



# Diel vertical distribution of planktonic ciliates within the surface layer of the NW Mediterranean (May 1995)

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Received 6 October 1997; received in revised form 17 March 1998; accepted 11 June 1998

## Abstract

The composition and vertical distribution of planktonic ciliates within the surface layer was monitored over four diel cycles in May 95, during the JGOFS-France DYNAPROC cruise in the Ligurian Sea (NW Mediterranean). Ciliates were placed into size and trophic categories: micro- and nano-heterotrophic ciliates, mixotrophic ciliates, tintinnids and the autotrophic *Mesodinium rubrum*. Mixotrophic ciliates (micro and nano) represented an average of 46% of oligotrich abundance and 39% of oligotrich biomass; nano-ciliates (hetero and mixotrophic) were abundant, representing about 60 and 17% of oligotrich abundance and biomass, respectively. Tintinnid ciliates were a minor part of heterotrophic ciliates. The estimated contribution of mixotrophs to chlorophyll *a* concentration was modest, never exceeding 9% in discrete samples. Vertical profiles of ciliates showed that chlorophyll-containing ciliates (mixotrophs and autotrophs) were mainly concentrated and remained at the chlorophyll *a* maximum depth. In contrast, among heterotrophic ciliates, a portion of the population appeared to migrate from 20–30 m depth during the day to the surface at night or in the early morning. Correlation analyses of ciliate groups and phytoplankton pigments showed a strong relationship between nano-ciliates and zeaxanthin, and between chlorophyll-containing ciliates and chlorophyll *a*, as well as other pigments that were maximal at the chlorophyll *a* maximum depth. Total surface layer concentrations showed minima of ciliates during nighttime/early morning hours. © 2000 Elsevier Science Ltd. All rights reserved.

**Keywords:** Planktonic ciliates; Vertical distribution; NW Mediterranean

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## 1. Introduction

Planktonic ciliates often dominate numerically the microzooplankton and contribute to the nanozooplankton. Among ciliates, different trophic modes can be distinguished with potentially different water column distributions. Autotrophy is found in the ciliate *Mesodinium rubrum*; it is a rapid swimmer (speeds up to  $5 \text{ mm s}^{-1}$ , Lindholm, 1981) and is reputed to be strongly phototactic (Lindholm, 1985) as well as rheotactic (Crawford and Purdie, 1992). These characteristics make it a potentially migrating organism, and diel vertical migrations have been reported for this species (e.g., Smith and Barber, 1979; Dale, 1987). Mixotrophic oligotrich ciliates, forms that retain functional plastids from ingested algae, are photosynthetic as well as phagotrophic feeders (Stoecker, 1991; Dolan, 1992). There is no evidence of plastid reproduction inside ciliate cytoplasm, hence the ciliates are dependent on algal food to replace their plastids. Mixotrophic ciliates also can display vertical migration (Dale, 1987; Stoecker et al., 1989; Jonsson, 1989), perhaps to exploit optimum light and nutrient levels or algal prey to serve as chloroplast sources. Heterotrophic ciliates, considered alone, are still a complex assemblage of aloricate forms and tintinnids; in terms of size they can belong to the nanozooplankton or the microzooplankton, and in terms of diet be bacterivorous, algivorous or predacious (e.g., Dolan, 1991). Such a multiplicity of trophic modes translates into the capacity of planktonic ciliates to exploit a large variety of prey types and thereby assume different roles in the marine ecosystem. Therefore, one would expect differences in their water column distribution and in their relative importance within the ciliate assemblage.

The vertical distribution and total stock size of the ciliate community as an undifferentiated assemblage have been studied in many marine systems (e.g., Beers et al., 1980; Sorokin et al., 1985; Leakey et al., 1996 and references therein). However, surprisingly little is known about the relative distribution of the different trophic categories within ciliate communities (Dale, 1987; Stoecker et al., 1989; Putt, 1990), and to our knowledge data from deep-water systems are rare and there is only one study in open Mediterranean waters (Dolan and Marrasé, 1995).

In this paper we present the results of a cruise in the NW Mediterranean performed in May 1995 during which samples were obtained to study differences in the vertical structure of distinct components of the ciliate assemblage and to monitor changes in the water column distribution of the most important ciliate categories through four diel cycles. Relationships with chlorophyll *a*, variabilities of total standing stocks, and ciliate consumption of daily primary production were estimated.

## 2. Methods

As part of the JGOFS-France cruise DYNAPROC, in May 1995 samples were taken at the reference station DYFAMED ( $43^{\circ}25,2'N$ ,  $07^{\circ}51,8'E$ ) in the NW Mediterranean. The site, removed from the frontal zone and beyond the influence of the Ligurian current, was chosen after extensive survey as a site with weak horizontal advective movements. Water samples were collected with a CTD-Niskin bottle

rosette. Samples were obtained from 6 depths in the surface layer (5, 10, 20, 30, 40 and 50 m) every 4 h over four separate 36 h cycles yielding a total of ten profiles per diel cycle. Sampling cycles started in the morning at 10 : 00 h (local time UTC  $\pm$  2 h) and ended 36 h later at 22 : 00 h. The first and second cycles were conducted on 11 and 14 May, respectively, cycles 3 and 4 were run two weeks later on 27 May and 30 May.

For ciliate enumerations, samples of 500 ml were fixed with acid Lugol's (2% final concentration) and stored in darkness at 4°C until examined. Fifty or 100 ml were settled, and the entire surface of the settling chamber was scanned at 200 $\times$  with a Zeiss axiovert inverted microscope. Ciliates were identified to genus when possible following Montagnes and Lynn (1991), except for tintinnid ciliates, which were classified on the basis of lorica morphology using the species descriptions of Balech (1959) and Kofoid and Campbell (1939). For the tintinnids, only loricae containing cells were enumerated.

Ciliates were placed into distinct categories: (1) Large mixotrophic oligotrichs: *Tontonia* spp. and a large 70–100  $\mu\text{m}$  *Strombidium* sp. e; (2) Mixotrophic nano-ciliates; (3) Autotrophic *Mesodinium rubrum*; (4) Heterotrophic micro-ciliates; (5) Heterotrophic nano-ciliates; (6) Tintinnids. As Lugol's fixative allows only the identification of mixotrophic oligotrichs with distinctive gross morphologies (e.g. *Tontonia* spp.), supplementary 500 ml water samples were collected and fixed with borate-buffered formaldehyde (2% final concentration) to identify by epifluorescence microscopy the trophic mode of oligotrich ciliates, for details see Pérez et al. (1997).

Chlorophyll *a* and phytoplankton pigments were measured by HPLC as described in Vidussi et al. (2000).

### 2.1. Biomass estimates

Biovolumes of non-tintinnid ciliates were estimated from average linear dimensions of 50 cells measured for each morphospecies within the trophic categories described above. Standard geometric assumptions were made to calculate cell volume. The biovolume estimates were converted into carbon using a conversion factor of 0.19  $\text{pg C } \mu\text{m}^{-3}$  for 2% Lugol's fixed oligotrichs (Putt and Stoecker, 1989). We did not estimate the biomass of tintinnids that were less abundant.

### 2.2. Regression analyses

Pearson's correlation coefficients were calculated to test the relationship of different pigment concentrations with the abundance and calculated biomass of hetero- auto- and mixotrophic ciliates. Correlation analyses were performed for the entire data set using either depth-integrated data or concentrations in discrete depth samples.

### 2.3. Estimation of photosynthetic ciliate chlorophyll

The chlorophyll *a* content of *M. rubrum* was calculated using a conversion factor for Lugol's fixed cells of 3.6  $\text{fg chlorophyll } a \mu\text{m}^{-3}$  (Stoecker et al., 1991). We estimated the chlorophyll content of mixotrophic ciliates found in our samples in the following

manner. Given that chlorophyll per unit cell volume is inversely related to cell size in phytoplankton (Malone, 1980), we examined the relationship between cell volume and volume-specific chlorophyll content in mixotrophic oligotrichs based on literature reports of direct measurements (Stoecker et al., 1987,1988,1988/1989; Putt, 1990; Perriss et al., 1994). An equation was generated (see results) relating cell size of mixotrophic oligotrichs to volume-specific chlorophyll content. The relationship generated was then used to estimate chlorophyll per cell, based on cell size, for the mixotrophic oligotrichs found in our samples.

