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Fine scale spatial correlations between planktonic ciliates and dinoflagellates[1]

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Abstract. Fine scale spatial distributions of planktonic ciliates which prey on dinoflagellates were investigated in a small estuary. The horizontal distributions of *Favella* sp., *Balanion* sp. and *Strobilidium* sp. were positively correlated with the patchy distribution of dinoflagellates. The vertical distribution of *Favella* was positively correlated with the distribution of dinoflagellates. Throughout the diel cycle, the vertical distribution of *Favella* was similar to the vertical distribution of dinoflagellates. We speculate that behavioral responses are responsible for the association of ciliates with their prey in the water column. Vertically coincident ciliate and algal populations should respond similarly to turbulent mixing and water displacement caused by wind stress, bathymetry, or frontal convergences. This would result in horizontal patches in which the ciliates and algae remain associated. This fine scale spatial coupling between ciliates and their prey should result in higher ciliate growth rates and greater impact of ciliate grazing on phytoplankton populations than would be predicted from average ciliate or algal densities. Coincident patches of algae and ciliates may also provide higher food concentrations for larger grazers which can use both resources.

Introduction

Fine scale patchiness (m to 100's of m) in the distribution of plankton is widely recognized (reviewed in Haury *et al.*, 1978; Reid, 1982). Phytophagous planktonic ciliates are an important component of the plankton (Beers and Stewart, 1967, 1969, 1971; Blackbourn, 1974; Heinbokel and Beers, 1979; Capriulo and Carpenter, 1983) with generation times (h to days) and rates of movement (a few m h^{-1}) on the same scales as the phytoflagellates on which they prey. We thus would expect positive correlations between ciliate abundance and that of their algal prey. This is in contrast to macrozooplankton populations which, because of their longer development times and faster swimming speeds, are often poorly or negatively correlated with phytoplankton abundance (Steeman Nielsen, 1937; Bainbridge, 1953; Mackas and Boyd, 1979).

Although the fine scale distribution of tintinnids and oligotrichs has been investigated (Johansen, 1976; Kuwahara *et al.*, 1975; Kume, 1979; Rassoulzadegan and Gostan, 1976) it is not possible to determine from these studies if the distribution of a particular ciliate was correlated with that of its food, because neither the feeding habits of specific ciliates nor the species composition of the phytoplankton were known. Some ciliates have very specific algal food requirements (Stoecker *et al.*, 1981). Thus, all algae of the proper size may not be suitable foods.

In order to test the hypothesis that the fine scale distribution of planktonic

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ciliates is positively correlated with that of their algal prey, we checked the horizontal and vertical distributions of these ciliates and their dinoflagellate prey in a small estuary. In this estuary (Perch Pond, Falmouth, MA), the large tintinnid, *Favella* sp. and the naked ciliates *Balanion* sp. and *Strobilidium* sp. commonly co-occur with dinoflagellate blooms (Stoecker *et al.*, 1983). *Favella* is a selective predator on dinoflagellates (Stoecker *et al.*, 1981), but it also consumes smaller ciliates (Stoecker and Evans, in preparation). Not all dinoflagellates are suitable prey, since *Favella* can only ingest particles less than ~45% of its oral diameter (Spittler, 1973), (i.e., <34 μm in diameter; Stoecker *et al.*, 1981). *Balanion* consumes only relatively small dinoflagellates in culture, while *Strobilidium* requires a mixture of a small dinoflagellate (such as *Heterocapsa triquetra*), and a flagellate from another taxon as food (Stoecker, unpublished data).

Methods

Sampling

Horizontal and diel vertical distribution studies were made during separate dinoflagellate blooms in Perch Pond, a small tidal estuary. Vertical distributions were determined twice (Study No. 1, September 28 and 29 and Study No. 2, October 5 and 6, 1981) at station A in Perch Pond (Figure 1). Sampling commenced at 0800 h and continued at 4 h intervals, for 28 h. A hand vacuum pump (Mityvac) attached to a flask and a length of weighted tubing was used to collect 2-l samples at one meter intervals from the surface (maximum depth 4 m). Water temperature was measured in each sample. Subsamples were saved for salinity determinations (250 ml, using an Autosal 8400) and for dinoflagellate and ciliate counts. One liter subsamples were preserved with formalin, concentrated using a 30 μm mesh, and the *Favella* counted using a dissecting microscope. Ciliates other than *Favella* and dinoflagellates were counted using 25 ml top (sedimentation) cylinders and an inverted microscope (Hasle, 1978). The ciliates were counted over the entire chamber, but dinoflagellates were counted along several diameter transects for each sample.

