

Planktonic ciliates in the oligotrophic Eastern Mediterranean: vertical, spatial distribution and mixotrophy

Paraskevi Pitta^{1,*}, Antonia Giannakourou²

¹Institute of Marine Biology of Crete, PO Box 2214, 71003 Heraklion, Crete, Greece

²National Centre for Marine Research, Aghios Kosmas, 16604 Hellinikon, Greece

ABSTRACT: Abundance, biomass, vertical distribution, species composition and mixotrophy of planktonic ciliates were investigated during March 1997 in the oligotrophic Eastern Mediterranean. Six depth layers were sampled in the euphotic zone (0 to 100 m) at 7 stations in the North and 4 in the South Aegean Sea, resulting in a total of 66 samples and 82 ciliate species. Abundance was in general very low (0 to 780 cells l⁻¹) except from specific stations in the North Aegean stations (20 to 2040 cells l⁻¹), influenced by the Black Sea Water. Aloricate species dominated the depth-integrated abundance and biomass in both the North and the South. South Aegean stations presented more diverse ciliate fauna, uniform distribution down to 100 m and higher values of integrated abundance and biomass than the North Aegean stations. Among North stations, those subjected to the influence of the Black Sea presented very pronounced stratification, with mixotrophs and heterotrophs decreasing sharply below 20 m; at these stations, mixotrophic species of 18 to 30 µm dominated the ciliate community at the surface whereas at the South as well as at the rest of the North stations, nanociliates were the major mixotrophic size class. Mixotrophs (20% of abundance in the South, 38% in the North) and nanociliates (28% of abundance in the South, 44% in the North) were found to be very important components of the community, which indicates that these organisms play also an important role in oligotrophic systems.

KEY WORDS: Planktonic ciliates · Eastern Mediterranean · Abundance · Biomass · Vertical distribution · Mixotrophy · Size classes · Nanociliates

INTRODUCTION

After several studies focusing on the biology of planktonic ciliates, these protozoa are now thought to play a much larger role in nature in terms of biomass and carbon flow than previously believed (Fenchel 1990). They comprise heterotrophic and mixotrophic forms (Stoecker et al. 1987, Laval-Peuto & Rassoulzadegan 1988). Ciliates, generally considered as microplanktonic organisms, comprise also nanociliates, an ecologically important, albeit not well-known group.

Being such a diversified group of organisms, ciliates are able to modulate their source of carbon and therefore

they may play an important role in a variety of environments; as protozoa and small cells, they are characterized by high growth rates (Fenchel 1990) and are capable of taking advantage very quickly when there are surplus resources during bloom periods. When resources are scarce, mixotrophic ciliates can take advantage of their double trophic mode, photosynthesis and phagocytosis. The importance of ciliates is expected to increase in oligotrophic waters where the microbial food web imposes the need for many different roles in terms of trophic mode or size classes (micro- or nanoplankton). Despite their importance, little information concerning the role of ciliates in oligotrophic systems is available (Strom et al. 1993, Stoecker et al. 1996).

The Eastern Mediterranean Sea has been characterized as one of the most oligotrophic areas in the world

*E-mail: vpitta@imbc.gr

with extreme properties such as high transparency, low nutrient concentrations and poor productivity (Azov 1986, Yacobi et al. 1995). In the Western Basin (the less oligotrophic part of the Mediterranean) considerably more effort has been devoted to the study of pelagic ciliates, regarding distribution (Rassoulzadegan 1977, 1979, Bernard & Rassoulzadegan 1994, Dolan & Marrasé 1995, Vaqué et al. 1997) or biological processes (Rassoulzadegan 1982, Sherr et al. 1989, Ferrier & Rassoulzadegan 1991, Pérez et al. 1997). However, in the Eastern Basin, information is restricted to the coastal waters (Pitta & Giannakourou 1995, Pitta et al. 1999) or mainly refers to the distribution of tintinnids only (Kimor & Wood 1975, Dowidar et al. 1983, Abboud-Abi Saab 1989).

The Aegean Sea shares all the characteristics of the extreme oligotrophic Eastern Mediterranean. Moreover, it presents additional interest since it combines extreme environmental conditions; its southern part, the South Aegean Sea or Cretan Sea, influenced by the Levantine waters (Souvermezoglou 1989, Theocharis et al. 1993), has been recently characterized as one of the most oligotrophic areas of the Mediterranean Sea on the basis of productivity and light attenuation (Ignatiades 1998); the North Aegean Sea is considered more productive than the South, with higher nutrient input, influenced by the colder and less saline Black Sea Waters passing through the Dardanelles straits (Poulos

et al. 1997) and receiving the outflow of several rivers discharging along the North coast.

The present paper addresses the vertical distribution of ciliates in an oligotrophic system during the mixing period of spring 1997. Two areas with contrasting characteristics are studied, the North (less oligotrophic) and the South (more oligotrophic) Aegean Sea. Particular attention has been given to specific groups such as mixotrophs and nanociliates. To our knowledge, no other study exists on the entire ciliate fauna from the open oceanic waters of this part of the Mediterranean.

MATERIALS AND METHODS

Four stations (S1, S2, S6, S7) were sampled in the South (6 to 9 March 1997) and 7 stations (N1 to N7) in the North Aegean Sea between 28 March and 2 April 1997 (Fig. 1). The South Aegean stations were established offshore, in the Cretan Sea, at a bottom depth ranging from 1300 to 2200 m. The North Aegean stations were either shallow (95 m N4, 120 m N6) or deep (420 to 1200 m). Stns N1, N4 and N5 were chosen in order to assess the impact of the Black Sea Water (BSW) outflow on the North Aegean pelagic ecosystem. CTD data from this sampling cruise (V. Zervakis, NCMR, unpubl. data) showed that during this period the mixed layer depth was extended below 100 m in

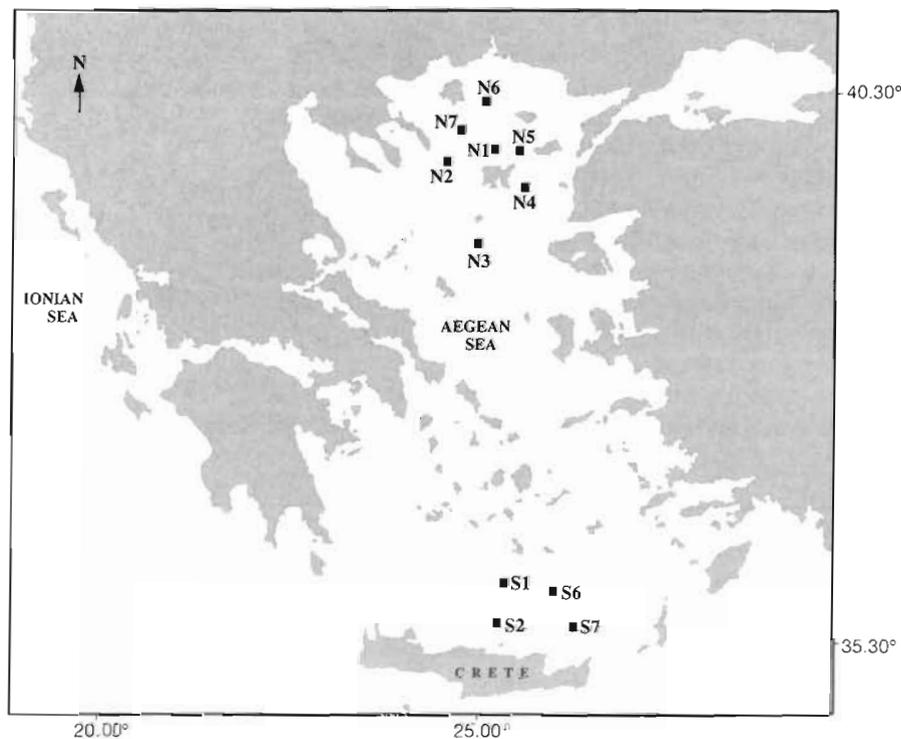


Fig. 1. Sampling stations in the South and the North Aegean Sea

the South Aegean (surface temperature 15°C and salinity 39.02 psu), the North Aegean Stns N2, N3, N6 and N7 showed lower surface temperature (13 to 13.5°C) and salinity (37 to 38.4 psu) whereas the BSW-influenced Stations showed a surface layer (20 to 30 m depth) with even lower temperature (11.5°C) and salinity (34.5 to 36.5 psu). Samples were collected during daytime (11:00 to 12:00 h) at 1, 10, 20, 50, 75 and 100 m water depth, by means of a CTD-rosette using 10 l Go-Flo bottles.

