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PART I

Planktonic ciliates in the Mediterranean Sea: longitudinal trends

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Abstract

We analysed samples taken through the euphotic zone from 18 stations between the Ligurian Sea (6°E) and the Levantin Basin (32°E) from 24 May to 25 June 1996. Both ciliate and chlorophyll concentrations ranged over a factor of about 7, but ciliate concentrations (0.4–2.8 mg C m³) varied irregularly compared to a longitudinal decline, west to east, in chlorophyll concentration (0.07–0.48 mg m³). The lower chlorophyll concentrations (0.1 mg m²) of the eastern basin stations corresponded with a relatively high stock of ciliates (0.5 mg C m²). Large mixotrophic ciliates were more abundant, in both absolute and relative terms, in the eastern Mediterranean stations with less chlorophyll. The species diversity of tintinnid ciliates appeared higher in the central and eastern basins compared to the west. Our results suggest a shift from the western to eastern Mediterranean in the planktonic food towards a microbially dominated system. © 1999 Elsevier Science Ltd. All rights reserved.

1. Introduction

In the Mediterranean Sea there is a gradient of oligotrophy from the western to eastern basins. Concentrations of both nitrate and phosphate are lower in the eastern compared to the western basins (Bethoux et al., 1992), and phosphorus limitation is thought to increase from west to east (Krom et al., 1991). From satellite maps, a clear decline can be seen in chlorophyll from west to east (e.g., Antoine et al., 1996;

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Williams, 1998), and from automated underway sampling, similar declines in abundances of specific autotrophs such as the picoplanktonic *Synechococcus* have been described (Jacquet et al., 1998).

Differences in trophic state often accompany differences in food web structure, and community structure is closely associated with basic ecosystem characteristics such as carbon export (e.g., Legendre and Rassoulzadegan, 1995). For example, in coastal vs ocean systems, the biomass of heterotrophic bacteria and protozoans is relatively high in open ocean waters of low chlorophyll content; a relative dominance of heterotrophic organisms corresponds with expectations of lower carbon export (Gasol et al., 1997). In the Mediterranean Sea, one might expect the west to east decline in chlorophyll to correspond with changes in food web structure. However, in contrast to a considerable body of data on nutrients and primary producers in the Mediterranean, very little is known concerning longitudinal gradients in the heterotrophic members of the planktonic food web.

We examined the stock size and composition of the ciliate portion of the planktonic protozoan community in the Mediterranean Sea from 6°E to 32°E. Ciliates, because they consume both picoplankton and nanoplankton, and because they serve as prey for metazoans, are often considered a key component of planktonic food webs, especially in systems in which primary production is dominated by small autotrophs (Sherr et al., 1985). We hypothesized that, corresponding with the longitudinal declines in chlorophyll, there would be declines in the biomass of ciliates, increases in the relative biomasses of certain trophic types of ciliates (mixotrophic vs heterotrophic), and increases in the species diversity of tintinnids, a ciliate group in which individual species are easily distinguished and diversity estimated with relative ease.

Our expectations concerning declines in ciliate stocks paralleling declines in chlorophyll, were based on previous comparisons of chlorophyll and ciliate concentrations in open water systems, which indicated, across systems, a rather constant ratio of about 3 mg of ciliate carbon for each mg of chlorophyll *a* (Dolan and Marrasé, 1995; Peréz et al., in press). Mixotrophic ciliates can supply most of their requirements of basal metabolism using the carbon fixed by functional chloroplasts sequestered from ingested phytoplankton. Thus, predictions concerning changes in the composition of the ciliate community reflected the idea that mixotrophic ciliates, as forms better able to survive food-poor periods, could be expected to be commoner in more oligotrophic environments (Dolan, 1992). Likewise, in oligotrophic environments, heterotrophic ciliates may be, on average, larger as large ciliates often appear to have lower minimum food concentrations compared to smaller ciliates (Rassoulzadegan, 1993). Systems in which primary production is pulsed, compared to systems in which it is more even, often appear to show lower diversity of both zooplankton (Angel, 1997) and phytoplankton (Venrick, 1982). We expected then the species diversity of tintinnid ciliates to follow a pattern of higher diversity in the more oligotrophic eastern areas, in which the spring blooms of the phytoplankton are less marked compared to the western basin (e.g., Fowler et al., 1991).

To examine these hypotheses we analysed samples obtained during the Mediterranean Investigation of Oligotrophic Systems (MINOS) cruise program, in which stations were sampled along a cruise track between the Ligurian Sea and the Levantin

Basin and back to the Ligurian Sea from 24 May to 25 June, 1996. Unexpectedly, we found that ciliate biomass, unlike chlorophyll, showed no longitudinal gradient, with the lower chlorophyll concentrations of the eastern basin stations corresponding with relatively high concentrations of ciliates, and the average cell size of heterotrophic ciliates was nearly constant. Confirming expectations, abundances of large mixotrophic oligotrichs were generally the highest, in both absolute and relative terms, in the more oligotrophic eastern stations, and the species diversity of tintinnid ciliates appeared higher in the central and eastern basins compared to the west. Overall, our results suggest an increased importance of ciliates in the planktonic food web from west to east, given the increased ratio of ciliates to chlorophyll, corresponding with shifts towards a more species-rich community with more mixotrophic ciliates.