A QSL 200 irradiance meter and submersible probe (Biospherical Instruments, Inc.) were used to make light measurements at each depth. The meter was not working properly during the second diel study so light measurements are not available.

On April 19, 1982, between 1300 and 1430 h, samples were taken for the horizontal study at 17 locations spaced ~50 m apart (Figure 1). Integrated water samples were collected using a rigid PVC pipe which was lowered to the bottom and sealed to capture the water column. Samples were preserved with 1.0% buffered formaldehyde.

An inverted microscope with 100 ml capacity top cylinders was used to examine samples from the horizontal study. Ciliates were counted over the entire chamber. Dinoflagellates were counted in crossed diameter transects, which were equivalent to 2.3 ml of each sample.

Statistical analyses

Multiple correlation analyses were used to determine if parameters were associated. When phytoplankton or ciliate concentrations were zero, the data were coded by adding 0.5 to each datum. A square root transformation was used to make the variance of count data independent of the means (Sokal and Rohlf, 1981). For the diel studies, each sample was treated as a data set, regardless of time or depth, in testing for association between ciliate abundance and dinoflagellate abundance, temperature, or salinity. For the horizontal distribution study, the coefficient of dispersion (C.D.), which is the variance divided by the mean (Sokal and Rohlf, 1981), was calculated for individual species based on counts of 100 ml sub-samples for ciliates and based on counts of transects which were equivalent to 2.3 ml for dinoflagellates.

Observations

Horizontal distribution

Three planktonic ciliates >30 μm in diameter were abundant, *Favella* sp., *Balanion sp., and Strobilidium* sp. on April 19, 1982 (Table I). *Favella* was abundant, with an average density for the water column of over 1000 cells l^{-1}. *Balanion* and *Strobilidium* were less abundant, with average densities of 46 and 152 l^{-1}, respectively. Calculated C.D's for all three ciliates were much greater than 1 indicating that the distributions were clumped.

The dominant dinoflagellates (in order of abundance) were *Gonyaulax spinifera, Gonyaulax longicornu, Scrippsiella troichoidea, Heterocapsa triquetra*, and *Dinophysis acuminata*. Unidentified dinoflagellates comprised ~5% of the total

Table I. Horizontal fine scale distribution study, April 9, 1982, 1400 h

	Approximate size (μm)	No. of cells l^{-1} Mean ± S.D.	C.D.[a]
Ciliates:			
Favella sp.	65 – 75 x 100 – 200	1375 ± 1340	122.77
Balanion sp.	32 x 34	46 ± 56	6.51
Strobilidium sp.	40 – 50	152 ± 153	15.42
Dinoflagellates			
Heterocapsa triquetra	16 x 22	8229 ± 5784	3.81
Scrippsiella troichoidea	23 x 30	11 047 ± 7263	4.49
Dinophysis acuminata	20 – 32 x 46 – 49	5055 ± 4061	2.90
Gonyaulax spinifera	30 x 50	87 341 ± 113 911	87.33
Gonyaulax longicornu	40 x 50	11 097 ± 9580	7.79
Total dinoflagellates		128 157 ± 129 730	123.55

[a] C.D., coefficient of dispersion.