For ciliate enumeration, 500 ml of whole water were preserved with borax-buffered formalin (final concentration 2% formaldehyde). The samples were stored at 4°C in the dark and examined within 4 wk of collection. Although other fixatives, such as acid Lugol's solution, may give higher counts (Gifford 1985), their use does not allow for the detection of plant pigments within cells by means of epifluorescence microscopy. According to Stoecker et al. (1994a), formaldehyde fixation may result in substantial abundance underestimation (30 to 80%); however counts under both fixation methods (Lugol and formaldehyde) in an adjacent coastal area of the Northern Aegean showed no significant differences between the 2 methods (Giannakourou unpubl. data). One hundred ml sub-samples were concentrated using settling chambers and examined on an Olympus IX-70 inverted microscope equipped for transmitted light, phase-contrast and epifluorescence microscopy (blue light: DM 500 nm dichroic mirror, BP 420 to 480 nm exciter filter, BA 515 nm barrier filter and a 100 W mercury burner).

In this study, the terms oligotrichs, choreotrichs and tintinnids are used to describe the taxonomic position of the ciliate species, according to Laval-Peuto (1994) and Laval-Peuto et al. (1994); they stand for the orders Oligotrichida, Choreotrichida and Tintinnida respectively, the first 2 comprising aloricate and the third one loricate species. Plastidic ciliates are those species retaining plastids (some members of the order Oligotrichida) while the terms mixotrophic and heterotrophic describe the trophic activity of the various ciliate species, this being both phagotrophic and phototrophic in the case of mixotrophs and just phagotrophic in the case of heterotrophs.

Oligotrich and choreotrich ciliates were identified down to genus or species level where possible, following Maeda & Carey (1985), Maeda (1986), Laval-Peuto & Rassoulzadegan (1988), Lynn et al. (1988, 1991a), Montagnes et al. (1988, 1990), and Montagnes & Taylor (1994). Tintinnids were identified under phase-contrast microscope, based on the lorica shape and dimensions, after Jorgensen (1924) and Balech (1959).

Cell sizes were measured with an ocular micrometer and converted into cell volumes using appropriate geometric formulae (Peuto-Moreau 1991). According

to Stoecker et al. (1992), the factors used to convert biovolumes to biomass are influenced by taxon as well as fixation method. During this study, the conversion factor 0.14 pg C μm^{-3} was used, as has been suggested for ciliates fixed with 2% formaldehyde (Putt & Stoecker 1989, Lessard 1991).

Two-way ANOVA (station by depth) was used in order to test whether significant differences existed or not among samples grouped according to certain criteria (i.e. depth or geographic location). This type of analysis was performed on total abundance and biomass as well as on particular sub-groups of species referring to taxonomic or trophic categories. The post hoc Tukey test was employed for multiple comparisons among groups of samples assembled according to the significant factors. In order to test whether the factors investigated had an impact on the community structure affecting the species composition and/or the relative abundance of the species present in the community, multivariate analysis was performed on the species abundance data, using non-metric multidimensional scaling (MDS, Field et al. 1982) in the PRIMER software package. Similarities among samples were calculated by means of the Bray-Curtis index (Bray & Curtis 1957) and a $\log(x + 1)$ transformation was applied on the abundance data prior to the analysis in order to normalize the data and to avoid skewness.

RESULTS

Ciliate fauna

A total of 82 ciliate taxa was identified and counted during this study. Species richness was higher in the South Aegean (70 species) than in the North (50 species). The ciliate assemblage included members of the orders Choreotrichida (*Strobilidium* spp.), Tintinnida, Oligotrichida (*Strombidium* spp., *Tontonia* spp. and *Laboea* spp.) and Scuticociliatida.

Ciliate species were dominated by aloricate forms (Choreotrichida and Oligotrichida) by 69.5% while tintinnids represented 18% of the total species number. Mixotrophs accounted for 23% of the ciliate species. These values were approximately the same for both the North and the South Aegean stations.

Ciliates ranged in length from 10 μm (a tiny *Strombidium* species) to almost 400 μm (the tintinnid *Xystonella treforti*). Twelve species were found in the nanoplankton fraction (<20 μm), 2 tintinnid species (*X. treforti* and *Xystonellopsis paradoxa*) exceeded 200 μm in length, while the rest of the species belonged to the microplankton fraction (20 to 200 μm). Seven species (mainly *Strombidium* spp.) were found to contribute

Table 1 Species exceeding 10% of ciliate abundance at any 1 sample, maximal concentration (cells l⁻¹) reached and the corresponding depth. *Nanociliate species

Group	Species	North Aegean		South Aegean	
		Max conc. l ⁻¹	Depth (m)	Max conc. l ⁻¹	Depth (m)
Mixotrophs oligotrichs	<i>Strombidinopsis batos</i> *	40	10		
	<i>Strombidium conicum</i>	490	1		
	<i>Strombidium conicum</i> like	190	1		
	<i>Strombidium dalum</i> *	170	10		
	<i>Strombidium delicatissimum</i> *	190	1	60	10
	<i>Strombidium</i> sp. tiny*	10	20		
	<i>Strombidium</i> sp. 1	450	1		
	<i>Strombidium vestitum</i>	140	10	40	100
	<i>Tontonia gracillima</i>	10	50		
	<i>Tontonia simplicidens</i>	10	75		
Heterotrophs oligotrichs	<i>Strombidium compressum</i>	40	20	60	20, 75
	<i>Strombidium crassulum</i>	10	75		
	<i>Strombidium epidemum</i> *			80	20
	<i>Strombidium inclinatum</i>	30	20		
	<i>Strombidium sphaericum</i> *	1020	1	70	10
	<i>Strombidium sulcatum</i>	20	20		
Choreotrichs	<i>Lohmaniella oviformis</i>	60	10	110	75
	<i>Lohmaniella oviformis</i> small*	20	50		
	<i>Strobilidium elegans</i>	30	10		
	<i>Strobilidium</i> sp. 1	10	75		
	<i>Strobilidium</i> sp. 2	20	50, 100		
	<i>Strobilidium</i> sp. 3	10	75		
	<i>Strobilidium</i> sp. 4*	20	10		
	<i>Strobilidium</i> sp. 5	70	1		
	<i>Strobilidium</i> sp. 6*	120	1		
	<i>Strombidinopsis cheshiri</i>	60	20		
Tintinnids	<i>Codonella galea</i>	30	1		
	<i>Stenosemella nivalis</i>	20	1		
	<i>Xystonellopsis paradoxa</i>	10	75		
Other	Scuticociliates	90	1	120	1, 20, 50, 75
	Ciliata sp.	10	75, 100		

more than 10% of abundance at any one sample in the South (Table 1) while 30 species (mainly of the genera *Strombidium*, *Strobilidium* and *Lohmaniella*) in the North Aegean Sea.

Vertical profiles

Water column profiles showed a pattern of vertical distribution of ciliates in the South quite different from that in the North (Fig. 2). In the South, both abundance and biomass were mostly uniform in the first 100 m. Average concentration (over all 6 depths sampled) ranged from 302 to 545 cells l⁻¹ and average biomass from 0.76 to 0.98 µg C l⁻¹. In the North Aegean, a decrease in abundance and biomass was observed with depth, this decrease being more pronounced in 3 out of 7 stations (N1, N4 and N5), where surface concentration reached 2040 cells l⁻¹ (Stn N4) and decreased to a mean value of 114 cells l⁻¹ below 20 m depth. In the 4 other North Aegean stations, density

decreased from around 300 to 20 cells l⁻¹ (N2, N7), or was very low at all depths (60 to 170 cells l⁻¹, N3) or even presented a subsurface maximum (N6), but in no case did they reach high densities.

The unusually high biomass at 75 and 100 m of Stn S2 is due to the presence of 1 individual of the large tintinnid species *Xystonella treforti*.

Standing stock (abundance and biomass)

Ciliate biomass integrated to 100 m depth was higher in the South than in the North (Table 2; range: 55.1 to 100.5 mg C m⁻², mean 87 ± 21.35 mg C m⁻², in the South, as compared to the first group of North stations [N1, N4 and N5], range: 23.2 to 38.4 mg C m⁻², mean 30.5 ± 7.65 mg C m⁻² and the second North group [N2, N3, N6 and N7], range: 8.4 to 18.3 mg C m⁻², mean 14.1 ± 4.73 mg C m⁻²).

