ANNALES
DE
L'INSTITUT
OCÉANOGRAPHIQUE

NOUVELLE SÉRIE

EXTRAIT

EFFECTS OF TEMPERATURE AND LIGHT ON THE FEEDING RATE OF *FAVELLA* SP. (CILIATED PROTOZOA, SUBORDER TINTINNINA)

BY

D. STOECKER and R. R. L. GUILLARD

Tome 58 — 1982 — Fascicule Supplémentaire

MASSON, ÉDITEUR
Paris New York Barcelone Milan

Ann. Inst. océanogr., Paris, 1982, **58** (S) : 309-318.

EFFECTS OF TEMPERATURE AND LIGHT ON THE FEEDING RATE OF *FAVELLA* SP. (CILIATED PROTOZOA, SUBORDER TINTINNINA) (1)

BY

D. STOECKER * and R. R. L. GUILLARD **

KEY-WORDS : Temperature.
Light.
Feeding rate.
Tintinnina.

MOTS-CLÉS : Température.
Lumière.
Taux d'ingestion.
Tintinnidiens.

Abstract

Laboratory experiments were used to determine the effects of temperature and light on the feeding rate of *Favella* sp., a coastal tintinnid which is a predator on dinoflagellates. At prey densities of 80-800 dinoflagellates ml^{-1}, clearance rates were relatively independent of temperature between 8 and 20 °C with a Q_{10} response of 1.0 to 1.1. Light intensity, prey density, and interactions between these two parameters usually had statistically significant effects on clearance rate. In culture vessels, *Favella* aggregates in areas of high prey density. We feel that the effects of light on feeding rate are due to aggregation of the prey and the subsequent aggregation of *Favella* and are thus prey density effects on a microspatial scale.

Résumé

Effets de la température et de la lumière sur le taux d'ingestion de *Favella* sp. (Protozoaires ciliés, sous-ordre des Tintinnidiens).

Des expériences au laboratoire ont permis de déterminer les effets de la température et de la lumière sur le taux d'ingestion de *Favella* sp., un tintinnidien côtier prédateur de dinoflagellés. Avec des densités de 80 à 800 dinoflagellés ml^{-1}, les taux de filtration étaient relativement indépendants de la température entre 8 et 20 °C avec un Q_{10} de 1,0 à 1,1. L'intensité de la lumière, la densité des proies, et les interactions entre ces deux paramètres avaient habituellement des effets significatifs sur le taux de filtration. Dans les récipients de culture, *Favella* se rassemble dans les zones où les proies sont très denses. Nous pensons que les effets de la lumière sur le taux de filtration sont dus à l'agrégation des proies et à l'agrégation de *Favella* qui en résulte et sont ainsi des effets de la densité des proies à une microéchelle spatiale.

(1) Contribution N° 4954 from the Woods Hole *Oceanographic Institution*. This research was supported by the *Department of Commerce NOAA Office* of Sea Grant Under Grant Nos. NA79A-D-00102 and NA80AA-D-00077.

* Woods Hole *Oceanographic Institution*, Woods Hole, Massachusetts 02543 (U.S.A.).
** *Present address :* The Bigelow Laboratory for Ocean Sciences, West Boothbay Harbor, Maine 04575 (U.S.A.).

Tintinnids (ciliated protozoa, suborder Tintinnina) are a major component of microzooplankton (BEERS & STEWART, 1967, 1969, 1971 ; JOHANSEN, 1976 ; CAPRIULO & CARPENTER, 1980) and are important consumers of nanophytoplankton (BLACKBOURN, 1974 ; JOHANSEN, 1976 ; HEINBOKEL & BEERS, 1979 ; CAPRIULO & CARPENTER, 1980 ; RASSOULZADEGAN & ETIENNE, 1981). Tintinnids, and other pelagic ciliates, by growing rapidly in response to phytoplankton blooms may act to stabilize planktonic communities (BEERS & STEWART, 1971 ; JOHANSEN, 1976 ; IBANEZ & RASSOULZADEGAN, 1977 ; CAPRIULO & CARPENTER, 1980 ; LANDRY *et al.*, 1980 ; STOECKER & ANDERSON, unpublished data).

Little information on the effect of temperature on the feeding rates of tintinnids is available, although a Q_{10} response of 2 has been assumed (HEINBOKEL & BEERS, 1979). Another assumption often applied to tintinnid feeding studies is that light has little or no influence on feeding rates. HEINBOKEL (1978 *b*), using relatively undisturbed field assemblages of tintinnids, found no significant diel periodicity in feeding behavior, which is consistent with BLACKBOURN's (1974) laboratory experiments using *Tintinnopsis parvula* and *T. cylindrica* grazing on *Pavlova* (formerly *Monochrysis*) *lutheri*. RASSOULZADEGAN (1978) found that ingestion rate was higher when *Favella ehrenbergii* was incubated in the light than in the dark with natural assemblages of particles ; however, RASSOULZADEGAN did not conclude that there was a direct relationship between ingestion rate and light.

