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Planktonic ciliate distribution relative to a deep chlorophyll maximum: Catalan Sea, N.W. Mediterranean, June 1993

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Abstract—Vertical distributions and relative contributions of distinct trophic guilds of ciliates were investigated in an oligotrophic system with a deep chlorophyll maximum (DCM) in early summer. Ciliates were classified as *heterotrophic*: micro and nano ciliates, tintinnids and predacious forms or *photosynthetic*: large mixotrophic oligotrichs (*Laboea strobilia*, *Tontonia* spp.), and the autotrophic *Mesodinium rubrum*. Variability between vertical profiles (0–200 m) was relatively low with station to station differences (C.V.s of ~30%) generally larger than temporal (1–4 day) differences (C.V.s of ~15%), for integrated concentrations. Total ciliate biomass, based on volume estimates integrated from 0–80 m, averaged ~125 mg C m^{-2}, compared to ~35 mg m^{-2} for chlorophyll *a* (chl *a*), yielding a ciliate to chl ratio of 3.6, well within the range of 1 to 6 reported for the euphotic zones of most oceanic systems. Heterotrophic ciliate concentrations were correlated with chl *a* concentration ($r = 0.83$ and 0.82, biomass and cells l^{-1}, respectively) and averaged ~230 cells l^{-1} in near surface samples (chl $a = 0.1\ \mu g\ l^{-1}$) to ~850 cells l^{-1} at 50 m depth, coinciding with the DCM (chl $a = 1$–$2\ \mu g\ l^{-1}$). Tintinnid ciliates were diverse (36 species in 19 genera) but a minor part of heterotrophic ciliates. Nanociliates represented <1% of heterotrophic or total ciliate biomass, in contrast to reports on near-shore ciliate communities. Predacious ciliates were very rare. Large mixotrophic oligotrichs, while a minor portion of ciliate cells l^{-1}, were an important part of total ciliate biomass, representing 63% at 5 m and 21% integrated over 0–80 m. *Mesodinium rubrum* was found throughout the water column, usually with a sub-surface peak (~100 cells l^{-1}). Concentrations of neither large mixotrophic oligotrichs, nor the autotrophic *M. rubrum*, were correlated with chl *a*. Estimates of the contribution of photosynthetic ciliate chl (mixotrophic and autotrophic) to total chl *a* (based on literature values of chl *a* $cell^{-1}$) ranged from ~20% in some surface samples to <0.5% in the DCM.

INTRODUCTION

In diverse marine systems, subsurface chlorophyll maximum layers are common, and a variety of governing mechanisms such as nutrient supply, differential grazing, and cell sinking have been proposed to account for them (e.g., Bienfang *et al.*, 1983). In the oligotrophic Catalan Sea, a deep chlorophyll maximum (DCM) is present from early spring to autumn, between 40 and 60 m depth, coinciding with depth of both nitrate and phosphate nutriclines (Estrada *et al.*, 1993). Production in the DCM ranges from 15 to

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30% of total carbon fixation, and *in situ* growth has been suggested as the primary mechanism maintaining the DCM (Estrada, 1985a). However, the role of phytoplankton grazers in the system is unclear. A relatively small contribution of phytoplankton to total plankton was invoked recently to explain a poor correlation between DNA and chlorophyll in this system when the DCM is present (Berdalet and Estrada, 1993). While significant diatom populations are occasionally found (e.g., Estrada, 1985a,b), phytoplankton composition during the stratified period is generally dominated by nano and picoplanktonic forms (Delgado *et al.*, 1992; Latasa *et al.*, 1992). Hence, one would expect a significant population of grazers on small phytoplankton. Grazing on picoplankton is usually attributed to nano and micro-sized protists (nanoflagellates and ciliates), and grazing on nanoplankton is generally assigned to micro-sized ciliates (Pierce and Turner, 1992).

Ciliates are commonly considered as herbivores, but rather than being a homogenous assemblege they are actually a community composed of variable proportions of more or less distinct trophic guilds (Dolan, 1991a). Among oligotrich ciliates, for example, are species which are strict heterotrophs which feed on pico and nanophytoplankton, as well as mixotrophic species which, in addition to phagotrophic feeding, sequester and exploit chloroplasts from ingested algae (see reviews by Stoecker, 1991; Dolan, 1992). Mixotrophic oligotrichs fix carbon at rates estimated to represent a substantial (>50%) fraction of cell carbon demand, 2.5–7.5% of total body carbon h^{-1} (Stoecker and Michaels, 1991). Estimates of the contribution of mixotrophic oligotrichs to total ciliates (% cell ml^{-1}) range from <10% for a Norwegian Fjord (Verity and Vernet, 1992) in June to over 70% in surface waters of the N. Atlantic during the spring bloom (Stoecker *et al.*, 1994a) and up to 100% in surface samples from the coastal Ligurian Sea during spring and summer (Bernard and Rassoulzadegan, 1994). Mixotrophic oligotrich ciliates can form an important part of the chlorophyll crop; estimates of their contribution to total chlorophyll range up to 24% for surface samples from the Nordic Seas (Putt, 1990).

The other type of photosynthetic ciliate, the autotrophic *Mesodinium rubrum*, has a cosmopolitan distribution (Crawford, 1989). Blooms of this species have been noted in nearshore waters for over a hundred years (see Taylor *et al.*, 1971), and as a major component of upwelling ecosystems, *M. rubrum* has been the focus of intensive studies (e.g., Packard *et al.*, 1978; Dugdale *et al.*, 1987; Wilkerson and Grunseich, 1990). In nearshore waters, it is often a member of the ciliate community year-round (e.g., Montagnes and Lynn, 1989; Verity *et al.*, 1993; Bernard and Rassoulzadegan, 1994). However, very little data exists on *M. rubrum* in oligotrophic systems in general, and *M. rubrum* is reputed to be rare in the open Mediterranean (Lindholm, 1985).

Among heterotrophic ciliates, different types can be distinguished. Herbivorous oligotrichs and tintinnids have received the greatest amount of attention (e.g., Pierce and Turner, 1992). In recent years, nanociliates (cell size <20 μm long) have been identified as potentially important grazers of picoplankton, both heterotrophic bacteria and ultraphytoplankton (Sherr and Sherr, 1987; Sherr *et al.*, 1991). These grazers on small particles are competitors of microflagellates, but unlike microflagellates, nanociliates are efficiently consumed by copepods (Gifford and Dagg, 1988; Tiselius, 1989; Dolan, 1991b) and also by other, predacious, ciliates (Dolan and Coats, 1991a). The abundance of predacious ciliates has been linked to the abundance of nanociliates (Dolan, 1991a). Recently, the loricate tintinnid ciliates have been proposed as distinct forms which depend on "patches" of relatively high nanoplankton abundance (Rassoulzadegan, 1993).

Added to the complexity of the ciliate community, little is known concerning water column distributions of ciliates, relative to our knowledge of mesozooplankton (Longhurst and Harrison, 1989). There is a limited amount of data on ciliate distributions relative to DCMs (e.g., Chester, 1978; Beers *et al.*, 1980; Tsuda *et al.*, 1989) and water column distributions of different trophic groups in productive waters (e.g., Stoecker *et al.*, 1989; Putt, 1990; Dolan, 1991a). However, data from different systems are needed on the different groups of ciliates to assess the relative importance of the various roles which these protists may assume, roles ranging from grazers on prokaryotic phytoplankton (e.g., *Synechococcus*, *Prochlorococcus*) to potentially significant contributors themselves to the chlorophyll crop. The present study concerns the vertical distribution and relative contributions of different groups of ciliates in an oligotrophic environment with a pronounced DCM. To our knowledge, no comparable data exist despite the widespread nature of DCMs and the predominance, on an areal basis, of oligotrophic marine systems.