The same was found to hold true for abundance integrated to 100 m (South: range 27.5 to 54.4 × 10⁶ cells

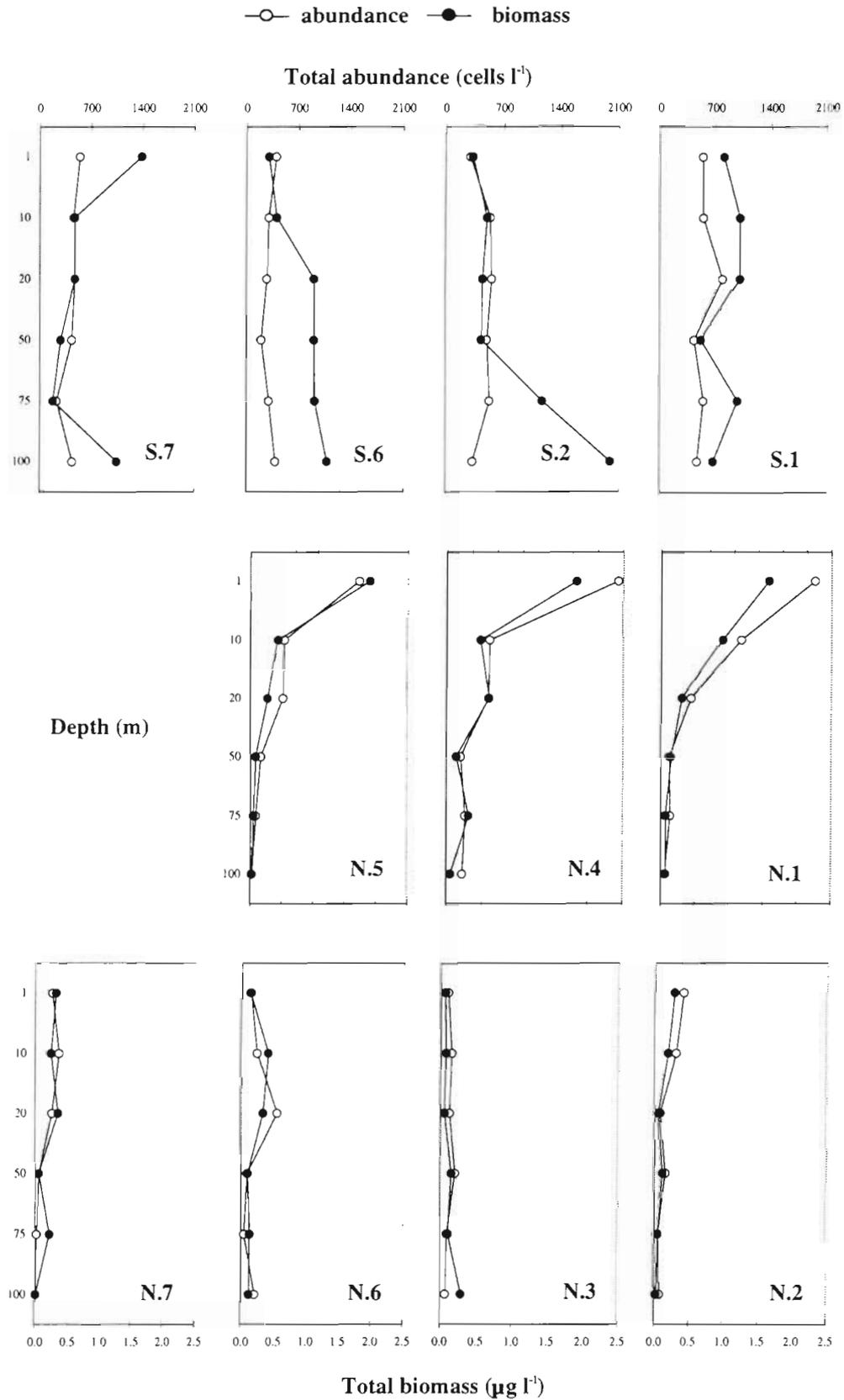


Fig. 2. Total ciliate abundance (cells l⁻¹) and biomass (μg C l⁻¹) versus depth at all stations sampled

Table 2. Integrated values (0 to 100 m) of ciliate abundance and biomass at all stations sampled

Stn	Abundance (10^6 cells m^{-2})	Biomass (mg C m^{-2})
S1	54.4	95.8
S2	48.1	96.4
S6	27.5	100.5
S7	39.5	55.1
N1	33.4	29.8
N4	37.8	38.4
N5	26.4	23.2
N2	10.8	8.4
N3	10.8	12.2
N6	16.4	18.3
N7	9.8	17.7

m^{-2} , mean $42.4 \pm 11.65 \times 10^6$ cells m^{-2} , first North group: range 26.4 to 37.8×10^6 cells m^{-2} , mean $32.5 \pm 5.7 \times 10^6$ cells m^{-2} , second North group: range 9.8 to 16.4×10^6 cells m^{-2} , mean $11.9 \pm 3 \times 10^6$ cells m^{-2}).

Aloricate species dominated the depth-integrated ciliate abundance and biomass (Table 3). Their relative contribution varied from 64 to 84% (mean 73.9%) and from 40 to 63% (mean 56.2%) respectively in the South while in the North it ranged from 80 to 93% (mean 87.8%) and from 41 to 86% (mean 70.8%) respectively. Tintinnids were a less important group numerically (0.6 to 7.2% of total abundance), but due to their large size they comprised an important part of the total biomass (up to 55.2% at Stn N7). The most abundant tintinnids in the North Aegean stations (Table 1) were *Codonella galea*, *Stenosemella nivalis* and *Xystonellopsis paradoxa*.

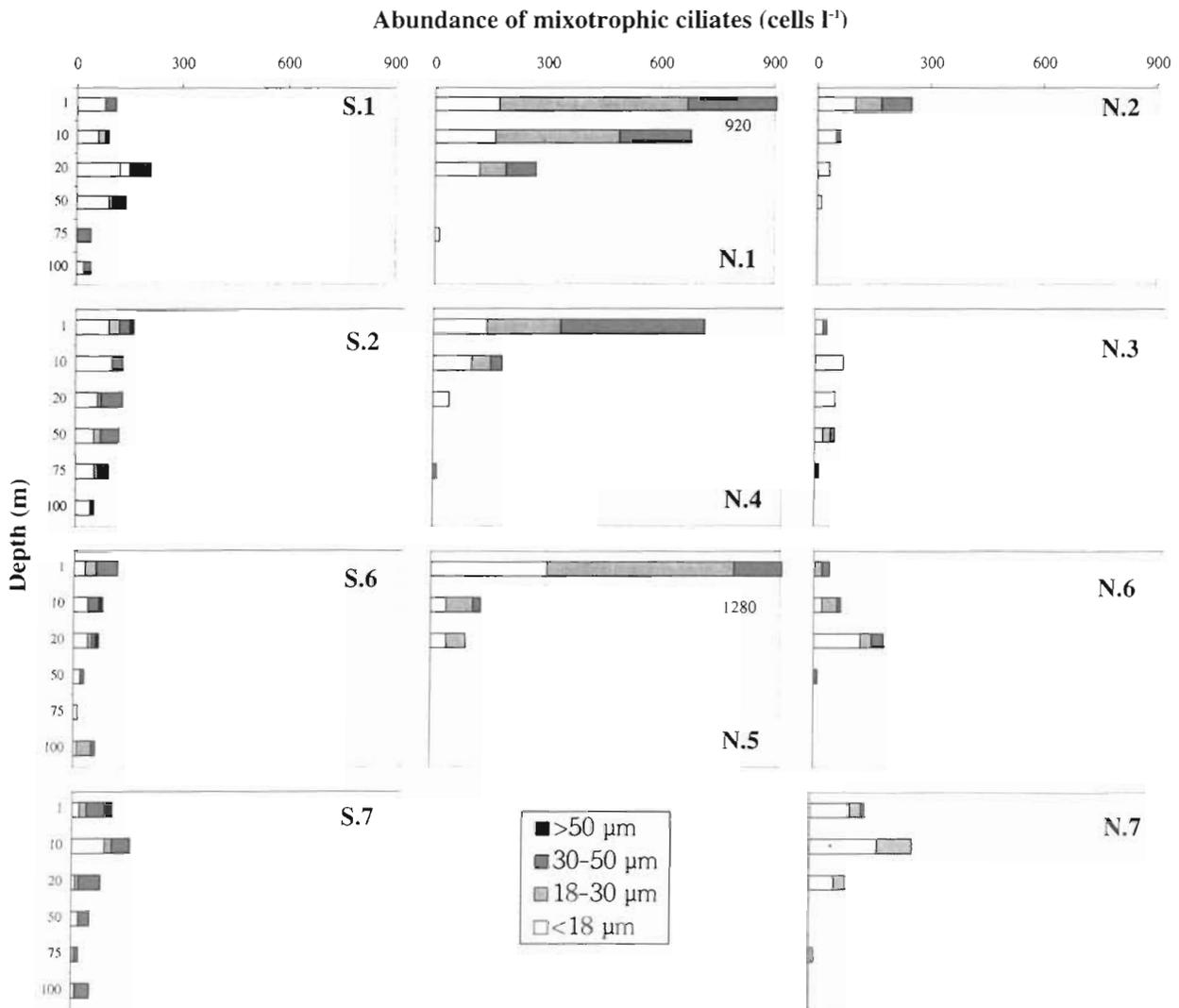


Fig. 3. Abundance (cells l^{-1}) of 4 size classes of mixotrophic ciliates versus depth at all stations sampled

Mixotrophs

Mixotrophs contributed to the total abundance (0 to 100 m integrated values) from 17 to 24% in the South and from 21 to 54% in the North. In terms of integrated biomass, the values varied from 13 to 27% in the South and from 18 to 62% in the North (Table 3).

