia* populations for *Favella* at the three dinoflagellate densities. Estimates of $K_e$ are from Stoecker et al. (1983; Table 6). The growth constants for *Favella* were slightly different in Experiments 1 and 2 (Stoecker et al., 1983), therefore, both data sets were used here resulting in two estimates of $r$ as a function of *Acartia* density for each *Heterocapsa* density. Estimates of $g$ are from Experiment 6 (Figure 6).

subjected to grazing (Table III and Figure 8). Turner and Anderson (1984) observed empty loricae of *Eutintinnus pectinis* in fecal pellets and free in jars grazed by *Acartia hudsonica*. These observations indicate that *Acartia* spp. may ingest some tintinnids whole, as suggested by Robertson (1983), but may also remove the contents and discard the empty loricae.

The presence of live tintinnids without a lorica or with a damaged or replacement lorica in the grazed treatments suggests that captured tintinnids may escape. The possession of a lorica appears to help freshwater rotifers escape from predatory copepods (Gilbert and Williamson, 1978; Williamson, 1983). Loricae in tintinnids may similarly reduce successful capture and ingestion by copepods (Capriulo et al., 1981).

To understand the population dynamics of tintinnids we need to combine estimates of predation with realistic data on specific growth rates of tintinnids (Robertson, 1983). This can be stated as $r = K_e - g$, where $r$ is the instantaneous rate of increase of tintinnids in the presence of predation, $K_e$ is the specific growth constant of the tintinnids, and $g$ is the grazing coefficient. The specific growth constant depends on food availability. For *Favella* sp., we have estimates of the specific growth constant at varying concentrations of *Heterocapsa triquetra* at 15 C (Stoecker et al., 1983). We calculated the grazing coefficient ($g$) of *Acartia* for *Favella* as a function of *Heterocapsa* density at 15 C using the relationship $g = N(F)/V$ with $F$ estimated from the data presented in Figure 6 ($N =$ number of copepods, $F =$ clearance rate, $V =$ volume). Over the range of *Favella* concentrations of $\sim 1-4$ ml$^{-1}$, the clearance rate of *Acartia* for *Favella* does not
change (Figure 5); this estimate of $g$ should hold over this range. However, the
daily $g$ may be less than we have estimated because the clearance rate of copepods
may be lower during the day than at night (our grazing experiments were done at
night).

The net rate of increase, $r$, for Favella was calculated from estimates of Ke and
g for three densities of Heterocapsa and are plotted as a function of adult Acartia
density in Figure 10. At a Heterocapsa density of about 100 cells ml$^{-1}$, a density
of about 3 - 4 adult Acartia 1$^{-1}$ could prevent a net increase in Favella but at a
Heterocapsa density of 1000 cell ml$^{-1}$, a density of $-10$ adult Acartia 1$^{-1}$
would be necessary (Figure 10). During blooms of Favella in Perch Pond, dinoflagellate
densities are often less than 100 cells ml$^{-1}$ (Stoecker et al., 1983; Stoecker et al.,
1984) and Acartia (A. hudsonica in spring and A. tonsa in the summer and fall)
densities often exceed 3 - 4 adults and copepodites 1$^{-1}$. These data suggest that
grazing by Acartia may at times prevent the net growth of Favella populations in
this estuary. At higher dinoflagellate densities or lower Acartia densities, Acartia
may depress, but not by itself prevent, net increases in Favella (Figure 10). In
Perch Pond and other similar estuaries, additional species occur along with the
Heterocapsa and Favella. Day and night grazing rates may vary. Figure 10 thus
presents a greatly simplified situation. Nevertheless, copepod predation and food
availability should interact in limiting ciliate populations. This hypothesis is fur-
ther supported by the observations of Smetacek (1981) on protozooplankton
cycles in Kiel Bight.

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