2. Methods

Between the 24th May and 25th June of the MINOS cruise, samples were obtained from 18 of 20 stations located along two transects between the French coast and Cyprus (Fig. 1 and Table 1). Samples for ciliates and chlorophyll determinations were obtained with a CTD-Niskin bottle rosette using 12 l Niskin bottles. Generally, in the early morning, six samples were taken from the surface to just below the chlorophyll maximum layer. For chlorophyll and other pigment determinations, 2 l aliquots were

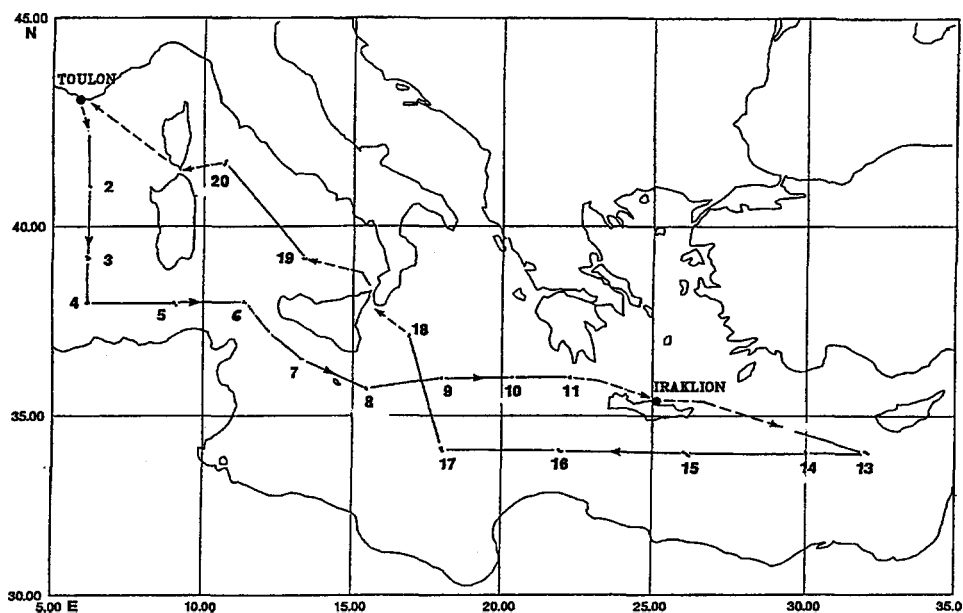


Fig. 1. Station map and cruise track of the Minos cruise program. See Table 1 for station coordinates and sampling depths.

Table 1

Station locations and characteristics: Layer sampled, chlorophyll max and euphotic zone depth in m, chlorophyll maximum concentration in ng l^{-1}

Station	Basin	Location	Date	Time	Layer sampled	Chl Max		Euphotic zone depth
						Z	Conc	
2	West	41°00'N, 6°10'E	May 24	07:45	80	50	1038	56
3	West	39°10'N, 6°10'E	May 25	06:53	90	80	302	70
4	West	38°00'N, 6°10'E	May 28	06:48	90	50	1792	58
5	West	37°00'N, 9°00'E	May 29	07:01	90	40	598	68
6	West	38°00'N, 11°20'E	May 30	06:39	90	50	963	60
7	Central	36°30'N, 13°15'E	May 31	06:52	90	70	451	76
8	Central	36°00'N, 15°45'E	June 1	08:00	90	80	826	77
9	Central	36°00'N, 18°45'E	June 2	06:51	120	110	324	92
10	Central	36°00'N, 20°20'E	June 3	06:45	90	80	198	80
11	East	36°00'N, 22°15'E	June 4	06:40	90	70	350	75
13	East	34°00'N, 32°00'E	June 9	07:00	200	110	309	100
14	East	34°00'N, 30°00'E	June 11	06:57	130	90	279	96
15	East	34°00'N, 26°00'E	June 13	07:00	140	120	270	110
16	East	34°00'N, 22°00'E	June 15	07:00	100	90	414	90
17	Central	34°00'N, 22°00'E	June 17	07:02	130	100	207	108
18	Central	37°05'N, 16°52'E	June 21	07:02	120	100	369	90
19	West	39°10'N, 13°20'E	June 23	06:57	80	70	1329	75
20	West	41°30'N, 10°40'E	June 25	07:00	120	80	458	80

filtered through GF/F filters, pigments extracted in methanol and samples processed using HPLC as detailed in Vidussi et al. (1996).

For ciliate enumerations, 500 ml samples of whole water were preserved with Lugol's (2% final conc.) and stored refrigerated and in darkness except during transport and sedimentation. The whole water samples were concentrated via sedimentation and examined following the protocol detailed in Dolan and Marrasé (1995). Briefly, samples were pre-concentrated in 500 ml graduated cylinders, and concentrates settled in standard sedimentation chambers. Concentrates equivalent to 333 ml of whole water were examined. Ciliates were placed in approximately 20 distinct size–shape and trophic categories. The autotrophic ciliate *Mesodinium rubrum*, which was rare, was pooled with taxa of large mixotrophic ciliates (*Tontonia*, *Laboea*). All remaining ciliates were considered heterotrophic. As the use of Lugol's fixative precluded identification of mixotrophic ciliates without distinctive gross morphologies (i.e., certain *Strombidium* species), the heterotrophic group likely contained some mixotrophs. Biovolumes were converted to carbon contents using the conversion factor of 0.19 pg C per μm^3 established for oligotrichs fixed with 2% Lugol's (Putt and Stoecker, 1989).

Pearson's correlation coefficients were calculated to examine relationships between pigment concentrations and biomasses of heterotrophic ciliates and mixotrophic ciliates (*M. rubrum* and large mixotrophic ciliates). For these analyses we examined relationships with chlorophyll *a* and three carotenoids: zeaxanthin,

hexanoyl-oxyfucoxanthin (19'-HF) and butanoylxyfucoxanthin (19'-BF), previously found to be related to ciliate abundance in the N. W. Mediterranean (Pérez et al., in press). Zeaxanthin is found in the autotrophic bacteria *Synechococcus* and *Prochlorococcus* and 19'-HF and 19'-BF are indicators of nanoflagellates with 19'-HF found in prymnesiophyte taxa and 19'-BF in chrysophyte and pelagophyte taxa (Claustre, 1994). Correlation analyses were performed on the entire data set using both discrete depth samples ($n = 114$) or averages of depth-integrated station data ($n = 18$). In the case of depth integrated data, integration through the euphotic zone or the total depth sampled yielded very small differences in parameter concentrations and statistical relationships. The trapezoidal method was used for water column integration.