In the North Aegean stations, mixotrophs were more abundant at the surface layers and they decreased below 20 m depth (Fig. 3), this being more pronounced in the stations influenced by the Black Sea; abundance reached 86.7% and biomass 93.1% of the total numbers at the surface while below 20 m mean values were 5.3% for abundance and 8.2% for biomass. In the South stations, mixotrophic ciliates decreased only slightly with depth. By contrast to the North, the percentage of mixotrophs in the samples taken at the South stations, below 20 m, was never lower than 16 and 15% of abundance and biomass respectively.

Table 3. Percentage of aloricates (oligotrichs and choreotrichs), tintinnids and others over the total ciliate fauna (integrated values 0 to 100 m) in terms of abundance and biomass and percentages of mixotrophs calculated over the entire ciliate abundance and biomass

Stn	Ciliate fauna							
	Oligotrichs + choreotrichs		Tintinnids		Other		Mixotrophs	
	Abund.	Biom.	Abund.	Biom.	Abund.	Biom.	Abund.	Biom.
S1	76.5	60.9	1.4	17.1	22.2	22.0	20.5	13.2
S2	84.3	60.6	1.8	36.0	13.9	3.5	23.7	20.8
S6	63.9	39.7	2.8	1.6	33.2	58.7	18.5	24.2
S7	70.8	63.5	3.6	24.7	25.5	11.8	17.0	27.2
N1	91.4	83.1	1.8	12.2	6.8	4.7	52.6	61.9
N4	92.0	64.3	2.6	33.1	5.4	2.6	20.8	18.1
N5	93.5	83.6	0.6	11.7	5.9	4.8	47.0	52.6
N2	82.9	85.9	2.6	0.9	14.5	13.2	27.1	20.7
N3	92.1	61.8	3.7	29.6	4.2	8.6	34.0	17.8
N6	82.5	75.0	0.6	9.3	16.9	15.6	29.0	29.9
N7	80.1	41.5	7.2	55.2	12.7	3.2	54.0	25.6

Table 4. Percentage of 4 size classes of aloricates (oligotrichs and choreotrichs) over the total aloricate fauna (integrated values 0 to 100 m) in terms of abundance and biomass

Stn	<18 μm		18 to 30 μm		30 to 50 μm		>50 μm	
	Abund.	Biom.	Abund.	Biom.	Abund.	Biom.	Abund.	Biom.
S1	31	4	30	18	13	21	2	17
S2	32	6	36	24	15	32	1	13
S6	23	3	29	13	13	16	2	23
S7	26	4	30	25	17	27	1	10
N1	42	11	21	34	13	26	0	0
N4	69	23	12	17	12	25	1	3
N5	39	11	38	57	8	11	0	0
N2	47	25	30	32	14	36	0	0
N3	44	24	34	32	12	22	0	0
N6	35	12	24	22	20	38	1	6
N7	35	10	30	26	8	17	0	0

In our study, mixotrophic nanociliates (<18 μm) numerically dominated (47%) the mixotrophic abundance in the South Aegean stations (Fig. 3) as well as at 4 out of 7 North Aegean stations (55% at N2, N3, N6 and N7). The mixotrophic fauna of the North Aegean stations receiving the outflow of the Black Sea was dominated by larger size (18 to 30 μm : 32% at Stn N1, and 30 to 50 μm : 32% at N4, N5).

Size classes

Nanociliates comprised a large amount of the ciliate fauna in the Aegean samples, especially at the North stations, 28% (mean values) in the South and 44% in the North (Table 4). In terms of biomass, nanociliates contributed only to a minor degree to the total ciliate biomass (4% in the South and 17% in the North). In the South, the most abundant size class was the 18 to 30 μm

species, while in the North it was the <18 μm species. Species in the >50 μm size class numerically contributed more in the South than in the North, where tintinnids were the most abundant (Table 3).

In the samples taken at the South Aegean there was no evident change in the structure of the ciliate community in respect of size classes nor was there a noticeable decrease of nanociliate abundance with depth (Fig. 4). In the North Aegean, nanociliates as well as all other ciliate groups decreased with depth, especially at the BSW stations.

Spatial structure

Multivariate analysis of species abundance data for all the samples taken, revealed 2 clusters corresponding to North and South Aegean (Fig. 5), whereas no other obvious pattern was found. The fact that MDS showed only these 2 clusters implies that the species of the ciliate community are not substantially different between the 2 groups of the North Aegean stations—neither is there a pronounced qualitative difference with depth in any of the clusters of stations sampled.

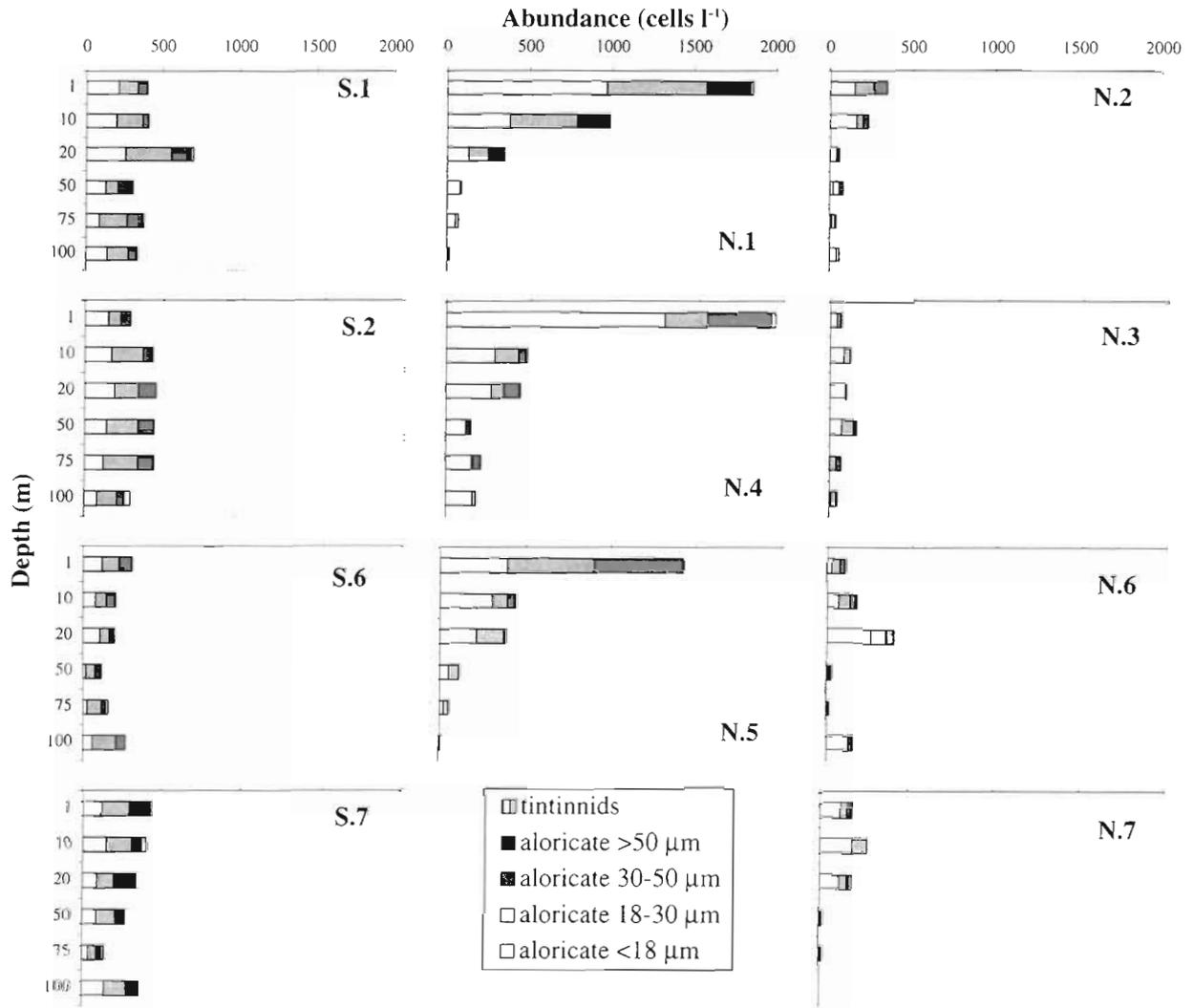


Fig. 4. Abundance (cells l⁻¹) of tintinnids and 4 size classes of aloricate ciliates versus depth at all stations sampled

