Effects of protozoan herbivory and carnivory in a microplankton food web

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ABSTRACT: The estuarine ciliates *Favella* sp. and *Balanion* sp. both feed on the dinoflagellate *Heterocapsa triquetra*, and *Favella* also feeds on *Balanion*. In laboratory experiments, transient dinoflagellate populations were higher than would be expected if the effects of the 2 grazers were additive; in some experiments the presence of *Favella* was associated with higher *H. triquetra* populations. In a theoretical model, increasing the rate of predation on a species could increase that species' steady-state concentration. The relative gross growth efficiencies in this model have an important influence on ecosystem structure. These effects may be important in regulating population densities in microplankton communities in which omnivory is common.

INTRODUCTION

Microzooplankton, including ciliates, are important consumers of phytoplankton in many marine planktonic communities (Heinbokel 1978, Heinbokel & Beers 1979, Capriulo 1982, Landry & Hassett 1982, Capriulo & Carpenter 1983, Verity 1984). In general, the larger planktonic ciliates (mostly tintinnids and oligotrichs) have been assumed to eat algae, but some may eat smaller ciliates as well (Blackbourn 1974, Robertson 1983). Carnivory among the microzooplankton would affect estimates of the feeding impact of microplankton as individuals (but perhaps not as a community) from incubation experiments using natural assemblages (Capriulo & Carpenter 1980, Landry & Hassett 1982). More interestingly, omnivory could partially control the trophic dynamics and structure of microplankton communities. Omnivorous habit may contribute to the resiliency of planktonic communities (Landry 1981) and decrease the potential secondary production by creating horizontal links (Steele 1974). Isaacs (1972, 1977) has suggested that most marine food webs are unstructured (omnivory is common), but within a highly structured part of a food web the consequences of being both a competitor of and a predator on another species would be different. We refer to such a situation as a trophic triangle.

We have investigated such a trophic triangle. Dino-flagellates often dominate the phytoplankton standing crop in salt ponds (small estuaries) on Cape Cod, Massachusetts. *Heterocapsa triquetra* (Ehr.) Stein is one of the most common dinoflagellates, often occurring in almost monospecific blooms. It is about 16×22 μm in size. The naked ciliate, *Balanion* (sp. nov., Coats & Small unpubl.) is sometimes associated with *H. triquetra* blooms in these estuaries (Stoecker et al. 1983). *Balanion* is about 32×34 μm in size. *Favella* sp., a large tintinnid (oral diameter 65 to 75 μm), is usually associated with spring and fall dinoflagellate blooms in these estuaries (Stoecker et al. 1984). In the laboratory, both *Favella* (Stoecker et al. 1981) and *Balanion* (Stoecker unpubl.) are selective predators on dino-flagellates. *Favella* is large enough to feed on *Balanion*. We determined the growth rates and gross production efficiencies of both ciliates, investigated predation by *Favella* on *Balanion*, and studied the effects of the interaction between *Favella* and *Balanion* on *H. triquetra* populations in multispecies cultures.

We then investigated a simple triangular model of this 3-species interaction. The properties of 3-species systems in which there is 1 predator and 2 prey (reviewed in Levandowsky 1977), 3 competitors (Rescigno 1968), or a linear food chain (Rescigno & Jones 1972) have been investigated. Although triangular interactions may be quite common in the plankton, this type of interaction had not been previously investigated.

EXPERIMENTAL METHODS AND MATERIALS

Culture of dinoflagellate and ciliates. Experiments were run with cultured *Heterocapsa triquetra* algae (Strain A984), *Balanion* sp., and *Favella* sp. All 3 were isolated from Perch Pond. The algae were grown in enriched seawater medium f/2 (Guillard 1975), except that silicic acid was omitted, on a 14:10 h light:dark cycle under 291 $\mu Em^{-2} s^{-1}$ of cool-white (Sylvania Co.) fluorescent light at 20 °C. *Favella* was cultured in aged, diluted Sargasso seawater (salinity about 31 ‰) to which 0.01 ml l^{-1} of f/2 iron-EDTA trace-metal solution (Guillard 1975) was added. This medium was autoclaved in teflon bottles, cooled, and then poured into sterile polycarbonate flasks. *Favella* were fed approximately 10^3 cells ml^{-1} of *H. triquetra* and grown at 15 or 20 °C. Culture methods for *Balanion* were similar to those for *Favella* except that *Balanion* was fed approximately 10^4 cells ml^{-1} of *H. triquetra* and maintained at 15 °C.

