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Dynamics of ciliate abundance, biomass and community composition in an oligotrophic coastal environment (NW Mediterranean)

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ABSTRACT: The importance of ciliates as components of the microbial community of the oligotrophic coastal area of the Bay of Blanes (NW Mediterranean Sea) was examined based on a 3 yr, high resolution study focused on the composition, abundance and biomass of the ciliate community. The most abundant components of the ciliate community were 'oligotrich' ciliates. Naked oligotrichs included heterotrophic genera represented by *Halteria*, *Strombidium*, *Strobilidium*, and *Lohmaniella*, as well as mixotrophic genera represented by *Laboea* and *Tontonia* and loricate ciliates represented by the group of tintinnids. Autotrophic ciliates were represented by the genus *Mesodinium*. Other, less abundant groups encountered throughout the study period included the orders Scuticociliatida, Pleurostomatida and Prorodontida. Ciliate community abundance and biomass did not show a simple seasonal pattern. Maximum values were observed in spring, following the winter phytoplankton blooms, throughout the study period. Ciliate communities showed significant interannual differences in abundance and cell size. However, total ciliate biomass (µg C l^{-1}) was similar among years. Changes in ciliate abundance and biomass were independent of temperature. Periods with persistent, heavy rainfall, which promotes pulses of allochthonous material from flushed rivers, were characterized by a reduced abundance of ciliates, and increased pico- and nanoplanktonic populations. Cross correlation analysis revealed that bacterial abundance and chlorophyll *a* (chl *a*) concentration were both significantly negatively correlated with ciliate abundance, with time lags of 15 d, suggesting a role for ciliates in the control of these communities. Examination of the variability of ciliate abundance and biomass at different time scales revealed a dominant scale of temporal variation in ciliate abundance at about 50 d, similar to that of chl *a* in the Bay of Blanes, whereas total ciliate biomass (µg C l^{-1}) did not show any dominant scale of variation.

KEY WORDS: Coastal area · Ciliate abundance and biomass · Community composition · Rainfall · Temporal variabilty

INTRODUCTION

Ciliates are important components of coastal microbial communities (Pierce & Turner 1992), where they can play an important role in nutrient and carbon cycling (Azam et al. 1983, Sherr et al. 1986, Ferrier-Pagès & Rassoulzadegan 1994, Dolan & Marrasé 1995). The abundance, biomass and composition of coastal microbial communities (i.e. phytoplankton, bacterioplankton, and protists) should be much more variable than those of open-sea communities, due to the greater variability in factors influencing their growth (e.g. temperature, salinity, turbulence, water turbidity) characteristic of coastal waters (Nielsen & Kiørboe 1991).

The Bay of Blanes (Catalan coast, NW Mediterranean Sea) is a heterotrophic system during most of the year, with primary production exceeding community respiration only during phytoplankton blooms (Satta et al. 1996). The Bay of Blanes is characterized by considerable environmental variability (Cebrián et al. 1996). This variability results from a number of processes, including intermittent pulses of allochthonous material inputs from rivers, and the effects of flow

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modifications by an adjacent submarine canyon (Masó et al. 1990, Masó & Tintoré 1991). The environmental variability characteristic of the Bay of Blanes should result in a similarly large variability in the pelagic microbial communities. Ciliate communities may respond to environmental variability through changes in abundance, biomass and composition, but these responses may be masked by the effects of the interactions of the ciliate communities with other planktonic communities.

Long-term studies of the distribution of ciliate communities in coastal waters and their response to physical and biological forcing are few, as most studies refer to a 1 or 2 yr period (e.g. Smetacek 1981, Nielsen & Kiørboe 1991, Bernard & Rassoulzadegan 1994, Ferrier-Pagès & Rassoulzadegan 1994). To extend our knowledge of the temporal patterns of ciliate abundance, biomass and composition on the NW Mediterranean coast, we conducted a 3 yr intensive sampling program in the oligotrophic coastal area of the Bay of Blanes. The primary goal of the study was to describe the pattern of seasonal and annual changes in ciliate community structure, density and biomass, with a temporal resolution ranging between 1 d and 1 wk. We also assessed the relationship between the changes observed and environmental and biological forcing. In particular, we examined the relationship between changes in the ciliate community and temperature (which showed a persistent seasonal pattern) and rainfall (as an example of sporadic events which produced pulses of organic and inorganic matter). Biological forcing was assessed through examination of the relationships among ciliate abundance and chlorophyll *a* (chl *a*) concentration, and the abundance of bacteria and heterotrophic nanoflagellates. Finally, we characterized the dominant scales of temporal variation in ciliate abundance and biomass.

MATERIALS AND METHODS

The study was conducted in the Bay of Blanes (NW Mediterranean Sea; Fig. 1), an exposed bay with a relatively steep slope (~2%), which receives intermittent discharge from the Tordera River after storm periods, as well as some urban sewage and runoff (cf. Cebrián et al. 1996). Subsurface (–0.5 m) samples were collected from March 1992 to February 1995, at a 12 m deep fixed station (41° 39.90' N, 2° 48.03' E). The samples were collected twice a week from March 1992 to February 1993, and once a week from March 1993 to February 1995. Sampling frequency was increased (daily or 3 times/week) during phytoplankton blooms. Subsurface (–0.5 m) water samples were collected in 5 l bottles from an outboard motor boat, and kept refrigerated until reaching the laboratory (30 to 60 min).

Subsurface temperature (–0.5 m) was recorded with an Aandera salinity-temperature probe, with sampling frequencies ranging from 0.3 to 12 d^{-1}. Rainfall data were obtained from a meteorological station located 500 m from the sampling site. Complementary data on rainfall were obtained from 2 additional meteorological stations within the watershed of the Tordera River.

At the laboratory, 500 ml was filtered through a Whatman GF/F filter for fluorometric analysis of chl *a* concentration (Parsons et al. 1984). The filters were homogenized and kept refrigerated in the dark while pigments were extracted in 90% acetone for ca 6 h. Fluorescence was then measured in a Turner Designs fluorometer calibrated with pure chl *a* (Sigma Co.).