### 3. Results

#### 3.1. Hydrologic structure of the water column

The time-course changes in physical and chemical parameters of the study site during the cruise and details of the hydrologic structure at the Station DYFAMED are given in Andersen and Prieur (2000). Briefly, from several types of observations, from Doppler-based current measures to CTD salinity and temperature data, horizontal advection at the sampling site remained weak throughout the DYNAPROC cruise (Andersen and Prieur, 2000). A single important event was the occurrence of strong winds up to  $16 \text{ m s}^{-1}$  on 13 May, after this wind event, between the 13 and 15 May, an upward advective shift of deeper layers, related to Ekman pumping, was observed, superimposed upon the wind-induced mixing of the superficial layers (0–10 m). Time-depth distributions of temperature and density excess are represented in Fig. 1. During the first cycle, the temperature gradient was strong: after May 12 the heat content of the 0–30 m layer decreased. During cycles 3 and 4, the 0–20 m layer warmed slowly while the thermocline depth did not vary. Density diagrams showed two structures: the main stratification represented by the narrowing of isopycnals 28.5 and  $28.6 \text{ kg m}^{-3}$  and a secondary one represented by isopycnals 28.9 and  $29 \text{ kg m}^{-3}$ . During cycles 1 and 2 the main stratification was located at 10–15 m depth, but during cycles 3 and 4 it was deeper (20 m) and was joined by isopycnals 28.9 and  $29 \text{ kg m}^{-3}$ .

#### 3.2. Ciliate assemblage

During the four diel cycles different ciliate taxa were commonly found (Table 1). Ciliate abundance was on average  $3300 \text{ cell l}^{-1}$  during May in the surface layer (5–50 m); peak values were up to  $10,000 \text{ cell l}^{-1}$ . The ciliate assemblage was dominated by oligotrichs. Tintinnids represented less than 5% of ciliate abundance in 82% of samples and less than 10% in 95% of samples. The tintinnid species found are reported in Table 2.

Among oligotrichs, *Strombidium* species dominated the number and the biomass of hetero- and mixotrophic ciliates. Nano-ciliates were present in all samples and were numerically the dominant size group of the ciliate assemblage, representing between 51 and 70% of oligotrich abundance (Table 3) depending on the diel cycle. In terms of biomass, their contribution was less important.

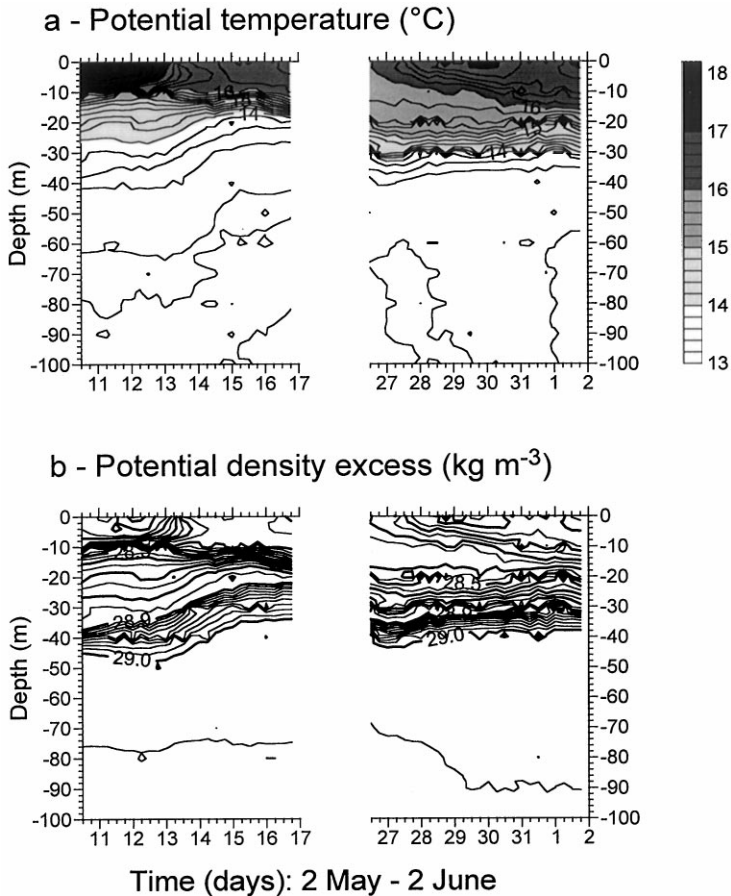


Fig. 1. Time-depth distributions of (a) temperature and (b) density excess for the 0–100 m water column at the site sampled. Isopycnals are drawn at 0.05 intervals with bold line at 0.1 intervals, except between 28.9 and 29  $\text{kg m}^{-3}$  where they are drawn at 0.01 intervals. (from Andersen and Prieur, this issue).

Mixotrophic ciliates were present in both sizes classes (nano- and micro-plankton), and their contribution to total oligotrich biomass and abundance ranged from 31 to 47% and from 42 to 54%, respectively (Table 3). *M. rubrum* was present only during cycles 3 and 4; its contribution to ciliate biomass ranged from 2 to 1%, and from 11 to 6% in terms of cells  $\text{ml}^{-1}$ .

### 3.3. Diel vertical distribution

The chlorophyll *a* maximum was situated at 30 m depth on May 11 and 12 with maximal chlorophyll concentration of 2  $\text{mg l}^{-1}$ ; on May 14 the chlorophyll maximum was at 20 m depth ( $\sim 1.4 \text{ mg l}^{-1}$ ), and during cycles 3 and 4 it was located again around 30 m depth (Fig. 2). The highest chlorophyll *a* concentrations were found

Table 1

Ciliate species commonly found in our samples during the diel cycles. *L* is total length in microns. Max [ ] is maximum concentration in cell l<sup>-1</sup>

Group	Species	<i>L</i> (μm)	Shape	Max [ ]	Depth	Date and time of day
Autotrophic ciliate	<i>Mesodinium rubrum</i>	15	—	1920	30 m	27 May 10 : 00 h
Mixotrophic oligotrich	<i>Tontonia spp.</i>	100	—	300	20 m	27 May 22 : 00 h
	<i>Strombidium sp. e</i>	70	Conical	1020	30 m	28 May 18 : 00 h
	<i>Strombidium sp. a</i>	16	Conical	5960	20 m	14 May 14 : 00 h
Heterotrophic oligotrich	<i>Strombidium sp. b</i>	15	Round	2460	20 m	11 May 10 : 00 h
	<i>Strombidium sp. c</i>	26	Conical	3300	10 m	31 May 06 : 00 h
	<i>Strombidium sp. f</i>	35	Round	280	30 m	31 May 14 : 00 h
	<i>Strombidium sp. g</i>	40	Mixed	960	20 m	31 May 18 : 00 h
Tintinnids	Table 2	35–300	—	460	5 m	27 May 14 : 00 h
Prostomid	<i>Balanion sp.</i>	15	—	1840	30 m	11 May 22 : 00 h

Table 2

Tintinnid species present in our samples during the diel cycles. *L* and OD are the total length and the oral diameter respectively. Max [ ] is the maximum concentration in cell l<sup>-1</sup>

Species	<i>L</i> and OD (μm)	Max [ ]	Depth
<i>Acanthostomella conicoides</i>	35/20	280	30 m
<i>Amphorella quadrilineata</i>	100/35	360	5 m
<i>Codonella aspera</i>	100/50	10	50 m
<i>Codonellopsis pusilla</i>	40/17	120	30 m
<i>Craterella protuberans</i>	35/30	40	30 m
<i>Dadaiella ganymedes</i>	100/25	280	30 m
<i>Dictyocysta mitra</i>	70/40	20	50 m
<i>D. elegans speciosa</i>	65/40	80	50 m
<i>Eutintinnus tubulosus</i>	145/30	120	5 m
<i>Ormosella sp.</i>	50/25	10	50 m
<i>Proplectella claparedei</i>	75/35	160	30 m
<i>Rhabdonella spiralis</i>	300/50	20	20 m
<i>Salpingella spp.</i>	80–300/n.d.	180	30 m

during the first diel cycle and decreased during the second cycle (14 May). The lowest concentrations were found during cycle 3, when the maximum chlorophyll *a* concentration was 1 mg l<sup>-1</sup>; during the last cycle (30 May), concentrations at the chlorophyll maximum ranged from 0.8 to 1.3 mg l<sup>-1</sup>.