Tintinnids were identified using lorica morphology and the species descriptions found in Balech (1959), Campbell (1942), Jörgensen (1924) and Kofoed and Campbell (1929,1939). To examine tintinnid ciliate diversity, data were divided into three sets corresponding to the West, Central and Eastern Mediterranean (Fig. 1), each consisting of 300–450 individuals. Species diversity of tintinnids was examined with plots of cumulative numbers of species vs cumulative numbers of individuals; species evenness of tintinnids was examined with plots of percent of total individuals versus species rank.

3. Results

Water column profiles showing the range of conditions encountered are shown in Figs. 2–4. At station 2 in the Ligurian Sea (Fig. 2), there was a broad, relatively shallow (40 m) chlorophyll maximum (1200 ng l^{-1}) located above the nutriclines. In the Tyreanean Sea (Fig. 3), higher concentrations of chlorophyll were found; the nutricline and chlorophyll maximum were deeper (60–80 m depth). Fig. 4 shows profiles typical of most central and eastern stations. Chlorophyll concentrations were low with deep chlorophyll maximum layers and nutriclines (100–120 m). In general, the vertical distribution of ciliates paralleled chlorophyll (Figs. 1–3). However, ciliate concentrations were less variable than chlorophyll. For example, similar peak concentrations of ciliates of about 700 ng C l^{-1} were recorded from both stations 2 and 14 with very different chlorophyll maximum concentrations of about 1200 and 500 ng chlorophyll l^{-1} , respectively.

A longitudinal gradient in chlorophyll concentration, consisting of a west to east decline of about 40–20 mg chlorophyll *a* per m^2 , was evident in depth-integrated values, corresponding to an average water column values ranging from 0.48 to 0.07 mg chlorophyll per m^3 (Fig. 5). Total ciliate biomass averaged about 1 mg carbon per m^3 (50 mg C per m^2) with no clear longitudinal trend. The distributions of the 3 phytoplankton pigments assumed to represent ciliate prey showed two distinct patterns. The prymnesiophyte pigment (19'-HF) and the pigment marker of chrysophyte and pelagophyte taxa (19'-BF) declined from west to east, corresponding closely with chlorophyll. The pigment found in the autotrophic bacteria *Synechococcus* and *Prochlorococcus* (zeaxanthin) showed no clear longitudinal trends, similar to ciliate biomass.

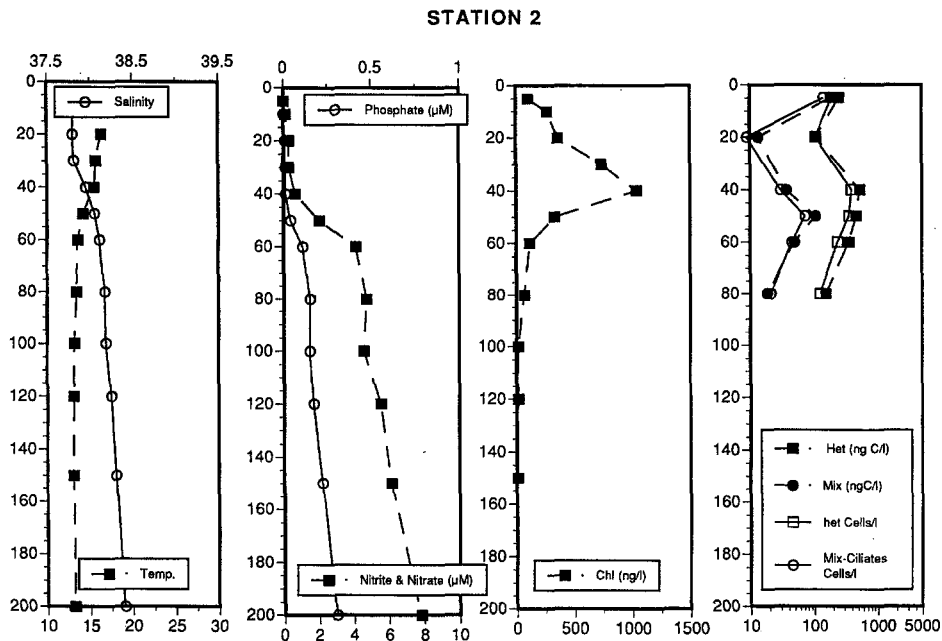


Fig. 2. Vertical profiles from Station 2, a typical western station. Note that ciliate stocks in carbon units, ng carbon l^{-1} , (heterotrophic ciliates, Het; mixotrophic ciliates, Mix) as well as in abundance (cells) roughly parallel the distribution of chlorophyll. The chlorophyll maximum of about 1000 ng l^{-1} coincides with about 750 ng l^{-1} of ciliate carbon.

The community composition of the ciliate community showed differences from west to east (Fig. 6). Among the oligotrich taxa, concentrations of large mixotrophic ciliates were quite variable; however, they were more abundant and represented a larger proportion of the ciliate community in the eastern stations, relative to the west. In contrast, heterotrophic ciliates were relatively invariant from west to east, both in terms of concentrations about $0.5 \text{ mg carbon per m}^{-3}$ (approx. 40 mg C per m^2) and an overall average cell size of $20\text{--}25 \mu\text{m}$ equivalent spherical diameter. Small oligotrichs ($20\text{--}30 \mu\text{m}$ length) were numerically dominant at all stations. There were no obvious changes in the size spectra of ciliates at the different stations.