METHODS

Sampling

Between 11 June and 15 June 1993, as part of the MESOSCALE 93 cruise, water samples were obtained from six stations located along a transect between the coast of Spain and the Balearic Islands in the Western Basin of the Mediterranean Sea (Fig. 1 and Table 1). Water column depth range from ~500 m at Sta. 1 to ~2000 m at Sta. 6. All six stations were sampled on 14 June, with additional water column samples taken from two stations at 1–4 day intervals, yielding a total of nine water column profiles. Samples for ciliates and chlorophyll *a* determinations were obtained with a CTD-Niskin bottle rosette using 5 l Niskin bottles. Depths samples were usually 5, 10, 20, 30, 40, 50, 60, 70, 80, 100, 200 m.

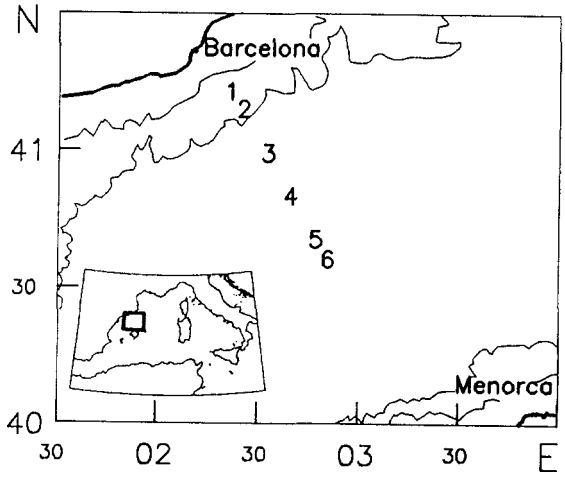

Fig. 1. Sampling stations along a transect of approximately 100 nautical miles between Barcelona and the island of Minorca in the N.W. Mediterranean Sea.

Table 1. *Station locations and sampling times; for station orientations see Fig.* 1. *Thin lines represent the* 500 m *and* 1000 m *isobaths*

Station	Location	Dates	Time
1	41°11.2′N, 2°19.5′E	14 June	16:05
2	41°7.2′N, 2°22.7′E	10 June	7:45
2	41°6.3′N, 2°23.4′E	14 June	10:00
3	40°57.6′N, 2°30.5′E	14 June	17:54
4	40°48.4′N, 2°37.7′E	14 June	19:45
5	40°39′N, 2°45.0′E	11 June	7:43
5	40°39.4′N, 2°44.8′E	14 June	21:41
5	40°39.4′N, 2°45.4′E	15 June	7:52
6	40°35.0′N, 2°48.5′E	14 June	22:58

Sample treatment

For chlorophyll determinations, 25–200 ml from each bottle were filtered through GF/F filters. The filters were homogenised in 90% acetone, the suspension cleared by centrifugation, and fluorescence determined with a Turner Designs fluorometer following standard protocols (Yentsch and Menzel, 1963).

For ciliate enumeration, 500 ml of whole water from each Niskin bottle was preserved with acid Lugol's (1–2% final concentration) and stored refrigerated and in darkness, except during transport and sedimentation. Samples were concentrated via sedimentation in 500 ml graduated cylinders. After settling for 2–4 days, the top 400 ml of sample was slowly siphoned off with small-bore (0.5 cm dia.) tubing. Examination of sedimented supernate revealed a negligible quantity of ciliates (<1% of total cells). 50 or 100 ml of concentrates, representing 250–500 ml whole water, were settled in standard Ziess settling chambers and the entire surface of the settling chamber was scanned at 480 × with an inverted microscope equipped with phase-contrast optics.

Oligotrich ciliates, were identified to genus when possible (following Montagnes and Lynn, 1991) and placed in cell-length categories ranging from 10 to 70 μm in 10 μm increments. Large (60–150 μm long) mixotrophic oligotrich species with very distinctive gross morphologies (see Laval-Peuto and Rassoulzadegan, 1988), *Laboea strobila*, *Tontonia appendiculariformis*, *T. gracillima* and the autotrophic ciliate *Mesodinium rubrum* were enumerated separately. Tintinnids were identified via lorica morphology using species descriptions found in Balech (1959), Campbell (1942), Jörgensen (1924), Kofoid and Campbell (1929, 1939) and the taxonomic scheme of Corliss (1979). Empty lorica were not enumerated.

Biomass estimates

Taxa were placed into trophic categories: (1) Nanociliates—ciliates less than 20 μm in length, (2) Autotrophic—*Mesodinium rubrum*, (3) Large mixotrophic oligotrichs—*Laboea strobila, Tontonia appendiculariformis*, *T. gracillima*, (4) Predacious ciliates—forms which feed on large particles (e.g., *Cyclotrichium*) or raptorially (e.g., *Didinium*, *Lacrymaria*), (5) Heterotrophic—the default category. The use of Lugol's fixative precluded identification of mixotrophic oligotrichs without distinctive gross morphologies

(e.g., *Strombidium* spp.). Hence, the heterotroph group likely contained some mixotrophic forms. For some analyses, all non-photosynthetic taxa were pooled.

Biovolumes of non-tintinnid heterotrophic ciliates were estimated from median dimensions of the size classes. For biovolume estimates of large mixotrophic oligotrichs, 50 cells each of the 3 species were measured with an ocular micrometer. The average cell volume of *Mesodinium rubrum* was calculated from the average dimensions of 100 cells. The biovolume estimates were converted to carbon equivalents by the factor experimentally derived for Lugol's-fixed marine oligotrichs, 0.2 pg C per μm^3 (Putt and Stoecker, 1989), except for tintinnid carbon, which was estimated from the experimentally derived factor, 0.053 pg C μm^3 lorica volume (Verity and Langdon, 1984).

Regression analyses

Pearson's correlation coefficients were calculated to examine the relationship of chl *a* concentration to the numerical abundance and calculated biomasses of heterotrophic ciliates, tintinnids, large mixotrophic oligotrichs, and *Mesodinium rubrum*. For these analyses, concentrations in discrete samples were used with no data transformation. Use of square root or log transformations resulted in very minor changes in correlation parameters.

Tintinnid diversity

From casual observations, the tintinnid fauna appeared unusually species-rich. Species diversity of tintinnids was examined with plots of cumulative numbers of species versus cumulative numbers of individuals, a common method in marine studies (Gray, 1994). Starting with the first depth sampled at the first station, cumulative total tintinnids counted was plotted against cumulative total number of species encountered from the first to the 90th sample. For comparison, data from a eutrophic coastal plain estuary, the Chesapeake Bay (detailed in Dolan and Coats, 1990, 1991b; Dolan, 1991a), was also plotted. Chesapeake data were from June–August from three stations, separated by 10 nautical miles, sampled at two week intervals. As tintinnids were restricted to oxygenated waters (Dolan and Coats 1991b), only data from samples from surface waters (4–5 depths per station) were used, yielding a total number of 65 samples over a sampling period of 2.5 months. It should be noted that, for both data sets, tintinnids were enumerated in samples of sedimented whole water, which yields significantly higher tintinnid cell counts than screened, or sieved, or net concentrated samples (Brownlee and Jacobs, 1987; Buck *et al.*, 1992).