Experiment 1: growth curves. The first experiment was designed to document the growth of *Favella* sp. and *Balanion* sp., alone and in each other's presence, over a period of days. Duplicate 2 l flasks containing 1 l of medium were used for each treatment. The 4 treatments were: (1) *Heterocapsa triquetra* alone; (2) *H. triquetra* plus *Balanion*; (3) *H. triquetra* plus *Favella*; (4) *H. triquetra* plus *Balanion* and *Favella*. Flasks were inoculated at the following densities on Day 0: *H. triquetra*, 1000 cells ml^{-1}; *Balanion*, 0.5 cells ml^{-1}; *Favella*, 0.5 cells ml^{-1}. These densities are within the ranges we have observed in the estuary (Stoecker et al. 1984). Flasks were incubated in the light at 15°C. On the day after inoculation (Day 1) each flask was gently mixed and a 60 ml sample was withdrawn with a serological pipette. The sample was fixed with acid Lugol's solution. Sampling was repeated daily until the populations declined. Subsamples were taken from the fixed samples, settled, and counted using the inverted-microscope method. The ciliates in 25 ml were counted, unless densities were greater than 15 ml^{-1}, when the ciliates in 10 ml were counted. Logarithms of mean densities were plotted against time to determine the periods of exponential growth. Growth rates and generation times in h were calculated for these periods using standard formulas (Guillard 1973). Frost's equations (Frost 1972) were used to calculate average cell concentrations (C), clearance (F), and ingestion (I) rates for these same periods. The average concentration of grazers (*Favella* or *Balanion*) was calculated assuming exponential growth (Heinbokel 1978).

Experiment 2: effects of initial Heterocapsa triquetra and Favella sp. densities. A 2-way matrix design was used in this experiment to test for the effects of initial

densities of *Heterocapsa triquetra* and *Favella* sp. and for effects due to the interaction of these 2 factors on *H. triquetra* and *Balanion* sp. populations after 48 h incubation. Initial *Balanion* density was 0.5 cells ml^{-1}. Initial *H. triquetra* densities were 100, 500, and 1000 cells ml^{-1}. Initial *Favella* densities were 0, 1, and 2.5 cells ml^{-1}. Six 250 ml capacity polycarbonate flasks containing 100 ml of medium were used for each treatment. After inoculation, the contents of 3 flasks from each treatment were fixed with acid Lugol's solution. The remaining 3 flasks in each treatment were incubated at 15 °C in the dark for 48 h and then the contents fixed. The cells in 50 ml volumes were counted using the inverted-microscope technique. A logarithmic transformation was done on the counts to correct for multiplicative effects (Sokal & Rohlf 1981). When the counts included zeros, the data were coded by adding 1 to each variate before the transformation. Two-way analysis of variance (2-way ANOVA) (Sokal & Rohlf 1981) was used to test for the effects of initial algal and *Favella* densities and of interaction between the 2 factors on *Balanion*. By the end of the experiment, *H. triquetra* had disappeared from 7 of the treatments, therefore a t-test for unequal variances (Sokal & Rohlf 1981) rather than analysis of variance were used with these data.

Experiment 3: gross production efficiencies. The gross production efficiencies (GPE) (production/ingestion; equivalent to gross growth efficiency, ecological efficiency or yield as used by some authors) of *Favella* sp. and *Balanion* sp., when feeding on *Heterocapsa triquetra* were compared in this experiment. It was not possible to determine the production efficiency for *Favella* when feeding on only *Balanion* because *Favella* does not survive on this diet.

Triplicate 250 ml capacity polycarbonate flasks containing 200 ml of medium were used for each treatment. To determine if efficiencies varied with algal food concentrations, 3 initial *Heterocapsa triquetra* densities were used: 500, 1000, and 3000 cell ml^{-1}. Triplicate control flasks at each algal density were not inoculated with ciliates. Experimental flasks were inoculated with either *Favella* sp., 1 cell ml^{-1}, or with *Balanion* sp., 2 cells ml^{-1}. Flasks were incubated at 15 °C in the dark. Volumes of 100 ml were removed from each flask after 24 and 48 h incubation. At both sampling times, 10 to 40 ml unfixed samples were electronically sized using a Model TA II Coulter counter with a population accessory and a 400 μm aperture tube. The aperture tube was calibrated with 21.84 μm polystyrene microspheres. Channel splitting was used to improve particle-size resolution. The sizes of *Balanion* and *Favella* were also checked using an ocular micrometer. Sixty ml subsamples were preserved with acid Lugol's solution and later counted. In

the treatments with *Balanion*, 25 ml settled samples were counted; with *Favella*, 50 ml samples were counted.

Cell counts for each replicate at each sampling time were converted to carbon (C) using the formula:

$$C = aV \qquad (1)$$

where C = pg C ml^{-1}; a = the conversion factor for volume to carbon (pg C μm^{-3}); V = average cell volume (μm^3). Conversion factors were determined from triplicate CHN analysis of the ciliates and volume determinations on cells from the same cultures.

Frost's equations (Frost 1972) were used to calculate the average concentration of *Heterocapsa triquetra* in pg C ml^{-1} and the ingestion rates (I) in pg C ciliate^{-1}h^{-1}. The average concentrations (N) of *Favella* sp. or *Balanion* sp. were calculated. Ciliate carbon at 24 h was subtracted from ciliate carbon at 48 h to get the production (P) for the 24 h time interval in pg C ml^{-1}.