Among the tintinnids, 1100 individual cells were examined consisting of a total of 81 species. About half of the tintinnid species found (39 out of 81) were common to two or more of the western, central or eastern populations (Table 2). However, the population characteristics of tintinnid ciliates showed distinct differences between western vs central or eastern stations. The central and eastern populations were very similar in terms of diversity and dominance but, compared to the western populations, were more species diverse and less highly dominated by a few species, showing more species 'evenness' (Fig. 7). There were also differences in the numbers of species found exclusively in a given region. Among the species encountered, only 5 were found

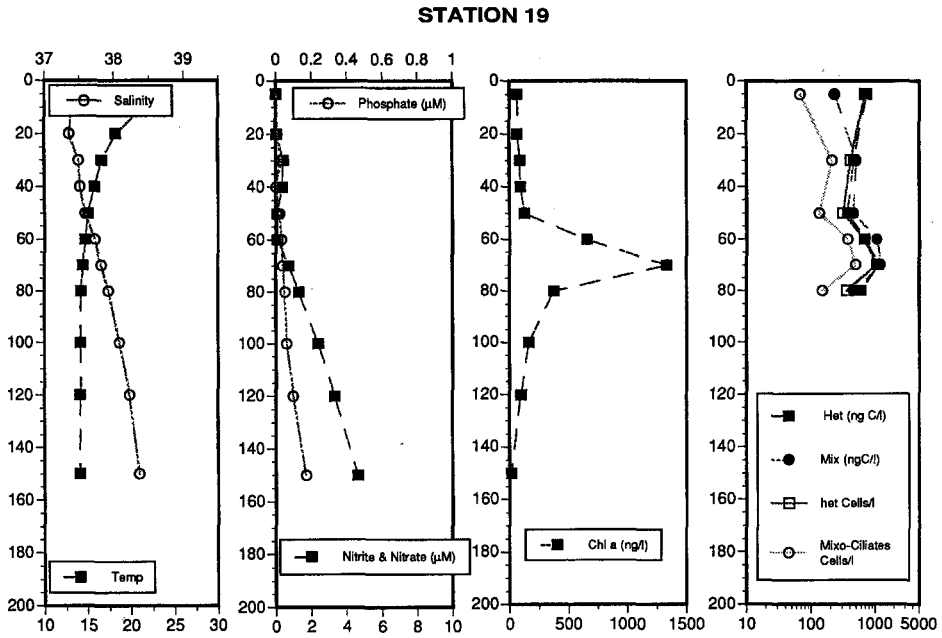


Fig. 3. Vertical profiles from Station 19 in the Tyrrhenian Sea, one of the most chlorophyll-rich stations. Units as in Fig. 2. Note the chlorophyll maximum of approximately 1500 ng l^{-1} chlorophyll coincided with about 1700 ng l^{-1} of ciliate carbon (total of both heterotrophic, Het, and mixotrophic, Mix, ciliate stocks).

exclusively at western stations, while 18 tintinnid species were restricted to central stations, and 17 tintinnid species were found only at eastern stations.

The statistical relationships using discrete depth samples were stronger between ciliate abundance and chlorophyll *a* than 19'-HF or 19'-BF (Table 3). Significant relationships were found between chl *a* and total ciliates, heterotrophic ciliates, and mixotrophic ciliates; 19'-BF (chrysophytes and pelagophytes) and 19'-HF (prymnesiophyte) concentrations were related to total and heterotrophic ciliates but not mixotrophic ciliate concentration. Zeaxanthin concentrations (*Synechococcus* and *Prochlorococcus*) were not significantly related to any ciliate group. There were no significant relationships among the averages of depth-integrated parameters. However, the highest r^2 values were found with chlorophyll *a* and zeaxanthin, the pigment marker, which, like total and heterotrophic ciliates, was relatively invariant with longitude.

4. Discussion

Compared to other open water systems, overall average ciliate concentrations in the western, central, and eastern stations were within the range expected of ciliate carbon of roughly 2–5 times chlorophyll concentration (Fig. 8). However, relative to

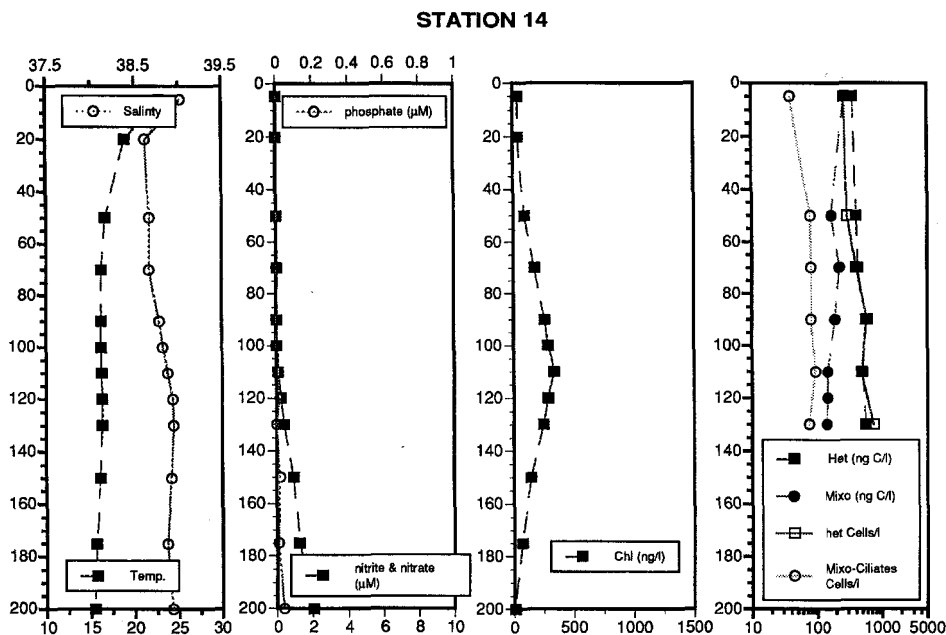


Fig. 4. Vertical profiles from an eastern Mediterranean station, Station 14. Units as in Fig. 2. Note the deep, broad chlorophyll maximum. Peak concentrations of chlorophyll, about 500 ng l^{-1} coincide with ciliate stocks of 750 ng l^{-1} carbon, similar to peak values of ciliate stocks in western stations of higher chlorophyll concentrations (e.g., Fig. 2).

chlorophyll, ciliates were more abundant in the central and eastern Mediterranean, corresponding with an increase in the relative importance of autotrophic bacteria. This relative increase in the apparent importance of ciliates from the west to the central and eastern Mediterranean was coupled with interesting shifts in ciliate community composition.