We conducted experiments in the laboratory to determine the effects of temperature and light on the feeding rate of *Favella* sp. (1). Members of this genus often co-occur with dinoflagellate blooms (KUTT & MARTIN, 1975 ; WHITE, 1979 ; STOECKER & ANDERSON, *in prep.*). The *Favella* sp. used in the experiments described herein not only requires dinoflagellates as food (GOLD, 1970), but is a selective predator on this algal taxon (STOECKER *et al.*, 1981) although it also preys on other ciliates (STOECKER, *in prep.*) ; other members of this genus may be less selective. RASSOULZADEGAN (1978) found that *Favella ehrenbergii* consumes particles up to 33 μM in equivalent spherical diameter and thus may compete with copepods for food. Conversely, *Favella* may serve as food for macrozooplankton. In the laboratory, copepods (*Centropeges* spp.) prey on *Favella* sp. (COWLES & STOECKER, unpublished data). *Favella* is also consumed by larval fish (NMFS, 1980). At least seasonally, *Favella* sp. may play an important role in some coastal ecosystems, both as a consumer of phytoplankton, particularly dinoflagellates, and as a consumer of other ciliates, and as a food for larger zooplankton.

METHODS

Feeding studies.

Five strains of *Favella* sp. isolated from coastal waters *(Table I)* were used in the feeding experiments. We used tintinnids from actively growing, non-cyst forming cultures in the feeding experiments. It was necessary to use different strains at different times because cultures of a particular strain did not always meet these criteria and because we lost several strains used in the early experiments. We used the procedures described in STOECKER *et al.* (1981) to isolate and culture *Favella* except that aged, diluted Sargasso seawater (5 parts seawater to 1 part distilled water) was used to make the tintinnid culture medium SWT, and the dinoflagellate culture called Strain Gymno, recently identified as *Heterocapsa pygmaea* by LOEBLICH *et al.* (1981), was the sole algal food for routine maintenance. For the feeding experiments, in addition to *Heterocapsa pygmaea,* the dinoflagellates used included *Scrippsiella trochoidea* (Stein) Loeblich III (Strain Peri), *Heterocapsa triquerta* (Ehr.) Stein (stain A 984) ; *Gonyaulax tamarensis* Lebour (Isolate 469, originally from A.R. Loeblich III) ; and *Thoracosphaera heimi* (Lohm) Kampt (Strain A 603), which has recently been shown to be a dinoflagellate rather than a coccolithophore (TANGEN *et al., unpublished*). *Thora-*

(1) Oral lorica diameter of our cultured individuals and the natural populations from which they were isolated is 72-75 μm. Specimens of this species have been referred to as *F. ehrenbergii* by STOECKER *et al.* (1981), following descriptions by GOLD & MORALES (1975), but these are consistently smaller than *F. ehrenbergii* (Clap and Lachm.) Jörg. described from European coastal waters (LAVAL-PEUTO & RASSOULZADEGAN, personal communications).

TABLE I. — Favella *Isolates.*

TABLEAU I. — *Origines des souches de* Favella.

Strain	Date isolated	Location	Surface water temperature (°C)
BHFav	10- 3-79	Boston Harbor, MA	15
PPFav	5- 1-80	Perch Pond, Falmouth, MA	11
MPFav	5-27-80	Mill Pond, Chatham, MA	17
SPFav	5-27-80	Salt Pond, Eastham, MA	17
NPP	10- 3-80	Perch Pond, Falmouth, MA	11

cosphaera, although a dinoflagellate, is non-motile except for a short time immediately after the onset of the light period. All were cultured as previously described (STOECKER *et al.,* 1981). We maintained our stock cultures, with the exception of *G. tamarensis* which was grown at 15 °C, at 20 ° because *Favella* and the dinoflagellates we used in the feeding experiments grew well at this temperature.