Analysis of variance

Concentrations of various components of ciliate fauna (reflecting either their morphology and taxonomy—aloricates vs tintinnids—or their trophic activity—mixotrophs vs heterotrophs) were compared through analysis of variance (2-way ANOVA) among stations and depth layers. In the South, no significant differences among depths were detected for any component of ciliate fauna in terms of either abundance or biomass (Table 5). Only Stns S1 and S6 were found to be different in

Table 5. Results of 2-way ANOVA (station by depth) for abundance and biomass of different components of the ciliate fauna in the South Aegean Sea. *p<0.05, **p < 0.01, ns: not significant

Variable		F	df	Stations		F	Depth	
				p	Tukey test		df	p
Total ciliates	Abund.	5.06	3	0.013	S1/S6**	0.86	5	ns
	Biom.	0.23	3	ns		1.17	5	ns
Aloricates	Abund.	5.11	3	0.012	S1/S6*	1.27	5	ns
	Biom.	0.28	3	ns		1.01	5	ns
Tintinnids	Abund.	1.00	3	ns		0.83	5	ns
	Biom.	1.08	3	ns		1.30	5	ns
Mixotrophs	Abund.	1.88	3	ns		3.39	5	ns
	Biom.	0.24	3	ns		0.79	5	ns
Heterotrophs	Abund.	4.35	3	0.021	S1/S6*	0.51	5	ns
	Biom.	0.92	3	ns		1.73	5	ns

terms of abundance of total ciliates, aloricates and heterotrophs.

By contrast, stations in the North Aegean when considered separately, were not found to be different in terms of most of the ciliate fauna components (Table 6). However, when North Aegean stations were regrouped into 2 major groups, one comprising the stations influenced by the Black Sea outflow (N1, N4 and N5) and the other comprising the rest of the North stations, the ANOVA revealed significant differences between these 2 groups of stations for all ciliate components (Table 6) except the tintinnid biomass. The abundance and biomass of almost all components (except tintinnids and heterotrophs) showed highly significant differences between the surface and the lower layers, indicating a strong reduction in all ciliate components below 20 m.

DISCUSSION

Mixotrophs

In both the South and the North Aegean, mixotrophs made up a large amount of ciliate abundance (17 to 54%) and biomass (13 to 62%). It is difficult to compare our data on mixotrophic species with data reported from other regions due to various methodological problems such as differences in sampling (particularly depth ranges) and different or unclear methods in reporting values (average values, integrated values, percentages). Furthermore, in some studies, not all mixotrophic taxa are enumerated due to the use of fixatives, such as Lugol's solution, which do not preserve fluorescence; this technique results in an underestimation of mixotrophic abundance since only large species known as mixotrophic (*Laboea strobila*, *Tontonia appendiculariformis*) are counted.

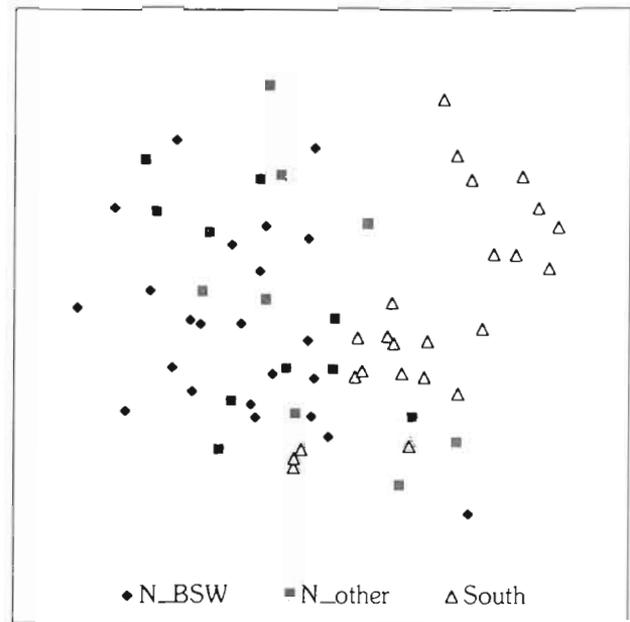


Fig. 5. MDS ordination plot of samples taken at all stations and in all depths. N_BSW: North Aegean Stns N1, N4 and N5 influenced by the Black Sea Water (BSW); N_other: North Aegean Stns N2, N3, N6 and N7; South: South Aegean Stns

Dolan & Marrasé (1995) found 70 l^{-1} *Laboea strobila* and *Tontonia* spp. at 20 m depth during the stratification period (June) in the Western Mediterranean. In comparison, the values reported in the present paper and during the mixing period for all mixotrophic oligotrichs were from 3 to 18 times more numerous although the total ciliate abundance was lower than in the Western basin. Mixotrophs were more abundant at the surface, particularly in the samples from the North Aegean. *L. strobila* was found only twice and *T. appendiculariformis* 3 times, occurring only in the South Aegean with their abundance never exceeding 10 cells l^{-1} . By

Table 6. Results of 2-way ANOVA (station by depth) for abundance and biomass of different components of the ciliate fauna in the North Aegean Sea. * $p < 0.05$, ** $p < 0.01$, ns: not significant

Variable	Stations separately				Stations grouped			Depth				
		F	df	p	Tukey test	F	df	p	F	df	p	Tukey test
Total ciliates	Abund.	2.40	6	ns		15.06	1	0.000	6.09	5	0.000	1/20*, 1/50**, 1/75**, 1/100**
	Biom.	1.81	6	ns		11.72	1	0.002	5.64	5	0.001	1/20*, 1/50**, 1/75**, 1/100**
Aloricates	Abund.	2.38	6	ns		15.17	1	0.000	6.30	5	0.000	1/20*, 1/50**, 1/75**, 1/100**
	Biom.	1.80	6	ns		11.65	1	0.002	5.75	5	0.001	1/20*, 1/50**, 1/75**, 1/100**
Tintinnids	Abund.	2.00	6	ns		4.45	1	0.042	1.09	5	ns	
	Biom.	2.20	6	ns		1.99	1	ns	0.91	5	ns	
Mixotrophs	Abund.	1.88	6	ns		10.45	1	0.003	6.47	5	0.000	1/20*, 1/50**, 1/75**, 1/100**
	Biom.	1.55	6	ns		8.48	1	0.006	5.37	5	0.001	1/20*, 1/50**, 1/75**, 1/100**
Heterotrophs	Abund.	2.64	6	0.035	N4/N7*	9.22	1	0.005	2.28	5	ns	
	Biom.	3.12	6	0.017	N4/N2*, N4/N3*	5.34	1	0.027	1.47	5	ns	

contrast, 50% of mixotrophs in our study were nanociliates. Mixotrophic species of larger size were dominant only in the North Aegean stations influenced by the Black Sea outflow (18 to 30 μm : 32% at Stn N1, and 30 to 50 μm : 32% at N4, N5).

The presence of oligotrichs that retain chloroplasts has been reported from both neritic and oceanic waters (Table 7). In general, and perhaps due to the above-mentioned problems in methodology, the mixotroph contribution to the total ciliate abundance varies from <10% (Stoecker et al. 1996) to around 50%, depending on the type of values used, i.e. when only surface layers are considered, mixotrophs are in general more abundant, whereas with integrated values their proportion decreases depending on the maximum depth used in the calculation. The values found during this study are generally within the range reported from other studies. However, in terms of abundance, the relative contribution of mixotrophic ciliates at the surface layers and particularly at the North Aegean stations (up to 88% of abundance) is among the highest surface values reported from either oceanic or neritic regions.

In terms of vertical distribution, in the North Stns N1, N4 and N5 (those receiving the Black Sea outflow) mixotrophs were very abundant at the surface layers (up to 87% of abundance) whereas they noticeably decreased below 20 m. According to Poulos et al. (1997) this depth layer (surface to 25 m) corresponds to the less saline BSW which flow towards the Aegean Sea through the Dardanelles Strait, this flow becoming largest in late spring and summer. According to Zodiatis (1994), BSW flows westward along the northern shoreline of Lemnos, therefore influencing the water masses of the area where Stns N4, N5 and N1 are located. In the second group of North Aegean Stations (N2, N3, N6 and N7), mixotrophs presented low densities compared to the rest of the stations (North and South), decreasing with depth albeit less sharply than at the BSW-influenced stations.