Estimates of photosynthetic ciliate chlorophyll

Estimates of the chl *a* contents of mixotrophic and autotrophic ciliates were made with values from the literature. For *Mesodinium rubrum*, chl *a* per cell was calculated as 3×10^{-5} μg $cell^{-1}$, based on an average cell volume of 8.5×103 μm^3 ($n = 100$ cells) and a conversion factor of 3.6 fg chl *a* per μm^3 for Lugol's-fixed *M. rubrum* (Stoecker *et al.*, 1991). For large mixotrophic oligotrichs, a value of 1.5×10^{-4} μg chl *a* $cell^{-1}$ was used, the average of $\sim 0.5 \times 10^{-4}$ reported by Putt (1990) for mixotrophic oligotrichs from the

Nordic Seas and ~2.5 × 10^{-4} reported by Stoecker *et al.* (1988) for cultured *Laboea strobila*. Unless otherwise noted, all data reported are ±S.D.

RESULTS

Ciliates of the Catalan Sea

Of the ciliate taxa commonly found (present in >10% of the samples), 15 non-tintinnid or aloricate forms were distinguished (Table 2). The autotrophic *Mesodinium rubrum* was often present throughout the water column; three species of large mixotrophic oligotrichs were found, generally restricted to waters above 60 m depth. Of the three mixotrophs, *Tontonia appendiculariformis* was the most common. The ciliate community was numerically dominated by oligotrichs of the genus *Strombidium*, considered in this study as exclusively heterotrophic. Both cell numbers and biomass of heterotrophic ciliates were usually dominated by *Strombidium* sp. e, a cone-shaped species, 50–60 μm in length. Among the nanociliates, forms ranging in length from 10 to 20 μm, were species of *Strombidium*, *Strobilidium*, *Balanion* and *Cyclidium*. Nanociliates were present in most samples, including those from 200 m, but rarely in excess of 50 cells l^{-1} and were a minor component heterotrophic ciliate biomass. The tintinnid fauna was diverse with 32 species in 19 genera. However, there were relatively few common species, only 9 out of 32 (Table 3) and tintinnids usually represented <5% of heterotrophic ciliate cells or biomass. Among the common tintinnid species, most forms had lorica diameters of ~40 μm.

Table 2. Ciliate species, or forms, commonly encountered (≥10% of the samples) with "L" referring to length in microns and "max conc" maximum concentration in organisms l^{-1}

Group	Species or type	L (μm)	Max conc	Depth
Autotrophic Ciliate	*Mesodinium rubrum*	30	180	70 m
Mixotrophic Oligotrichs	*Laboea strobila*	150	135	5 m
	Tontonia appendiculariformis	100	44	5 m
	T. gracillima	60	26	5 m
Heterotrophic Oligotrichs	*Strombidium* sp. a	15	56	50 m
	Strombidium sp. b	25	176	20 m
	Strombidium sp. c	35	176	40 m
	Strombidium sp. d	45	400	50 m
	Strombidium sp. e	55	596	40 m
	Strombidium sp. f	85	68	60 m
	Strobilidium sp. a	15	88	20 m
	Strobilidium sp. b	25	104	70 m
Tintinnids	(See Table 3)	35–300	304	45 m
Prostomid Ciliates	*Balanion* sp. a	25	72	40 m
	Balanion sp. b	15	24	20 m
Scuticociliates	*Cyclidium* sp.	20	16	5 m
Radiolarians	*Acanthocorys* sp.	100	24	40 m
	Monocyrtoinid sp.	75	8	20 m
Copepods	nauplii	—	80	44 m
	post-naupliar	—	20	40 m

Table 3. Tintinnid species found in the Catalan Sea samples with length and oral diameter in microns referring to lorica dimensions. Max Conc gives maximum abundance in cell l^{-1}. *Species are listed as rare if found in <10% of the samples. Cysts refers to presumptive cysts observed in loricas. Parasites refers to observations of specimens with apparent* Dubosquella*-type infections* (i.e., Coats 1988, Coats *et al.*, 1994)

Species	Length, Oral Diameter (μm)	Max conc	Depth	Notes
Acanthostomella conicoides	40, 20	4	50 m	rare
A. obtusa	35, 15	20	50 m	rare
Amphorides gaarderae	50, 30	196	45 m	rare
A. laackmanni	50, 20	12	40 m	rare
A. quadrilineata	100, 45	44	40 m	common, cysts
Canthariella brevis	50, 20	4	200 m	rare
Climacocylis scalaroides	100, 30	8	45 m	rare
Codonella cuspidata	70, 20	4	45 m	rare
C. elongata	85, 40	2	5 m	rare
C. galea	60, 40	4	44 m	rare
Dadayiella ganymedes-cuspis-acutiformis	75, 30	48	40 m	common
Daturella emarginata	250, 50	4	50 m	rare
D. recta	200, 50	4	100 m	rare
Dictyocysta elegans	70, 45	8	100 m	rare
D. magna	75, 50	12	40 m	common
D. minor	50, 30	12	100 m	rare
Eutinttinnus inquilinus	70, 25	4	5 m	rare
E. lusus-undae	150, 40	16	40 m	common, cysts, parasites
E. macilentus	200, 40	4	80 m	rare
E. tenuis	250, 40	8	40 m	common, cysts
Metacylis jörgensenii	70, 45	8	60 m	rare
M. sp.	35, 50	4	60 m	rare
Ormosella trachelium	70, 20	4	100 m	rare
Petalotricha major	90, 75	20	50 m	common
Proplectella globosa	80, 45	4	50 m	rare
Salpingella decurtata	120, 20	16	50 m	rare
S. gracilis	300, 32	32	60 m	common
S. minutissima	100, 10	64	50 m	common
S. laminata	75, 15	4	5 m	rare
S. rotundata	100, 15	8	20 m	rare
Steenstrupiella gracilis	65, 10	8	50 m	rare
S. steenstrupi	120, 40	2	5 m	rare
Stensomella steini	70, 40	108	50 m	common
Tintinnopsis parva	40, 20	20	50 m	rare
Undellopsis marsupialis	100, 50	4	40 m	rare
Xystonellopsis pinnata	110, 25	4	60 m	rare

Predacious ciliates were very rare with only one specimen of *Cyclotrichium* and three specimens of *Lacrymaria* encountered.

Water column distributions

Water column profiles from the 14 June transect showed marked DCMs at all six stations (Fig. 2). The average chl *a* concentration ($\mu g\ l^{-1}$) increased from 0.11 ± 0.03 at 5 m to 1.12 ± 0.19 at 40–50 m depth. Corresponding with chl *a*, heterotrophic ciliate concentrations increased with depth from 190 ± 67 cells l^{-1} at 5 m to 850 ± 298 cells l^{-1} in DCM samples and then decreased to 50 ± 17 cells l^{-1} at 200 m depth. Nanociliates and tintinnids both formed only minor contributions to the cell numbers and biomass of heterotrophic ciliates. Large mixotrophic oligotrichs were usually most abundant in samples from 5 to 20 m depth, 44 ± 22 cells l^{-1}, and absent from samples below 60 m depth. The depth of peak mixotroph cell concentration varied from station to station and was not clearly related to the time of day the water column was sampled. *Mesodinium rubrum* distributions varied from an almost even distribution (~80 cells l^{-1}) throughout the top 60 m of the water column (Sta. 4) to displaying subsurface maxima of very similar magnitudes (110±17 cells l^{-1}) but at different depths ranging from 20–80 m; again, the variability was not clearly related to the time of day samples were taken (Table 1).