Bacterioplankton and heterotrophic nanoflagellate abundances were determined by epifluorescence microscopy (Porter & Feig 1980). Duplicate subsamples of 5 to 10 ml (bacterioplankton) and 20 to 30 ml (hetero-

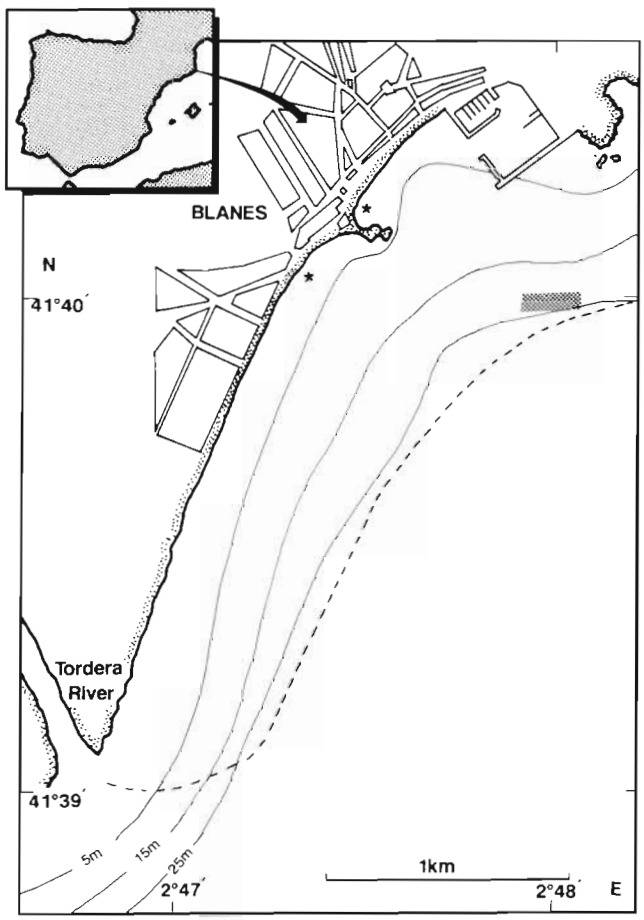

Fig. 1. Map of study area (Bay of Blanes, NW Mediterranean Sea). Shaded area: sampling site; (*) point of intermittent water discharge; (– –) water discharge from Tordera River

trophic nanoflagellates) were stained with DAPI and filtered through 0.2 µm and 0.6 µm to collect bacterioplankton and heterotrophic nanoflagellates, respectively. Error between duplicates ranged from 5 to 20%. Data on heterotrophic nanoflagellates covered the period from March 1992 to February 1994.

Ciliate abundance was examined in single 100 ml samples, which were preserved in a 1% final concentration of acidic Lugol's solution, and sedimented in 100 ml chambers for at least 48 h before enumeration, at 200× or 400× magnification, using an inverted microscope. Ciliate cells were determined to genus, when possible, following Lee et al. (1985) and Aladro Lubel et al. (1990). Taxa were placed into groups as 'oligotrichs' which included some genera considered heterotrophic, e.g. *Halteria*, *Strombidium*, *Strobilidium*, and *Lohmaniella*, and large mixotrophic genera, *Laboea* and *Tontonia*. We considered loricate tintinnids separately, and empty lorica were not enumerated. Other ciliate taxa were pooled by order: Haptorida which included mainly *Mesodinium* although in a few (<1%) cases *Askenasia* was present. Other orders present in the samples were Scuticociliatida (mainly *Cyclidium* and *Uronema*), Pleuroestomatida (*Amphyleptus*) and Prorodontida (*Urotricha*). Ciliate biomass was estimated as ciliate biovolume, which was calculated by approximation to the nearest geometric shape from measurements of cell length and width of at least 20 ciliate cells per sample. To avoid the probable underestimation of ciliate biovolume due to fixation with Lugol's solution (Leakey et al. 1994, Stoecker et al. 1994), the average cell volume for each genus was converted to carbon equivalents using the factor experimentally derived for Lugol's-fixed marine oligotrichs, 0.2 pg C μm^{-3} (Putt & Stoecker 1989), except for tintinnid carbon, which was estimated using the experimentally derived factor of 0.053 pg C μm^{-3} lorica volume (Verity & Langdon 1984).

The relationship between temperature and biological variables was examined by means of Pearson's correlation analysis, and the differences in biological properties between rainy and dry periods were tested by ANOVA. Cross correlation analyses were used to test the relationship between ciliate abundance and other components of microbial food webs.

The structure of the temporal variability observed in the Bay of Blanes was examined by first quantifying, using ANOVA, the significance of the variance at difference scales of variation. We then identified the dominant time scales of variation. Semivariance (S-V) at the time scale t (days) was calculated according to the equation (Robertson 1987):

$$\text{S-V}\ (t) = (1/2\ \text{n})\ (c_x - c_{x+t})^2$$

where c_x is ciliate abundance at time x, n is the number of observations for each time difference, and t is the time elapsed between c_x and c_{x+t} (i.e. the time scale evaluated). In practice, S-V is calculated for lag times up to half the length of the total record, which is the largest time scale that can be resolved with the analysis (Robertson 1987). The shape of the semivariogram typically shows an increase in S-V with increasing time scale up to a plateau (i.e. sill value; Robertson 1987), which indicates the dominant time scale in the process examined. Semivariogram analysis is particularly well suited to investigating the dynamic behavior of time series sampled with different intensity, such as the ciliate abundance and biomass reported here, which were sampled once or twice per week, or daily during the study.

RESULTS

Relationship between environmental and biological variables

Surface water temperature fluctuated from minimal values of 11 to 12°C in late January and February, to maximal values of 25 to 26°C in late August and September (Fig. 2a). Despite the strong temperature seasonality, chl *a* concentration did not show a simple seasonal pattern (Fig. 3a). The pattern was highly variable among years, however a distinct winter and summer bloom of phytoplankton was present in each year, concurrent with winter minimum and summer maximum temperatures (Figs. 2a & 3a), despite an overall negative correlation between surface temperature and chl *a* concentration ($r = -0.442$, $p = 0.007$). The abundance of microheterotrophs (bacteria, heterotrophic nanoflagellates, and ciliates) fluctuated greatly throughout the study period (Figs. 3b, c & 4), independently of temperature (Fig. 2a).

Examination of the cumulative monthly rainfall (Fig. 2b) shows that periods of heavy rainfall (>20 l m^{-2} d^{-1}), sufficient to cause torrential river discharge, were more frequent and more intense in 1992 compared with the following years, with the period 1993–1994 being particularly dry, except for October 1994 (Table 1, Fig. 2b). The heaviest rainfall was recorded in spring 1992, when storms discharged 44 l m^{-2} in a few hours in June, and in October 1994, when 61 l m^{-2} were discharged in a short period (Fig. 2b).

The comparison of changes in microheterotroph abundance and chl *a* concentration during periods of heavy rainfall showed a significant increase in the abundance of bacteria and heterotrophic nanoflagellates during heavy rain periods (Table 2). Hence, increased bacteria and heterotrophic nanoflagellate