Large mixotrophic ciliates increased in absolute and relative importance from west to east (Fig. 6). It should be noted that only *Tontonia* and *Laboea* species were enumerated as mixotrophs, but these species generally dominate the biomass of mixotrophs (Pérez et al., in press). In low-chlorophyll waters, finding an increased proportion of large mixotrophic ciliates, as forms able to supplement grazing with photosynthesis, may be expected. However, an increase in their absolute abundance is difficult to explain. Concentrations of mixotrophs were not related to pigment markers of particular nanoflagellate taxa or autotrophic bacteria (Table 3). Recently, it was suggested that, although mixotrophic ciliates have lower maximum growth rates, they may be less subject to predation by copepods (Pérez et al., 1997). The abundance of mixotrophic ciliates may then be in part positively related to copepod carnivory on their competitors, heterotrophic ciliates and copepod carnivory could be higher in low-chlorophyll waters. Unfortunately, there is at present very little data concerning copepod concentrations in the central or eastern open Mediterranean Sea.

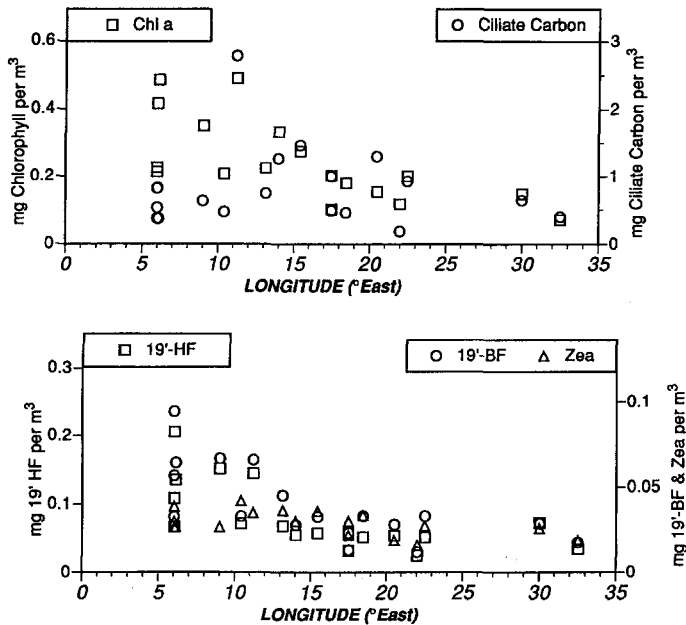


Fig. 5. Averages of water column integrated values of chlorophyll, ciliate stocks (top panel) and selected phytoplankton pigments (bottom panel). Note the decline in chlorophyll concentrations from west to east and the lack of a corresponding decline in total ciliate biomass concentrations. Longitudinal changes in the concentrations of the pigment marker for prymnesiophyte phytoplankton, 19'-HF, paralleled chlorophyll while the pigment markers of autotrophic bacteria, zeaxanthin (Zea) and the marker pigment for chrysophyte and pelagophyte taxa, 19'-BF, were similar to ciliate biomass, relatively invariant.

The differences in the community composition of tintinnid ciliates suggest that ciliate communities in the east and central Mediterranean are more diverse in terms of numbers of 'endemic' species, numbers of species, and species evenness (Fig. 7). There are many theories that attempt to explain diversity in general, and mechanisms responsible for diversity in the plankton have long been a subject of dispute (Hutchinson, 1961). Commonly, among plankton communities, diversity does not show a simple relationship with productivity, but rather species richness increases and dominance decreases as organic inputs are less seasonally pulsed (Angel, 1997). Here we wish only to remark that tintinnid diversity conforms to such a general expectation when the western and eastern Mediterranean are compared.

From west to east, the increase in mixotrophs and the increase in diversity of tintinnids appear to occur against a background of a nearly invariant community of heterotrophic ciliates, which dominated ciliate biomass. There were no obvious changes in the composition of the heterotrophs, as reflected in the lack of marked differences in average cell size (Fig. 6). The overall stability of the ciliate community, relative to differences in the communities of primary producers, suggest a more important role for ciliates in carbon flow in the central and eastern areas relative to

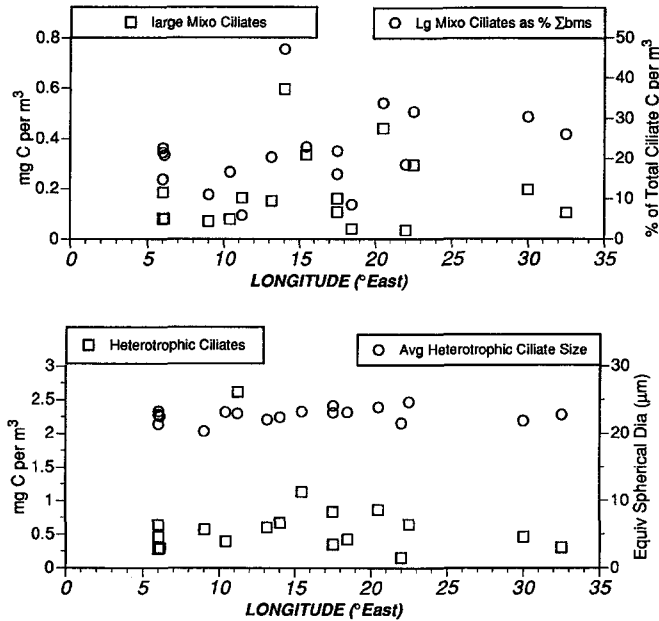


Fig. 6. Averages of water column integrated values of the biomass of large mixotrophic ciliates and their % contribution to total ciliate biomass (top panel) and heterotrophic ciliate biomass with average heterotrophic ciliate cell size (bottom panel). Note an overall trend of a west to east increase of large mixotrophic ciliate concentrations and relative importance. In contrast, heterotrophic ciliate biomass and average cell size was nearly invariant.

the western Mediterranean. We have no direct estimates of carbon consumption by ciliates, but rough calculations based on estimates of primary production and some simple assumptions can yield order of magnitude estimates and support a hypothesis of an increased importance of ciliates in biogenic flux from the western to the central and eastern Mediterranean.