Here we consider the diel vertical distribution of individual ciliate forms only for the 4 most abundant taxa or groups in our samples: (1) the nano-mixotroph *Strombidium sp. a*, (2) the heterotrophic nano-ciliate *Strombidium sp. b*, (3) heterotrophic micro-ciliates and (4) the autotrophic *Mesodinium rubrum*. *M. rubrum*, present only during

Table 3

Averaged contribution of different ciliate categories to oligotrich abundance and biomass. Mixotrophs and heterotrophs are either nano- or micro-ciliates. Nano-ciliates include mixotrophic and heterotrophic forms. With chloro-plasts are mixotrophs and *M. rubrum*

Cycle	Date	Mixotrophs		With chloroplasts		Heterotrophs		Nano-ciliates	
		Biomass (%)	Abundance (%)	Biomass (%)	Abundance (%)	Biomass (%)	Abundance (%)	Biomass (%)	Abundance (%)
Cycle 1	11 May	34	44	34	44	66	56	23	67
Cycle 2	14 May	46	54	46	54	55	46	30	70
Cycle 3	27 May	47	45	49	55	52	45	9	51
Cycle 4	30 May	31	42	32	48	68	52	7	52

cycles 3 and 4, was mainly concentrated at the chlorophyll *a* maximum depth (around 30 m depth) during both cycles regardless of the time of day (Fig. 3).

The mixotrophic nano-ciliate displayed a relatively invariant vertical distribution. Most of the population (Fig. 4) was found at 30 m throughout the first cycle independent of the hour of day, except on 12 May at 18 : 00 h, when the maximal abundance was recorded at 40 m. During the second cycle, the nano-mixotroph was mainly found in the layer between 20 m depth and the surface. During cycles 3 and 4, the maximal abundances were found again at 30 m depth from the beginning of the cycle until 06 : 00 h, and at 20 m depth during the second light period.

Heterotrophic nano and micro-size species (Figs. 5 and 6) were mainly located just above the chlorophyll *a* maximum depth in a layer between 5 and 20 m depth during cycles 1 and 2, but their vertical distribution was more dispersed during cycles 3 and 4. In all the cycles, we noted the presence of heterotrophic ciliates, especially micro-ciliates, near the surface during nighttime hours, usually between 22 : 00 and 02 : 00 h, although sometimes we detected this phenomenon in early morning 06 : 00–10 : 00 h.

### 3.4. Diel variability of integrated biomass

The total biomass of ciliates varied considerably over each of the cycles (Fig. 7). Usually, integrated biomass was minimal during the nighttime hours and represented about 50% of daytime peak values. Similarly, chlorophyll *a* concentration oscillated with nighttime minima and maximum-min differences of about 50%.

### 3.5. Chlorophyll *a* content estimates

The relationship found between the chlorophyll *a* content and mixotrophic oligotrich biovolume (Fig. 8) is expressed by the equation  $y = -7.97 \times 10^{-6}(V) - 2.34$  ( $R^2 = 0.56$ ;  $p = 0.0013$ ), where  $y$  is the log transformed volume-specific chlorophyll *a* content in pg chlorophyll *a*  $\mu\text{m}^{-3}$  and  $V$  is the Lugol's fixed cell volume in  $\mu\text{m}^3$ . Using this relationship, we estimated the chlorophyll *a* content of mixotrophs present in our samples. The equation generated may be criticised as a spurious correlation of the form  $a/b$  vs.  $b$  (e.g., Berges, 1997), but a significant non-linear formulation with

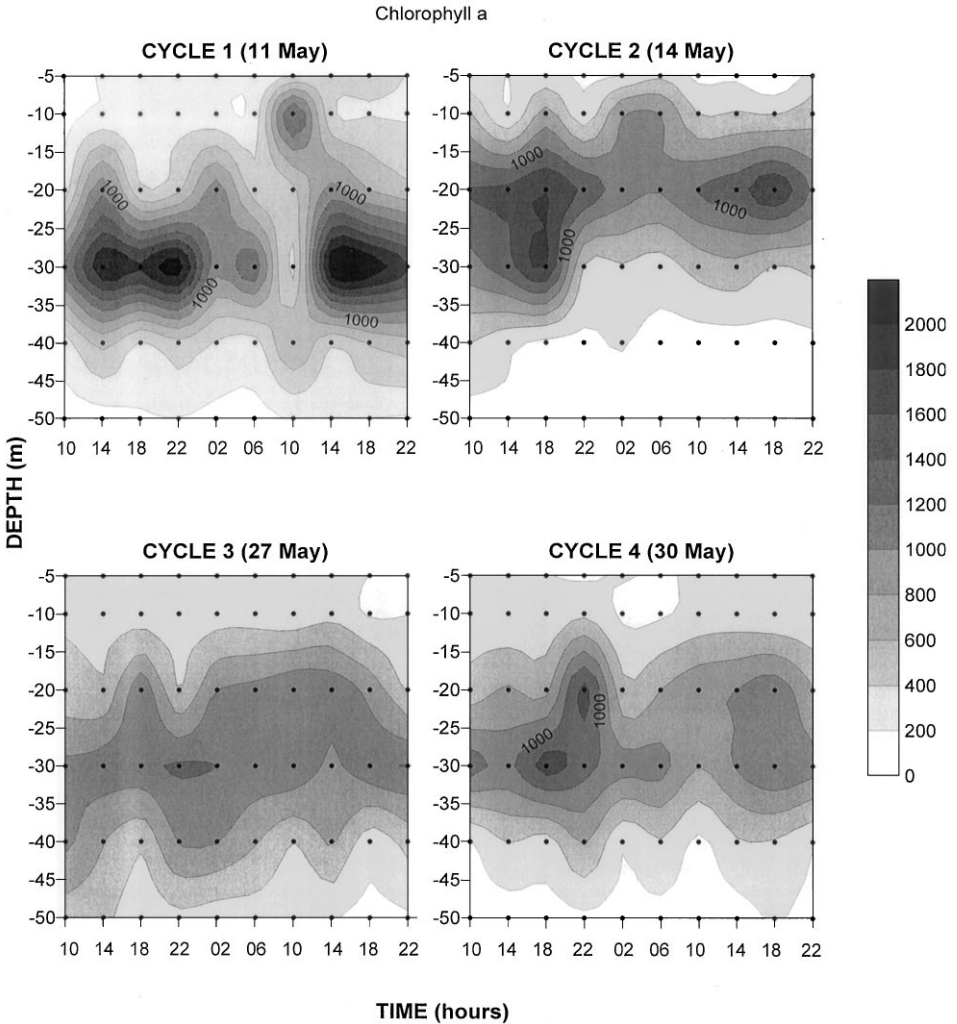


Fig. 2. Vertical distribution of chlorophyll *a* concentration ( $\text{ng chlorophyll } a \text{ l}^{-1}$ ) during the four diel cycles. Time is local time (UTC + 2 h).

independent variables yielded the same parameter estimates. We believe the linear relation is correct and reflects a “packaging effect” of chloroplasts in the ciliates.

For *Tontonia* spp. and for *Strombidium* sp. e our estimates of chlorophyll content were  $0.73 \times 10^{-3}$  and  $3.70 \times 10^{-3}$   $\text{pg chlorophyll } a \mu\text{m}^{-3}$ , respectively. We assumed a chlorophyll *a* content of  $4.26 \times 10^{-3}$   $\text{pg } \mu\text{m}^{-3}$  for the small *Strombidium* sp. a. This value is the last we could generate using our equation, as the volume of the nano-sized mixotroph was beyond the limits of the regression model data base. Rather than extrapolate the linear model, we preferred to utilise the last value contained within the data base. Our assumption is that even if the relationship changes for the small values of biovolume, our estimates would be conservative.



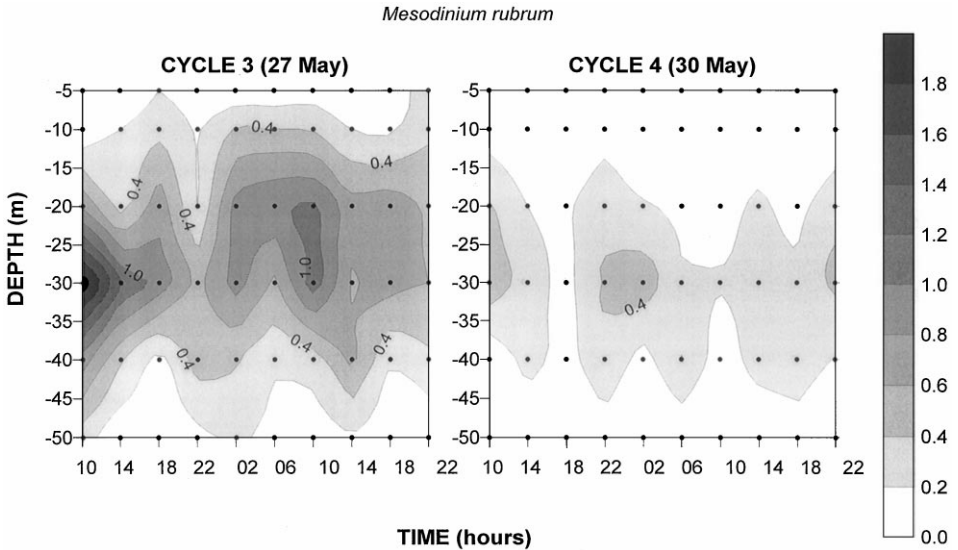


Fig. 3. Vertical distribution of *Mesodinium rubrum* concentration (cell ml<sup>-1</sup>) during the four diel cycles. Time is local time (UTC + 2 h).