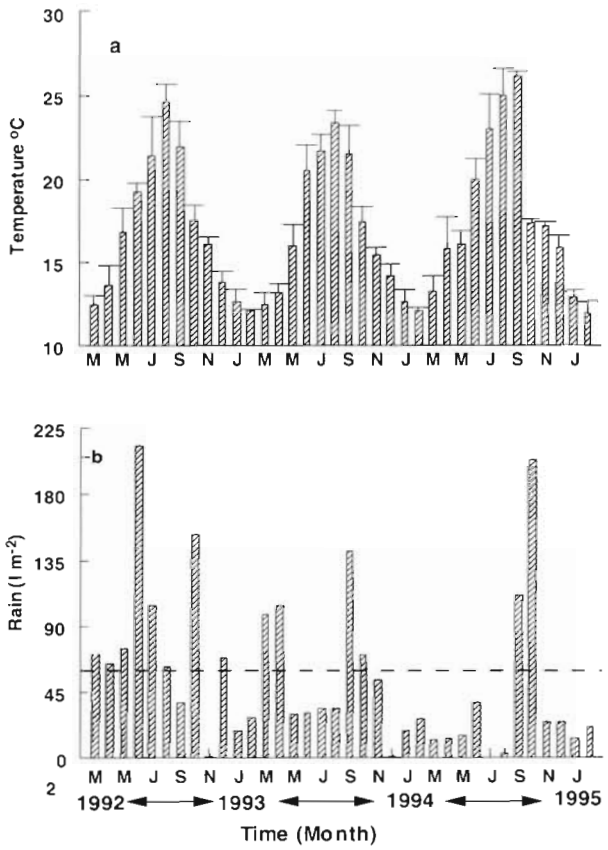

Fig. 2. (a) Average of monthly values of temperature (bars indicate standard deviation) and (b) cumulative monthly rainfall values. Dashed line refers to values of cumulative monthly rainfall greater than 50 l m^{-2}

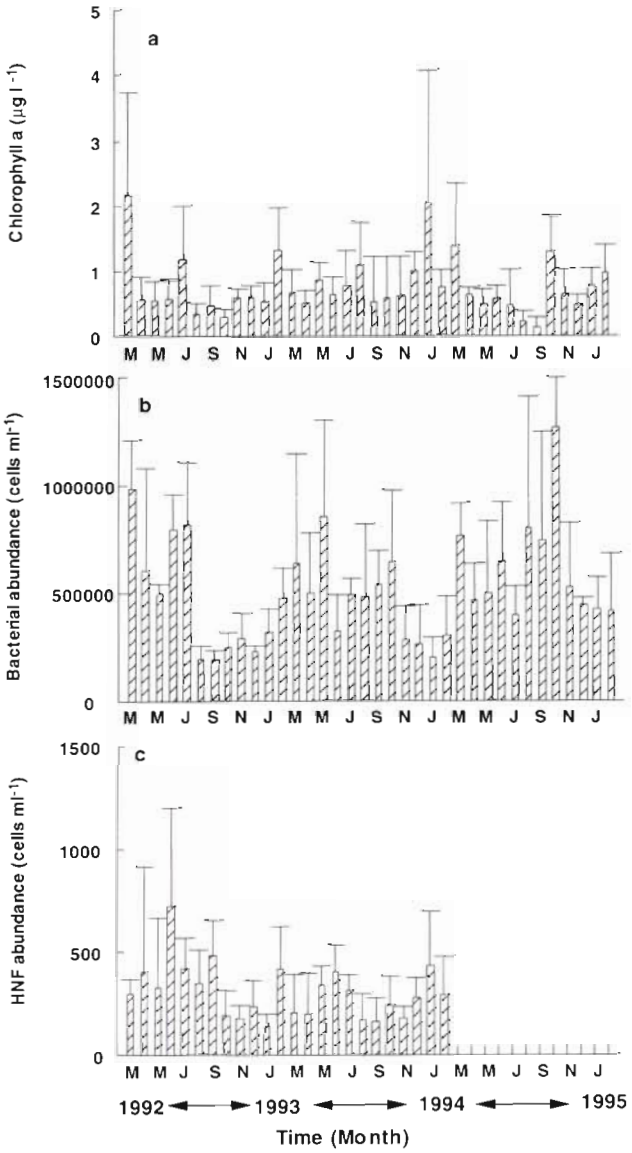

Fig. 3. Monthly average of (a) chlorophyll *a* concentration and (b) bacterial and (c) heterotrophic (HNF) nanoflagellate abundance (bars indicate standard deviation)

abundance was observed in spring and summer 1992, and in autumn 1994 for bacterial abundance, and in spring 1992 for heterotrophic nanoflagellates (Table 2). In contrast, ciliate abundance tended to decline during periods of heavy rain (Table 2). This effect was particularly evident during spring 1992 (Table 2, Figs. 2b & 4a). The decline in ciliate abundance during periods of heavy rain was mainly due to a decline in heterotrophic oligotrichs ($p < 0.05$ and $p < 0.018$ for abundance and biomass, respectively) and *Mesodinium* ($p < 0.013$ for biomass).

Chl *a* concentration, bacterial and heterotrophic nanoflagellate abundance

Chl *a* concentration over the study period ranged from 0.010 µg l^{-1} in August 1994 to 5.75 µg l^{-1} in March 1992. Maximum values for 1993 and 1994 were recorded in February (2.74 µg l^{-1}) and January (5.01 µg l^{-1}), respectively. These phytoplankton blooms in winter are a consistent feature of the Catalan coast. Bacterial abundance values ranged from 0.5×10^5 cells ml^{-1} in August 1993 to 18.7×10^5 cells ml^{-1} in August 1994. The peak bacterial abundances for 1992 and 1993 were both observed in March (14.4×10^5 and 14.9×10^5 cells ml^{-1}, respectively). Finally, the abundance of heterotrophic nanoflagellates ranged from 20 cells ml^{-1} in September 1993 to 1.7×10^3 cells ml^{-1} in June 1992, with the maximum values for 1993 (0.79×10^3 cells ml^{-1}) being recorded in February. The monthly mean chl *a* concentration and bacterial abundance showed similar trends (Fig. 3), with chl *a* blooms being followed by increased bacterial abundance. In contrast, the monthly mean abundance of heterotrophic nanoflagellates was low when mean bacterial abundance was high (Fig. 3).

Table 1. Seasonal rain frequency (%) in the study period

Year	Rainfall (range) (l m^{-2})	Spring	Summer	Autumn	Winter
1992–1993	>20	6.59	4.35	3.33	2.24
	10–20	5.49	4.35	3.33	7.86
	5–10	9.89	2.17	6.67	4.49
	0.01–5	21.86	16.00	23.3	13.48
	0	56.17	73.13	63.37	71.93
1993–1994	>20	1.08	0.00	3.33	0.00
	10–20	4.35	2.19	5.55	3.30
	5–10	7.61	5.49	4.44	1.12
	0.01–5	15.2	19.78	44.44	8.98
	0	71.76	72.54	42.24	86.60
1994–1995	>20	0.00	2.22	5.49	0.00
	10–20	1.09	2.22	4.39	1.47
	5–10	0.00	0.00	3.30	0.00
	0.01–5	16.48	10.00	16.48	17.65
	0	82.43	85.56	70.34	80.88

Table 2. Differences in bacterial and heterotrophic nanoflagellate abundance (BN and HNF: cells ml^{-1}), chlorophyll *a* concentration (chl *a*: µg l^{-1}), and ciliate abundance (CIL: cells l^{-1}) and biomass (BCIL: µg C l^{-1}) between rain vs no rain periods performed by means of a multifactorial ANOVA (* $p < 0.05$, marginally significant; ns: not significant; nd: not determined). Positive (+) and negative (–) symbols indicate values were higher during heavy rain periods (>10 l m^{-2}) or lower with respect to no rain periods, respectively