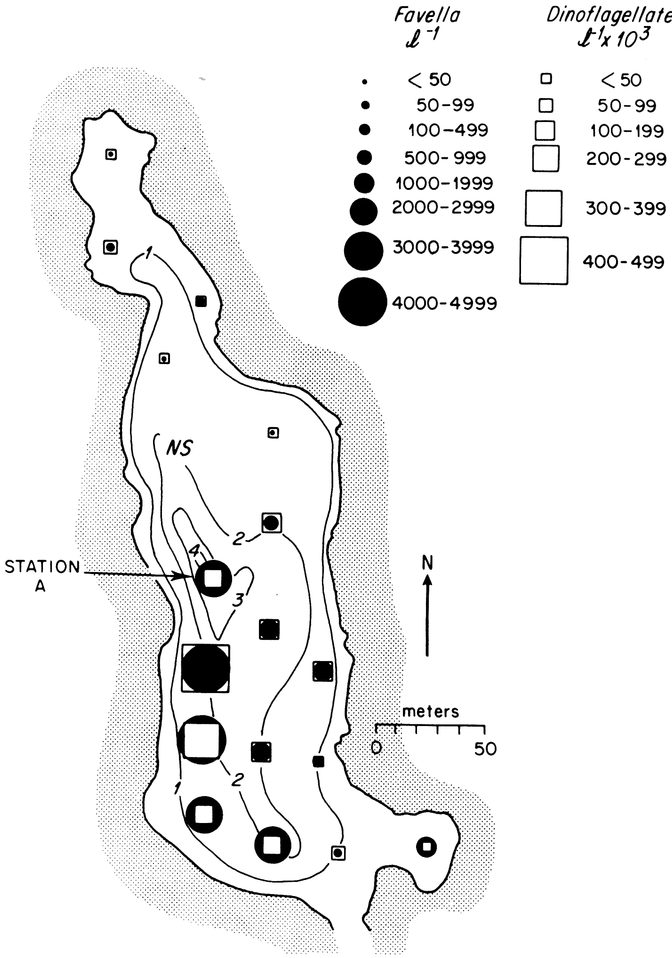


Fig. 1. Horizonal distribution of *Favella* and dinoflagellates, Perch Pond, May 19, 1982. Depth contours are in meters.

dinoflagellate density, which was $\sim 128 \times 10^3$ cells l^{-1} (Table I). Of the five common dinoflagellates, only two, *H. triquetra* and *S. trochoidea*, were < 34 μm in diameter (Table I). The calculated C.D.'s for all dinoflagellates were much greater than 1, again indicative of aggregation.

Both dinoflagellates and ciliates were most abundant in the deeper, south central portions of Perch Pond (Figures 1, 2 and 3). *Favella* ($r = 0.72$; $p < 0.01$), *Balanion* ($r = 0.59$; $p < 0.05$) and *Strobilidium* sp. ($r = 0.85$; $p < 0.01$) were positively correlated with total dinoflagellates. *Balanion* was more associated with *H. triquetra* ($r = 0.87$, $p < 0.01$) than with total dinoflagellates.

Microscopic observations of *Favella* revealed that this tintinnid had preyed on *H. triquetra, S. troichoidea*, and some small *Gonyaulax* cells. *Balanion* contained mostly *H. triquetra* in their digestive vacuoles. In *Strobilidium*, the only

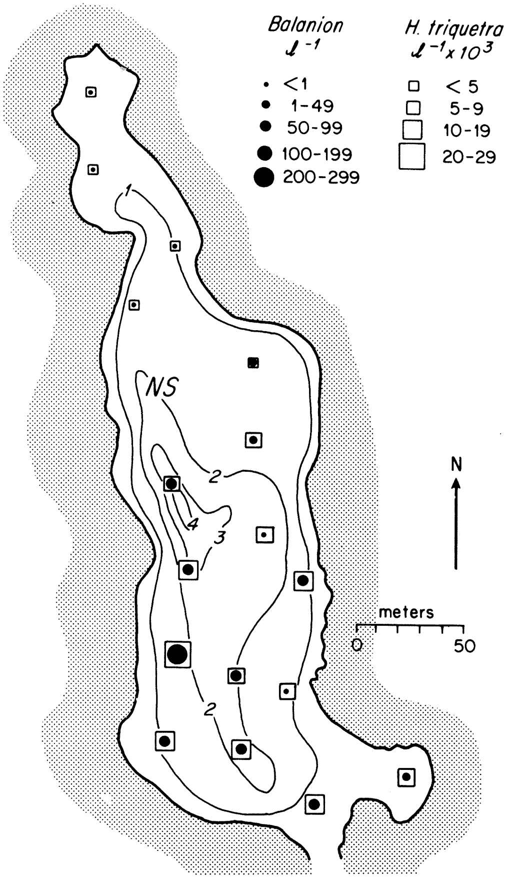


Fig. 2. Horizontal distribution of *Balanion* and *Heterocopsa triquetra*, Perch Pond, May 19, 1982. Depth contours are in meters.

recognizable dinoflagellate in the digestive vacuoles was *H. triquetra* although remnants of other types of cells were present.