All experiments, except for the *Favella distribution* experiment *(Fig. 1),* were run in duplicate or triplicate in 5 ml of SWT in 25 × 150 mm Pyrex glass culture tubes incubated with 25 tintinnids, without prior acclimatization, for 7 to 10 h at 8, 15, or 20 °C. These experimental conditions were used for several reasons. *Favella* sp. occurs in Massachusetts during the spring and fall when water temperatures are changing rapidly. The highest *Favella* densities (5 *Favella* ml^{-1} have been observed at certain depths ; lower concentrations are observed in whole water column samples) occur at temperatures between 15 and 20 °C although *Favella* has also been observed at higher (23°) and lower (11°) temperatures (STOECKER *et al.,* in prep.). In these shallow waters, the temperature differential between the surface and bottom can be as great as 5 °C ; *Favella* appear to cross these vertical thermal gradients (STOECKER *et al.,* in prep.). We believe that *Favella* is exposed to wide and rapid changes in temperature. Thus, except for 8 °C, the temperatures used in this study are typical of those to which *Favella* is exposed to *in situ.*

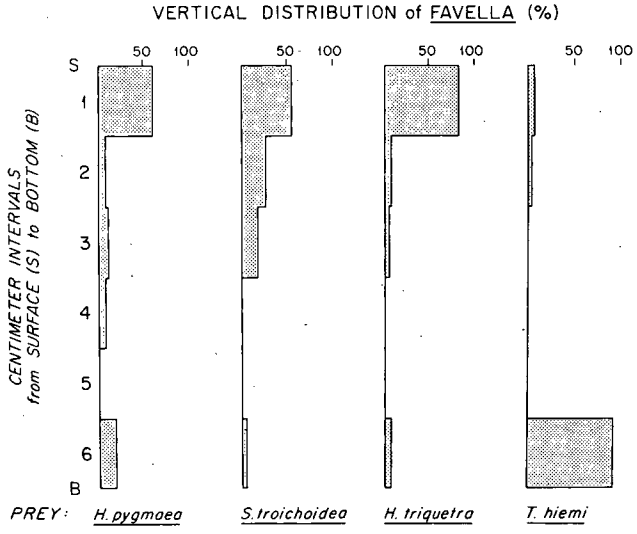

FIG. 1. — *Vertical distribution of* Favella *in tissue culture flasks in the presence of four dinoflagellates in the light. (Interval 1 is at surface, interval 6 is at bottom.)*

FIG. 1. — *Distribution verticale de* Favella *dans des flacons pour culture de tissus en présence de quatre dinoflagellés à la lumière. (Intervalle 1 en surface, intervalle 6 au fond.)*

The culture chambers were illuminated by cool-white *(Sylvania Co.)* fluorescent lighting and light intensities were determined using a QSL-100 irradiance meter (Biospherical Instruments, Inc.). The light intensities employed (53 to 230 μE m^{-2} sec^{-1}) are similar to those at the depths (3 to 4.5 m) at which we found the greatest density of *Favella* in one field study although subsequently we have also observed *Favella* nearer the surface during the day (STOECKER *et al.,* in prep.). To keep tubes in the dark we wrapped them in aluminium foil.

With the exception of *T. heimi,* the dinoflagellate species used in the feeding experiments are ones which co-occur with *Favella* sp. in Massachusetts estuaries. With the exception of one experiment with *T. heimi* (Experiment No. 5, *Table III*), the experimental dinoflagellate densities are within the upper range of dinoflagellate densities which have been observed in the estuaries where we find *Favella* sp. After incubation, the contents of the tubes were fixed with Lugol's solution, the algal densities were determined by counting 200 to 300 cells using appropriate counting chambers for the cell sizes and densities (GUILLARD, 1973), and

all tintinnids were counted by removal with a micropipette using a dissecting microscope.

FROST's equations (1972) were used to calculate the average algal cell concentration (« C »), volume swept clear (F), and ingestion rate (I) for the feeding experiments. In all experiments for which data are presented, the number of tintinnids at the end of the experiment was about the same as the number initially added, therefore, use of exponential equations to calculate the average number of tintinnids (HEINBOKEL, 1978 *a*) was not necessary. Experiments in which tintinnid survival was poor are not included.

The Q_{10} for F was calculated as :

$$Q_{10} = \frac{F_2}{F_1}^{\frac{10}{T_2 - T_1}}$$

where F_1 and F_2 are the volumes swept clear at temperatures T_1 and T_2 (SCHMIDT-NIELSEN, 1975).

Observations on microdistribution.

We used disposable 50 ml Falcon tissue culture flasks to observe the distribution of *Favella* in the presence of different dinoflagellates. The flat-sided tissue culture flasks (which for tissue culture are used with the long axis horizontal) were stood on end and marked at 1 cm intervals for 6 cm. Forty-five ml of SWT (which fills the flasks to 6 cm) containing 10^4 cells ml^{-1} *H. pygmaea* or *Thoracosphaera,* 10^3 cells ml^{-1} *H. triquetra,* or 5×10^2 cells ml^{-1} of *Scrippsiella* was put in each flask, and, after the motile dinoflagellates had resumed swimming, 100 *Favella* (Strain NPP) were added. The flasks were then incubated for 2 h at 20 °C in the light. We used a 10 X hand lens 4 cm in diameter to observe the *Favella* and count the number of individuals in each centimeter interval ; about 70 percent of the *Favella* added were counted using this technique.