Gross production efficiency (GPE), that is production/ingestion, was calculated as:

$$GPE = \frac{P}{24 \times N \times I} \qquad (2)$$

Gross production efficiencies were calculated separately for each of the 3 replicates at each food concentration. Because GPE is a proportion, an arcsine transformation was applied (Sokal & Rohlf 1981) before the data were analysed with a 2-way ANOVA to determine if the GPE's of the 2 ciliates were different and to determine if GPE's were different at different food levels.

Experiment 4: effects of ciliate species composition on grazing impact, numerical growth, and secondary production. This experiment was designed to simultaneously determine if the presence of both ciliates influences grazing impact, the growth of either, and the production of ciliate biomass compared with single ciliate species culture. Additional data were also obtained on the GPE of both ciliates for comparison with Experiment 4. Two initial densities of *Heterocapsa triquetra*, 500 and 1000 cells ml^{-1}, were used so that the interactions of the 2 ciliates at different algal food levels could be compared. The 4 initial ciliate densities at each algal food level were: (1) control (no ciliates); (2) 1 *Favella* ml^{-1}; (3) 0.5 *Balanion* ml^{-1}; (4) 1 *Favella* and 0.5 *Balanion* ml^{-1}. Triplicate cultures were incubated at 15 °C for 46 h. Experimental protocols for determining cell numbers and for measuring production were the same as in previous experiments. A 2-way ANOVA was used to test for the effects of algal density and initial ciliate densities.

EXPERIMENTAL RESULTS

Experiment 1: growth curves

With *Heterocapsa triquetra* present but no *Favella* sp. the *Balanion* sp. populations reached 350 ml^{-1} on Day 4 and then rapidly declined (Fig. 1). With *Favella* present, *Balanion* reached a lower maximum density, 22 ml^{-1}, on Day 3, and declined by Day 5. *Favella* in the treatment with *Balanion* contained the remains of *Balanion* in their food vacuoles. *Favella*'s growth was similar whether *Balanion* was present or absent (Fig. 1) except on Day 8 when the *Favella* without *Balanion* appeared to be declining more slowly than the *Favella* which had been with *Balanion*.

Algal concentrations were similar in the grazed treatment groups until Day 3 when the cultures with *Favella* sp. as the only grazer had the highest and the cultures with only *Balanion* sp. had the lowest *Heterocapsa triquetra* concentrations (Fig. 2). The cultures with both ciliates had intermediate *H. triquetra* densities. This trend persisted until the algae were almost completely removed by grazing. The reduced *Balanion* densities in the treatments with *Favella* cannot be ascribed to competition for food because more food was present on Days 3 and 4 in the treatments with *Favella* than without *Favella*.

From Fig. 1 & 2, the periods during which exponential growth occurred were identified; for these periods growth rates were estimated (Table 1). In Treatment 1 (*H. triquetra* alone) the generation time for *H. triquetra*
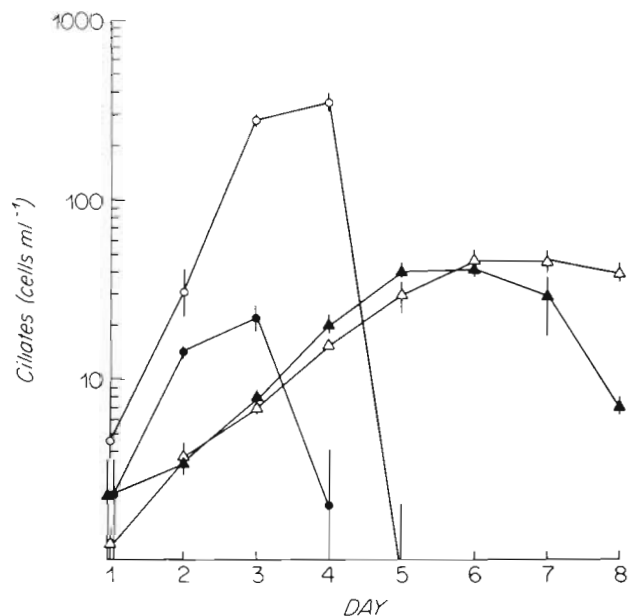

Fig. 1. Average densities of *Balanion* sp. and *Favella* sp.; Experiment 1. Ranges indicated by vertical bars. ○ *Balanion* alone; ● *Balanion* with *Favella*; △ *Favella* alone; ▲ *Favella* with *Balanion*
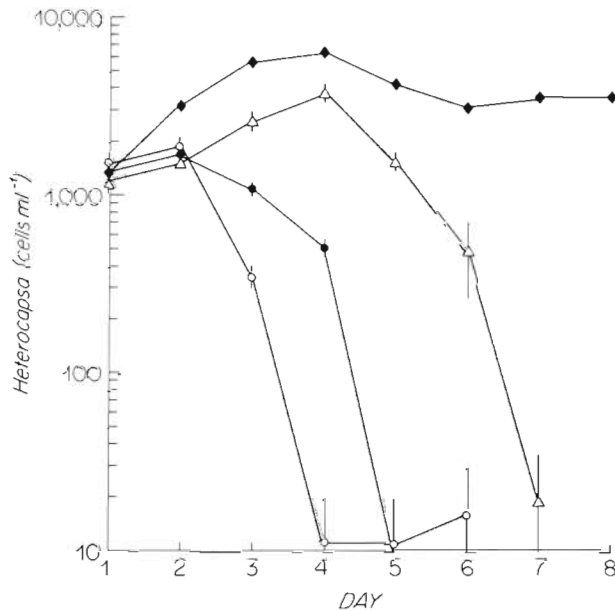
Fig. 2. Average densities of *Heterocapsa triquetra*; Experiment 1. Ranges indicated by vertical bars. ◆ control; ○ with *Balanion* sp.; △ with *Favella* sp.; ● with *Balanion* and *Favella*