On this basis, we estimated the contribution of mixotrophic ciliates to chlorophyll *a* concentration in the surface layer (Fig. 9). Their contribution was variable during a diel cycle, but in general the highest values, ranging from 4 to 8%, were found near the surface between 18 : 00 and 22 : 00 h occasionally we found contributions of 8%: during the first cycle at 10 : 00 h at surface and at 30 m depth at 10 : 00 h (5%). During the second cycle, mixotroph contribution to chlorophyll *a* represented 4% at 22 : 00 h in the 40 and 50 m depth layer. During cycle 3, from 10 : 00 to 18 : 00 h, mixotrophs represented 4% of chlorophyll *a* concentration at 30 m depth.

Within the chlorophyll maximum layer, mixotrophic ciliate contribution to chlorophyll was negligible. Mixotrophs represented 0.1 to 1.3% of the chlorophyll during the first sampling cycle, from 0.1 to 2.7% during the second diel cycle, from 1.4 to 5.1% during cycle 3 and from 0.7 to 2.1% during the last cycle.

### 3.6. Relationships with chlorophyll *a* and carotenoids

Details of pigment concentrations and distribution appear elsewhere (Vidussi et al., this issue). Briefly, during the DYNAPROC cruise, the major carotenoids were zeaxanthin, mostly from coccoid cyanobacteria as prochlorophytes were almost absent, fucoxanthin from diatoms and some prymnesiophytes, 19' HF (19' hexanoyloxyfucoxanthin) from prymnesiophytes and 19' BF (butanoyloxyfucoxanthin) from chrysophytes and pelagophytes. Prasinoxanthin (indicator of prasinophytes), alloxanthin from cryptophytes, and peridinin from dinoflagellates were present but in small amounts.

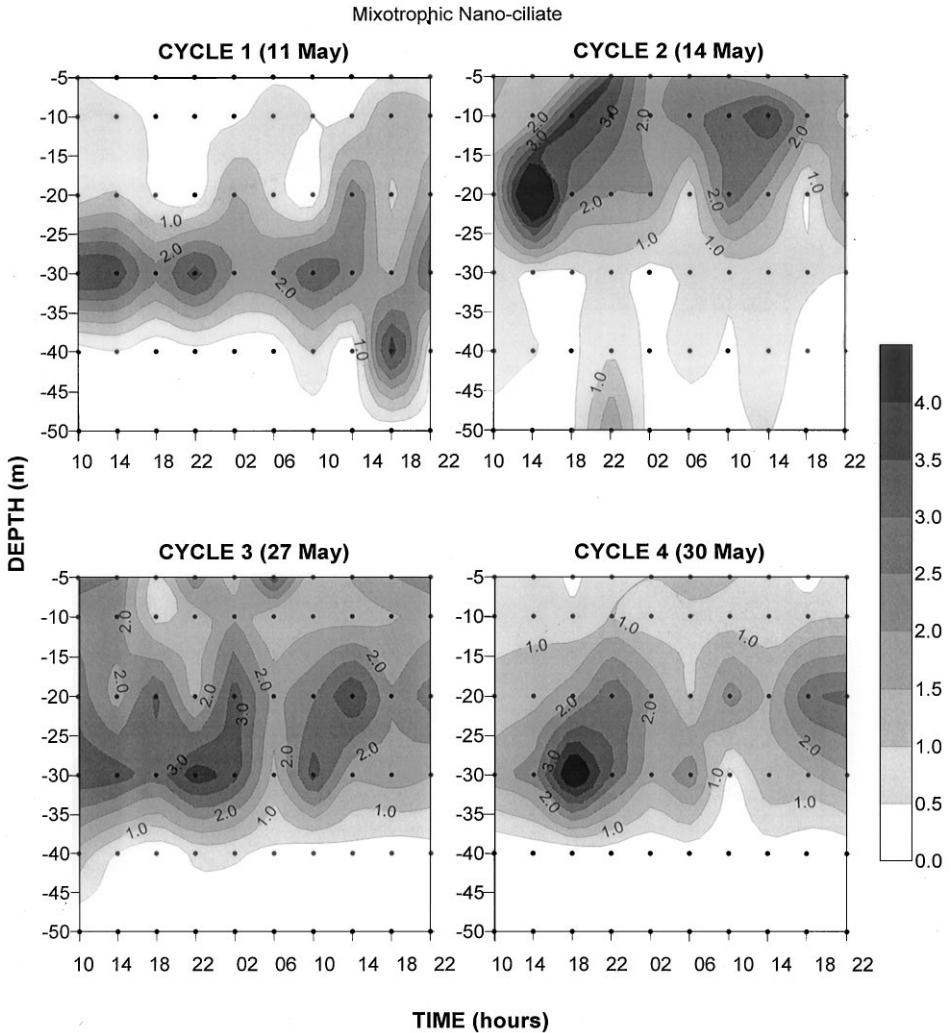


Fig. 4. Vertical distribution of mixotrophic nano-sized oligotrich concentration ( $\text{cell ml}^{-1}$ ) during the four diel cycles. Time is local time (UTC + 2 h).

Table 4 shows the Pearson correlation coefficients obtained between ciliate abundance and biomass and pigment concentrations. Using depth integrated data, we found all ciliates positively related to zeaxanthin, except for the biomass of heterotrophic nano-ciliates. *M. rubrum* and the heterotrophic nano-ciliates were also correlated with chlorophyll *a*. Fucoxanthin was positively correlated with heterotrophic nano-ciliate biomass. The correlation coefficient with micro-heterotrophic biomass and fucoxanthin was negative.

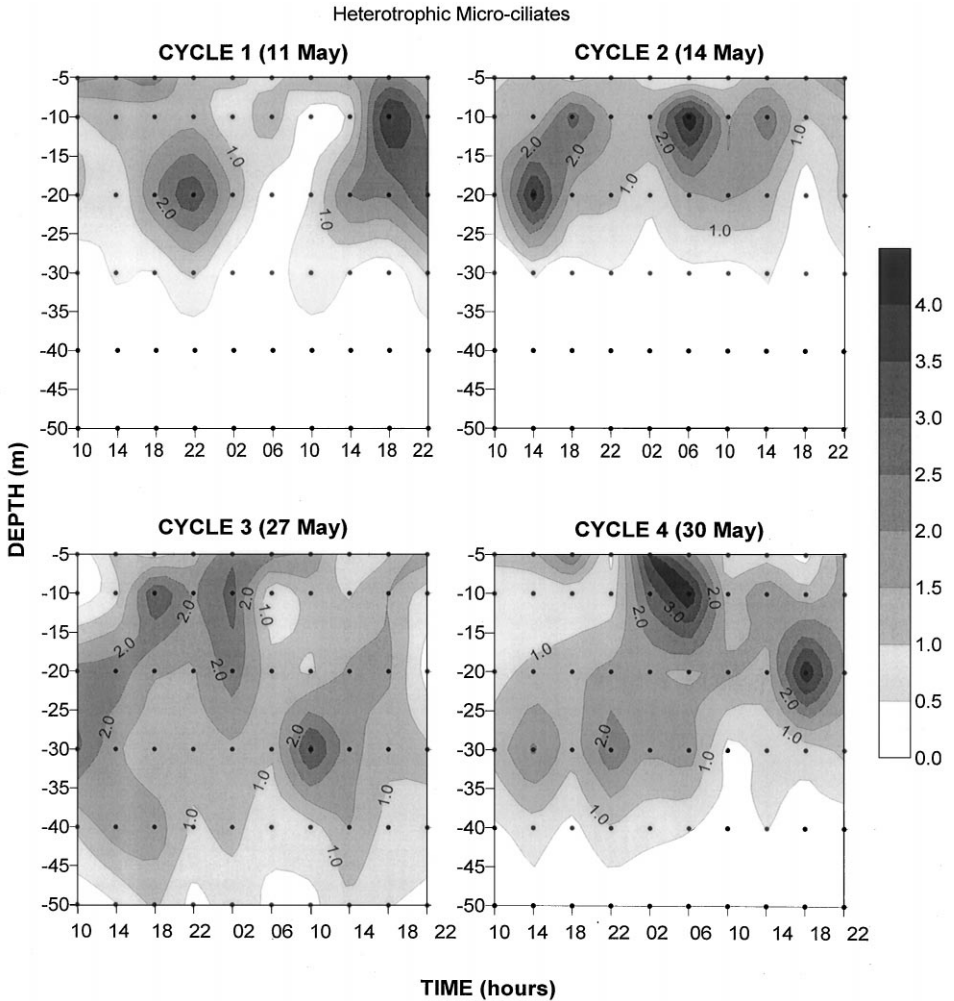


Fig. 5. Vertical distribution of heterotrophic micro-ciliates concentration ( $\text{cell ml}^{-1}$ ) during the four diel cycles. Time is local time (UTC + 2 h).