Diel vertical distribution

Study No. 1 (September 28 and 29). On the first morning, surface salinities were low (23.20 p.p.t.) due to rainfall the night before, with the highest salinity water (29.13 p.p.t.) at 2 – 3 m depths. From the surface to 1 m depth the water was cool (15°C) at night but warmed to 19°C during the day. Calculation of δ_T values showed that the water column was slightly stratified most of the time. The weather was calm with scattered clouds. During mid-day the surface light intensity was between 1460 and 1750 μE m^{-2} s^{-1} (Figure 4).

At station A the dominant dinoflagellates were *Cochlodinium helicoides* (32 x 35 μm), *Prorocentrum minimum* (15 – 25 x 17 μm), and *Prorocentrum redfieldi* (26 x 10 μm). Most of the other, less common dinoflagellates were less than

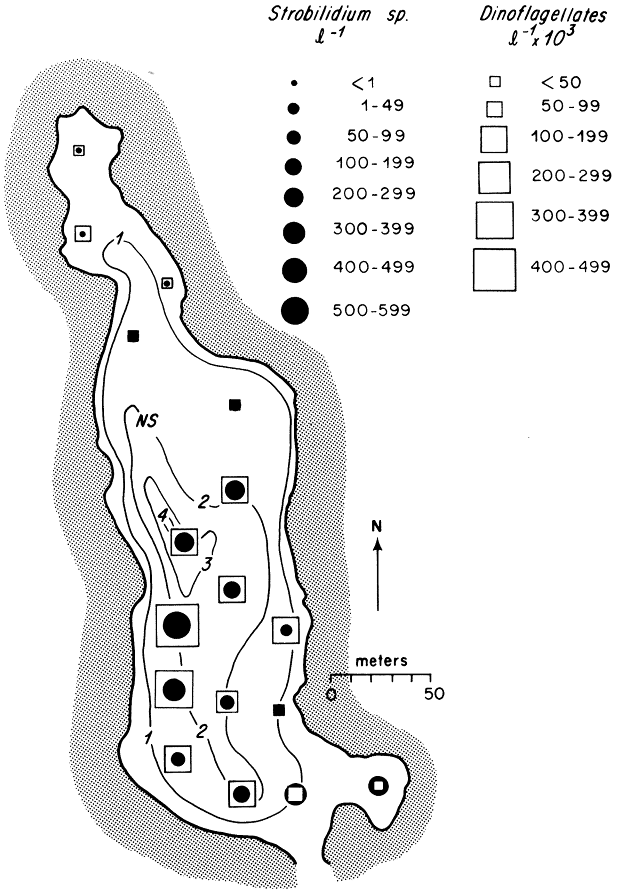
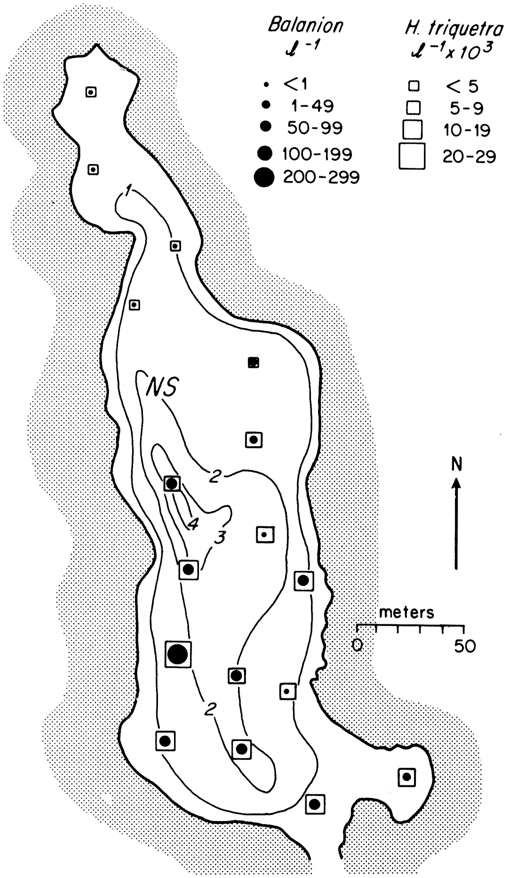


Fig. 3. Horizontal distribution of *Strobilidium* sp. and dinoflagellates, Perch Pond, May 19, 1982. Depth contours are in meters.