Table 1. Feeding rates of *Favella* sp. and *Balanion* sp. (Experiment 1). $<C>$: av. cell concentration (cells ml^{-1}); F: = volume swept clear (μl $ciliate^{-1}$ h^{-1}); I: ingestion rate (cells $ciliate^{-1}$ h^{-1})

	Repli-cate	$<C>$	F	I
Balanion on *Heterocapsa*				
Day 1–2	1	1893	1.2	2.3
	2	1299	1.2	1.6
Day 2–3	1	1012	0.8	0.8
	2	786	1.0	0.8
Favella on *Heterocapsa*				
Day 1–2	1	1460	9.9	14.5
	2	1341	11.4	15.3
Day 2–3	1	2032	1.4	2.8
	2	2052	1.0	2.0
Favella on *Balanion*				
Day 2–3	1	16.6	12.2	0.2
	2	19.4	15.0	0.3

over Days 1 to 3 was about 23 h. In Treatment 2 (*H. triquetra* plus *Balanion*) the generation time for *Balanion* for Days 1 to 3 was about 8 h. The generation time for *Favella* was estimated for Days 1 to 4; in Treatment 3 (*H. triquetra* plus *Favella*) it was about 20 h and in Treatment 4 (*H. triquetra, Balanion,* and *Favella*) it was about 23 h.

For the periods in which exponential growth occurred, feeding rates were also estimated (Table 1). It was assumed that the growth of *Heterocapsa triquetra* was similar in all flasks for the first 3 d of the experiment. The volume swept clear (F) by *Balanion* is about 1 μl $ciliate^{-1}h^{-1}$; the number of algae ingested appears to be proportional to the algal density. This is consistent with earlier results (Stoecker unpubl.). *Favella* con-

sumed 14.9 dinoflagellates $ciliate^{-1}h^{-1}$ on Days 1 and 2 when *H. triquetra* densities averaged 1401 cells ml^{-1}. On Days 1 and 2 *Favella* only consumed 2.4 dinoflagellates $ciliate^{-1}h^{-1}$; during this period *H. triquetra* densities averages 2042 cells ml^{-1} (Table 1). These values are within the range previously reported for *Favella* grazing on dinoflagellates (Stoecker & Guillard 1982) and are consistent with inhibition of feeding at *H. triquetra* densities over 1000 to 1500 ml^{-1} (Stoecker unpubl.). The predation rate of *Favella* on *Balanion* (at an average *Balanion* concentration of 18 ml^{-1}) was 0.25 *Balanion* $Favella^{-1}h^{-1}$. The volume swept clear by *Favella*, 14 μl $ciliate^{-1}h^{-1}$, with *Balanion* as prey was within the range, 1 to 25 μl $ciliate^{-1}h^{-1}$, reported with dinoflagellates as prey (Stoecker & Guillard 1982).

Table 2. Effect of initial *Heterocapsa* (H) and *Favella* (F) conc. (cells ml^{-1}) on *Heterocapsa* and *Balanion* conc. after 48 h. Experiment 2; initial *Balanion* conc. 0.5 cells ml^{-1}

	No. *Heterocapsa* ml^{-1} ± SD			No. *Balanion* ml^{-1} ± SD		
	H 100	H 500	H 1000	H 100	H 500	H 1000
0F	0 ± 0	0 ± 0	0 ± 0	13.2 ± 0.1	34.4 ± 6.2	32.4 ± 2.9
1F	0 ± 0	0 ± 0	101 ± 49	0.6 ± 0.4	0.9 ± 1.1	0.5 ± 0.1
2.5F	0 ± 0	0 ± 0	46 ± 25	0 ± 0	0 ± 0	0 ± 0

2-way ANOVA:

t-Test (unequal variances):		Source of *variation*	df	F	p
0 *vs* 101	p < 0.05	Initial *Heterocapsa*	2	1.11	ns
0 *vs* 46	p < 0.05	Initial *Favella*	2	295.4288	p < 0.001
101 *vs* 46	ns	Interaction	4	0.6775	ns
		Error	18		

Experiment 2: effects of initial *Heterocapsa triquetra* and *Favella* sp. densities

Favella sp. had a significant inhibitory effect on the density of *Balanion* sp. by 48 h (Table 2). In this experiment, the effects of initial *Heterocapsa triquetra* density were not significant (Table 2). At the end of the incubation, there were significantly more *H. triquetra* when *Favella* was present than when it was absent in the highest food density treatments; at the lower food densities all the algae had been grazed.