Measures of primary production made during the MINOS cruise (T. Moutin, pers. com.) showed a gradient from west to east of primary production from about 530 to 220 mg C per m² per day. For each station, from primary production and chlorophyll concentration values, a community generation time for the phytoplankton community can be calculated by dividing primary production by total phytoplankton carbon, estimated using a carbon to chl a ratio of 50. If we assume that ciliates are growing at the same rate as the phytoplankton, we can estimate ciliate carbon production rate as the product of growth rate times standing stock.

Having calculated ciliate biomass production, we can estimate ciliate consumption rates by assuming a growth efficiency of 33% (Hansen et al., 1997). The results of such calculations are presented in Fig. 9. We estimate ciliate carbon consumption, as a percent of primary production, to range from 14% as an average in the western stations, to 29 and 23% for the central and eastern stations. Clearly, such estimates

Table 2

Tintinnid species and occurrence in western (w), central (c), eastern (e) stations

Acanthostomella	Daturella	Rhabdonella
obtusa ^{w,c,e}	angusta ^c	amor ^c
conicoides ^{w,c,e}	Dictyocysta	apophysata ^c
gracilis ^c	elegans ^{w,c}	elegans ^c
minutissima ^{w,c,e}	lepida ^{w,c,e}	Rhabdosella
Amphorella	minor ^{w,c}	cuneolata ^c
intumescens ^c	mitra ^{w,c,e}	Salpingacantha
gaarderae ^c	mulleri ^c	unquicutata
lackmanni ^{w,c,e}	Epiplocylix	perca ^{w,c}
lata ^w	acuminata ^w	acuminata ^{w,c,e}
oxyura ^{w,c}	undella ^{c,e}	curta ^{w,c,e}
pachytoecus ^{w,c,e}	Epiorella healdi^c	attenuata ^c
pyramidata ^{w,c,e}	Eutintinnus inquilinus^c	cuneolata ^c
quadrilineata ^{w,c,e}	fraknoi ^{w,c,e}	decurtata ^{w,c,e}
steenstrupi ^{w,c,e}	Iusus-undae ^{w,c,e}	faurie ^{w,e}
torulata ^{w,c,e}	maclentus ^c	minuta ^w
trachelium ^c	pectina ^c	Undella
urceolata ^{c,e}	tubulosis ^c	aculeata ^{w,e}
Ascampbelliella	sp. a ^{w,c,e}	acuminata ^w
acuta ^c	Favella azorica ^c	caudata ^w
Canthariella	serrata ^c	claparedel ^c
septinaria ^c	Metacylix	clevel ^{w,c,e}
Climacocylix	serrata ^c	hyalina ^{c,e}
scalaria ^{w,c}	sp. a ^c	subacuta ^{w,c,e}
anthriease ^c	Parundella	turida ^{w,c}
Codonella	laachmanni ^{c,e}	Xystonella
amphorella ^c	Petalotrichs	lanceolata ^c
galea ^c	serrata ^c	longicaudata ^{w,c}
nationalis ^c	Proplectalla	lohmanni ^{w,c}
Craterella	perpusilla ^{w,e}	paradoxa ^c
tortulata ^c	Protorhabdonella	treforti ^{c,e}
Cyttarocylix	curta ^{w,c,e}	Xystonelopsis
encecryphalus ^{w,c}	simplex ^{w,c,e}	brandti ^c
Dadayiella		constricta ^c
ganymedes ^{w,c,e}		cymatica ^c
		paradoxi ^c

are subject to many sources of error: however, the generation times estimated for the ciliate community do not appear unreasonable as they are very similar to experimental measures of 2–3 days made in May in the N. W. Mediterranean (Pérez et al., 1997).

The degree of match or mismatch between primary production and grazing in the microbial food web can be used to predict carbon export (Legendre and Rassoulzadegan, 1996). Therefore, the differences noted in the importance of ciliates, relative to

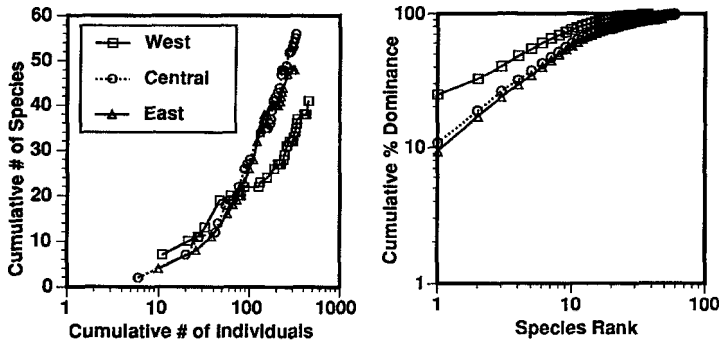


Fig. 7. Plots of species richness and relative dominance of tintinnid species for western, central and eastern stations. The central and eastern stations, with more species and a more even distribution of dominance, appear distinct from the western stations.