RESULTS

The feeding rates at 8, 15, and 20 °C in light and dark using several prey species are shown in Table II. There was little variation in clearance or ingestion rates between replicates. Our first Q_{10} experiment was run in the light and we observed lower clearance and ingestion rates at 15 °C than at the bracketing temperatures *(Table II).* This anomalous result led us to check the light intensities in the incubators used for this feeding experiment and we found that the light in the 15 ° incubator was lower than in the other two incubators *(Table II).* We then ran a similar Q_{10} experiment in the dark and found that under these conditions the 15 °C feeding rates were not lower than the rates at 8 and 20 °C. These results made us suspect that light alone may have an effect on *Favella's* interaction with its prey, however, an interaction between light and temperature can not be ruled out by these results. If the anomalous result at 15 ° in the light is ignored, the Q_{10} response between 8 ° and 20 °C for clearance rate is between 1.0 and 1.1 *(Table II).*

In experiment 3 *(Table III),* we used Two-Way Analyses of Variance (SOKAL & ROHLF, 1969) to test for significance of the effects of dinoflagellate density and illumination (light vs. dark) on clearance rates. In the experiment with *Heterocapsa triquetra* as prey, the effects were non-significant at the 5 % level (Fs for subgroups = 5.6045). When *Gonyaulax tamarensis* was used as prey, the effect of concentration was non-significant (Fs = 0.2339) but clearance rates were higher in the light than dark (Fs = 41.8097 ; $p < 0.005$). Interaction between the two factors was non-significant (Fs = 3.4065). With *Scrippsiella trochoidea,* clearance rates were higher at the lower algal cell concentrations (Fs = 122.6449; $p < 0.001$) and in the light (Fs = 141.8245; $p < 0.001$). Interaction between the two factors affected clearance rates (Fs = 23.0627 ; $p < 0.01$).

The experiments with *Thoracosphaera heimi* (numbers 4 and 5, *Table III*) were analysed using a Single Classification Analysis of Variance (SOKAL & ROHLF, 1969) to test for the effects of light on clearance rate. The differences were not statistically significant at the 5 % level in experiments 4 (Fs = 1.9974) or 5 (Fs = 0.0202).

The predation rates of *Favella* were compared at

TABLE II. — *Feeding Rates of* Favella [a] *at 3 Temperatures.*

TABLEAU II. — *Taux d'ingestion de* Favella *à 3 températures.*

Exp. No.	Illumination	Dinoflagellate	Temperature (°C)	Mean ± S.D.			Q_{10}
				$< C >$	F	I	
1	Light [b]	*H. triquetra*	8	795 ± 21	22.2 ±1.5	16.9 ± 1.2	1.10
			15	759 ± 28	19.3 ± 0.9	14.6 ± 0.5	
			20	779 ± 19	24.9 ± 0.7	19.4 ± 0.7	
		G. tamarensis	8	410 ± 6	17.4 ± 0.8	7.1 ± 0.3	1.11
			15	411 ± 6	14.0 ± 1.4	5.8 ± 0.6	
			20	413 ± 6	19.7 ± 1.3	8.2 ± 0.6	
		S. trochoidea	8	83 ± 3	14.1 ± 1.7	1.2 ± 0.2	1.09
			15	82 ± 9	12.7 ± 3.8	1.0 ± 0.2	
			20	82 ± 3	15.7 ± 2.5	1.3 ± 0.2	
2	Dark	*H. triquetra*	8	210 ± 0	3.5 ± 0.2	0.7 ± 0.0	1.00
			15	210 ± 1	3.4 ± 0.0	0.7 ± 0.0	
			20	200 ± 6	3.3 ± 0.6	0.7 ± 0.1	
		G. tamarensis	8	108 ± 4	8.8 ± 0.5	0.9 ± 0.0	1.09
			15	107 ± 3	8.9 ± 0.8	1.0 ± 0.1	
			20	108 ± 1	8.9 ± 0.2	1.0 ± 0.0	

(a) Strain BHFav; 3 replicates in Exp. 1, 2 replicates in Exp. 2.
(b) Approximately 200 $\mu E\ m^{-1}$ at 8 and 20°, 40-100 $\mu E\ m^{-2}\ sec^{-1}$ at 15 °C.
S.D. = Standard deviation.
$< C >$ = Av. cell algal concentration (cells ml^{-1}).
F = Volume swept clear (μl tintinnid^{-1} h^{-1}).
I = Ingestion rate (cells eaten tintinnid^{-1} h^{-1}).
Q_{10} = Q_{10} for F calculated from 8 to 20 °C.