In most studies carried out in other temperate regions or in the Nordic Seas, the abundance of mixotrophic ciliates decreases with depth (Lindholm 1985, Stoecker et al. 1989, Putt 1990, Dolan & Marrasé 1995) and at 50 or 80 m, the densities are 2 to 3 times less than at the surface; even in the case of the stratified Catalan Sea during June, where heterotrophic ciliates were more abundant at 50 m than near the surface, mixotrophs showed an inverse pattern of vertical distribution and were more abundant at the surface (Dolan & Marrasé 1995).

While in the North Aegean the vertical distribution of mixotrophic ciliates is in agreement with patterns found in other regions, in all South Aegean stations mixotrophs were more abundant at the surface layers

but they occupied the entire euphotic zone, down to 100 m, probably due to mixing. The South Aegean Sea is known to be one of the most oligotrophic areas of the Mediterranean Sea and its waters have been classified as Jerlov's Optical Type I, i.e. the most transparent (Ignatiades 1998).

The results of this study indicate the quantitative importance of mixotrophic ciliates in an extreme oligotrophic area (South Aegean) as well as in the less oligotrophic stations of the North Aegean, i.e. those influenced by the Black Sea outflow.

Nanociliates

Compared to microciliates, nanociliates have been found to predominate in neritic waters (Lynn et al. 1991b), to constitute a large amount (57%) of the nanoplankton biomass in tidal creek waters (Sherr et al. 1986), to predominate by far (72%) the non-tintinnid ciliates in the Northern Adriatic (Revelante & Gilmartin 1983) or, on the contrary, to contribute only a minor part of the total ciliate fauna (8%) in the open Catalan Sea (Dolan & Marrasé 1995). Dolan & Marrasé (1995) suggested that in oceanic systems nanociliates play only a minor role in the food web compared to the coastal systems.

Our study in the open waters of the Eastern Mediterranean showed however that nanociliates accounted for 28% of abundance in the South and 44% in the North. In oligotrophic areas such as the Aegean Sea, where resources are by and large scarce, the picoplankton fraction is of great importance as has been found in the Levantine Basin (Eastern Mediterranean, Li et al. 1993) as well as in other oligotrophic regions (Gieskes et al. 1979, Platt et al. 1983). We may assume that the scarcity of resources forces the system towards a web of smaller organisms, this concerning not only autotrophic components such as cyanobacteria, prochlorophytes and eukaryotic flagellates (according to their attributes; Fenchel 1988) but also their predators, heterotrophic flagellates and ciliates. The importance of nanociliates becomes even greater when considering the contribution of this group to the mixotrophic community: 35% of nanociliates in the South and 31% in the North Aegean were mixotrophic.

These results indicate that in the oligotrophic Aegean Sea, small size characterizes not only the autotrophic fraction of the ecosystem but also a large proportion of the heterotrophic or the mixotrophic ones. As also found by Lessard & Murrell (1996) in the Sargasso Sea, the present study shows that small ciliates do exist in considerable abundance in oligotrophic systems.

Table 7. Concentrations and relative importance of mixotrophic ciliates in marine systems. N_{NSV}: North Aegean Stns N1, N4 and N5 influenced by the Black Sea Water; N_{Other}: North Aegean Stns N2, N3, N6, N7

Region	Depth (m)	Sampling period	Mixo abund. (cells l ⁻¹)	% of ciliate abund.	% of ciliate biomass	Organisms counted	Source
Neritic waters							
Woods Hole	0	Spring, summer		47–51			Stoecker et al. (1987)
	0	Autumn, winter		22			
	0–9	July	2380	52 of total		All plastidic	
Villefranche Bay	0	Oct–Feb		41 of oligo spp.			Laval-Peuto & Rassoulzadegan (1988)
Villefranche Bay	0	22 mo			51 of oligo ^b	All fluorescent ciliates	Bernard & Rassoulzadegan (1994)
Jamaica, Caribbean	5	1 yr		12	25	<i>Laboea</i> , <i>Tontonia</i>	Lynn et al. (1991b)
E. Pacific fjord	2	Feb	57	1.60	7	<i>Laboea</i> , <i>Tontonia</i> , <i>Strombidium capitatum</i>	Martin & Montagnes (1993)
Nordic Seas	0	Summer	497	58–65 of total	59–63 of oligo	All plastidic	Putt (1990)
	50		65	14–24			
Shelf/slope waters							
Georges Bank, NW Atlantic	0 to 35 ^a	July		21–70		All plastidic	Stoecker et al. (1989)
Oceanic waters							
Sargasso Sea		Late spring		37			Unpubl. data in Stoecker (1991)
Gulf Stream		Late spring		25			Unpubl. data in Stoecker (1991)
Subarctic Pacific	5–30	Jun, Sep, May, Aug		30–50		Mixotrophic	Booth et al. (1993)
North Atlantic	0–20	May–Jun bloom	558–3006	52 of total		Plastidic oligotrichs	Stoecker et al. (1994b)
Weddell-Scotia Seas, Antarctic	0–85	Jun–August		10		Plastidic oligotrichs	Gowing & Garrison (1992)
Equatorial Pacific		Mar–April	5	10 of total		Plastidic oligotrichs	Stoecker et al. (1996)
		Oct	2	<10			
Mediterranean Sea							
Catalan Sea	5	Jun	54	19 of total	63 of total	<i>Laboea</i> , <i>Tontonia</i>	Dolan & Marrasé (1995)
	0–20		70	18	48		
	0–80		24	6	21		
Aegean Sea, South	0–20	Mar	70–210	17–55	5–89	Plastidic oligotrichs	This study
	20–100		20–140	7–33	0.1–39		
Aegean Sea, N _{SSW}	0–20	Mar	40–1280	8–88	30–86		
	20–100		0–10	0–14	0–5		
Aegean Sea, N _{Other}	0–20		30–260	28–87	18–93		
	20–100		0–30	0–20	0–15		

^a integrated

^b biovolume

North versus South Aegean Sea or the Aegean Sea as a whole?

The abundance of ciliates encountered during this study is among the lowest reported from oceanic waters (Strom et al. 1993, Suzuki et al. 1998). It is low also compared to values found in the Western Mediterranean (Dolan & Marrasé 1995) and the Adriatic Sea (Krsinic 1995), thus reflecting the extreme oligotrophic regime of this part of the Eastern Mediterranean. If we consider the fact that this study was undertaken during the spring bloom period when one would expect high abundance of all pelagic components, and if the underestimation due to the fixation method used is relatively low, then the ciliate abundance found in the Aegean Sea may be the lowest encountered in the literature. Despite the low abundance, ciliate assemblages proved to be very diverse, comprising 82 different ciliate taxa found during one sampling period while 55 taxa were found during a 1 yr study in the Southampton Water (Leakey et al. 1993).

South Aegean stations presented typical characteristics of an oceanic ecosystem with mixed water column during this period. The water column was mixed down to 100 m and this was evident in the abundance and biomass of total ciliates as well as of different groups of ciliates, such as mixotrophs, heterotrophs, tintinnids and aloricates (Table 5). Low abundance was found in the entire euphotic zone, which was however more extended compared to the North Aegean euphotic zone; in the South, ciliate fauna had the potential of exploiting resources deeper in the water column, resulting in higher integrated values for the 0 to 100 m layer. A more even exploitation of resources occurred in the South since in most of the samples the 2 most abundant species never exceeded 52%, whereas at the North stations they ranged from 76 to 90%. As a consequence, in the South only 7 out of 70 species reached more than 10% of the total abundance and ciliate fauna was more diverse than in the North. Also, in contrast to the North, all the stations in the South Aegean were found to be homogeneous with respect to ciliate abundance and biomass with the exception of Stn S6 that was found to be different from Stn S1 in terms of abundance of aloricates and heterotrophs.

In contrast to the South, in the North Aegean 2 types of stations were identified. Stns N2, N3, N6 and N7 showed extremely low ciliate abundance and biomass whereas the stations close to the Dardanelles showed very high abundance at the surface, noticeably decreasing below the depth of 20 m. This is probably related to distinct characteristics of the BSW masses coming out from the Dardanelles strait (Poulos et al. 1997); the influence of the BSW results in salinity and temperature stratification of the water masses at these stations which is noticeable even during the winter mixing period.