Year	Season	BN	HNF	Chl *a*	CIL	BCIL
All	Pooled	0.001(+)	0.02(+)	ns	0.05(–)	ns
1992	Pooled	0.014(+)	0.08*(+)	ns	ns	ns
1993	Pooled	ns	ns	ns	ns	ns
1994	Pooled	0.066*(+)	nd	ns	ns	ns
1992	Spring	0.031(+)	0.05(+)	n.s	0.045(–)	0.018(–)
	Summer	0.013(+)	ns	ns	ns	ns
1994	Autumn	0.028(+)	nd	0.03(+)	ns	ns

Ciliate abundance and biomass

Total ciliate abundance averaged 3851 cells l^{-1} over the 3 yr period, ranging from 135 cells l^{-1} in August 1994 to 25960 cells l^{-1} in March 1994 (Table 3). Oligotrichs were the most important group. Heterotrophic oligotrichs (*Halteria*, *Strombidium*, *Strobilidium* and *Lohmaniella*) dominated the ciliate community with an average abundance of 1884 cells l^{-1}. Mixotrophic oligotrichs (*Laboea* and *Tontonia*) were less abundant (mean 417 cells l^{-1}), and tintinnids contributed an average abundance of 629 cells l^{-1}. Oligotrichs were consistently present throughout the entire study period. The peak abundance of mixotrophic oligotrichs and tintinnids occurred simultaneously with the maximum abundance of the ciliate community (Table 3). In the third year of this study, however, the abundance of oligotrichs was exceeded by that of loricate ciliates, due to a remarkable increase in tintinnid abundance. Interestingly, this tintinnid bloom did not suffice to overcome oligotrich dominance of ciliate biomass (Table 3). The autotrophic *Mesodinium* (order Haptorida) was also an important contributor to ciliate abundance, with an average density of 499 cells l^{-1}. Other orders contributing to the ciliate community, listed from maximum to minimum abun-

Table 3. Mean, maximum and minimum values of ciliate abundance (cell l^{-1}) and biomass (µg C l^{-1}) in the Bay of Blanes (NW Mediterranean) from March 1992 to March 1995, and the percent contribution (%) of each ciliate group

Group	Variable	Mean	Max.	Min.	Percent overall	Percent Year 1	Percent Year 2	Percent Year 3
Total ciliate community	Abundance	3851	25960 (Mar 94)	135				
	Biomass	5.37	96.27 (Mar 94)	0.031				
Heterotrophic oligotrichs	Abundance	1884	11202 (Nov 94)	0.0	50	55	61	29
	Biomass	1.66	27.13 (Mar 94)	0.0	41	33	47	50
Mixotrophic oligotrichs	Abundance	417	8923 (Mar 94)	0.0	11	13	9	7
	Biomass	1.02	52.28 (Mar 94)	0.0	17	17	16	17
Tintinnids	Abundance	629	7436 (Mar 94)	0.0	16	7	7	41
	Biomass	0.28	10.15 (Mar 93)	0.0	7	7	3	13
Mesodinium	Abundance	499	4272 (May 92)	0.0	11	10	13	13
	Biomass	0.44	14.53 (Mar 94)	0.0	11	7	15	16
Scuticociliatida	Abundance	236	2974 (Jun 94)	0.0	8	7	8	9
	Biomass	0.62	19.49 (Jun 93)	0.0	12	15	15	3
Pleurostomatida	Abundance	71	1984 (Jul 92)	0.0	2	4	1	<1
	Biomass	0.51	42.95 (Jul 92)	0.0	6	12	2	<1
Prorodontida	Abundance	9	657 (Mar 93)	0.0	<1	<1	<1	<1
	Biomass	0.04	3.60 (Mar 93)	0.0	1	1	<1	<1

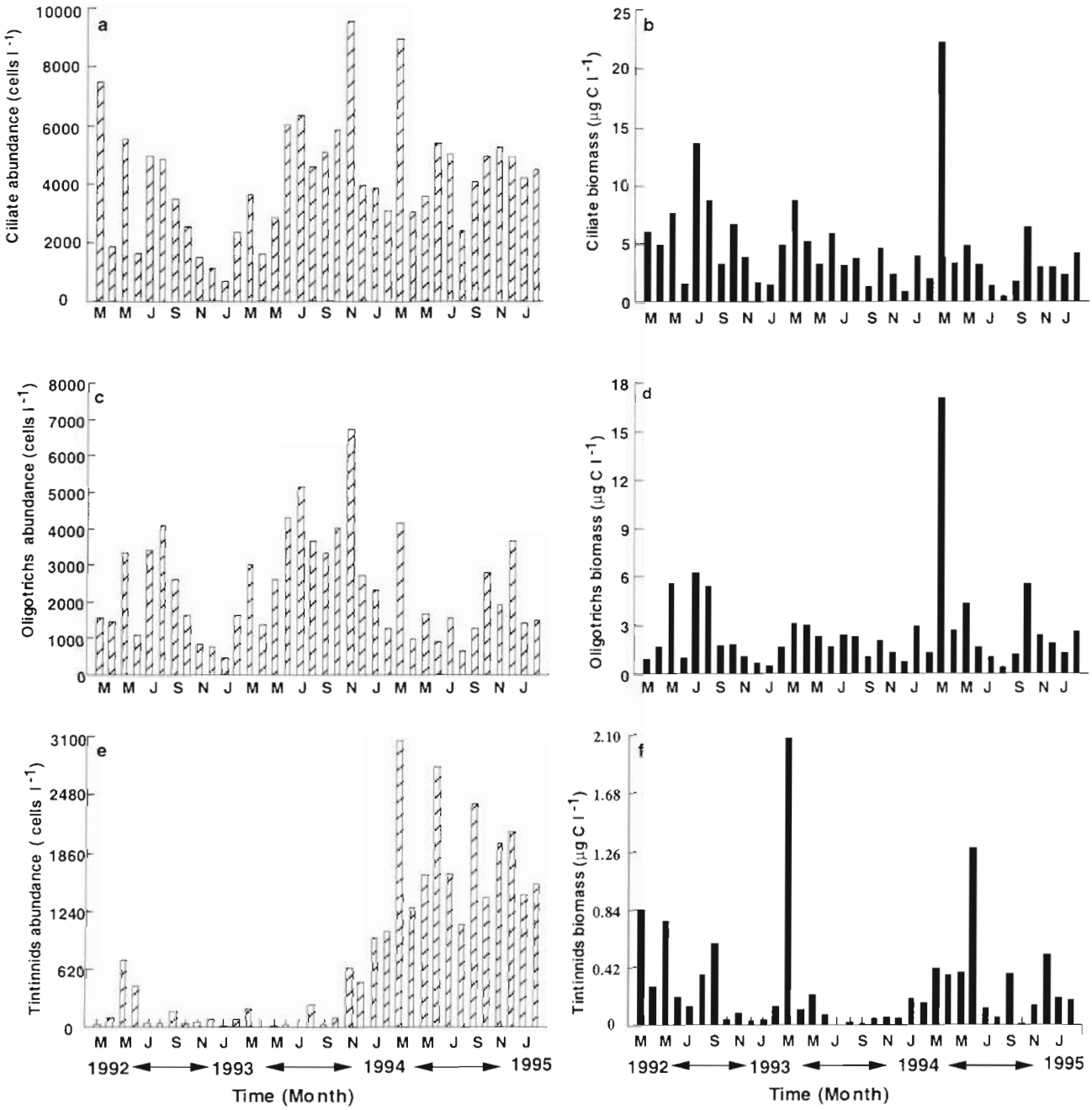

Fig. 4. Monthly averages of (a) ciliate community abundance (coefficient of variation, CV: 18 to 137%) and (b) biomass (CV: 11 to 198%), (c) oligotrich (heterotrophic plus mixotrophic) abundance (CV: 13 to 151%) and (d) biomass (CV: 14 to 205%), and (e) tintinnids abundance (CV: 36 to 224%) and (f) biomass (CV: 30 to 264%)