TABLE III. — *Feeding rates of* Favella [a] *in light and dark.*

TABLEAU III. — *Taux d'ingestion de* Favella *à la lumière et à l'obscurité.*

Exp. No.	Illumination	Dinoflagellate	C_i	Mean ± S.D. [b]		
				$< C >$	F	I
3	Light	*H. triquetra*	500	398 ± 9	22.8 ± 1.7	9.1 ± 0.4
	Dark		500	544 ± 7	7.7 ± 0.6	4.2 ± 0.4
	Light		100	171 ± 36	8.2 ± 8.2	1.3 ± 1.1
	Dark		100	155 ± 3	9.0 ± 2.3	1.4 ± 0.4
	Light	*G. tamarensis*	500	422 ± 3	24.0 ± 1.2	10.1 ± 0.6
	Dark		500	674 ± 4	7.7 ± 1.4	5.2 ± 1.0
	Light		100	150 ± 16	21.3 ± 3.3	3.2 ± 0.2
	Dark		100	189 ± 9	12.3 ± 4.0	2.3 ± 0.7
	Light	*S. trochoidea*	500	550 ± 18	14.1 ± 1.7	7.7 ± 0.7
	Dark		500	555 ± 21	7.5 ± 1.3	4.1 ± 0.6
	Light		100	134 ± 7	28.8 ± 1.5	3.9 ± 0.0
	Dark		100	146 ± 5	13.3 ± 0.2	2.0 ± 0.1
4	Light	*T. heimi*	803	705 ± 11	3.1 ± 0.4	2.2 ± 0.2
	Dark		803	721 ± 11	2.6 ± 0.4	1.9 ± 0.3
5	Light	*T. heimi*	8 460	7 694 ± 317	0.9 ± 0.4	6.7 ± 2.7
	Dark		8 460	7 653 ± 243	0.9 ± 0.3	6.8 ± 2.1

(a) Exp. 3 : Strain PPFav, 15 °C, 100 $\mu E\ m^{-2}\ sec^{-1}$ in light;
Exp. 4 : Strain NPP, 20 °C, 215 $\mu E\ m^{-2}\ sec^{-1}$ in light;
Exp. 5 : Strain SPFav, otherwise same as Exp. 4.
(b) Two replicates.
S.D. = Standard deviation.
C_i = Nominal cell concentration at time t_i (cells ml^{-1}).
$< C >$ = Av. algal cell concentration (cells ml^{-1}).
F = Volume swept clear (μl tintinnid^{-1} h^{-1}).
I = Ingestion rate (cells eaten tintinnid^{-1} h^{-1}).

TABLE IV. — *Feeding rates of* Favella [a] *at different light intensities.*

TABLEAU IV. — *Taux d'ingestion de* Favella *à différentes intensités lumineuses.*

Dinoflagellates	Light intensity ($\mu Em^{-2} sec^{-1}$)	Mean ± S.D.		
		< C >	F	I
G. tamarensis	0	371 ± 17	4.1 ± 1.0	2.7 ± 0.1
	53	338 ± 2	9.1 ± 1.4	2.2 ± 0.2
	108	337 ± 2	6.6 ± 0.8	3.0 ± 0.5
	208	315 ± 3	8.5 ± 0.4	1.5 ± 0.3
S. trochoidea	0	756 ± 11	4.7 ± 0.3	3.6 ± 0.2
	53	695 ± 13	8.1 ± 0.7	5.6 ± 0.4
	108	726 ± 26	5.8 ± 1.2	4.2 ± 0.8
	208	679 ± 8	7.6 ± 1.3	5.2 ± 0.8

[a] Strain MP-Fav; 15 °C, 2 replicates.
S.D. = Standard deviation.
< C > = Av. algal cell concentration.
F = Volume swept clear (μl tintinnid^{-1} h^{-1}).
I = Ingestion rate (cells eaten tintinnid^{-1} h^{-1}).

four light intensities using *Gonyaulax tamarensis* and *S. trochoidea* as prey *(Table IV)*. Data were analysed using a Two-Way Analysis of Variance with the Least Significant Difference (LSD) statistic used for *a priori* comparisons among means (SOKAL & ROHLF, 1969). The combined effect of algal species and density was insignificant at the 5 % level (Fs = 1.1903) but light intensity did have a significant effect (Fs = 15.6365 ; $p < 0.005$). At the 5 % significance level (LSD = 2.2193), clearance rates of cultures exposed to dim light (53 μE m^{-2} sec^{-1}) were higher than those in the dark or exposed to 108 μE m^{-2} sec^{-1}.