Experiment 3: gross production efficiencies

The conversion factor, *a* (see Eq. [1]), for volume to carbon is 0.136 pg C μm^{-3} for *Heterocapsa triquetra* and 0.10 for *Favella* sp. and *Balanion* sp. *Favella* and *Balanion* had a similar response, in terms of gross production efficiency (GPE), to variations in algal food density (Table 3). At initial *H. triquetra* densities of 500 and 1000 cells ml^{-1} (average food biomass 20 to 100 μg carbon l^{-1}), both ciliates had a GPE above 50 %. At an initial *H. triquetra* density of 3000 cells ml^{-1} (average food biomass 344 to 393 μg carbon l^{-1}), both *Favella* and *Balanion* had a lower GPE, 21 and 25 % respectively; however, these were not statistically different from each other ($p > 0.05$). At the highest food density, some of the fecal particles produced by the ciliates contained undigested *H. triquetra* cells.

Table 3. Mean ($\pm$ SD) Gross Production Efficiencies (GPE) of *Favella* sp. and *Balanion* sp. at 15 °C. Food: *Heterocapsa triquetra*

Food availability			
Initial *Heterocapsa* (cells ml^{-1})	Av. *Heterocapsa* (cells ml^{-1})	(μg C l^{-1})	GPE (%)
Favella			
500[a]	131	26	64 $\pm$ 4
500[a]	135	21	51 $\pm$ 4
1000[a]	422	82	69 $\pm$ 5
1000[b]	499	76	54 $\pm$ 11
3000[a]	1765	344	21 $\pm$ 5
Balanion			
500[a]	218	43	53 $\pm$ 4
500[b]	278	42	50 $\pm$ 4
1000[a]	462	90	54 $\pm$ 6
1000[b]	648	98	61 $\pm$ 12
3000[a]	2017	393	25 $\pm$ 8

[a] Experiment 3
[b] Experiment 4

Experiment 4: effects of ciliate species composition on grazing impact, numerical growth, and secondary production

At the end of the 46 h incubation, grazing had reduced the *Heterocapsa triquetra* density in all treatments with ciliates (Fig. 3). However, the effects of *Favella* sp. and *Balanion* sp. grazing on *H. triquetra*
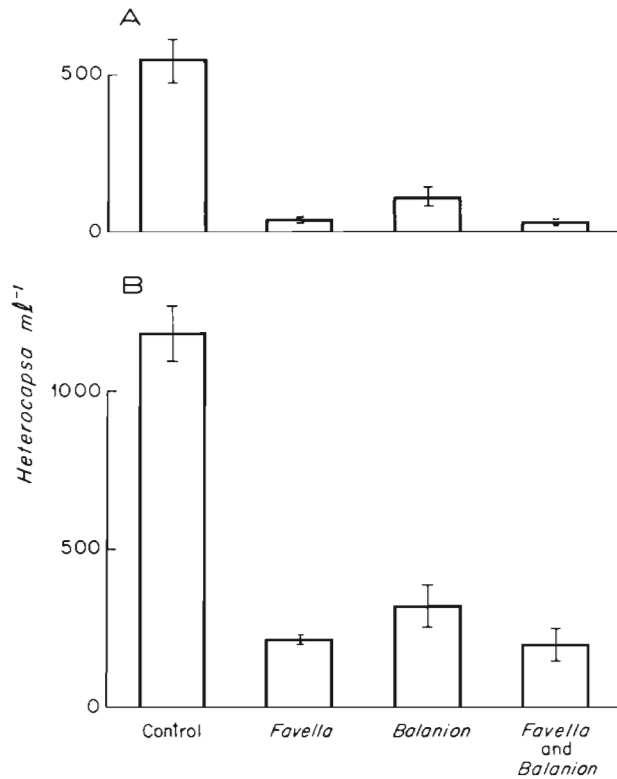

Fig. 3. *Heterocapsa triquetra* density (mean $\pm$ SD) 46 h after inoculation with *Favella* sp., *Balanion* sp., and both. Initial densities were 1.0 *Favella*, 0.5 *Balanion*, and 500 (A) or 1000 (B) *H. triquetra* ml^{-1}; Experiment 4

2-way ANOVAS:

A

Source of variation	df	F	p
Initial *Balanion*	1	70.75	< 0.001
Initial *Favella*	1	187.96	< 0.001
Interaction	1	50.27	< 0.001
Error	8		

B

Source of variation	df	F	p
Initial *Balanion*	1	69.42	< 0.001
Initial *Favella*	1	132.71	< 0.001
Interaction	1	60.36	< 0.001
Error	8		

were not additive; *H. triquetra* numbers were greater than expected. This interaction was significant at both algal densities (Fig. 3). The effect was not as striking as in Experiment 1, where adding *Favella* to *H. triquetra* and *Balanion* appeared to have increased the number of *H. triquetra* (Fig. 2). As in Experiment 2, *Balanion* concentrations were lower in the presence of *Favella* but the impact of *Favella* on *Balanion* was greater at the higher algal density (Fig. 4). *Balanion* did not have a significant effect on the number of *Favella* (Fig. 5).