Water column profiles of Sta. 5 (Fig. 3), sampled on 11, 14 and 15 June, showed the same trends found among the six transect stations. Although the DCM appeared more pronounced in the 11 June samples relative to the 14 or 15 June samples, stocks integrated over the top 20 or 80 m of the water column were very similar (Table 4). Variability was lower among the three profiles of Sta. 5 than among the six transect stations in terms of chl and heterotrophic and mixotrophic ciliate biomasses (Table 4). Station 2 profiles were not compared due to the loss of the DCM sample from the 10 June profile.

Relationships with chlorophyll a

The relationships between selected ciliate groups and chl in discrete depth samples are shown in Fig. 4. Significant correlations were found only with cells l^{-1} ($r = 0.82$; $n = 88$; $p < 0.01$) or biomass ($r = 0.83$; $n = 88$; $p < 0.01$) of heterotrophic ciliates. Concentrations of large mixotrophic oligotrichs, when present ($n = 43$), were not related to chl, nor were concentrations of *Mesodinium rubrum* ($n = 80$).

Tintinnids

Tintinnid ciliate abundance was not correlated with chl *a* concentration. Plots of cumulative tintinnid species encountered versus cumulative number of individuals counted (Fig. 5) showed a much higher number of species in Catalan Sea samples compared to Chesapeake Bay samples. The shape of the Catalan Sea curve indicates that the number of species would likely continue to increase with the number of individuals counted. In contrast, data from the Chesapeake Bay showed a plateau in the number of species after approximately 250 individuals, despite the larger temporal coverage of the samples (2.5 months for the Chesapeake Bay versus 4 days for the Catalan Sea).

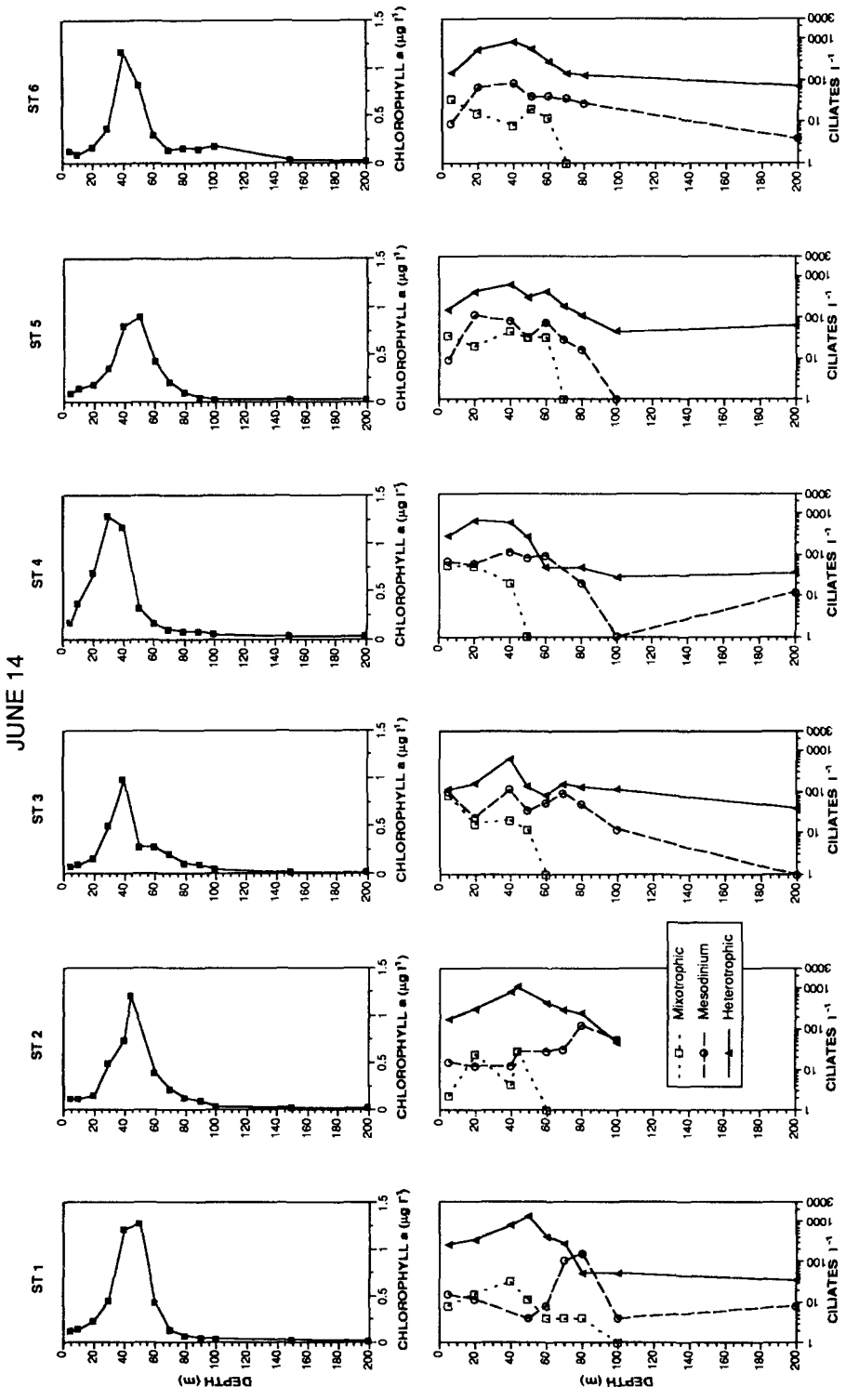

Fig. 2. Spatial variability of water column profiles of chlorophyll *a* and ciliates of distinct trophic guilds. Large mixotrophic ciliates (*Laboea. Tontonia* spp.) were maximal in near surface waters; the autotrophic ciliate Mesodinium rubrum showed variable distributions with maxima occasionally below the DCM. Heterotrophic ciliates were most abundant in the DCM layer.