Table 3

Results of correlation analysis, r^2 values. Significant relationships denoted with '*'

Pigments	Total ciliates	Heterotrophic ciliates	Lg Mixociliates	Mixo % total ciliates
A. Individual samples ($n = 114$)				
chl <i>a</i>	0.232*	0.203*	0.113*	0.002
19'-BF	0.091*	0.103*	0.003*	0.056
19'-HF	0.117*	0.133*	0.004	0.036
Zea	0.027	0.035	0.009	0.005
B. Averages of integrated data ($n = 18$)				
Chl <i>a</i>	0.181	0.211	0.002	0.041
19'-BF	0.025	0.054	0.038	0.087
19'-HF	0.023	0.053	0.053	0.096
Zea	0.062	0.087	0.004	0.118

primary production, probably correspond with different food web structures from west to east and, concomitantly, differences in export from surface layers of biogenic carbon. Within the microbial food web, ciliates commonly represent about half the stock of microzooplankton with heterotrophic dinoflagellates making up the rest. (e.g., Lessard and Murrell, 1996). The microzooplankton community itself is often about equal to the stock of nanozooplankton (e.g., Christaki et al., 1996). Ciliate biomass then likely represents about 25% of the heterotrophic protist community. If ciliate carbon demand is proportional to that of total heterotrophic protists, ciliates probably represent approximately $\frac{1}{4}$ total heterotrophic protistan carbon demand. Our very rough calculations suggest then that the microbial food web consumes a quantity of carbon equal to about half the carbon fixed in the west compared to all the carbon fixed in the central and eastern Mediterranean.

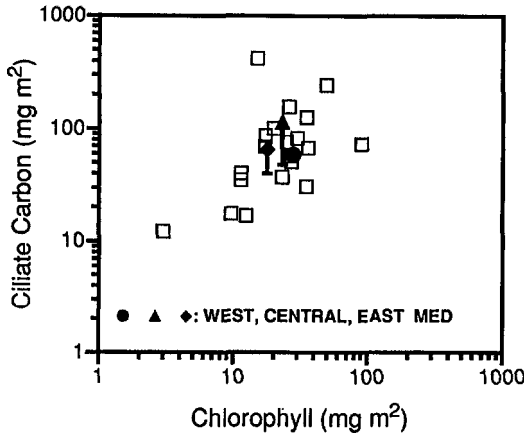


Fig. 8. Comparison of ciliate stocks and chlorophyll content in the western, central and eastern Mediterranean with data from a variety of open water marine systems. Data: Beers and Stewart (1969,1971), Chester (1978), Dolan and Marrasé (1995), Garrison and Buck (1989), Paranjape et al. (1985), Pérez et al. in press, Sime Ngando et al. (1992), Leakey et al. (1996), Lessard and Murrell (1996), Strom et al. (1993), Suzuki et al. (1998). In most cases, water column depths integrated were about the first 100 m.

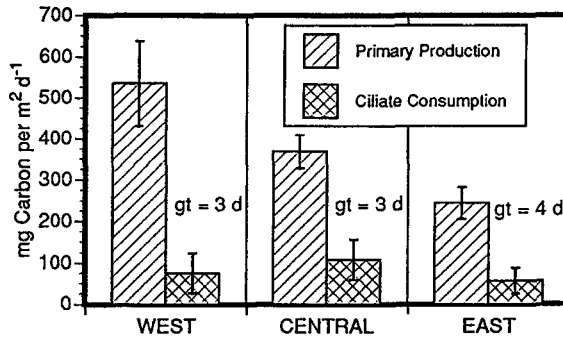


Fig. 9. Estimates of primary production, station averages \pm S.D., for the western, central and eastern basins (unpublished data of T. Moutin) with rough estimates of ciliate consumption rates, station averages \pm S.D., for the three basins. For details on calculations, see discussion- briefly, for each station, a phytoplankton community generation time was estimated and ciliates were assumed to grow at the same rate as phytoplankton and consume three times their production; average generation times (gt) given for each basin.

Thus, based on simple consideration of the stocks of ciliate microzooplankton, we would predict a longitudinal gradient of reduced carbon export from the surface layer in the Mediterranean from west to east. The longitudinal shifts in total chlorophyll, in contrast to relatively invariant quantities of heterotrophic ciliates and markers of certain small phytoplankton taxa such as autotrophic bacteria, suggests that a gradient of carbon export is superimposed on a stable microbial food web in the Mediterranean Sea.

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References

- Angel, M.V., 1997. Pelagic biodiversity. In: Ormond, R.F.G., Gage, J.D., Angel, M.V. (Eds.), *Marine Biodiversity: Patterns and Processes*. Cambridge University Press, Cambridge.
- Antoine, D., André, J.-M., Morel, A., 1996. Oceanic primary production 2. estimation at global scale from satellite (coastal zone color scanner) chlorophyll. *Global Biogeochemical Cycles* 10, 57–69.
- Balech, E., 1959. *Tintinoinea del Mediterraneo*. Instituto Espanol de Oceanografía, Madrid.
- Beers, J.R., Stewart, G.L., 1969. Microzooplankton and its abundance relative to the larger zooplankton and other seston. *Marine Biology* 4, 182–189.
- Beers, J.R., Stewart, G.L., 1971. Micro-zooplankton in the plankton communities of the upper waters of the eastern tropical Pacific. *Deep-Sea Research* 18, 861–883.
- Bethoux, J.P., Morin, P., Madec, C., Gentili, B., 1992. Phosphorous and nitrogen behaviour in the Mediterranean Sea. *Deep-Sea Research* 39, 1641–1654.
- Campbell, A.S., 1942. *The Oceanic Tintinnoida of the Plankton Gathered during the Last Cruise of the Carnegie*. Carnegie Institution of Washington, Publication 537, Washington DC.
- Chester, A.J., 1978. Microzooplankton relative to a subsurface chlorophyll maximum layer. *Marine Science Communications*, 4 275–292.
- Christaki, U., Van Wambeke, F., Christou, E.D., Conan, P., Gaudy, R., 1996. Food web structure in the surface layer, at a fixed station influenced by the North Western Mediterranean Current. *Hydrobiologia* 321, 145–153.
- Claustre, H., 1994. Phytoplankton pigment signatures of the trophic status in various oceanic regimes. *Limnology and Oceanography* 39, 1207–1211.
- Dolan, J.R., 1992. Mixotrophy in ciliates: a review of *Chlorella* symbiosis and chloroplast retention. *Marine Microbial Food Webs* 6, 115–132.
- Dolan, J.R., Marrasé, C., 1995. Planktonic ciliate distribution relative to a deep chlorophyll maximum: Catalan sea, N.W. Mediterranean, June 1993. *Deep-Sea Research* 42, 1965–1987.
- Fowler, S.W., Small, L.F., La Rosa, J., 1991. Seasonal particulate carbon flux in the coastal northwestern Mediterranean Sea, and the role of zooplankton fecal matter. *Oceanologica Acta* 14, 77–85.
- Garrison, D.L., Buck, K.R., 1989. Protozooplankton in the Weddell Sea, Antarctica: abundance and distribution in the Ice-edge zone. *Polar Biology* 9, 341–351.
- Gasol, J.P., del Giorgio, P.A., Duarte, C., 1997. Biomass distribution in marine planktonic communities. *Limnology and Oceanography* 42, 1353–1363.
- Hansen, P.J., Bjornsen, P.K., Hansen, B.W., 1997. Zooplankton grazing and growth: scaling within the 2–2000 μm body size range. *Limnology and Oceanography* 42, 687–704.
- Hutchinson, G.E., 1961. The paradox of the plankton. *American Naturalist* 95, 137–144.
- Jacquet, S., Lennon, J.F., Vaulot, D., 1998. Application of a compact automatic sea water sampler to high frequency picoplankton studies. *Aquatic Microbial Ecology* 14, 309–314.
- Jørgensen, E., 1924. *Mediterranean Tintinnidae*. Report of the Danish Oceanographical Expeditions 1908–1910 to the Mediterranean and adjacent seas. Vol. II. Biology, No. 8, J.3 (Thor expedition), Copenhagen.