We observed the spatial distribution of *Favella* incubated in tissue culture flasks in light (230 μE m^{-2} sec^{-1}) with different dinoflagellates. *Favella*'s distribution was influenced by that of the dinoflagellate prey *(Fig. 1)*. With the motile dinoflagellates *Heterocapsa pygmaea, Heterocapsa triquetra,* and *Scrippsiella,* over 50 % of the *Favella* counted were found in the top centimeter where the dinoflagellates were swarming ; many *Favella* were observed feeding with the oral end oriented towards the air-water interface. However, in the flask containing *Thoracosphaera,* which lies on the bottom, over 50 % of the *Favella* counted were in the bottom centimeter interval ; most of these were feeding with the oral end oriented toward the bottom.

DISCUSSION

In our Q_{10} experiments *(Table II)*, clearance and ingestion rates were little influenced by temperature over a temperature range (8-20 °C) bracketing the temperatures at which we collected *Favella (Table I)*. This is consistent with BLACKBOURN's (1974) laboratory experiments using *Tintinnopsis subacuta* and *T. parvula.* However, we do not know whether filtering or food particle handling was the rate limiting step in our feeding experiments.

In laboratory experiments using algal monocultures as food, ingestion rates of tintinnids typically increase with increasing food concentrations until a maximum rate is obtained (HEINBOKEL, 1978 *a*). Likewise, RASSOULZADEGAN & ETIENNE (1981), using natural assemblages of particles, found that the ingestion rate of the tintinnid *Stenosemella ventricosa* (Clap and Lachm) Jorg. feeding on particles beween 1.3 and 27 μm seemed to be a function of particle concentration. Clearance rate (volume swept clear tintinnid^{-1} h^{-1}) could be expected to remain relatively constant with increasing food concentrations as long as the food concentration was below that at which the maximum ingestion rate is obtained ; at this food concentration ingestion

and clearance rates are probably limited by the time it takes a food particle to be phagocytized (FENCHEL, 1980) rather than limited by the filtering rate.

It is possible that temperature changes influence the filtration rate differently than food particle handling time. Therefore the Q_{10} response for clearance rate could depend on food concentration, because food concentration should control which step is rate limiting. In the experiments reported herein, prey densities generally were in the upper range of those *Favella* sp. would encounter *in situ*, it is possible that *Favella* would exhibit a more typical Q_{10} response for feeding at lower prey densities.

In the laboratory, light had a positive, statistically significant effect on clearance rate of *Favella* when motile dinoflagellates were prey except in the experiment with *Heterocapsa triquetra (Tables III* and *IV)*. However, we believe that light may have had a positive effect on feeding in the *Heterocapsa* experiment but that the lack of statistical significance could be due to the large amount of variation in the light 100 treatment group. These results are consistent with RASSOULZADEGAN's (1978) observation that predation by *Favella ehrenbergii* on natural particle assemblages was greater in bottles incubated in the light than in the dark. However, these results with *Favella* species are different from results obtained with other tintinnids. BLACKBOURN (1974), using *T. parvula* and *T. cylindrica*, found no statistically significant difference between feeding rates in dim light and in the dark. HEINBOKEL (1978 *b*) found no pronounced diel periodicity in feeding behavior of total assemblages of field collected tintinnids (which did not contain *Favella*) which could be separated from the variability in the individual grazing estimates.

With a non-motile prey, *Thoracosphaera heimi*, there was no pronounced, consistent difference between light and dark clearance rates *(Table III)*. However, because of the low clearance rates with *T. heimi* as prey, the results should be interpreted with caution.

Differences in the behavior of the dinoflagellate prey in the light and dark, rather than solely light effects on the tintinnids themselves, may be responsible for the observed differences in feeding rates. The simplest explanation is that under certain light conditions the distribution of dinoflagellates in the culture vessels is clumped (i.e. swarms occur) and that this can increase the predation rate of *Favella* on the dinoflagellate cells. This interpretation is consistent with the phototactic response of dinoflagellates and their concentration at particular depths under certain light conditions (EPPLEY *et al.*, 1968), with the ability of *Favella* to aggregate in areas of high prey density *(Fig. 1)*, and with the dependence of ingestion rates on food concentrations (HEINBOKEL, 1978 *a* ; FENCHEL, 1980 ; RASSOULZADEGAN & ETIENNE, 1981 ; and *Table III*). This interpretation suggests that other factors that can effect the behavior of dinoflagellates such as nutrient availability (CULLEN & HORRIGAN, 1981) and temperature gradients (KAMYKOWSKI, 1981), can also affect their susceptibility to tintinnid predation.