dance, included Scuticociliatida (*Uronema* and *Cyclidium*), Pleurostomatida (*Amphyleptus*) and Prorodontida (*Urotricha*). The maximum abundance of these forms was independent of that of the total ciliate community (Table 3). The biomass of the ciliate community averaged 5.37 µg C l^{-1}, reaching the highest value in March 1994, and was dominated by oligotrichs (Table 3).

Seasonal variation of ciliate abundance and biomass

Ciliate abundance was highly variable on both a seasonal and a monthly time scale (Figs. 4 & 5). The coefficient of variation of the monthly ciliate abundance ranged from 18 to 137% and that for ciliate biomass ranged from 11 to 198%. This variability was even higher when for individual ciliate groups. In the first

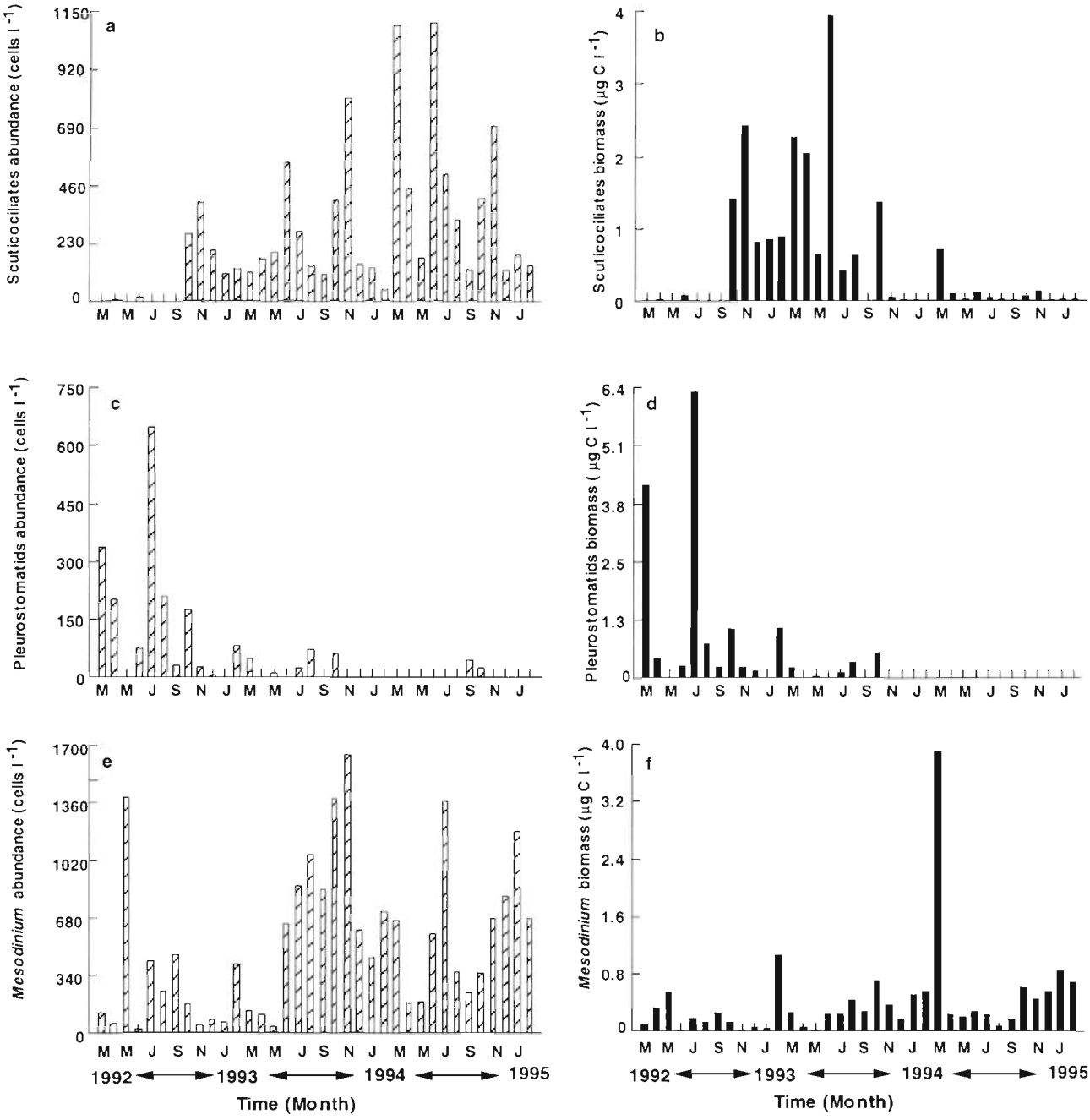

Fig. 5. Monthly average of (a) Scuticociliatida abundance (CV: 44 to 283%) and (b) biomass (CV: 55 to 283%), (c) Pleurostomatida abundance (CV: 71 to 245%) and (d) biomass (CV: 97 to 245%), and (e) *Mesodinium* abundance (CV: 26 to 204%) and (f) biomass (CV: 37 to 259%)

and second years total ciliate abundance showed a late spring bloom, summer bloom, and additional blooms in the fall of the second and third years, after the phytoplankton blooms and increases of bacterial abundances (Figs. 3 & 4a). Cross correlation analysis revealed that bacterial abundance and chl *a* concentration were both significantly negatively correlated with ciliate abundance, with a time lag of about 2 wk ($p < 0.05$).

Total ciliate biomass peaked in late winter/early spring and in the fall of every year, while an additional summer peak was observed in the first year (Fig. 4b).

Oligotrich abundance and biomass (heterotrophic and mixotrophic) followed those of the ciliate community (Fig. 4c, d). Tintinnids showed a small spring bloom in the first year followed by a decline in abundance throughout the remaining seasons. There was

considerable seasonal variability in the second and third year, with a small summer peak, followed by a greater peak in the fall of the second year, and peak tintinnid abundance in late winter/early spring, followed by several peaks in late spring, summer, and fall of the third year (Fig. 4e). Tintinnid biomass was characterized by maxima in late winter/early spring for 1992 and 1993, the first and third year showed secondary peaks at the end of the summer (September), and a small winter peak in the third year (Fig. 4f).