34 μm in diameter (Table II). *Favella* was common, but not abundant, with average water column densities of 18–56 cells l^{-1} (Table II). *Strobilidium, Myrionecta* (formerly *Mesodinium) rubrum*, and *Eutintinnuis pectinis* were present but not sufficiently abundant to be accurately counted in the 25 ml settled samples.

During the diel cycle, both the abundance and species composition of the microplankton at Station A varied (Table II). The vertical distributions of *Favella* and the two most abundant dinoflagellates are shown in Figure 4 with associated profiles of temperature, salinity, and light intensity. *Favella* was most abundant near the surface on the first morning, and then gradually descended through the water column during the day such that the maximum was centered at ~3 m depth by 0400 h. On the second morning (0800 and 1200 h), *Favella*'s distribution did not show a surface maximum (Figure 4).

Dinoflagellates did not demonstrate a clear diel migration pattern. Total



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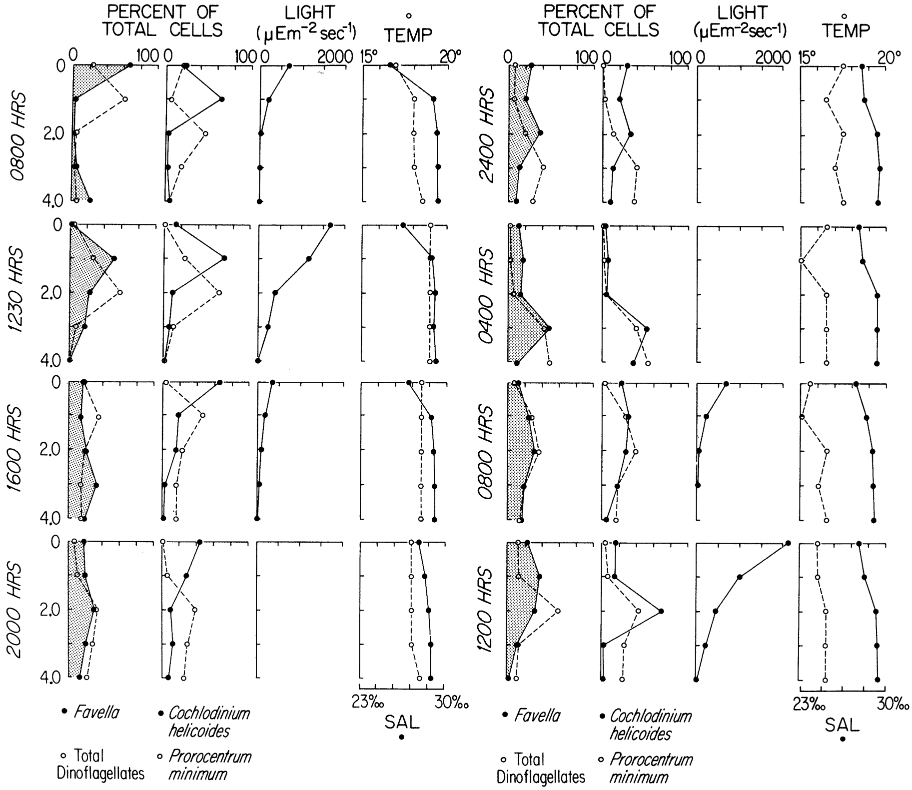

Fig. 4. Diel vertical distribution of *Favella*. Study No. 1, dinoflagellates, light, temperature, and salinity at station A, September 28 and 29, 1981.

dinoflagellate densities were highest at 1 and 2 m depths during the day and at 2 and 3 m at night (Figure 4). *C. helicoides* and *P. minimum* had different diel distribution patterns, with the former found closer to the surface than the latter (Figure 4).

During the diel study *Favella* sp. abundance was not significantly correlated with temperature or salinity but was positively correlated with total dinoflagellate abundance (Table III). At a more detailed level, *Favella* was associated with *C. helicoides* abundance and with some of the less-common dinoflagellates but not significantly with *P. minimum* or *P. redfieldi*. The distribution of *C. helicoides* positively correlated with the less common dinoflagellates, while the two *Prorocentrum* species were also positively associated.

Study No. 2 (October 5 and 6). The temperature ranged from 12 to 14°C with the coldest water found at the surface in the morning (Figure 5). The salinity ranged from 23.77 to 29.64 with the saltier water below 2 m (Figure 5). The water column was slightly stratified. The weather was calm, but overcast on the first morning and then cleared, but remained calm. Light measurements are not available for this second diurnal study.