- Kofoid, C.A., Campbell, A.S., 1929. A conspectus of the marine and freshwater ciliata belonging to the suborder tintinninea, with descriptions of new species principally from the Agassiz expedition to the eastern tropical Pacific 1904–1905. University of California Publications in Zoology 34, 1–403.
- Kofoid, C.A., Campbell, A.S., 1939. The tintinninea of the eastern Tropical Pacific. Bulletin of the Museum of Comparative Zoology at Harvard College 84, 1–473.
- Krom, M.D., Kress, N., Brenner, S., Gordon, L.I., 1991. Phosphorous lilitation of primary production in the eastern Mediterranean Sea. *Limnology and Oceanography* 36, 424–432.
- Leakey, R.J.G., Burkill, P.H., Sleigh, M.A., 1996. Planktonic ciliates in the northwestern Indian Ocean: their abundance and biomass in waters of contrasting productivity. *Journal of Plankton Research* 18, 1063–1071.
- Legendre, L., Rassoulzadegan, F., 1995. Plankton and nutrient dynamics in Marine Waters. *Ophelia* 41, 153–172.
- Legendre, L., Rassoulzadegan, F., 1996. Food-web mediated export of biogenic carbon in oceans: hydrodynamic control. *Marine Ecology Progress Series* 145, 179–193.
- Lessard, E.J., Murrell, M.C., 1996. Distribution, abundance and size composition of heterotrophic dinoflagellates and ciliates in the Sargasso Sea near Bermuda. *Deep-Sea Research* 43, 1045–1065.
- Paranjape, M.A., Conover, R.J., Harding, J.C.H., Prouse, N.J., 1985. Micro and macrozooplankton on the Nova Scotian Shelf in the prespring bloom period: a comparison of their potential resource utilization. *Canadian Journal of Fisheries and Aquatic Sciences* 42, 1484–1492.
- Pérez, M.T., Dolan, J.R., Fukai, E., 1997. Planktonic oligotrich ciliates in the NW Mediterranean: growth rates and consumption by copepods. *Marine Ecology Progress Series* 155, 89–101.
- Peréz, M.T., Dolan, J.R., Vidussi, F., Fukai, E., in press. Diel vertical distribution of planktonic ciliates within the surface layer of the NW Mediterranean (May 1995). *Deep-Sea Research I*.
- Putt, M., Stoecker, D.K., 1989. An experimentally determined carbon: volume ratio for marine “oligotrichous” ciliates from estuarine and coastal waters. *Limnology and Oceanography* 34, 1097–1103.
- Rassoulzadegan, F., 1993. Protozoan patterns in the Azam-Ammerman’s bacteria-phytoplankton mutualism In: Guerro, R., Pedros-Alio, C. (Eds.), *Trends in Microbial Ecology*. Spanish Society for Microbiology, Barcelona, pp. 435–439.
- Sherr, E.B., Sherr, B.F., Paffenhöfer, G.-A., 1985. Phagotrophic protozoa as food for metazoans: a ‘missing’ trophic link in marine pelagic food webs? *Marine Microbial Food Webs* 1, 61–80.
- Sime-Ngando, T., Juniper, K., Vézina, A., 1992. Ciliated protozoan communities over Cobb Seamount; increase in biomass and spatial patchiness. *Marine Ecology Progress Series* 89, 37–51.
- Strom, S.L., Postel, J.R., Booth, B.C., 1993. Abundance, variability and potential grazing impact of planktonic ciliates in the open subarctic Pacific Ocean. *Progress in Oceanography* 32, 185–203.
- Suzuki, T., Yamada, N., Taniguchi, A., 1998. Standing crops of planktonic ciliates and nanoplankton in oceanic waters of the western Pacific. *Aquatic Microbial Ecology* 14, 49–58.
- Venrick, E.L., 1982. Phytoplankton in an oligotrophic ocean: observations and questions. *Ecological Monographs* 52, 129–154.
- Vidussi, F., Claustre, H., Bustillo-Guzman, J., Cailliau, C., Marty, J.-C., 1996. Rapid HPLC method for determination of phytoplankton chemotaxonomic pigments: separation of chlorophyll *a* from divinyl-chlorophyll *a* and zeaxanthin from lutein. *Journal of Plankton Research* 18, 2377–2382.
- Williams, N., 1998. The Mediterranean beckons to europe’s oceanographers. *Nature* 279, 483–484.