The relative contribution of heterotrophic oligotrichs to total oligotrich abundance was highest in 1992 to 1994 (58 to 98%), while tintinnids were the most important components (40 to 78%) of the heterotrophic oligotrichs (naked and loricate) from 1994 to 1995 (Fig. 6a). The contribution of mixotrophic oligotrichs to the oligotrich community was substantially lower than that of heterotrophic oligotrichs (Fig. 6a). However, large mixotrophic oligotrichs contributed a high percentage of the total oligotrich biomass in spring and/or summer over the study period (Fig. 6b).

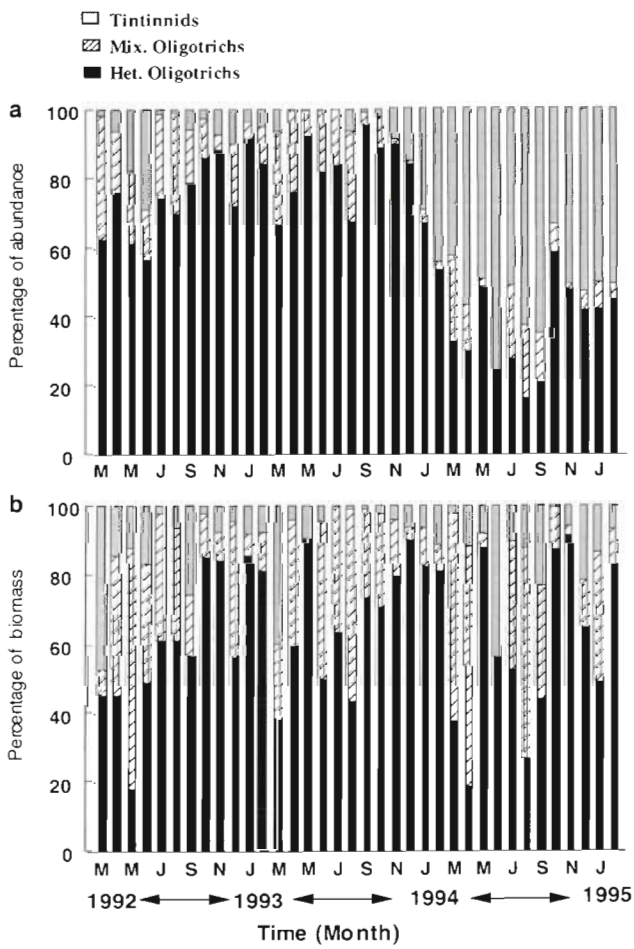

Fig. 6. Relative contribution of naked heterotrophic, mixotrophic, and tintinnid (a) abundance to total oligotrich abundance and (b) biomass to total oligotrich biomass

The abundance and biomass of Scuticociliatida and Pleurostomatida were lower than those of oligotrichs. Scuticociliatida showed persistent blooms in the fall of every year, with substantial summer blooms recorded in the second and third years, when a significant bloom occurred in late winter/early spring as well (Fig. 5a). The biomass of Scuticociliatida showed a significant peak in the fall of the first and second years, and blooms in late winter/early spring in the second and third years (Fig. 5b). The order Pleurostomatida produced blooms in late winter/early spring, summer, with its abundance being substantially greater in the first year (Fig. 5c). Biomass did not reflect significant seasonal variation within the second or third year, except for a small peak in the fall of the second year. Three peaks were detected in the first year, including a late winter/early spring peak, a large summer peak (coinciding with that of total ciliate biomass for this year), and an additional autumn peak, also recorded in the second year (Fig 5d). The order Prorodontida presented very low abundance and biomass during the whole period.

The seasonal pattern of the autotrophic *Mesodinium* varied greatly among years. In the first year *Mesodinium* sp. produced a strong bloom later in the spring and 2 smaller blooms in the summer. In contrast, the second year was characterized by a substantial summer peak, followed by an even greater autumn bloom, and blooms occurred in late winter/early spring, summer and mid-winter of the third year (Fig. 5e). With respect to biomass, the first year seasonal pattern was characterized by a small peak later in the spring. A late winter/early spring peak, together with an smaller autumn peak, was observed in the second and third years. The large biomass peak observed in the spring of the third year coincided with that of the oligotrich and total ciliate biomass (Fig. 5f).

The abundance and biomass of *Mesodinium* were not directly correlated with chl *a* concentration, despite the autotrophic nature of *Mesodinium*. However, the abundance and biomass of *Mesodinium* were significantly correlated with chl *a* at seasonal scales (Figs. 3a & 5e, f). These positive correlations were observed in winter 1993 ($r_{abundance} = 0.509$, $p < 0.031$ and $r_{biomass} = 0.576$, $p < 0.012$, respectively) and in summer 1994 ($r_{biomass} = 0.599$, $p < 0.05$).

Interannual variability in ciliate abundance and biomass

The preceding description of seasonal patterns provides indication of major interannual differences in the abundance and biomass of ciliates over the study period (Tables 4 & 5). The abundance of ciliates dif-

Table 4. Mean annual values of ciliate abundance (cells l^{-1}), biomass (µg C l^{-1}) and biomass ciliate^{-1} (ng C cell^{-1}). CV: coefficient of variation for each variable

Variable	Year	Abund.	CV	Biomass	CV	Biom./cil.	CV
Ciliate community	1992–1993	2833	90	6.35	168	2.35	108
	1993–1994	4679	74	4.02	150	1.22	132
	1994–1995	4759	80	4.98	270	0.72	90
Heterotrophic oligotrichs	1992–1993	1576	105	1.54	140	0.97	86
	1993–1994	2950	81	1.39	117	0.60	81
	1994–1995	1334	86	2.17	193	1.21	82
Mixotrophic oligotrichs	1992–1993	411	163	1.00	196	2.29	102
	1993–1994	426	164	0.62	162	1.93	86
	1994–1995	425	297	1.50	492	1.89	111
Tintinnids	1992–1993	157	240	0.24	297	2.86	208
	1993–1994	282	164	0.27	511	2.13	230
	1994–1995	1875	77	0.35	192	0.17	120
Mesodinium	1992–1993	317	211	0.30	247	1.21	138
	1993–1994	713	122	0.34	122	0.71	132
	1994–1995	616	119	0.79	277	1.12	143
Scuticociliatida	1992–1993	99	261	0.59	226	7.86	106
	1993–1994	271	131	1.15	275	4.64	162
	1994–1995	454	129	0.13	233	0.27	166
Pleurostomatida	1992–1993	137	226	1.00	449	7.86	99
	1993–1994	20	367	0.12	416	5.20	37
	1994–1995	5	523	0.001	547	0.14	22

fered significantly (Tukey multiple comparison test, $p < 0.05$) in the first year with respect to the following 2 years, when mean annual abundance was lowest and cell size largest ($p < 0.01$, Tables 4 & 5). The abundance of naked heterotrophic oligotrichs differed significantly in the second year with respect to the first and third years, when the maximum mean density was observed (mean = 2950 cells l^{-1}; Table 4). The abundance of tintinnids increased remarkably over the third year. The abundance of *Mesodinium* and Pleurostomatida was significantly different in the first year from the other years, whereas Scuticociliatida showed great