Table II. Average concentrations (cell l^{-1}) for water column at station A, September 28 and 29, 1981

Time	*Favella*	*Cochlodinium helicoides*	*Prorocentrum minimum*	*Prorocentrum redfieldi*	Other dinoflagellates
0800	30	163×10^3	8×10^3	4×10^3	8×10^3
1200	50	39×10^3	147×10^3	51×10^3	14×10^3
1530	39	11×10^3	38×10^3	5×10^3	9×10^3
2000	38	26×10^3	136×10^3	14×10^3	37×10^3
2400	52	52×10^3	184×10^3	8×10^3	16×10^3
0400	53	94×10^3	331×10^3	12×10^3	18×10^3
0800	18	20×10^3	149×10^3	5×10^3	13×10^3
1200	56	197×10^3	98×10^3	18×10^3	34×10^3

Table III. Correlation matrices and multiple correlation coefficients (R); vertical distribution data, September 28 and 29, 1981

N = 40; R = 0.43 n.s.

	Temperature	Salinity	Dinoflagellates
Favella	−0.08 n.s.	−0.11 n.s.	0.37*
Temperature		0.05 n.s.	−0.20 n.s.
Salinity			0.29 n.s.

N = 40; R = 0.5315*

	Dinoflagellate species			
	Cochlodinium helicoides	*Prorocentrum minimum*	*Prorocentrum redfieldi*	Other dinoflagellates
Favella	0.39*	0.23 n.s.	0.32 n.s.	0.39*
Cochlodinium sp.		0.12 n.s.	0.11 n.s.	0.40*
Prorocentrum minimum			0.44**	0.12 n.s.
P. redfieldi				0.15 n.s.

N, sample size.
*p <0.05.
**p <0.01.
n.s. not significant.

During this diel study at station A, the dominant dinoflagellates were *P. redfieldi* and *P. minimum*. Dinoflagellate abundance and species composition varied through the diel cycle with time (Table IV). *Favella* densities for the water column ranged from 33 to 227 cells l^{-1} (Table IV). Other ciliates including *Strobilidium, Balanion*, and small tintinnids were present but not abundant.

Throughout the diel cycle, the two *Prorocentrum* species had somewhat similar vertical distribution patterns (Figure 5). On the first morning, which was overcast, the bulk of the *Prorocentrum* population was at 2 m or deeper but by midday the populations were centered at 1 m. By evening, the cells had descended to