When concentrations in discrete depths were considered, for all the ciliate types the highest correlation coefficients were found with zeaxanthin, except for *M. rubrum*, for which higher correlation coefficients were found with chlorophyll *a* and 19' HF.

Mixotrophic nano-ciliate numbers and biomass were highly and positively correlated with all pigments. Heterotrophic micro-ciliate abundance was positively correlated with zeaxanthin and 19' HF. Their biomass was negatively correlated with fucoxanthin. Heterotrophic nano-ciliate abundance and biomass were positively correlated with all pigment concentrations except fucoxanthin.

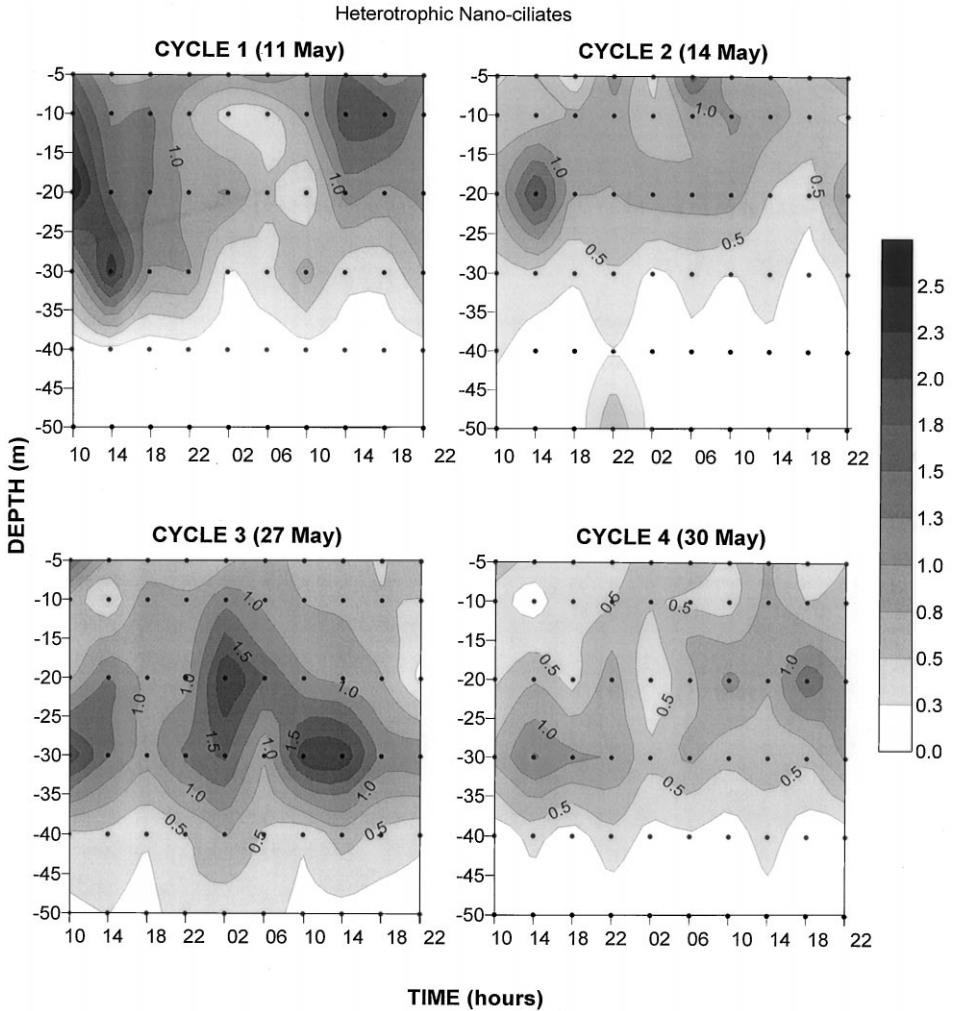


Fig. 6. Vertical distribution of heterotrophic nano-ciliates concentration ( $\text{cell ml}^{-1}$ ) during the four diel cycles. Time is local time (UTC + 2 h).

#### 4. Discussion

During May 1995, the ciliate assemblage at the study site in the NW Mediterranean was characterised by relatively high concentrations of ciliates compared to the ranges previously reported for different areas of the Mediterranean Sea (Table 5). The contribution of nano-sized oligotrichs to ciliate biomass appear to be somewhat lower than in other nearshore systems (Beers et al., 1980; Sherr et al., 1986; Lynn et al., 1991) but higher than the percentage estimated in the Catalan Sea ( $\sim 1\%$ ) by Dolan and Marrasé (1995).

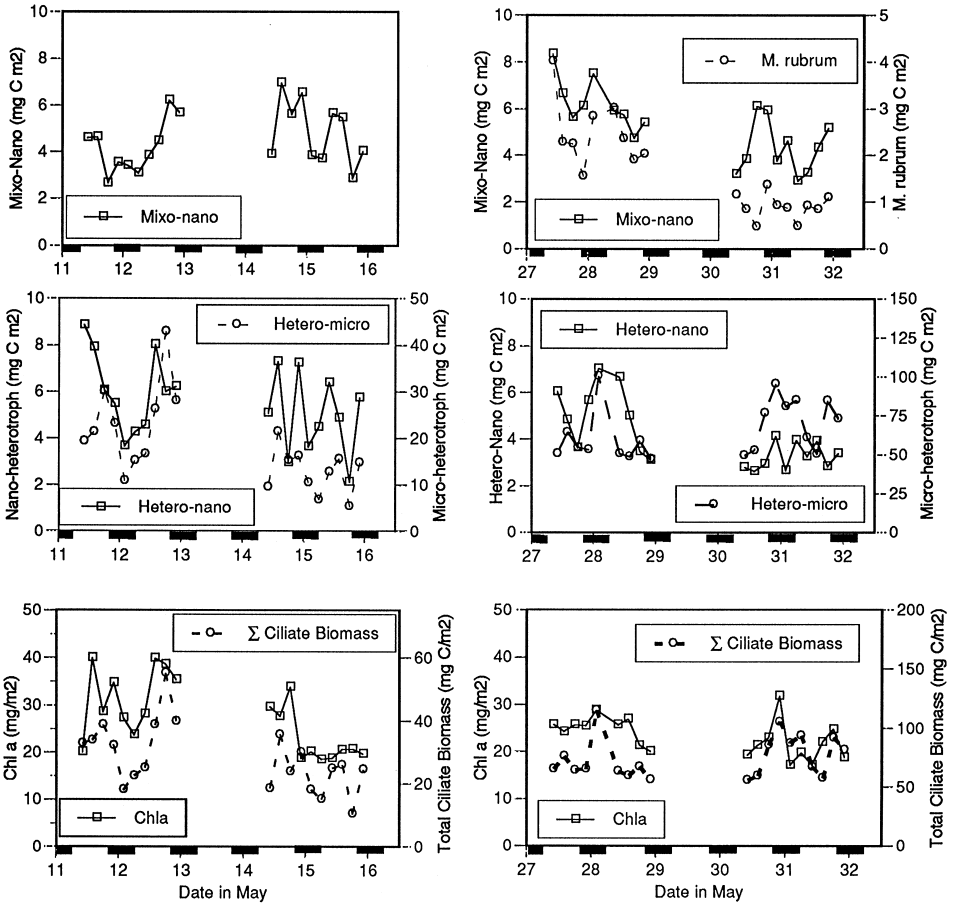


Fig. 7. Diel variability of the different types of ciliates and chlorophyll integrated through the water column (5–50 m) during the four cycles.

In the NW Mediterranean, ciliates with chlorophyll represented 20 to 50% of ciliate biomass and 6 to 30% of ciliate numbers in the surface layer (Table 6). In our samples, the average contribution of mixotrophs to oligotrich biomass ( $\sim 40\%$ ) was within the range reported above, whereas the estimated contribution to ciliate numbers (46%) was much higher. Probably because only some mixotrophic species, such as *Laboea* and *Tontonia*, were considered in previous reports.