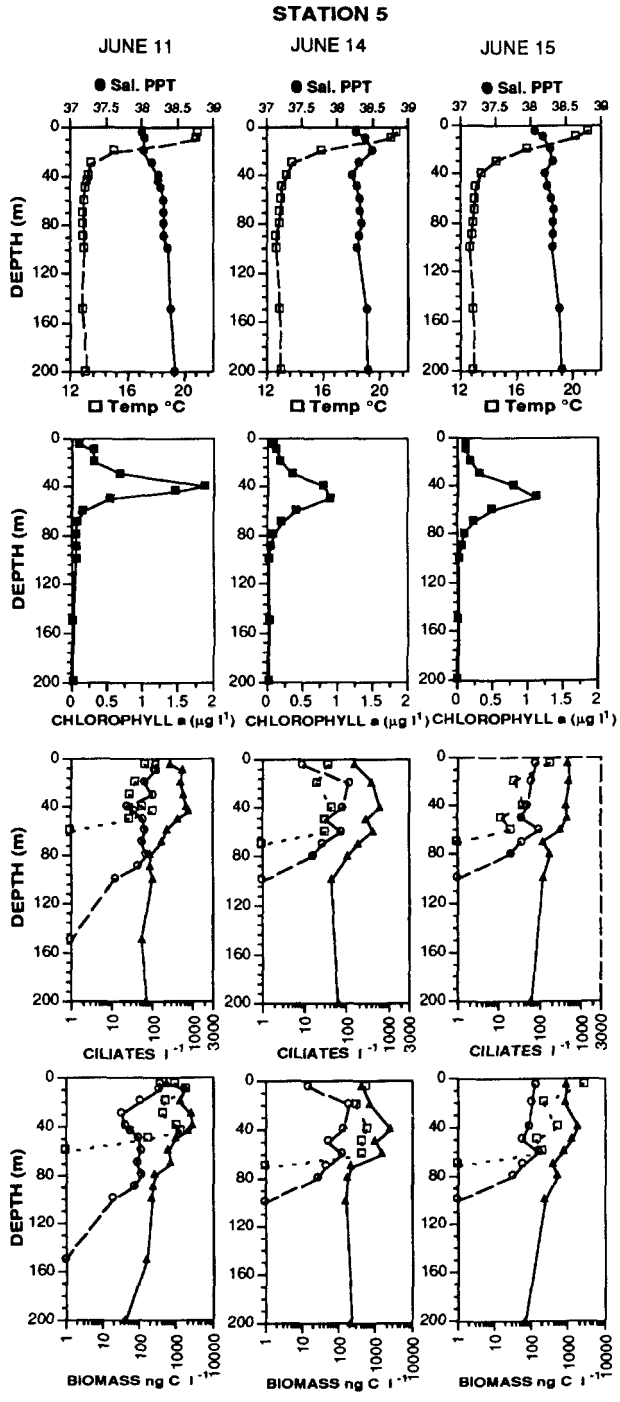

Fig. 3. Temporal variability of water column profiles for Sta. 5. Symbols representing distinct ciliate trophic guilds as in Fig. 2. Note that the vertical distributions of ciliates were similar in terms of cells l^{-1} and ng C l^{-1}.

Table 4. Spatial and temporal variability of integrated concentrations of different ciliate groups. Concentrations were integrated throughout surface waters low in chl a concentration and from the surface to the bottom of the DCM. Spatial variability was calculated based on the six stations sampled on 14 June *and temporal variability from the three profiles obtained at* Sta. 5 *from* 11–15 June (*Table* 1)

	Depth interval integration	Chl *a* (mg m^{-2})	Heterotrophs (10^6 cells m^{-2})	Heterotrophs (mg C m^{-2})	Mixotrophs (10^6 cells m^{-2})	Mixotrophs (mg C m^{-2})	Nanociliate (mg C m^{-2})
Spatial variability							
(avg m^{-2} ± SD, $n = 6$)	0–20 m	3.8 ± 1.93	4.4 ± 2.66	14.3 ± 7.71	0.6 ± 0.41	9.9 ± 6.93	0.1 ± 0.11
	0–80 m	34.9 ± 6.09	31.3 ± 8.31	95.0 ± 29.82	1.4 ± 0.53	20.9 ± 8.34	0.8 ± 0.58
Temporal variability							
(avg m^{-2} ± SD, $n = 3$)	0–20 m	3.6 ± 1.04	7.9 ± 2.57	17.7 ± 6.32	1.5 ± 0.88	22.9 ± 1.04	0.3 ± 0.24
	0–80 m	35.1 ± 1.03	31.6 ± 2.86	92.7 ± 14.35	2.9 ± 0.71	35.1 ± 1.03	1.1 ± 0.41

Table 5. Estimates of water column concentrations of ciliate biomass relative to chflorophyll a in oceanic systems

System	Depth (m) integration	Ciliate Biomass (mg C m^{-3})	Chlorophyll *a* (mg m^{-3})	Ciliates:Chlorophyll (C:chl *a*)	Remarks	Reference
N.E. Pacific	100	17.5	9.6	1.8	avg. of 5 profiles, Feb.	Beers and Stewart, 1969
N.E. Pacific (Slope)	100	100	20	5	avg. of 3 profiles, July	Chester, 1978
N.E. Pacific (Shelf)	40	73	90	0.8	avg. of 3 profiles, July	Chester, 1978
Weddell and Scotia Seas	100	35	11.4	3.1	avg. of 17 profiles, winter ice edge	Garrison *et al.*, 1993
E. Tropical Pacific	60–100	40	11.4	3.5	avg. of 12 profiles, Feb. and Mar.	Beers and Stewart, 1971
Nova Scotia Shelf	50	82	29.8	2.8	avg. of 6 profiles, Mar.	Paranjape *et al.*, 1985
Sub-Arctic Pacific	80	155	25.9	6.0	avg. of 16 profiles, May–Sept.	Strom *et al.*, 1993
Pacific Seamount	80	415	15.1	27.7	avg. of 18 profiles, Aug.	Sime-Ngando *et al.*, 1992
N.W. Mediterraean	80	125	35	3.6	avg. of 8 profiles, June	This study

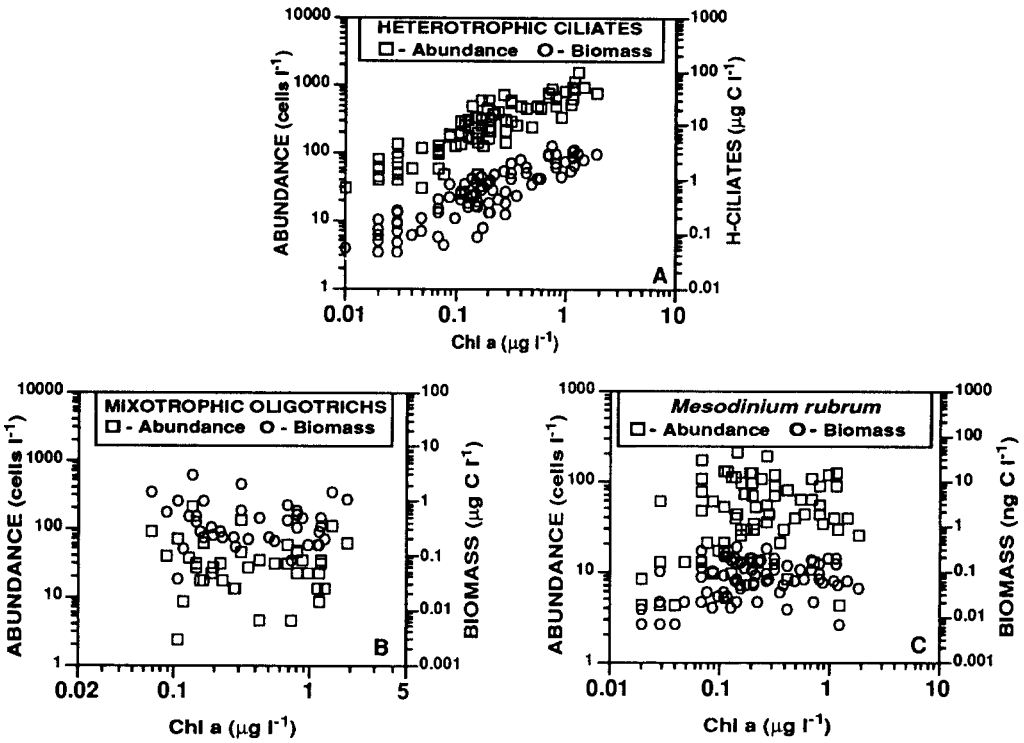

Fig. 4. Relationships between chlorophyll *a* concentrations and the different ciliate groups in discrete depth samples: (A) abundance and biomass of heterotrophic ciliates as a function of chlorophyll concentration; (B) abundance and biomass of large mixotrophic oligotrichs as a function of chlorophyll in samples from 5–50 m depth; (C) abundance and biomass of the autrophic ciliate *Mesodinium rubrum* as a function of chlorophyll concentration. Both cell numbers and biomass of heterotrophic ciliates were correlated with chl *a* concentration (ciliate cells l^{-1} = 540 × chl *a* µg l^{-1} + 127, r = 0.82; ciliate µg C l^{-1} = 1.83 × chl *a* µg l^{-1} + 0.24, r = 0.83).