Since nutrient availability is generally higher in the North Aegean than in the South (Friligos 1980) and consequently primary production could also be expected to be higher, the general impoverishment in ciliate fauna in the North Aegean Stns N2, N3, N6 and N7 could be attributed to increased predation by metazoan predators (top-down regulation) as has also been indicated in mesocosm experiments (Pitta et al. 1998). This is a hypothesis to be tested in the frame of the entire microbial food web. According to the same hypothesis, higher ciliate abundance in the South is due to weaker predation by copepods which agrees with the extreme oligotrophic character of the Cretan Sea, giving advantage to the microbial food web, inside which the energy is recycled and not transferred to higher trophic levels.

In terms of qualitative composition of the ciliate assemblages, aloricate ciliates numerically dominated (by 70%) both regions, this being in agreement with other studies in the Mediterranean (Ferrier-Pagès & Rassoulzadegan 1994, Dolan & Marrasé 1995) or other marine ecosystems (Beers et al. 1980, Sherr et al. 1986, Dolan & Coats 1990). Mixotrophic species represented 33% of the aloricate species during spring in the Eastern basin whereas Laval-Peuto & Rassoulzadegan (1988) found 40.6% in the coastal Western Mediterranean during autumn and winter.

The relative abundance of nanociliates and mixotrophs was different in these 2 environments. In addition, in the South, most of the mixotrophic abundance was found in the nanoplanktonic fraction while in the North, at least in the BSW-influenced stations, larger mixotrophic species dominated.

All the above seem to imply that there are marked differences between the North and the South Aegean in terms of community structure, abundance, biomass and vertical distribution of ciliates. However, this argument needs to be tested on a seasonal basis since ciliate distribution and biomass may change from one week to another or even more from one month to another.

Our results indicate that the ciliate community of the Aegean Sea, despite the low abundance, even during the bloom period, is a diverse component of the pelagic ecosystem, in terms of species, size groups and trophic modes. In particular, the high percentage of mixotrophs and nanociliates indicates that these components of the ciliate community may also be compatible with extreme oligotrophic conditions.

Acknowledgements. The authors wish to thank the Captain and the crew of the RV 'Aegaeo'. Thanks are due to Vassilis Zervakis for providing CTD data. Comments and helpful suggestions for the improvement of the manuscript were provided by Michele Peuto-Moreau and 4 anonymous reviewers.

This study forms the contribution No. 39 to the MTP-II project 'MATER: Mass Transfer and Ecosystem Response' jointly founded by the European Commission's Marine Science and Technology III (MAST-III) Programme (contract: MAS3-CT96-0051) and the Greek General Secretariat of Research and Technology.

LITERATURE CITED

- Abboud-Abi Saab M (1989) Distribution and ecology of tintinnids in the plankton of Lebanese coastal waters (Eastern Mediterranean). *J Plankton Res* 11:203–222
- Azov Y (1986) Seasonal patterns of phytoplankton productivity and abundance in nearshore oligotrophic waters of the Levant Basin (Mediterranean). *J Plankton Res* 8:41–53
- Balech E (1959) *Tintinnoinea del Mediterraneo*. Trabajos del Instituto Español de Oceanografía, Madrid, No 28
- Beers JR, Reid FMH, Stewart GL (1980) Microplankton population structure in Southern California nearshore waters in late spring. *Mar Biol* 60:209–226
- Bernard C, Rassoulzadegan F (1994) Seasonal variations of mixotrophic ciliates in the northwest Mediterranean Sea. *Mar Ecol Prog Ser* 108:295–301
- Booth BC, Lewin J, Postel JR (1993) Temporal variation in the structure of autotrophic and heterotrophic communities in the subarctic Pacific. *Prog Oceanogr* 32:57–99
- Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. *Ecol Monogr* 27:325–349
- Dolan JR, Coats DW (1990) Seasonal abundances of planktonic ciliates and microflagellates in mesohaline Chesapeake Bay waters. *Estuar Coast Shelf Sci* 31:157–175
- Dolan JR, Marrasé C (1995) Planktonic ciliate distribution relative to a deep chlorophyll maximum: Catalan Sea, NW Mediterranean, June 1993. *Deep-Sea Res* 42:1965–1987
- Dowidar NM, Khalil AN, El-Maghraby AM, El-Zawawy DA (1983) Zooplankton composition of the eastern harbour of Alexandria, Egypt. *Rapp Comm Int Mer Médit* 28:195–196
- Fenchel T (1988) Marine plankton food chains. *Annu Rev Ecol Syst* 19:19–38
- Fenchel T (1990) The role of protozoa in nature in terms of functional properties related to size. *Zool Sci* 7:51–58
- Ferrier C, Rassoulzadegan F (1991) Density-dependent effects of protozoans on specific growth rates in pico- and nanoplanktonic assemblages. *Limnol Oceanogr* 36:657–669
- Ferrier-Pagès C, Rassoulzadegan F (1994) Seasonal impact of the microzooplankton on pico- and nanoplankton growth rates in the northwest Mediterranean Sea. *Mar Ecol Prog Ser* 108:283–294
- Field JG, Clarke KR, Warwick RM (1982) A practical strategy for analysing multispecies distribution patterns. *Mar Ecol Prog Ser* 8:37–52
- Friligos N (1980) Nutrients in Greek waters. *Ves journées étud pollutions 1025–1034*, Cagliari, CIESM
- Gieskes WWC, Kraay GW, Baars MA (1979) Current ¹⁴C methods for measuring primary production: gross underestimates in oceanic waters. *Neth J Sea Res* 13:58–78
- Gifford DJ (1985) Laboratory culture of marine planktonic oligotrichs (Ciliophora, Oligotrichida). *Mar Ecol Prog Ser* 23:257–267
- Gowing MM, Garrison DL (1992) Abundance and feeding ecology of larger protozooplankton in the ice edge zone of the Weddell and Scotia Seas during the austral winter. *Deep-Sea Res* 39:893–919
- Ignatiades L (1998) The productive and optical status of the oligotrophic waters of the Southern Aegean Sea (Cretan Sea), Eastern Mediterranean. *J Plankton Res* 20:985–995
- Jørgensen E (1924) Mediterranean Tintinnidae. *Rept Danish Oceanograph Exped 1908–1910 to the Mediterranean and adjacent seas* 2:1–110
- Kimor B, Wood EJM (1975) A plankton study in the Eastern Mediterranean Sea. *Mar Biol* 29:321–333
- Krsinic F (1995) Changes in the microzooplankton assemblages in the northern Adriatic Sea during 1989 to 1992. *J Plankton Res* 17:935–953
- Laval-Peuto M (1994) Classe des Oligotrichea Büstchli, 1887. *Ordre des Tintinnida Kofoid et Campbell, 1929*. In: Grassé PP (ed), *Traité de zoologie II, 2, Infusoires ciliés*. Masson, Paris, p 181–219
- Laval-Peuto M, Rassoulzadegan F (1988) Autofluorescence of marine planktonic Oligotrichina and other ciliates. *Hydrobiologia* 159:99–110
- Laval-Peuto M, Grain J, Deroux G (1994) Classe des Oligotrichea Büstchli, 1887. *Ordres des Oligotrichida Büstchli, 1887 et des Choreotrichida Small & Lynn, 1985*. In: Grassé PP (ed), *Traité de zoologie II, 2, Infusoires ciliés*. Masson, Paris, p 153–179
- Leakey RJG, Burkill PH, Sleigh MA (1993) Planktonic ciliates in Southampton water: quantitative taxonomic studies. *J Mar Biol Assoc UK* 73:579–594
- Lessard EJ (1991) The trophic role of heterotrophic dinoflagellates in diverse marine environments. *Mar Microb Food Webs* 5:49–58
- Lessard EJ, Murrell MC (1996) Distribution, abundance and size composition of heterotrophic dinoflagellates and ciliates in the Sargasso Sea near Bermuda. *Deep-Sea Res* 43:1045–1065
- Li WKW, Zohary T, Yacobi YZ, Wood AM (1993) Ultraphytoplankton in the eastern Mediterranean Sea: towards deriving phytoplankton biomass from flow cytometric measurements of abundance, fluorescence and light scatter. *Mar Ecol Prog Ser* 102:79–87
- Lindholm T (1985) *Mesodinium rubrum*—a unique photosynthetic ciliate. *Adv Aquat Microbiol* 3:1–48
- Lynn DH, Montagnes DJS, Small EB (1988) Taxonomic descriptions of some conspicuous species in the family Strombidiidae (Ciliophora: Oligotrichida) from the isles of Shoals, Gulf of Maine. *J Mar Biol Assoc UK* 68:259–276
- Lynn DH, Montagnes DJS, Dale T, Gilron GL, Strom SL (1991a) A reassessment of the genus *Strombidinopsis* (Ciliophora, Choreotrichida) with descriptions of four new planktonic species and remarks on its taxonomy and phylogeny. *J Mar Biol Assoc UK* 71:597–612
- Lynn DH, Roff JC, Hopcroft RR (1991b) Annual abundance and biomass of aloricate ciliates in tropical neritic waters off Kingston, Jamaica. *Mar Biol* 110:437–448
- Maeda M (1986) An illustrated guide to the species of the families Halteriidae and Strombidiidae (Oligotrichida, Ciliophora), free swimming protozoa common in the aquatic environment. *Bull Ocean Res Inst* 21:1–67
- Maeda M, Carey PG (1985) An illustrated guide to the species of the family Strombidiidae (Oligotrichida, Ciliophora), free swimming protozoa common in the aquatic environment. *Bull Ocean Res Inst* 19:1–68
- Martin AJ, Montagnes DJS (1993) Winter ciliates in a British Columbian fjord: six new species and an analysis of ciliate purative prey. *J Eukaryot Microbiol* 40:535–549
- Montagnes DJS, Taylor FJR (1994) The salient features of five marine ciliates in the class Spirotrichea (Oligotrichia), with notes on their culturing and behaviour. *J Eukaryot Microbiol* 41:569–586
- Montagnes DJS, Lynn DH, Stoecker DK, Small EB (1988)