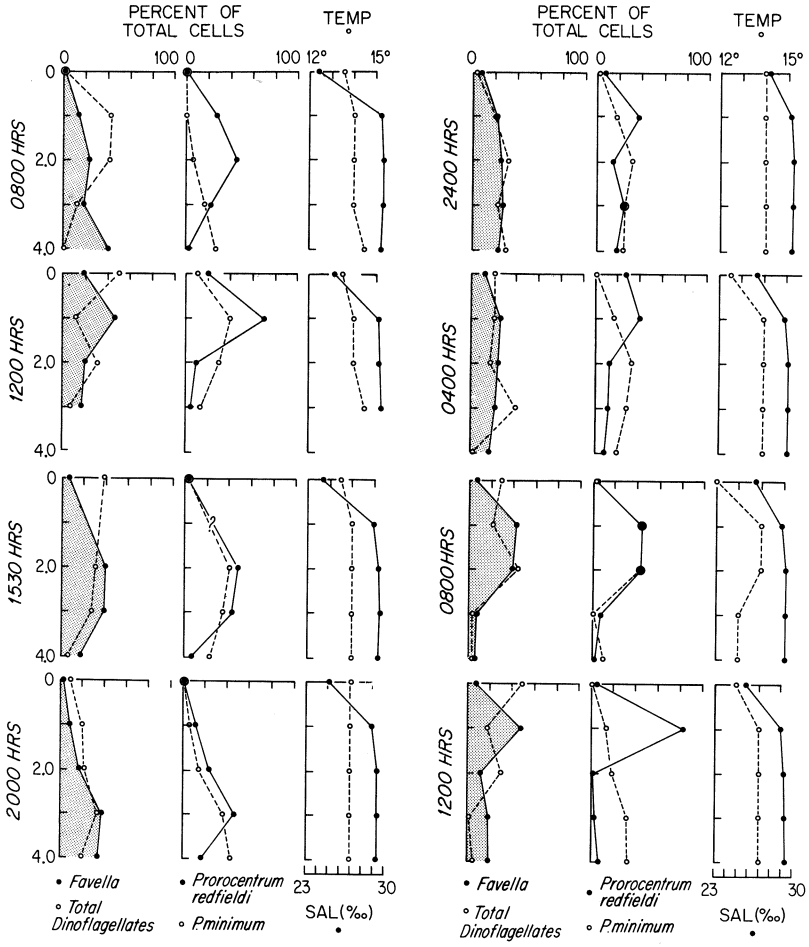

Fig. 5. Diel vertical distribution of *Favella*, dinoflagellates, temperature, and salinity at station A, Study No.2, October 5 and 6, 1981.

2 m and below. On the second morning, which was clear, the *Prorocentrum* were found between 1 and 2 m depth.

The vertical diel distribution of *Favella* was most similar to that of *P. redfieldi* (Figure 5). *Favella* were concentrated at 2 m and deeper on the first, overcast, morning and were at 2 m and above on the second, clear morning. At mid-day, *Favella* were concentrated at ~1 m, descending to 3–4 m depths in the afternoon. During the night, the *Favella* were more evenly distributed in the water column (Figure 5).

In this second diel study *Favella* was also positively correlated with total dinoflagellates but not with temperature or salinity. However, dinoflagellate abundance was associated with temperature and salinity (Table V). *Favella* was positively correlated with *P. redfieldi* and other dinoflagellates but not with

Table IV. Average concentrations (cells l^{-1}) for water column at Station A, October 5 and 6, 1981

Time	*Favella*	*Prorocentrum redfieldi*	*Prorocentrum minimum*	Other dinoflagellates
0800	51	148×10^3	167×10^3	23×10^3
1200	98	42×10^3	106×10^3	51×10^3
1530	82	20×10^3	72×10^3	33×10^3
2000	168	201×10^3	360×10^3	68×10^3
2400	227	173×10^3	332×10^3	185×10^3
0400	99	94×10^3	140×10^3	62×10^3
0800	53	68×10^3	59×10^3	72×10^3
1200	33	112×10^3	101×10^3	59×10^3

Table V. Correlation matrices and multiple correlation coefficients (R); vertical distribution data, October 5 and 6, 1981

N = 38; R = 0.58**

	Temperature	Salinity	Dinoflagellates
Favella	0.05 n.s.	0.05 n.s.	0.50**
Temperature		0.52**	0.48**
Salinity			0.55**

N = 38; R = 0.48*

	Dinoflagellate species		
	Prorocentrum redfieldi	*Prorocentrum minimum*	Other dinoflagellates
Favella	0.40*	0.26 n.s.	0.36*
Prorocentrum redfieldi		0.39*	0.26 n.s.
Prorocentrum minimum			0.45**

N, sample size.
*$p < 0.05$.
**$p < 0.01$.
n.s., not significant.

P. minimum. The two *Prorocentrum* species were positively associated (Table V).

Summary and Discussion

The distribution of dinoflagellates and of ciliates that eat dinoflagellates was patchy on horizontal and vertical spatial scales of meters to tens of meters in the estuary (Figures 1–5). In both the horizontal and vertical distribution studies, ciliate abundance was positively correlated with dinoflagellate abundance. Ciliates were not significantly correlated with temperature or salinity (Tables III and V). Through the diel cycle, the vertical distribution of *Favella* paralleled the vertical distribution of dinoflagellates, with both found near the surface in the morning and near the bottom at night (Figures 4 and 5).

The mechanisms for this fine scale association between ciliates and their prey remain speculative. Differential growth in prey patches is one possible explanation, but this seems unlikely unless the movement of dinoflagellates was mediated primarily by physical circulation patterns, not by behavior, since the changes in the vertical distribution of dinoflagellates and ciliates occurred over much shorter time scales than that required for division.

Interactions between turbulent mixing, water displacement, and migration are generally thought to be responsible for the vertical and horizontal patchiness of dinoflagellate populations (Heaney and Talling, 1980; George and Heaney, 1978; Incze and Yentsch, 1981; Tyler and Seliger, 1978). During both of our diel studies, the water column was stratified most of the time and it was calm; thus it is unlikely that wind-induced turbulent mixing was significant. However, horizontal advection of microplankton populations probably occurred due to tides. The normal tidal range in Perch Pond is 40 – 70 cm. During both diel studies, the ciliate and dinoflagellate populations at Station A changed in species composition and abundance during the 4 h periods between sampling (Tables II and IV); this dramatic change could only be due to water displacement.