Chlorophyll of photosynthetic ciliates

Estimates of the contribution of photosynthetic ciliate chlorophyll to total chlorophyll are given in Fig. 6. The peak values of ~20% reflect the low concentration of chlorophyll in surface waters coupled with the peak abundances of large mixotrophic oligotrichs. In the DCM, estimated ciliate chlorophyll represented a very small fraction (0.1–1%) of total chl *a*. In the chlorophyll maximum samples ciliate chlorophyll was largely *Mesodinium rubrum*.

DISCUSSION

Ciliate community composition

The ciliate community in the Catalan Sea shows some similarities as well as singularities compared to other marine systems. Total ciliate biomass, relative to chl concentration, is very similar to other oceanic systems (Table 5). The ratio of ciliate carbon to chl *a* concentration for the Catalan Sea is 3.6 compared to ratios from ~1 to 6 for systems

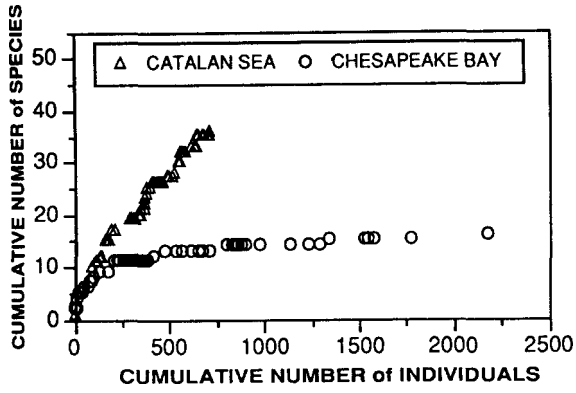

Fig. 5. Cumulative species curves for tintinnid species from samples of the Catalan Sea and the Chesapeake Bay. Chesapeake Bay data from samples gathered from three stations from June to August 1986 (details on sampling in Dolan, 1991). The cumulative volumes of water examined were approximately 25 l for the Catalan Sea and 1 l for the Chesapeake Bay.

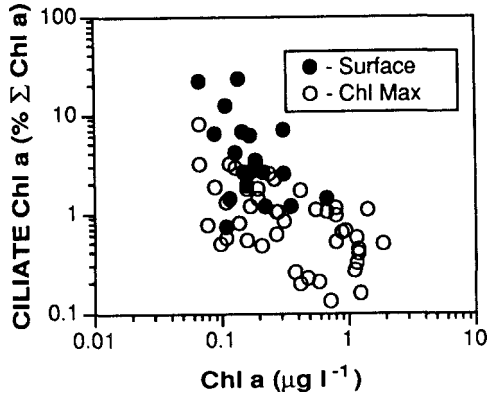

Fig. 6. Estimates of the contribution of photosynthetic ciliates to the chlorophyll crop as a function of chlorophyll concentration in discrete depth samples from the top 80 m of the water column. Chlorophyll contents of ciliates were calculated from literature values; see Methods for details. Note that ciliate chlorophyll is a much larger percentage (up to 20%) of the chlorophyll crop in surface waters (5–15 m) relative to samples from the DCM layer (20–80 m).

ranging from the subarctic Pacific to the Weddell Sea, with the exception of a recent study of an unusual Pacific Seamount community (Sime-Ngando *et al.*, 1992). The ratios are surprisingly consistent when possible sources of variability in ciliate estimates are considered (e.g., microscope measurement errors, differential fixative effects, differences in conversion factors) and differences in the depths of the water columns compared.

The relative contributions of different trophic groups to the Catalan Sea community are considerably more difficult to compare to other systems than total biomass values. For example, nanociliates, those species ≤ 20 μm in length which are thought to feed on

heterotrophic bacteria and ultraphytoplankton (Sherr *et al.*, 1986), are a very minor component of the ciliate community in the Catalan Sea (Table 4). Comparison of nanociliate stock with other systems is hampered as nanociliates have been described as underestimated when samples are examined at magnifications <250×, which is commonly the case (Sherr *et al.*, 1986), and in any event nanociliates are very rarely enumerated separately (Lynn *et al.*, 1991). The few available estimates of nanociliate abundance are from shallow coastal systems (Table 7) in which nanociliate abundances appear to be in excess of total ciliate abundances for the Catalan Sea. Unless the Catalan Sea is unusual among open water systems, and judging from concentrations of total ciliates and chl the system is not (Table 5), nanociliates may be much less important in deep water systems than in coastal systems, both as a component of the ciliate community, and as competitors of microflagellates for picoplanktonic prey.

Equally problematic is comparing the role of mixotrophic oligotrichs in the Catalan Sea to other systems. The fixative we used in our study, acid Lugol's, was employed as it minimises oligotrich cell loss (Ohman and Snyder, 1991; Leakey *et al.*, 1994; Stoecker *et al.*, 1994a,b) and is much more agreeable to work with than an aldehyde-based fixative when a large number of large-volume samples is processed. The distinct disadvantage of Lugol's relative to aldehyde-fixed material is the loss of chl *a* autofluorescence. Mixotrophic oligotrichs, in Lugol's-fixed material, can be identified only from characteristics of gross morphology. Thus, the mixotrophic taxa enumerated in this study were restricted to large taxa with very distinctive gross morphologies (*Laboea strobila* and *Tontonia* spp.) and likely represent an under-estimate of the importance of mixotrophic species in the ciliate community. Despite this probable underestimation in our analysis, mixotrophic taxa in the Catalan Sea appear to be a very significant component of the ciliate community.

Large mixotrophic oligotrichs dominated ciliate biomass in shallow depths (5 m), formed about half the ciliate biomass in the segment 0–20 m, and represented about 20% of total ciliate biomass from 0 to 80 m. Direct comparison to other systems is difficult due to differences in: (a) methodologies used (i.e., enumeration of all plastidic oligotrichs via chl autofluorescence), (b) types of data reported (i.e., cell numbers or biovolumes, or simply proportions), and (c) depths sampled. However, despite these problems, percentage biomass values for the Catalan Sea ciliate community do not appear unusual relative to other systems. In studies which report taxon-specific biomasses (taxa identified via gross morphology), known mixotrophic taxa represent 7–70% of total ciliate biomass, while studies reporting data on all plastidic oligotrichs (identified via chl autofluorescence) have yielded average figures of 51–60% of total biomass (Table 6). In contrast to biomass, the number of mixotrophic oligotrichs in cells l^{-1} appears low (24–70 cells l^{-1}) in the Catalan Sea samples, as it does in reports on other systems in which only *Laboea* and *Tontonia* are considered as mixotrophic taxa. This suggests again that consideration of only the large, distinctive forms of mixotrophs results in underestimation of mixotrophic ciliate cell numbers. However, the similarity in relative importance of mixotrophs (% total ciliate biomass), whether calculated as all plastidic oligotrichs or only *Laboea* and *Tontonia*, suggests that the large distinctive species may often dominate mixotrophic biomass.