From our observations we do not know if *Favella* is actively attracted to high prey densities or if *Favella* accumulates in areas of high prey density because of changes in its swimming behavior upon entering a prey patch. The non-random distribution of *Favella* in the culture vessels is consistent with TAYLOR & BERGER's (1980) observations of the patchiness on a microspatial scale of ciliates in freshwater ponds and with the vertical distributions of *Favella* and dinoflagellates in shallow estuaries (STOECKER *et al.*, in prep.). Tintinnids and other microzooplankters may often be exposed to very different prey concentrations than those estimated by using standard sampling techniques.

Many factors have to be taken into account to extrapolate from laboratory experiments on feeding rates to field situations. Even from shipboard experiments, such as those of CARPRIULO & CARPENTER (1980), it may be difficult to estimate *in situ* grazing or predation rates because changes in illumination or containment iself may change the microspatial distribution of predators and their prey as well as altering physical and chemical parameters (ROMAN & RUBLEE, 1980) all of which can alter clearance and ingestion rates.

ACKNOWLEDGEMENTS. — We thank D. M. ANDERSON for a culture of *Gonyaulax tamarensis* (isolate 429) and L. BRAND for a culture of *Thoracosphaera heimi* (strain A603), L. BRAND, T. COWLES, J. HEINBOKEL, F. RASSOULZADEGAN, and an anonymous reviewer for their comments on the manuscript, and R. M. KAVEE and M. NORMAN for volunteer technical assistance.

BIBLIOGRAPHICAL REFERENCES

BEERS, J. R., STEWART, G. L., 1967. — Microzooplankton in the euphotic zone at five locations across the California current. *J. Fish. Res. Bd. Can.*, **24** : 2053-2068.

BEERS, J. R., STEWART, G. L., 1969. — Microzooplankton and its abundance relative to the larger zooplankton and other seston components. *Mar. Biol.*, **4** : 182-189.

BEERS, J. R., STEWART, G. L., 1971. — Microzooplankters in the plankton communities of the upper waters of the eastern tropical Pacific. *Deep Sea Res.*, **18** : 861-883.

BLACKBOURN, D. J., 1974. — The feeding biology of tintinnid protozoa and some other nearshore microzooplankton. *Ph. D. Thesis,* The University of British Columbia.

CAPRIULO, G. M., CARPENTER, E. J., 1980. — Grazing by 35 to 202 µm microzooplankton in Long Island Sound. *Mar. Biol.*, **56** : 219-326.

CULLEN, J. J., HORRIGAN, S. G., 1981. — Effects of nitrate on the diurnal vertical migration, carbon to nitrogen ratio, and the photosynthetic capacity of the dinoflagellate *Gymnodinium splendens*. *Mar. Biol.*, **62** : 81-89.

EPPLEY, R. W., HOLM-HANSEN, O., STRICKLAND, J. D. H., 1968. — Some observations on the vertical migration of dinoflagellates. *J. Phycol.*, **4** : 333-340.

FENCHEL, T., 1980. — Suspension feeding in ciliated protozoa : functional response and particle size selection. *Microb. Ecol.*, **6** : 1-11.

FROST, B. W., 1972. — Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacifecus*. *Limnol. Oceanogr.*, **17** : 805-815.

GOLD, K., 1970. — Cultivation of marine ciliates (Tintinnida) and heterotrophic flagellates. *Helogander Wiss. Meeresunters,* **20** : 264-271.

GOLD, K., MORALES, E. A., 1975. — Seasonal changes in lorica sizes and the species of Tintinnida in the New York Bight. *J. Protozool.*, **22** : 520-528.

GUILLARD, R. R. L., 1973. — Chapter 19 : Division Rates, p. 289-311, *in :* J. R Stein, ed., *Handbook of Phycological Methods, Culture Methods and Growth Measurements. Cambridge University Press,* Cambridge, England.

HEINBOKEL, J. F., 1978 *a*. — Studies on the functional role of tintinnids in the Southern California Bight. I. Grazing and growth rates in laboratory cultures. *Mar. Biol.*, **47** : 177-189.

HEINBOKEL, J. F., 1978 *b*. — Studies on the functional role of tintinnids in the Southern California Bight. II. Grazing rates of field populations. *Mar. Biol.*, **47** : 191-197.