In single ciliate species culture, secondary production was greater for *Balanion* sp. than for *Favella* sp. (Fig. 6). Secondary production for the 24 to 46 h interval was significantly lower when both ciliates were present than when either was grown separately. The negative effect of the presence of both ciliates on production was more dramatic at the lower algal density (Fig. 6). For *Favella* or *Balanion* grown singly, the GPE was 50 % or greater (Table 3).

MODEL

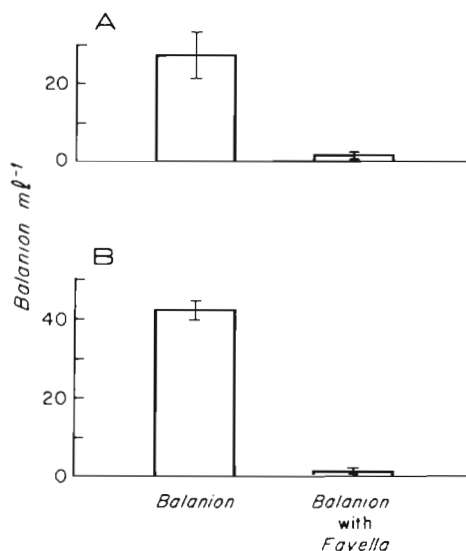We investigated the type of food web structure exemplified by interactions among *Favella* sp., *Balan-*

Fig. 4. *Balanion* sp. density (mean ± SD) 46 h after inoculation with *Balanion* (0.5 ml⁻¹) in the presence and absence of *Favella* sp. at 2 initial *Heterocapsa triquetra* densities, 500 (A) and 1000 (B) ml⁻¹; Experiment 4

2-way ANOVAS:

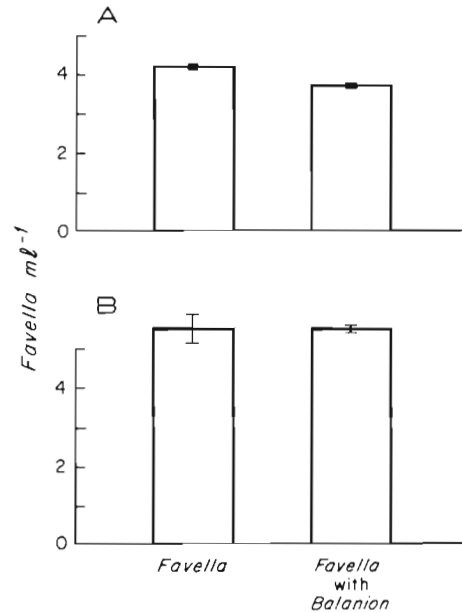| Source of variation	df	F	p
Initial *Heterocapsa*	1	8.75	< 0.05
Favella	1	226.11	< 0.001
Interaction	1	11.89	< 0.05
Error	8		

Fig. 5. *Favella* sp. density (mean ± SD) 46 h after inoculation with *Favella* (1.0 ml⁻¹) in the presence and absence of *Balanion* sp. (0.5 ml⁻¹) at 2 initial *Heterocapsa triquetra* densities, 500 (A) and 1000 (B) ml⁻¹; Experiment 4

2-way ANOVAS (ns: not significant):

Source of variation	df	F	p
Initial *Heterocapsa*	1	118.00	< 0.001
Balanion	1	2.13	ns
Interaction	1	2.27	ns
Error	8		

ion sp., and *Heterocapsa triquetra* using a theoretical model. We did not intend (indeed, we do not know enough) to construct a simulation model of the system. We omitted important features of *in situ* population dynamics such as formation and hatching of cysts, satiation of predators, and carnivore population dynamics. Our intention was to seek effects similar to those we observed in laboratory experiments in a setting simple enough to be analysed.

We considered the following model of populations of *Heterocapsa triquetra* (*H*), *Balanion* sp. (*B*) and *Favella* sp. (*F*):

$$\frac{dH}{dt} = rH - sH^2 - \alpha HB - \gamma HF \qquad (3)$$

$$\frac{dB}{dt} = \varepsilon_\alpha \alpha HB - \beta BF - \psi B \qquad (4)$$

$$\frac{dF}{dt} = \varepsilon_\beta \beta BF + \varepsilon_\gamma \gamma HF - \varphi F \qquad (5)$$