The autotrophic ciliate, *Mesodinium rubrum*, was generally present throughout the water column down to 200 m, despite its reputed rarity in Mediterranean waters (Lindholm, 1985). Abundance in the Catalan Sea (10–100 cells l^{-1}) is modest relative to concentrations in upwelling systems, for example, 10^6 cells l^{-1} reported for the Baja California upwelling system (Packard *et al.*, 1978). However, reports of concentrations of

Table 6. Concentrations and relative importance of mixotrophic oligotrichs in marine systems

System	Depths sampled	Sampling period	Mixotroph abundance cell per liter	Mixotrophs as % Σ cells per liter	Mixotrophs as % Σ ciliate biomass	Mixotrophic taxa enumerated	Reference
Nordic Seas	0 m	Jul. Aug.	373	54	—	All Plastidic Oligotrichs	Putt, 1990
	50 m		42	13	—		
Georges Bank (NW Atlantic)	0–35 m	Jul.	1011	37.6	—	All Plastidic Oligotrichs	Stoecker *et al.*, 1989
Villefranche Bay (N.W. Mediterranean)	0 m	1 yr	—	—	51	All Plastidic Oligotrichs	Bernard and Rassoulzadegan, 1993
Great Harbor (N.W. Atlantic coast)	0 m	1 yr	1167	45	—	All Plastidic Oligotrichs	Stoecker *et al.*, 1987
MA Coastal (NW Atlantic coast)	0–9 m	Jul.	2380	52.4	—	All Plastidic Oligotrichs	Stoecker *et al.*, 1987
N Atlantic NABE site	0–20 m	May–June	1774	50.3	60	All Plastidic Oligotrichs	Stoecker *et al.*, 1994
Subarctic Pacific	5–30 m	Jun., Sept. May, Aug.	—	30–50	—	"mixotrophic ciliates"	Booth *et al.*, 1993
Lame Cay (Caribbean coastal)	5 m	1 yr	20	10	25	only *Laboea*, *Tontonia*	Lynn *et al.*, 1991
E. Pacific fjord	2 m	Feb.	57	1.6	7.1	only *Laboea*, *Tontonia*, *Strombidium capitatum*	Martin and Montagnes, 1993
N.E. Pacific							
Seamount	0–24 m	Jul.	—	—	76.9	only *Laboea*, *Tontonia*	Sime-Ngando *et al.*, 1992
Off Summit	0–80 m		—	—	20		
Catalan Sea	5 m		54	19	63		
(NW Mediterranean)	0–20 m	Jun.	70	18	48	only *Laboea*, *Tontonia*	This study
	0–80 m		24	6	21.4		

Table 7. Concentrations and relative importance of nanociliates (species ≤20 μm in length) in marine systems

System	Depths sampled	Sampling period	Nanociliates l^{-1}	% Σ Ciliates l^{-1}	Biomass ($\mu g\ C^{-1}$) of nanociliates	% Σ Ciliate biomass	Reference
N.E. Pacific Coastal (S. California nearshore)	0–40 m	May–June	8300	74	0.76	30	Beers *et al.*, 1980
Carribean Coastal (Lime Cay, Jamaica)	5 m	1 yr	1953	87	0.33	43	Lynn *et al.*, 1991
N.W. Atlantic Coastal (S.E. U.S.A., continental shelf)	—	April–Sept.	2400	—	0.30	—	Sherr *et al.*, 1986
Catalan Sea	0–20 m	June	20	8	0.005	0.7	This study
	0–80 m		32	8	0.01	0.7	

M. rubrum outside of upwelling systems or under non-bloom conditions are very rare (Crawford, 1989). Several studies of near-shore waters have found *M. rubrum* to be a year-round component of the plankton (Bernard and Rassoulzadegan, 1994; Montagnes and Lynn, 1989; Verity *et al.*, 1993). Modest concentrations, similar to those found in the Catalan Sea, may be common to many marine systems. During the summer, in the Iceland/Greenland seas, *M. rubrum* concentrations were found to average 50 cell l^{-1} at 0 m and 15 cell l^{-1} at 50 m, while in the Barents Sea/North Svalbard average concentrations were 199 cells l^{-1} at 0 m and 32 cells l^{-1} at 50 m (Putt, 1990). In N.W. Atlantic shelf and slope waters, *M. rubrum* concentrations were found to vary from 8 to 1258 cells l^{-1} (integrated averages from 0 to ~35 m depth) during early summer (Stoecker *et al.*, 1989).

Relationships with chlorophyll

Heterotrophic ciliate distribution appears to be closely linked to chl in the Cata lan Sea (Figs 2, 3), and highly significant linear correlations were found between chl and both cells and biomass (Fig. 4A). In other systems, tight linkages have been found. For example, in the coastal waters of the NE Pacific, marked increases of ciliate concentrations were noted in "pigment layers" (Beers and Stewart, 1970) or, more specifically, chlorophyll maximum layers (Chester, 1978). Recently, correlations of ciliate carbon and phytoplankton carbon in discrete depth samples were reported for the Subarctic Pacific (Booth *et al.*, 1993). In contrast, markedly higher ciliate biomasses were reported for surface water relative to the DCM in the subtropical northern Pacific (Tsudi *et al.*, 1989). When ciliate and chl *a* concentrations represent water column integrations, lack of correlations have been reported for systems as diverse as Georges Bank (Stoecker *et al.*, 1989) and Pacific seamounts (Sime-Ngando *et al.*, 1992). Discrepancies among reports may represent distinct differences between systems (for example, in the size-structure of the chlorophyll crop) or be the result of considering relationships at different spatial scales, i.e., the whole water column.

For large mixotrophic oligotrichs, the lack of a relationship between concentrations and chl *a* in the Catalan Sea echoes findings from previous studies of other systems (Stoecker *et al.*, 1989; Sime-Ngando *et al.*, 1992) and is reasonable, as mixotrophic oligotrichs appear to be largely restricted to near-surface depths. While the abundances of mixotrophic oligotrichs generally decline with depth, distributional patterns are quite possibly complicated by vertical migrations; furthermore, the vertical migration patterns of a given mixotrophic oligotrich species may vary from system to system. For example, the maximum concentrations of *Laboea strobila* in near surface samples occurred at 14:00 in Long Island Sound (McManus and Fuhrman, 1986) and at 4:00 in Georges Bank (Stoecker *et al.*, 1989). If mixotrophic oligotrichs display diverse migrational habits, lack of a consistent relationship with chl *a* is not surprising.

Like mixotrophic oligotrichs, abundances of the autotrophic ciliate, *Mesodinium rubrum*, showed no relationship to chl concentration (Figs 2, 3, 4C). Peak concentrations of *M. rubrum* among the nine profiles were surprisingly consistent in magnitude, 110 ± 17 cells^{-1}, but variable in depth location. The depths of the population maxima were not clearly related to the time of day. Similar to *Laboea strobila*, the autotrophic *M. rubrum* is known as a vertical migrator, but also with apparently variable migration patterns. It may react to light cues in some systems (Lindholm and Mork, 1990; Passow, 1991) and turbulence in other systems (Crawford and Purdie, 1992).

Tintinnids

For the Catalan Sea samples, tintinnid abundance (average 80 ± 64 cells l^{-1}) varied little over chl concentrations ranging from 0.15–2.0 $\mu g\ l^{-1}$. The lack of relationship between abundance and chl tends to support the idea that, in contrast to oligotrichs, tintinnids exploit patches of high prey density (Rassoulzadegan, 1993), so that bulk measurements such as chl *a* l^{-1} are of very limited predictive value even when the chl represents small cells. The comparison of curves of cumulative numbers of species as a function of numbers of individuals (Fig. 5) showed, not surprisingly but for the first time, that diversity was higher in the N.W. Mediterranean compared to a coastal plain estuary. While the findings with regard to tintinnid diversity are not unreasonable, it should be noted that there is no comparative data, and furthermore, estimating diversity in tintinnids is complicated by uncertainties in species identifications.