The interaction between vertical (and perhaps horizonal) migration and water movements could produce complex patterns of horizontal patchiness similar to that observed in Perch Pond (Figures 1 – 3). Light wind stress can cause horizontal flow of surface waters, resulting in the advective transport of surface algal populations and the upwelling of subsurface accumulations. In addition, small-scale frontal convergences can create dinoflagellate patches in estuaries (Tyler and Seliger, 1978; Incze and Yentsch, 1981). Ciliates coincident with dinoflagellates in the water colum should be acted upon similarly by water movements and remain closely associated.

Although advective displacement undoubtedly occurred, the general similarity between dinoflagellate patterns and those of *Favella* throughout the diel cycle is evident from Figures 4 and 5. Both dinoflagellates and ciliates were near the surface in the morning and near the bottom at night. Dinoflagellates migrate vertically in a complex response to light, gravity, temperature, salinity, and nutrients (Eppley *et al.*, 1968; Heaney and Eppley, 1981; Kamykowski, 1981; Cullen and Horrigan, 1981). Planktonic ciliates can migrate at rates of 2.5 – 4.6 m h^{-1} (Zaika and Ostrovskaya, 1972), and thus should be able to maintain their position among migrating dinoflagellates if their movements are directed. Three possible mechanisms for the correlated movements of ciliates to dinoflagellates are: a similar behavioral response to physical and chemical factors; chemotaxis of the ciliates to the algae; and a locomotory response to food density.

In both diel studies, *Favella* was more closely correlated with dinoflagellate abundance than with temperature or salinity. *Favella* and *Balanion*, unlike dinoflagellates, are not phototactic in the laboratory. It thus seems unlikely that a common behavioral response to physical or chemical factors can explain the correlated vertical movements of ciliates and dinoflagellates.

In the laboratory, the microscale distribution of planktonic ciliates, can be controlled by prey distribution (Stoecker and Guillard, 1982). There is, however, no evidence for a direct, chemotactic response of phytophagous planktonic ciliates to their prey although chemotaxis has been observed in bacterivorous freshwater ciliates (Antipa *et al.*, 1983).

The aggregation of ciliates within algal patches in the field and laboratory may be due to changes in the locomotory pattern of ciliates when they encounter food. When tintinnids contact algal cells they interrupt their standard helical swimming pattern (Blackbourn, 1974; Heinbokel, 1978). We have observed that when *Favella* touches or closely approaches a dinoflagellate, the tintinnid stops, backs-up and then resumes swimming, but at a slight angle to the original direction. This locomotory response occurs whether or not the food particle is ingested. The shorter interval between reversals in the presence of food particles would result in a shorter mean path length within food patches than in areas of lower food density. Tintinnids would thus accumulate in areas of higher prey density. The response of ciliates to dinoflagellate density could occur even if the dinoflagellates were too big to be ingested. This may explain the positive correlations we observed between *Favella* and *C. helicoides*, a dinoflagellate too large to be eaten by *Favella*. This locomotory response to food density by some ciliates is functionally analogous to looping behavior which has been described in copepods (Williamson, 1981).

Identification of the factors regulating the fine scale spatial distribution of these two classes of microplankters is clearly beyond the scope of our descriptive study. The relatively sheltered environment of Perch Pond suggests to us that the distributions reflect an active behavioral association of ciliates with their prey. Both chemotaxis and changes in swimming behavior within high concentrations of food are possible explanations. These associations are then subject to the complex hydrography of a stratified embayment with both tidal and freshwater inflow.

The observed fine scale spatial coupling between planktonic ciliates and their phytoplankton prey has several consequences. This association should result in higher ciliate growth rates and greater grazing impact on phytoplankton populations than would be predicted from average ciliate or algal densities. Coincident patches of algae and ciliates may also provide higher food concentrations for larger grazers which can use both resources such as certain copepods (Stoecker and Sanders, in preparation) and certain fish larvae (Govoni *et al.*, 1983; Stoecker and Govoni, in press). Thus, the role of ciliates in food webs and the stability of these trophic interactions (Wiens, 1976) may partly depend on fine scale distribution patterns.

Acknowledgements

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