If we compare our data with oceanic systems other than the Mediterranean Sea (Table 6), it is apparent that the absolute concentrations of mixotrophic ciliates and their contribution to total ciliate biomass are quite variable. Differences in ciliate assemblages across seasons and places can be expected, and direct comparison is sometimes difficult due to the lack of consistent methods: differences in the part of the water column sampled and mixotrophic species enumerated. Nevertheless, the spring

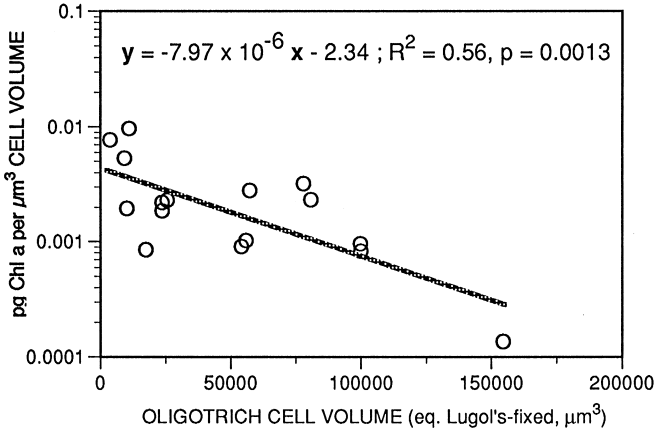


Fig. 8. Linear regression relating the volume-specific chlorophyll *a* content, chlorophyll per cubic micron, as a function of the cell volumes of different sized mixotrophic oligotrichs. Cell volumes were those of Lugol's-fixed cells. Data source citations are given in the Methods section.

ciliate assemblage in the NW Mediterranean does not seem to be basically different from the springtime assemblages of other temperate systems.

In addition to mixotrophic ciliates, the other chlorophyll-containing ciliate, the haptorid *Mesodinium rubrum*, was present at concentrations ranging from 20 to 1920 cell l<sup>-1</sup> (avg. 270 cell l<sup>-1</sup>). This range of concentration is similar to those recorded in other marine systems under non-bloom conditions (Stoecker et al., 1989; Putt, 1990; Dolan and Marrasé, 1995; Vaqué et al., 1997). The presence of *M. rubrum* during our study supports assertions that this species is common in the plankton assemblage of the NW Mediterranean (Bernard and Rassoulzadegan, 1994; Dolan and Marrasé, 1995).

#### 4.1. Water column distribution

Chlorophyll-containing ciliates (mixotrophs and *Mesodinium rubrum*) accumulated around the chlorophyll maximum depth, and despite their reputed migratory capacity (Smith and Barber, 1979; Dale, 1987; Stoecker et al., 1989) remained at this depth during all the diel cycles. Changes in the depth of ciliate maxima were about 10 m; in general, such changes were concomitant with changes in depth of the chlorophyll *a* maximum. While nano-flagellates, mainly prymnesiophytes, were responsible for most of chlorophyll biomass at the chlorophyll *a* maximum, the maximal concentrations of the other carotenoids also occurred at this depth (Vidussi et al., 2000). In mixotrophic ciliates, chloroplasts can be sequestered from a large variety of chlorophytic and chromophytic algae (Blackbourn et al., 1973; Laval-Peuto et al., 1986; Jonsson, 1987). Consequently, one hypothesis to explain their consistent coincidence with the chlorophyll *a* maximum is their requirement for certain algae that are adequate chloroplast donors.

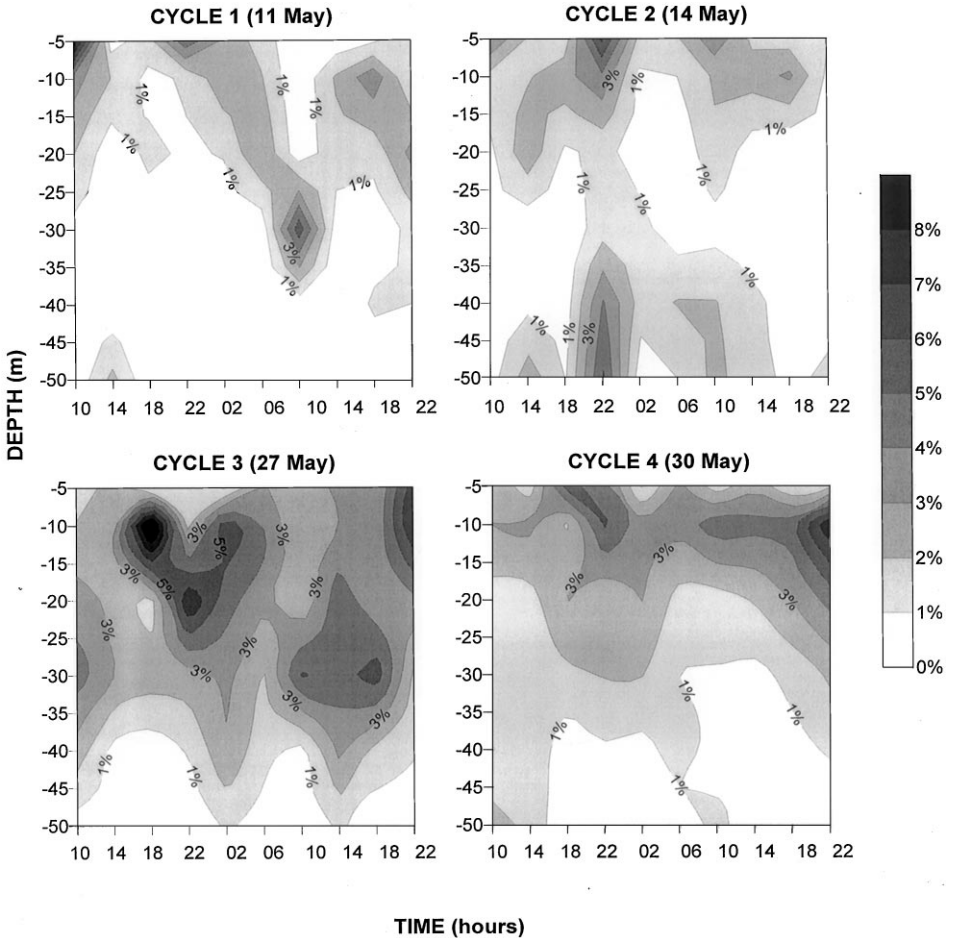


Fig. 9. Estimated contribution of chlorophyll-containing ciliates to total chlorophyll concentration in terms of % total chlorophyll in samples from the surface layer during the four diel cycles.

In the case of *M. rubrum* its maximum concentration at the chlorophyll maximum depth is more difficult to explain because *M. rubrum* is an autotroph that harbors true algal endosymbionts and does not ingest algal food. Nevertheless, depth maxima of *M. rubrum* have been reported (Lindholm, 1981; Lindholm and Mörk, 1990; Passow, 1991), and this species has been observed at 45 and 60 m in the eastern Mediterranean Sea (Lindholm, 1985). Moreover, during our survey *M. rubrum* did not vertically migrate following a diurnal pattern, although photoaxis has been reported in this species (Smith and Barber, 1979; Lindholm, 1985). In addition to light, many factors, such as nutrient levels or turbulence, may influence the vertical distribution of the haptorid *M. rubrum* (Crawford and Lindholm, 1997).

Table 4  
Pearson correlation coefficients found between ciliate abundance and biomass and pigment concentrations

Pigment	Nano-Mixotroph		<i>M. rubrum</i>		Nano-heterotroph		Micro-heterotroph	
	Abundance	Biomass	Abundance	Biomass	Abundance	Biomass	Abundance	Biomass
(a) Concentrations in discrete depth samples								
Chlorophyll <i>a</i>	0.527 <sup>a</sup>	0.527 <sup>a</sup>	0.665 <sup>a</sup>	0.661 <sup>a</sup>	0.371 <sup>a</sup>	0.339 <sup>a</sup>	0.139	0.086
19' BF	0.479 <sup>a</sup>	0.479 <sup>a</sup>	0.495 <sup>a</sup>	0.495 <sup>a</sup>	0.411	0.375 <sup>a</sup>	0.190 <sup>a</sup>	0.132
Fucoxanthin	0.219 <sup>a</sup>	0.219 <sup>a</sup>	0.473 <sup>a</sup>	0.473 <sup>a</sup>	0.049	0.089	– 0.151	– 0.169 <sup>a</sup>
19' HF	0.459 <sup>a</sup>	0.451 <sup>a</sup>	0.634 <sup>a</sup>	0.634 <sup>a</sup>	0.292 <sup>a</sup>	0.283 <sup>a</sup>	0.069	0.014
Zeaxanthin	0.736 <sup>a</sup>	0.736 <sup>a</sup>	0.585 <sup>a</sup>	0.585 <sup>a</sup>	0.613 <sup>a</sup>	0.486 <sup>a</sup>	0.480 <sup>a</sup>	0.421 <sup>a</sup>
Alloxanthin	0.415 <sup>a</sup>	0.415 <sup>a</sup>	0.450 <sup>a</sup>	0.450 <sup>a</sup>	0.302 <sup>a</sup>	0.231 <sup>a</sup>	0.053	0.074
(b) Water column (5–50 m) integrated concentrations								
Chlorophyll <i>a</i>	0.189	0.160	0.473 <sup>b</sup>	0.398 <sup>b</sup>	0.347 <sup>b</sup>	0.354 <sup>b</sup>	0.138	– 0.114
19' BF	0.166	0.130	– 0.118	– 0.153	0.292	0.200	0.254	0.184
Fucoxanthin	0.032	0.027	0.264	0.169	0.139	0.372 <sup>b</sup>	– 0.176	– 0.441 <sup>b</sup>
19' HF	0.094	0.074	0.352	0.250	0.300	0.415 <sup>b</sup>	0.028	– 0.243
Zeaxanthin	0.457 <sup>a</sup>	0.400 <sup>a</sup>	0.524 <sup>b</sup>	0.502 <sup>b</sup>	0.419 <sup>a</sup>	– 0.028	0.652 <sup>a</sup>	0.672 <sup>a</sup>
Alloxanthin	0.003	– 0.050	0.099	– 0.032	0.221	0.082	0.002	– 0.049