Growth, grazing and mortality are described by familiar Lotka-Volterra terms: r = *per capita* growth rate of *H. triquetra* at low densities; r/s = carrying capacity
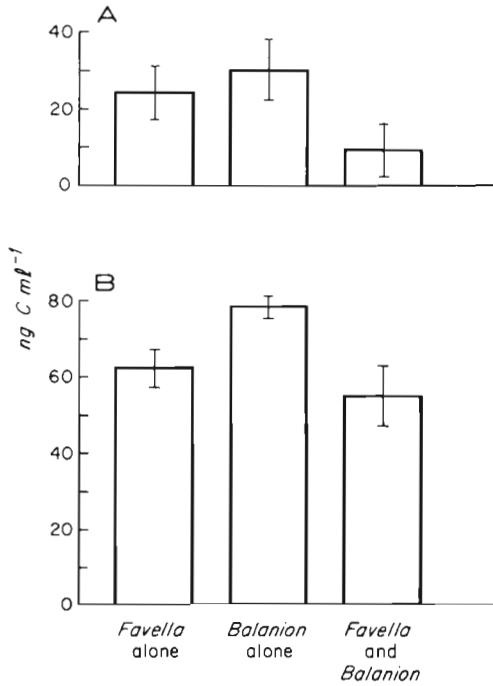
Fig. 6. Production of ciliate biomass (mean ± SD) over 22 h incubation when *Favella* sp. and *Balanion* sp. were grown separately and together at low (A) and high (B) *Heterocapsa triquetra* densities; Experiment 4

2-way ANOVAS (ns: not significant):

Source of variation	df	F	p
Initial *Heterocapsa* density	1	114.9	< 0.001
Ciliate species composition	2	14.7	< 0.002
Interaction	2	0.1	ns
Error	12		

for *H. triquetra* in the absence of specific predators. The total rate of grazing of *Balanion* on *H. triquetra* is αHB, proportional to the product of their concentrations. Grazing of *Favella* on *Balanion* is βBF; of *Favella* on *Heterocapsa*, γHF. The terms ψB and φF represent constant *per capita* mortality rates of B and F. The factors ε_α, ε_β, and ε_γ represent gross production efficiencies: the fraction of ingested grazer material converted to growth. Because of the triangular nature of the model, it is possible to compare efficiencies of different food pathways between 2 species, something which would make no sense in a food chain model. The relative values of these efficiencies will have an important effect on ecosystem structure.

The experiments reported here did not approach a steady state; and neither does the estuary which inspired them. In the estuary, there is instead a transient outburst, initiated by the germination of dinoflagellate and perhaps protozoan cysts, which lasts a few weeks, and which is terminated largely by the

formation of new dinoflagellate cysts (Anderson et al. 1983, Stoecker et al. 1983). Nevertheless, we investigated this model by examining steady-state solutions. It is at least plausible that changes in the steady state would entail similar changes in the annual cycle. We can draw conclusions that apply to other systems which may be governed for a longer time by differential equation models, and the analysis of steady state can be carried further than the analysis of transient behavior.

It is possible to choose parameters so that the system has a positive, stable equilibrium. Details will be furnished by G.T.E. on request.

The question: How does omnivory influence the system? can now be expressed more precisely (bearing in mind the difference between precision and accuracy) as: How do changes in the coefficients of Eq. (3) to (5) alter the steady-state concentrations?

If *Favella* sp. increases its grazing on *Heterocapsa triquetra* (γ increases), the direct effect is to reduce the *H. triquetra* concentration; but indirect effects, brought about by increased *Favella* populations increasing the grazing pressure on *Balanion* sp., cannot be predicted on the basis of verbal descriptions alone. Within the model, if we assume $\psi = 0$ (predation by *Favella* is the only source of *Balanion* mortality) then the long-term effect of changing γ depends on the sign of $(\varepsilon_\alpha \varepsilon_\beta - \varepsilon_\gamma)$. If this term is positive (if it is more efficient for *Favella* to feed on *H. triquetra* in the form of *Balanion* than directly; a human analogy is eating grass in the form of cattle) then increasing γ decreases H*, the steady state value of H. If, however, $(\varepsilon_\alpha \varepsilon_\beta - \varepsilon_\gamma)$ is negative, so that it is more efficient for *Favella* to feed on *H. triquetra* directly (a human analogy is eating fish directly rather than as chickens that have been fed fish-meal), then increasing γ produces an increase in H*. In this instance, it might be to the long-term detriment of a population to develop defences against one of its predators.

Next, suppose that *Favella* sp. were to alter its pattern of grazing. We suppose that $\beta + \gamma$ represents the total effort that *Favella* puts into feeding, and consider the consequences of a reduction of γ together with an increase of β so that $\beta + \gamma$ remains constant. Rather than looking at the abstract equations with effects going in all directions, consider the following examples:

Example 1 ($\gamma = 3.2$, $\beta = 1.6$)

$$\frac{dH}{dt} = H(1 - H - 1.6\,B - 3.2\,F) \tag{6}$$

$$\frac{dB}{dt} = B(H - 1.6\,F - 0.5) \tag{7}$$

$$\frac{dF}{dt} = F(0.8\,B + 0.95\,H - 0.7) \tag{8}$$

Example 2 ($\gamma = 4.8$, $\beta = 0$)

$$\frac{dH}{dt} = H(1 - H - 1.6B - 4.8F) \qquad (9)$$

$$\frac{dB}{dt} = B(H - 0.5) \qquad (10)$$

$$\frac{dF}{dt} = F(0.95[1.5]H - 0.7) \qquad (11)$$

In both examples, $\beta + \gamma = 4.8$, and $\varepsilon_\alpha = 0.625$, $\varepsilon_\beta = 0.5$, $\varepsilon_\gamma = 0.2969$, so that $\varepsilon_\alpha \varepsilon_\beta - \varepsilon_\gamma > 0$. In Example 1, the steady state is $H^* = 0.55$, $B^* = 0.23$, $F^* = 0.03$. In Example 2, where *Favella* does not prey on *Balanion*, there is no steady state with all 3 species present, F outcompetes B, and the stable steady state is $H^* = 0.49$, $B^* = 0$, $F^* = 0.11$. *Balanion* can survive in the system only if *Favella* grazes partly on *Balanion* (the more efficient but less abundant path) instead of wholly on *Heterocapsa triquetra*.

CONCLUSION

Favella sp. and *Balanion* sp. have different patterns of grazing pressure on dinoflagellates. For comparable initial populations, the higher ingestion rate of *Favella* gives it a greater initial impact, but the shorter generation time of *Balanion* gives it a potentially greater long-term impact.

The gross production efficiencies (GPE) were within the range reported for marine ciliates by Heinbokel (1978), Rassoulzadegan (1982) and Verity (1984). The decrease in GPE of *Favella* sp. and *Balanion* sp. grown at high food concentrations (Table 3) is consistent with Heinbokel's (1978) and Verity's (1984) observations of declines in GPE at high food densities.

The production experiment (Fig. 6) demonstrated that the horizontal link created by *Favella* sp. predation on *Balanion* sp. could decrease secondary production. However, the magnitude of this effect on yield is determined by the relative importance of the *Heterocapsa-Favella* and *Heterocapsa-Balanion-Favella* pathways. The impact of *Favella* on *Balanion* was influenced by both *Heterocapsa* and *Balanion* densities, thus the relative importance of the horizontal links must vary.

Our experiments all demonstrated the same qualitative effects. The differences in magnitude are not surprising, because the experiments were done with batch cultures and thus all 3 organisms varied in physiological state. As would be expected, both growth and feeding rates of the ciliates changed during incubation (Table 1). In the estuary also, growth, and probably feeding rate, varies from day to day (Stoecker et al. 1983). However, an important difference between our experiments and nature is that in nature the dino-

flagellates, at least some of the time, must be growing rapidly, whereas in our experiments algal growth was limited by light and nutrients.

In our model of the *Heterocapsa-Balanion-Favella* trophic triangle, the relative gross production efficiencies of the *Heterocapsa-Favella* and the *Heterocapsa-Balanion-Favella* pathways have an important effect on ecosystem structure. Our experimental results are consistent with the alternative in our model in which it is less efficient for *Favella* sp. to eat *Heterocapsa triquetra* in the form of *Balanion* ($\varepsilon_\alpha \varepsilon_\beta - \varepsilon_\gamma$ is negative). At 15 °C and moderate *H. triquetra* densities (Table 3), *Favella* sp. and *Balanion* sp. have similar gross growth efficiencies ($\varepsilon_\beta \simeq \varepsilon_\gamma$). Because ε_α must be < 1, $\varepsilon_\alpha \varepsilon_\beta$ must be less than ε_γ. This conclusion is supported by Experiment 4, in which production of ciliate biomass was less with both ciliates present than with only one (Fig. 6). The effect on total ciliate production was greater at lower *H. triquetra* densities than at higher *H. triquetra* densities probably because the *Balanion-Favella* link was relatively more important at the lower algal density.

In a triangular food web, where trophic position is ambiguous, we have 2 examples where increasing the rate of predation on a species can increase its stable, steady-state concentration. As with all such models, restriction to 3 species entails *ad hoc* allowances for interactions with the rest of the estuarine community, with the attendant danger that our conclusions will depend as much on these allowances as on the features in which we are interested. This is a problem, not of modelling, but of trying to understand an isolated part of a large system; the model only makes the problem explicit.

Under our experimental conditions, the system does not reach a steady state and both alga and the ciliate populations ultimately decline. In the field this also is true, but perhaps for different reasons. During spring and fall dinoflagellate blooms, both physical-chemical conditions and biotic factors change. Omnivory by *Favella* sp. may not be capable of making these systems stable but may have important influences on the length of blooms. Reduced grazing pressure on *Heterocapsa triquetra* because of *Favella* predation on *Balanion* sp. may allow greater opportunity for *H. triquetra* to form cysts which can seed new blooms (Anderson et al. 1983).

Our results suggest that triangular trophic structure may have important consequences for ecosystem structure. This type of trophic structure may be common among the microplankton because many heterotrophic microplankters are about the same size as their prey and thus competitors may often also be predators and prey. These complex trophic relationships are probably important in regulating grazing pressure by mi-

crozooplankton and microzooplankton secondary production.

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