HEINBOKEL, J. F., BEERS, J. R., 1979. — Studies on the functional role of tintinnids in the Southern California Bight. III. Grazing impact of natural assemblages. *Mar. Biol.*, **52** : 23-32.

IBANEZ, F., RASSOULZADEGAN, F., 1977. — A study of the relationships between pelagic ciliates (Oligotrichina) and planktonic nanoflagellates of the neritic ecosystem of the Bay of Villefranche-sur-Mer. Analysis of chronological series. *Ann. Inst. Oceanogr. Paris,* **53** : 23-32.

JOHANSEN, P. L., 1966. — A study of tintinnids and other protozoa in eastern Canadian waters with special reference to tintinnid feeding, nitrogen excretion, and reproduction rates. *Ph. D. Thesis,* Dalhousie Univ.

KAMYKOWSKI, D., 1981. — Laboratory experiments on the diurnal vertical migration of marine dinoflagellates through temperature gradients. *Mar. Biol.*, **62** : 56-64.

KUTT, E. C., MARTIN, D. F., 1975. — Report on a biochemical red tide repressive agent. *Environ. Letters,* **9** : 195-205.

LANDRY, M. R., HASSETT, R. P., ZAFAR, K., 1980. — Implications of grazing by marine microzooplankton. Abstract of paper presented at ASLO, Third Winter Meeting, Seattle, WA.

LAVAL-PEUTO, M., 1977. — Reconstruction d'une lorica de forme *Coxliella* par le trophonte nu de *Favella ehrenbergii* (Ciliata, Tintinnia). *C. R. Acad. Sci. Paris,* Serie D, **284** : 547-550.

LOEBLICH, A. R. III, SCHMIDT, R. J., SHERLEY, J. L., 1981. — Scanning electron microscopy of *Heterocapsa pygmaea* sp. nov., and evidence for polyploidy as a speciation mechanism in dinoflagellates. *J. Plankton Res.*, **3** : 67-79.

NATIONAL MARINE FISHERIES SERVICE, U.S., 1980. — Relationship between contaminants and food web dynamics in the Gulf of Mexico. Annual Progress report for FY 1980 submitted to OMPA, NOAA from the Division of Estuarine and Coastal Ecology, NMFS, Southeast Fisheries Center, *Beaufort Laboratory,* Beaufort, N.C., USA.

RASSOULZADEGAN, F., ETIENNE, M., 1981. — Grazing rate of the tintinnid *Stenosemella ventricosa* (Clap. and Lachm.) Jorg. on the spectrum of the naturally occurring particulate matter from a Mediterranean neritic area. *Limnol. Oceanogr.*, **26** : 258-270.

RASSOULZADEGAN, F., 1978. — Dimensions et taux d'ingestion de particules consommées par un tintinnide : *Favella ehrenbergii* (Clap. et Lachm.) Jorg., Cilié pélagique marin. *Ann. Inst. Océanogr.*, Paris, **54** : 17-24.

ROMAN, M. R., RUBLEE, P. A., 1980. — Containment effects in copepod grazing experiments : a plea to end the black box approach. *Limnol. Oceanogr.*, **25** : 982-990.

SCHMIDT-NIELSEN, K., 1975. — Animal physiology, adaptation and environment. *Cambridge University Press,* London, 699 p.

SOKAL, R. R., ROHLF, F. J., 1969. — Biometry. *W. H. Freeman and Co.,* San Francisco, 776 p.

STOECKER, D., GUILLARD, R. R. L., KAVEE, R. M., 1981. — Selective predation by *Favella ehrenbergii* (Tintinnia) on and among dinoflagellates. *Biol. Bull.*, **160** : 136-145.

STOECKER, D., ANDERSON, D. M. — Relationships between dinoflagellates and *Favella* sp. (ciliated protozoa, suborder Tintinnia). *In prep.*

TANGEN, K., BRAND, L. E., BLACKWELDER, P. L., GUILLARD, R. R. L. — *Thoracosphaera heinii* (Lohmann) Kamptner is a dinoflagellate : observations on its morphology and life cycles. *In prep.*

TAYLOR, W. D., BERGER, J., 1980. — Microspatial heterogeneity in the distribution of ciliates in a small pond *Microb. Ecol.*, **6** : 27-34.

WHITE, A. W., 1979. — Dinoflagellate toxins in phytoplankton and zooplankton fractions during a bloom of *Gonyaulax excavata. In :* D. L. Taylor and H. H. Seliger (eds.). *Toxic dinoflagellate blooms,* pp. 381-384, *Elsevier / North Holland,* New York.

(*Manuscript* received *15 September 1981,* accepted *3 April 1982.*)