Table 5. Comparison (Tukey HSD test) of the abundance (cells l^{-1}), biomass (µg C l^{-1}) and biomass ciliate^{-1} (ng C cell^{-1}) of each ciliate group among years, and ANOVA test of the significance of interannual differences in abundance and biovolume for the 3 yr period (1992 to 1995). •Marginally significant; ns: not significant

Group	Variable	Year 1–2	Year 2–3	Year 1–3	Total
Total ciliate	Abundance	0.001	ns	0.001	<0.0001
	Biomass	ns	ns	ns	ns
	Biomass/ciliate	0.001	ns	<0.0001	<0.0001
Heterotrophic oligotrichs	Abundance	<0.0001	<0.0001	ns	<0.0001
	Biomass	ns	ns	ns	ns
	Biomass/ciliate	0.01	<0.0001	0.081•	0.001
Mixotrophic oligotrichs	Abundance	ns	ns	ns	ns
	Biomass	ns	ns	ns	ns
	Biomass/ciliate	ns	ns	ns	ns
Tintinnids	Abundance	ns	<0.0001	<0.0001	<0.0001
	Biomass	ns	ns	ns	ns
	Biomass/ciliate	ns	0.060•	0.003	0.009
Mesodinium	Abundance	0.002	ns	0.023	0.004
	Biomass	ns	0.067•	0.026	0.067•
	Biomass/ciliate	0.091•	ns	ns	ns
Scuticociliatida	Abundance	0.012	0.019	<0.0001	<0.0001
	Biomass	0.084•	0.007	ns	0.024
	Biomass/ciliate	0.030	0.003	<0.0001	<0.0001
Pleurostomatida	Abundance	0.002	ns	0.001	<0.0001
	Biomass	ns	ns	0.068•	ns
	Biomass/ciliate	ns	ns	ns	ns

variability across all 3 years (Table 5). Ciliate biomass (µg C l^{-1}) remained much more uniform than ciliate abundance over the 3 yr period (Tables 4 & 5). This suggests a compensatory increase in cell size when ciliate abundance declined (Tables 4 & 5).

Dominant scales of variation for ciliate community abundance and biomass

Analysis of the variance in ciliate abundance showed interannual variance to be similar to that between months (8 and 6% of the variance, respectively, $p < 0.01$ and $p < 0.06$, respectively). However, the seasonal pattern of ciliate abundance also differed between years, these differences accounting for a larger (16%, $p < 0.001$) share of the variance. Yet, most of the variance in ciliate abundance occurred at time scales other than annual or monthly (i.e. 68% unexplained variance). We therefore examined the dependence of ciliate abundance on time scale using a semivariogram. The results obtained indicate a steady increase in semivariance with increasing time scale to reach a plateau at about 50 d (Fig. 7a). This indicates the dominant scale of temporal variation in ciliate abundance to be about 2 mo, resulting from the interaction of the characteristic time scales of multiple processes influencing ciliate abundance. Variation in ciliate biomass is, however, buffered relative to that in numerical abundance (Fig. 7b), since changes in ciliate density are compensated by opposite changes in mean cell size (Table 4).

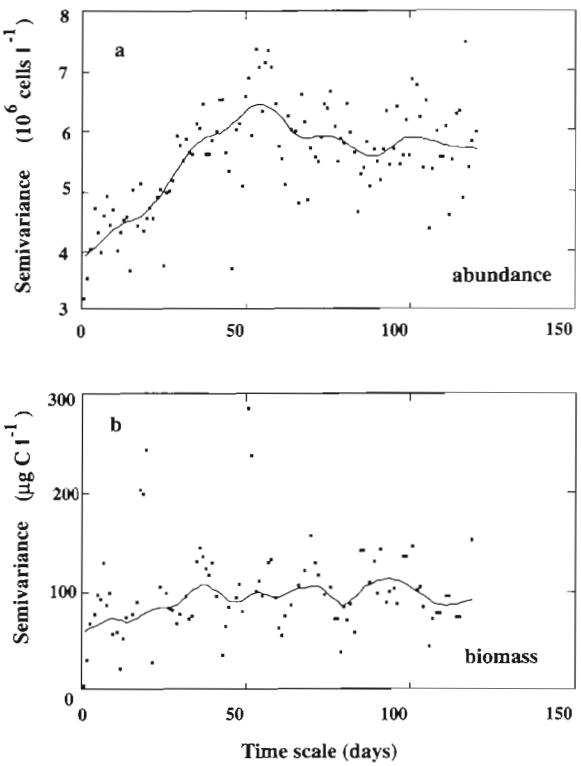

Fig. 7. Dominant scale of temporal variation in ciliate (a) abundance and (b) biomass, using a semivariogram

DISCUSSION

The Bay of Blanes is considered a temperate oligotrophic coastal area where a late winter phytoplankton bloom (mainly diatoms, cf. Mura et al. 1996) occurs concurrent with the annual minimum temperatures. This late winter bloom appears to be a general feature of the Catalan coast, and is recurrently associated with a period of low sea level, promoted by a sustained period of atmospheric stability, characterized by high atmospheric pressure, calm waters, lack of rainfall (Cebrián et al. 1996), low biomass of herbivorous zooplankton (Andreu & Duarte 1996), and high abundance of fish larvae (Palomera & Olivar 1996). These fish larvae may relax the pressure mesozooplankton normally exert on microplankton. The input of organic matter during the winter bloom leads to increased abundance of bacteria and protists. However, phytoplankton (mainly dinoflagellates; Mura et al. 1996) can also bloom during the summer, with high water temperature and a stratified water column. The concentration of chl *a* during summer time is always lower than that recorded during winter/spring (Fig. 3a). Andreu & Duarte (1996) found an increase of zooplankton (mainly copepods and cladocerans) in August 1992 in the Bay of Blanes, which could have been responsible for the reduced abundance of phytoplankton and ciliates at the end of summer 1992. These seasonal phytoplankton blooms are similar to those observed for the Chesapeake Bay area (Dolan & Coats 1990) and the French Mediterranean coast (Ferrier-Pagès & Rassoulzadegan 1994). However, the ciliate spring bloom in the Bay of Blanes appears to occur slightly earlier than these other blooms, presumably in response to the phytoplankton bloom in late winter observed in this area. Cross correlation analysis showed bacterial abundance and chl *a* concentration to be negatively correlated with ciliate abundance ($p < 0.05$). These correlations indicate that an increase in ciliate abundance is associated with a decline in bacteria and phytoplankton abundance with a delay of about 2 wk, and suggests, therefore, a role for ciliates in the control of these populations. Furthermore, the monthly coefficient of variation for bacterial abundance (range: 8.9 to 80%) was moderate in comparison with those of heterotrophic nanoflagellates (range: 26 to 106%), and ciliates (range: 18 to 137%). Heterotrophic nanoflagellates and ciliate abundance were

much more variable than bacteria in the study period, as expected based on predator-prey models (Wright 1988, Vaqué & Pace 1992). These results support the existence of seasonal differences in microplanktonic food web structure in temperate coastal areas (Pierce & Turner 1992).