- Taxonomic descriptions of one new species and redescription of four species in the family Strombidiidae (Ciliophora, Oligotrichida). *J Protozool* 35:189–197
- Montagnes DJS, Taylor FJR, Lynn DH (1990) *Strombidium inclinatum* n. sp. and a reassessment of *Strombidium sulcatum* Clarapède and Lachmann (Ciliophora). *J Protozool* 37:318–323
- Pérez MT, Dolan JR, Fukai E (1997) Planktonic oligotrich ciliates in the NW Mediterranean: growth rates and consumption by copepods. *Mar Ecol Prog Ser* 155:89–101
- Peuto-Moreau M (1991) Symbiose plastidiale et mixotrophie des ciliés planctoniques marins Oligotrichina (Ciliophora). Thèse de doctorat d'état, Université de Nice-Sophia Antipolis
- Pitta P, Giannakourou A (1995) Seasonal variability of nano- and microplankton in Heraklion Bay (South Aegean). *Rapp Comm Int Mer Médit* 34:215
- Pitta P, Giannakourou A, Divanach P, Kentouri M (1998) Planktonic food web in marine mesocosms in the Eastern Mediterranean: bottom-up or top-down regulation? *Hydrobiologia* 363:97–105
- Pitta P, Karakassis I, Tsapakis M, Zivanovic S (1999) Natural vs. mariculture induced variability in nutrients and plankton in the Eastern Mediterranean. *Hydrobiologia* 391:181–194
- Platt T, Rao DVS, Irwin B (1983) Photosynthesis of picoplankton in the oligotrophic ocean. *Nature* 300(5902):702–704
- Poulos SE, Drakopoulos PG, Collins MB (1997) Seasonal variability in sea surface oceanographic conditions in the Aegean Sea (Eastern Mediterranean): an overview. *J Mar Syst* 13:225–244
- Putt M (1990) Abundance, chlorophyll content and photosynthetic rates of ciliates in the Nordic Seas during summer. *Deep-Sea Res* 37:1713–1731
- Putt M, Stoecker DK (1989) An experimentally determined carbon: volume ratio for marine 'oligotrichous' ciliates from estuarine and coastal waters. *Limnol Oceanogr* 34:1097–1103
- Rassoulzadegan F (1977) Evolution annuelle des ciliés pélagiques en Méditerranée Nord-Occidentale. Ciliés oligotriches 'Non Tintinnides' (Oligotrichina). *Ann Inst Oceanoogr (Paris)* 53:125–134
- Rassoulzadegan F (1979) Evolution annuelle des ciliés pélagiques en Méditerranée Nord-Occidentale. II. Ciliés Oligotriches. Tintinnides (Tintinnina). *Invest Pesq* 43:417–448
- Rassoulzadegan F (1982) Dependence of grazing rate, gross growth efficiency and food size range on temperature in a pelagic Oligotrichous ciliate *Lohmaniella spiralis* Leeg., fed on naturally occurring particulate matter. *Ann Inst Oceanoogr (Paris)* 58:177–184
- Revelante N, Gilmartin M (1983) Microzooplankton distribution in the Northern Adriatic Sea with emphasis on the relative abundance of ciliated protozoans. *Oceanol Acta* 6:407–415
- Sherr EB, Sherr BF, Fallon RD, Newell SY (1986) Small, aloricate ciliates as a major component of the marine heterotrophic nanoplankton. *Limnol Oceanogr* 31:177–183
- Sherr EB, Rassoulzadegan F, Sherr BF (1989) Bacterivory by pelagic choreotrichous ciliates in coastal waters of the VW Mediterranean Sea. *Mar Ecol Prog Ser* 55:235–240
- Sherr EB, Sherr BF, Berman T, Hadas O (1991) High abundance of picoplankton-ingesting ciliates during late fall in Lake Kinneret, Israel. *J Plankton Res* 13:789–799
- Souvermezoglou E (1989) Distribution of nutrients and oxygen in the Eastern Mediterranean Sea. Proceedings of the UNESCO/IOC Second Scientific Workshop, Trieste, Italy, POEM Sci. Repts, 3, Cambridge, MA, p 85–102
- Stoecker DK (1991) Mixotrophy in marine planktonic ciliates: physiological and ecological aspects of plastid-retention by oligotrichs. In: Reid PC (ed) *Protozoa and their role in marine processes*. NATO ASI Series G25:161–179, Springer-Verlag, Berlin
- Stoecker DK, Michaels AE, Davis LH (1987) Large proportion of marine planktonic ciliates found to contain functional chloroplasts. *Nature* 326(6115):790–792
- Stoecker DK, Taniguchi A, Michaels AE (1989) Abundance of autotrophic, mixotrophic and heterotrophic planktonic ciliates in shelf and slope waters. *Mar Ecol Prog Ser* 50:241–254
- Stoecker DK, Buck KR, Putt M (1992) Changes in the sea-ice brine community during the spring-summer transition, McMurdo Sound, Antarctica. I. Photosynthetic protists. *Mar Ecol Prog Ser* 84:265–278
- Stoecker DK, Gifford DJ, Putt M (1994a) Preservation of marine planktonic ciliates: losses and cell shrinkage during fixation. *Mar Ecol Prog Ser* 110:293–299
- Stoecker DK, Sieracki ME, Verity PG, Michaels AE, Haugen E, Burkill PH, Edwards ES (1994b) Nanoplankton and protozoan microzooplankton during the JGOFS North Atlantic bloom experiment: 1989 and 1990. *J Mar Biol Assoc UK* 74:427–443
- Stoecker DK, Gustafson DE, Verity PG (1996) Micro- and mesoprotozooplankton at 140° W in the equatorial Pacific: heterotrophs and mixotrophs. *Aquat Microb Ecol* 10:273–282
- Strom S, Postel JR, Booth BC (1993) Abundance, variability, and potential grazing impact of planktonic ciliates in the open subarctic Pacific Ocean. *Prog Oceanogr* 32:185–203
- Suzuki T, Yamada N, Taniguchi A (1998) Standing crops of planktonic ciliates and nanoplankton in oceanic waters of the western Pacific. *Aquat Microb Ecol* 14:49–58
- Theocharis A, Georgopoulos D, Lascaratos A, Nittis K (1993) Water masses and circulation in the central region of the Eastern Mediterranean: Eastern Ionian, South Aegean and Northwest Levantine, 1986–1987. *Deep-Sea Res* 40:1121–1142
- Vaqué D, Blough HA, Duarte CM (1997) Dynamics of ciliate abundance, biomass and community composition in an oligotrophic coastal environment (NW Mediterranean). *Aquat Microb Ecol* 12:71–83
- Yacobi YZ, Zohary T, Kress N, Hecht A, Robarts RD, Waiser M, Wood AM, Li WKW (1995) Chlorophyll distribution throughout the southeastern Mediterranean in relation to the physical structure of the water mass. *J Mar Syst* 6:179–190
- Zodiatis G (1994) Advection of the Black Sea water in the North Aegean Sea. *Global Atmos Ocean Syst* 2:41–60

Editorial responsibility: Fereidoun Rassoulzadegan (Contributing Editor), Villefranche-sur-Mer, France

Submitted: December 21, 1998; Accepted: July 5, 1999
Proofs received from author(s): February 25, 2000