<sup>a</sup>  $p < 0.01$ .

<sup>b</sup>  $p < 0.05$ .



The vertical distribution of the two common heterotrophic ciliates was quite different. The nano-sized heterotrophic oligotrich generally co-occurred with chlorophyll *a* and the mixotrophic nano-ciliate (Fig. 6). In contrast, peak concentrations of the micro-sized heterotrophic oligotrich often occurred above the chlorophyll maximum, especially during nighttime hours when part of the population appeared to migrate up to near surface depths (Fig. 5).

As stated by Jonsson (1989), planktonic ciliates usually show a non-random vertical distribution, often characterised by accumulations close to the surface or around the pycnocline. This seems to be a consequence of the combined effects of negative geotaxis (upwards swimming) and rheotaxis. Our results are consistent with this point of view. Nano-ciliates and *M. rubrum* accumulated at the chlorophyll maximum depth located below the pycnocline where turbulence is low. However, the micro-heterotrophs showed a bimodal distribution with peaks at surface and below the pycnocline and temporal changes, a variable distribution more difficult to explain simply on the basis of ciliate behaviour.

#### 4.2. Relations with chlorophyll *a* and carotenoids

The positive correlation found between plastidic ciliates and chlorophyll *a* in discrete depth samples (Table 4a) reflects the co-incident distributions apparent in Figs. 2 and 4. This finding contradicts results obtained in the Catalan Sea (Dolan and Marrasé, 1995), where mixotrophic ciliates, considered as exclusively *Laboea* and *Tontonia*, were mostly restricted to the near-surface layer. Correlations of this ciliate category of large mixotrophs with carotenoids indicates coincident distributions as well (Table 4a).

Similar to our findings (Table 4b), previous studies report a lack of correlation between chlorophyll *a* and mixotrophic oligotrichs when data are integrated through the water column (Stoecker et al., 1989; Sime-Ngando et al., 1992), although a positive relationship was found for some species when considered independently (*Laboea strobila* and *M. rubrum* in Stoecker et al., 1989). Among chlorophyll-containing ciliates, we found only *M. rubrum* to be correlated with chlorophyll *a* (Table 4b).

Heterotrophic nano-ciliates were correlated with chlorophyll *a* both for discrete depth samples or integrated through the water column. In contrast, there was a lack of correlation between heterotrophic micro-ciliates and chlorophyll *a*. In other marine systems, both positive relationships (Booth et al., 1993; Dolan and Marrasé, 1995) and lack of correlation have been reported (Stoecker et al., 1989; Sime-Ngando et al., 1992). Obviously, this relationship may vary from one system to another depending on the water column properties and plankton structure.

We found an overall positive correlation of the carotenoid zeaxanthin from cyanobacteria with all types of ciliates; a strong relationship was even detected between zeaxanthin and *M. rubrum*. Clearly, for *M. rubrum*, this relationship reflects a co-occurrence without trophic interaction. In contrast, we might expect a trophic relationship between mixo- and heterotrophic ciliates < 30 µm and cyanobacteria as stated by Rassoulzadegan et al. (1988). Another interesting point is the negative relationship between heterotrophic micro-ciliate biomass and fucoxanthin (mainly

Table 5  
Estimates of ciliate abundance and biomass in different marine systems

System	Interval of Integration	Ciliate abundance ( $10^7$ cell $m^{-2}$ )	Ciliate biomass ( $mg\ C\ m^{-2}$ )	Comments	Reference
N W Mediterranean	5–50 m	14.6	75.9 <sup>a</sup>	avg. 40 profiles, May	This study
	0–80 m	3.3	125	avg. 8 profiles, June	Dolan and Marrassé (1995)
	0–30 m	2.1	37.8	avg. 12 profiles, July	Revelante and Gilmartin (1990)
Pacific Ocean	0–80 m	42.0	213	avg. 8 profiles, May–June	Strom et al. (1993)
	0–80 m	7.4	416	avg. 18 profiles, August	Sime-Ngando et al. (1992)
	0–20 m	0.24	11	Samples at the Reef face, February	Ayukat (1991)
	0–120 m	0.59	10.2	avg. 5 profiles, March–April	Stoecker et al. (1996)
Subarctic Pacific	0–120 m	0.88	23.1	avg. 4 profiles, October	
	0–113 m	63.7	842.2	avg. 6 profiles, Summer	Tumantseva (1982)
Subantarctic Pacific	0–75 m	28.8	846.8	avg. 6 profiles, Summer	
	0–82 m	61.3	1432.6	avg. 9 profiles, Summer	
Indian Ocean	(0–12°N)	1.7 <sup>b</sup>	25	avg. 4 profiles, September–October	Leakey et al. (1996)
	(12–24°N)	3.6 <sup>b</sup>	49	avg. 5 profiles, September–October	
Central	(0–10°S)	3.75 <sup>c</sup>	326.5	avg. 5 profiles, August–September	
	(10–20°S)	2.3 <sup>c</sup>	155.3	avg. 6 profiles, August–September	Sorokin et al. (1985)
	(20–30°S)	2 <sup>c</sup>	197.3	avg. 5 profiles, August–September	

Atlantic Ocean								
Georges Bank	0–36 m	10.3	—	—	—	—	—	Stoecker et al. (1989)
Lime Cay	0–20 m	2.9–11.8	5.6–41.6	—	—	—	—	Lynn et al. (1991)
NABE Site 89	0–20 m	7.65	127.3 <sup>b</sup>	—	—	—	—	Stoecker et al. (1994)
NABE Site 90	0–20 m	4.24	53.7 <sup>b</sup>	—	—	—	—	Lessard and Murrell (1996)
Sargasso Sea	0–150 m	6	45	—	—	—	—	
	0–150 m	16.5	90	—	—	—	—	
Polar Regions								
Iceland/Greenland Sea	0–50 m	2.69	—	—	—	—	—	Putt (1990)
Barents Sea/N. Svalbard	0–50	2.97	—	—	—	—	—	
Hjeltefjorden	0–100 m	16.9	—	—	—	—	—	Verity and Vernet (1992)
Fauskangerpollen	0–70 m	22.6	—	—	—	—	—	
McMurdo Sound	0–150 m	—	342	—	—	—	—	Stoecker et al. (1995)
Weddell Sea	0–100 m	0.14–2.34	3–570	—	—	—	—	Garrison and Buck (1989)

<sup>a</sup>Based on oligotrich biomass.

<sup>b</sup>Data from a figure.

<sup>c</sup>Maximal estimates.