Tintinnid species identifications are always based on lorica morphology, because the infraciliature, the basis of alpha-level ciliate taxonomy (Corliss, 1979), is known for only a handful of species (Choi *et al.*, 1992; Petz and Foissner, 1993). However, some tintinnid species are apparently capable of expressing different lorica morphologies (Gold and Morales, 1976; Davis, 1981; Laval-Peuto, 1983; Wasik and Mikolajczyk, 1993). The magnitude of this problem is difficult to judge but appears minor, as studies of field populations have rarely shown co-existence of different lorica morphotypes of the same species.

Estimated grazing impact of heterotrophic ciliates

For the Catalan Sea, estimates of ciliate ingestion rates can be made with some assumptions concerning ciliate energetics. One may assume an average growth efficiency estimate of ~50% for marine oligotrichs (Verity, 1991) and calculate ingestion over a range of growth rates. A probable *in situ* growth rate can be identified, based on established numerical response curves (Verity, 1985, 1991) and literature values of phytoplankton carbon concentrations for the Catalan Sea in summer (Delgado *et al.*, 1992). The results of such calculations, combined with values of primary production in surface and DCM (Estrada, 1985a) waters, are presented graphically in Fig. 7. Our calculations yield estimates of ciliate ingestion rates equivalent to 25 and 40% of primary production in the surface waters and DCM, respectively.

Comparison of grazing estimates among systems is most often done in terms of percent primary production consumed, which reveals a range of values from near zero to over 100% (see reviews in Gifford, 1988; Capriulo *et al.*, 1991; Pierce and Turner, 1992). Given the variety of methods employed, and groups considered (i.e., Σ microzooplankton, only tintinnids or oligotrichs), such a range is not unexpected, especially since such figures necessarily combine errors in estimating grazing as well as primary production. The large range of reported values makes choosing a typical figure hazardous. However, averaging the means of each range presented in the latest available review (Pierce and Turner, 1992, Table 3), yields an estimate of 44 ± 21.6% primary production consumed by microzooplankton on a daily or annual basis among systems ranging from the Canadian Arctic to the eastern tropical Pacific. Our estimate of ciliate ingestion of 40% primary production in the DCM approaches the grand average, while our estimate for surface waters, 25% of primary production, comes in below. It should be noted that the surface water community contained, in addition to heterotrophic grazers, an approximately equivalent biomass of

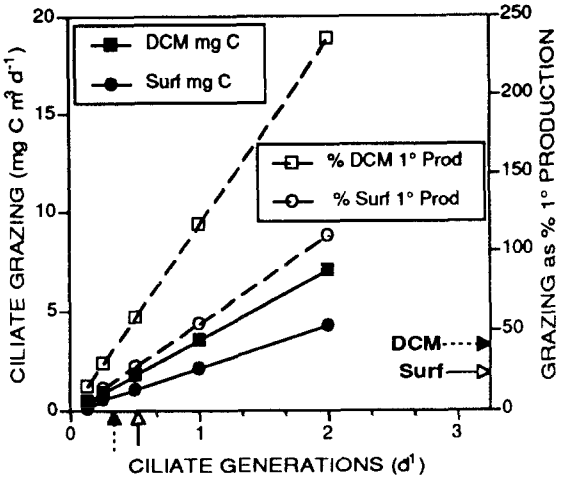

Fig. 7. Estimates of heterotrophic ciliate grazing, in terms of carbon and percent daily primary production for the surface (5 m) and DCM (40–60 m) segments of the water column, as a function of ciliate growth rate. Values were calculated based on (a) average ciliate stocks (n = 9) for 5 m (0.5 ± 0.25 mg C m^3) and integrated from 40 to 60 m (1.8 ± 0.78 mg m^3), (b) a ciliate gross growth efficiency of 50% (Verity, 1991) and (c) primary production estimates for 5 m depth (4 ± 2.28 mg C m^3 d^{-1}) and the DCM layer (3 ± 1.0 mg C m^3 d^{-1}) from Estrada (1985a).

mixotrophic oligotrichs, which do ingest phytoplankton. Thus, if mixotrophs and heterotrophs are pooled to calculate ingestion, their combined consumption would equal about 50% of primary production, similar to the figure for the DCM.

Chlorophyll contribution of photosynthetic ciliates

The estimates of photosynthetic ciliate chlorophyll presented here should be considered as approximate. Only large, morphologically distinct forms were categorised as mixotrophic oligotrichs, which most likely yielded underestimates. Values of chl *a* cell $^{-1}$ were drawn from the literature (see Methods) and averaged; using the high or low values would shift the estimates provided here by a factor of 5. With these caveats in mind, our findings still indicate a role of some importance for photosynthetic ciliates, especially in surface waters where large mixotrophic oligotrichs were dominant.

Our estimates indicate that, while insignificant contributors to the DCM, a large part of the chl crop (≥20%) in surface waters of the Catalan Sea may be in the form of ciliates (Fig. 6). As these ciliates are cells ≥20 μm in size, their primary production would be directly available to metazoan grazers such as copepods, in contrast to the dominant component of the phytoplankton community, which is composed of cells ≤5 μm in size (Delgado *et al.*, 1992). Considered in these terms, even if photosynthetic ciliates provide only modest contributions to primary production, they may be disproportionately important in carbon flux to higher trophic levels.

The Catalan Sea is probably not unusual with regard to the potentially important role of photosynthetic, especially mixotrophic, ciliates based on recent abundance data from other systems (Table 6). In terms of the contribution of mixotrophic oligotrichs to the chl crop, comparative data are sparse. In the Nordic Seas, Putt (1990) noted that in near-surface samples where chl concentrations are low ≤0.2 μg l^{-1}, a single mixotrophic species

could represent 24% of the chl crop. For the shelf and slope waters of Georges Bank, ciliate chl (mixotrophic and *Mesodinium rubrum*) were estimated to equal 7% of total chl for values integrated throughout the euphotic zone (Stoecker *et al.*, 1989).

In many marine systems, photosynthetic ciliates may represent a significant, previously overlooked, part of the chlorophyll crop in surface waters. Their contribution is easily underestimated or not detected. There is ample evidence that ciliate chl can not be determined by traditional chl size-fractionation techniques, as filtration of water samples results in the lysis of ciliates (Putt, 1990).

CONCLUSION

Data presented here show that different types of planktonic ciliates display different vertical distributions, relative to chl *a*, in a system with a well-defined DCM. Heterotrophic ciliate biomass appeared closely linked to chl *a* concentration. In contrast, large mixotrophic forms were largely restricted to the surface layer, where chl *a* concentrations were low. In near surface samples, they formed an important part of total ciliate biomass and likely contributed significantly to the chl *a* crop. The autotrophic species *Mesodinium rubrum* displayed variable vertical distributions. The ciliate community differed in some fundamental respects compared to better-known near shore communities with relatively few nanociliates found and diversity, at least that of tintinnid ciliates, high. In the N.W. Mediterranean, ciliate biomass relative to phytoplankton biomass as measured by chl *a*, is largely similar to stocks of oceanic systems. Rough calculations of grazing impact for ciliates suggest that about 50% of primary production is probably consumed by planktonic ciliates.

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