Table 6  
Incidence of mixotrophic ciliates in different marine systems. Mixotroph abundance and biomass are in cell  $l^{-1}$  and  $\mu g C l^{-1}$ , respectively

Marine system	Period sampled	Depth sampled	Mixotroph abundance	Mixotroph biomass	% of ciliate abundance	% of ciliate biomass	Remarks	Reference
NW Mediterranean								
Ligurian Sea	May	5–50 m	1120	0.59	46	39	All plastidic oligotrichs	This study
Blanes Bay	3 years	0.5 m	417	1.02	11	19	Only <i>Tontonia</i> , <i>Laboea</i>	Vaqué et al. (1997)
Catalan Sea	June	0–20 m	70	—	18	48	Only <i>Tontonia</i> , <i>Laboea</i>	Dolan and Marrasé (1995)
Ligurian Sea	June	0–80 m	24	—	6	21.4	Only <i>Tontonia</i> , <i>Laboea</i>	Bernard and Rassoulzadegan (1994)
Adriatic Sea	1 year	0 m	—	—	—	51	All plastidic oligotrichs	Revelante and Gilmartin (1990)
	July	0–30 m	—	—	29	—	Only <i>S. conicum</i> , <i>S. delicatissimum</i>	
Other Systems								
NABE 89	May	0–20 m	3006	4.6 <sup>a</sup>	73	67	All plastidic oligotrichs	Stoecker et al. (1994)
NABE 90	May–June	0–20 m	1364	1.8 <sup>a</sup>	60	58.5	All plastidic oligotrichs	Stoecker et al. (1994)
Georges Bank	July	0–36 m	978	1.9	33.5	—	All plastidic oligotrichs	Stoecker et al. (1989)
Great Harbor	1 year	0 m	1167	2.0	—	—	All plastidic oligotrichs	Stoecker et al. (1987)
Nantucket Sound	July	0–9 m	2204	2.9	55	—	All plastidic oligotrichs	Stoecker et al. (1987)
Lime Cay	1 year	5 m	—	—	12	25	Only <i>Tontonia</i> , <i>Laboea</i>	Lynn et al. (1991)
Pacific Seamount	August	0–20 m	—	—	—	76.9	All plastidic oligotrichs	Sime-Ngando et al. (1992)
Off summit	August	0–80 m	—	—	—	20	All plastidic oligotrichs	Stoecker et al. (1996)
Equatorial Pacific	March–April	0–120 m	4.53	0.02	9	26	All plastidic oligotrichs	Stoecker et al. (1996)
	October	0–120 m	1.77	0.01	2	6	All plastidic oligotrichs	Verity and Vernet (1992)
Hjeltefjorden	June	0–100 m	117	—	4.5	—	All plastidic oligotrichs	
Fauskangerpollen	June	0–70 m	67	—	1.9	—	All plastidic oligotrichs	Putt (1990)
Iceland/Greenland	Summer	0 m	428	3	52	—	All plastidic oligotrichs	
		50 m	201	—	8	—	All plastidic oligotrichs	
Barents/N Svalbard	Summer	0 m	318	1.7	40	—	All plastidic oligotrichs	
		50 m	63	—	16	—	All plastidic oligotrichs	
McMurdo Sound	Spring bloom	5 m	—	—	25	—	All plastidic oligotrichs	Stoecker et al. (1995)

<sup>a</sup>Data from a figure.

from diatoms). The presence of diatoms suggests the occurrence of a “herbivorous” trophic chain with an increased presence of copepods and copepod grazing pressure to which micro-ciliates may have been particularly sensitive. We have found that copepods preferentially consume micro-sized oligotrichs relative to nano-sized forms (Pérez et al., 1997).

#### 4.3. Diel variability of integrated biomass of ciliates

As expected at the site, horizontal advective movements remained weak throughout the period sampled. Thus temporal changes in integrated biomass are likely due to actual changes rather than horizontal flow of water masses. The cyclical changes we found in integrated biomass were quite marked; unfortunately, comparative data are virtually non-existent. The pattern we observed was similar to that found for *Laboea strobila* at 3 m depth in Long Island Sound (McManus and Fuhrman, 1986), which exhibited nighttime minima and late afternoon maxima.

The observed changes may be related to the nocturnal upward migration of copepods. In general, the minima in ciliate concentrations occurred around sunrise and could be a consequence of copepod feeding during the night. Estimates of nighttime feeding of copepods support this hypothesis. From estimates of copepod abundance, an average of 12 copepod  $l^{-1}$  (Pérez et al., 1997), and of filtration rates, an average of 2 ml copepod $^{-1}$  h $^{-1}$  (Pérez et al., 1997), and the assumption that copepod concentrations in the surface layer are 2 to 3 times higher during the night relative to daylight hours, as observed in coastal Mediterranean waters (Pagano et al., 1993; Christaki et al., 1998), we estimate that copepods would clear 50–75% of the surface layer of ciliates during a 10 h night. As the changes we observed represent about 50% of the ciliate biomass, it seems possible that they could be the result of copepod feeding during the night.

#### 4.4. Estimated grazing impact of ciliates

We can provide rough estimates of the grazing impact of ciliates within the surface layer (5–50 m) during the cruise on the basis of: (1) the biomass of dominant ciliate species stocks, (2) net growth rates estimated at 20 m depth during in situ incubations (Pérez et al., 1997), (3) values of daily primary production estimated by Chiaverini et al. (1995), and (4) assumption of a growth efficiency of 50% for marine oligotrichs (Verity, 1991). The results of these calculations are presented in Fig. 10. While carbon consumed by ciliates increased slightly from 1.1 mg m $^{-3}$  d $^{-1}$  on 11 May to 2.2 mg m $^{-3}$  d $^{-1}$  on 30 May, the estimated grazing impact of ciliates on primary production varied greatly. The largest impact was estimated for the 30 and 14 May with  $\sim$  40 and 17% of primary production consumed by ciliates; on 11 and 27 May the grazing impact represented only 8% to 10% of primary production. Such variability is due primarily to differences in primary production on four dates. Values of primary production on 11, 14, 27, and 30 May were 13.2, 8.4, 18.0 and 5.5 mg C m $^{-3}$  d $^{-1}$ , respectively. Our estimates may be conservative because they involved only three oligotrich species for which net growth rates were measured.

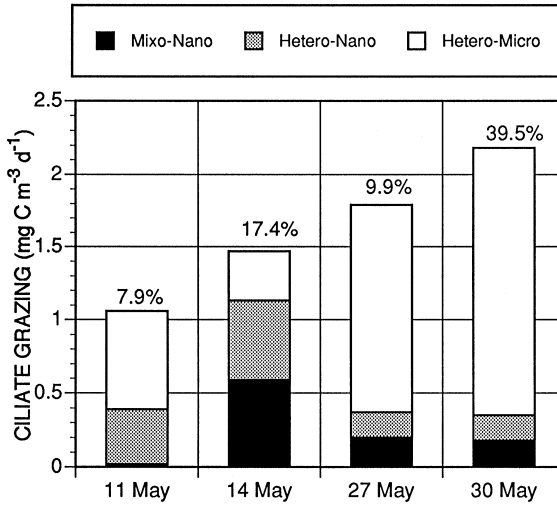


Fig. 10. Estimated grazing impact of the three dominant oligotrich ciliates found. Ciliate grazing is in  $\text{mg m}^{-3} \text{d}^{-1}$ . Numbers on the bars give the percent of primary production consumed on four dates by the three oligotrichs.

Nevertheless they are in the range reported in the review of Pierce and Turner (1992), and the last estimate on 30 May approaches the value of 44% given by Dolan and Marrasé (1995), who averaged the mean of ranges reported in the review of Pierce and Turner (1992). It should be noted, however, that calculations of consumption rates are highly dependent on estimates of growth efficiency (e.g., Straile, 1997).

#### 4.5. Contribution of photosynthetic ciliates to chlorophyll *a*

The estimated contribution of plastidic ciliates to chlorophyll *a* in the surface layer was less important than one might expect, especially at depths above or below the chlorophyll *a* maximum depth. This largely reflected the facts that the water column distribution of the chlorophyll-containing ciliates coincided with chlorophyll *a* and the chlorophyll *a* concentrations were relatively high. Earlier works reported mixotroph maximal concentrations in near-surface samples and in consequence larger contributions to chlorophyll *a* crop in the generally chlorophyll-poor extreme upper water column. For example, in the Nordic Seas, Putt (1990) estimated the contribution of a single species to be up to 24% when chlorophyll is  $\leq 0.2 \mu\text{g l}^{-1}$ , and Dolan and Marrasé (1995) reported peak values around 20% in the surface of the Catalan Sea. During May 1995 at our site, chlorophyll *a* concentration was  $\leq 0.2 \mu\text{g l}^{-1}$ , even at 5 m depth, and mixotrophs represented a modest contribution. However, as suggested by Putt (1990), mixotrophic ciliates may account for a substantial part of chlorophyll in more oligotrophic systems, or seasons, and in the microplankton size fraction of chlorophyll.

## Acknowledgements

The work reported is part of the doctoral dissertation of M.T. Pérez. We are indebted to V. Andersen for organising the DYNAPROC Cruise Program, and the captain and crew of the *Sûroit* for ship operations. We also thank two anonymous referees who greatly improved an earlier version of the manuscript. Financial support was provided by the C.N.R.S., the Commission of the European Communities through the contract “MEDEA” (MAS3 CT95-0016) and a Eusko Jaurlaritz (Basque government) grant to M.T. Pérez.

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