Our results also provide evidence of the importance of heavy rainfall for the abundance of bacterioplankton and heterotrophic nanoflagellates in the Bay of Blanes (Tables 1 & 2). This response presumably reflects the increase in allochthonous inputs of DOM from river flushing after rainstorms, which promotes the growth of bacteria and, in turn, leads to an increase in heterotrophic nanoflagellate abundance. The response of ciliate abundance and biomass to heavy rainfall was not as clear as those for heterotrophic picoplankton and nanoplankton, but showed a tendency for ciliate abundance and biomass to decrease during heavy rainfall (Table 2). This observation is consistent with the results of Nielsen & Kiørboe (1991), who observed a decrease in ciliate abundance and biovolume during wind storm periods.

The mean ciliate abundance observed in the Bay of Blanes (Table 3) was slightly higher than that reported for the French Mediterranean coast (1 to 2 $\times$ 10^3 cells l^{-1}) by Ferrier-Pagès & Rassoulzadegan (1994), but lower than values reported for more eutrophic systems (Table 6). Mean ciliate biomass and the range of biomass variation observed were higher than values reported in the literature (Table 6). The wider range of variation observed in the Bay of Blanes may simply reflect the larger number of biomass estimates available there (Table 6). The dominance by naked heterotrophic oligotrichs of the ciliate community growing in the Bay of Blanes is in agreement with previous studies in the Mediterranean Sea (Ferrier-Pagès & Rassoulzadegan 1994, Dolan & Marrasé 1995) and appears to be characteristic of most marine and brackish water ecosystems (Beers et al. 1980, Smetacek 1981, Andersen & Sørensen 1986, Sherr et al. 1986, Dolan & Coats 1990, Nielsen & Kiørboe 1991). Maximum values for mixotrophic oligotrichs were 1 order of magnitude higher in this coastal area (Table 3) than those in the open northwestern Mediterranean Sea (205 ciliates l^{-1} in June 1993; Dolan & Marrasé 1995). These large ciliates represented about 20% of the total ciliate biomass (Table 3) in the Bay of Blanes, compared to about half of the ciliate biomass in the northwestern Mediterranean (Dolan & Marrasé 1995). The relative contribution of mixotrophic oligotrichs could be underestimated in our acidic Lugol's-preserved samples, where we could only recognize 2 genera as mixotrophic (*Laboea* and *Tontonia*), although some of the ciliates we considered heterotrophic oligotrichs may also be mixotrophic (Dolan & Marrasé 1995, and references therein).

Tintinnids were, on average, the third most abundant group, as observed on the French Mediterranean coast (Ferrier-Pagès & Rassoulzadegan 1994). Tintinnid biomass represented only 7% of total ciliate biomass for the 3 yr period, similar to their low contribution to the ciliate community of the open northwestern Mediterranean Sea (Dolan & Marrasé 1995). Hargraves (1981) and Verity (1987) reported strong seasonal cycles in temperate near-shore environments (Narragansett Bay, Rhode Island, USA), with tintinnid

Table 6. Mean and range (in parentheses) of ciliate abundance and biomass in different marine systems for surface waters. nc: not comparable data; nd: not determined

Location	Mean (range) (ciliates l^{-1} $\times$ 10^3)	Mean (range) (μg C l^{-1})	Source
Sea of Japan	(0.3–15)	nc	Sorokin (1977)
Pacific coastal waters[a]	11.2 (5.0–24)	3.6 (0.8–9.0)	Beers et al. (1980)
Kiel Bight Estuary[b]	(<0.02–92)	(1.0–56)	Smetacek (1981)
Oslofjord, Sweden	(2.2–14.7)	nd	Paasche & Kristiansen (1982)
Kaneohe Bay, Hawaii, USA	(1.0–1.4)	1.96	Landry et al. (1984)
Limfjord Sound	17.1 (1.4–162)	nd	Andersen & Sørensen (1986)
Maine Estuary	(<0.02–>540)	nd	Sanders (1987)
Open Sound, Georgia, USA	14.0	nd	Sherr et al. (1989)
Tidal Creek, Georgia, USA	71.0	nd	Sherr et al. (1989)
Chesapeake Bay area	(4.0–22)	(8.4–16)	Dolan & Coats (1990)
Northern Baltic	(0.3–10.2)	(0.3–4.0)	Leppänen & Brunn (1986)
Adriatic Sea	0.88	0.72	Revelante & Gilmartin (1990)
NW Mediterranean Sea	(1–2)	(0.2–1.2)	Ferrier-Pagès & Rassoulzadegan (1994)
Blanes Bay (NW Med.)	3.81 (0.13–26)	5.37 (0.031–96)	This study

[a]Ciliate abundance and biomass for 5–40 m
[b]Ciliate abundance and biomass for 5–20 m

abundance fluctuating between 10^2 and 10^4 cells l^{-1}. This was not the case in the Bay of Blanes, where no clear seasonality in tintinnid abundance, which was generally low, was observed. Tintinnid abundance fluctuated greatly at short scales of 1 to 2 wk (coefficient of variation of monthly tintinnid abundance ranged from 36% in January 1994 to 224% in August 1993). These short-term fluctuations appear to be characteristic of this group (Gold & Morales 1976, Graziano 1989) and may reflect the confounding effect of patchiness (Stoecker et al. 1984). The biomass of tintinnids presented even broader temporal fluctuations than their abundance (coefficient of variation of monthly tintinnid biomass ranged from 30% in August 1994 to 264% in August 1992).

The orders Scuticociliatida and Pleurostomatida were much less abundant than the aforementioned groups, as has been described for other parts of the Mediterranean Sea (Ferrier-Pagès & Rassoulzadegan 1994, Dolan & Marrasé 1995) and other marine systems such as Chesapeake Bay (Dolan & Coats 1990). The abundance of *Mesodinium* in the Bay of Blanes was significantly greater than that observed in the open Mediterranean Sea (mean ≈ 100 cells l^{-1}) by Dolan & Marrasé (1995). The lack of a significant correlation between *Mesodinium* abundance and biomass and chl *a* concentration is also similar to reports from the open Mediterranean Sea (Dolan & Marrasé 1995).

The bulk of the ciliate community, represented by naked oligotrichs, showed a seasonal pattern characterized by spring peaks, as well as peaks in summer 1992 and 1993, and in autumn 1993 and 1994. The seasonal patterns of tintinnids, Scuticociliatida, Pleurostomatida and *Mesodinium* were distinctly different, suggesting that each group responds differently to changes in the environment and food web.

Although total ciliate abundance and biomass were significantly correlated, this correlation was weak, resulting in mostly independent seasonal trends for total ciliate abundance and biomass. A similar difference between the seasonal patterns between ciliate abundance and biomass has been reported for Chesapeake Bay by Dolan & Coats (1990).

The interannual differences in ciliate abundance and cell size were much larger than those in total ciliate biomass (µg C l^{-1}), due to a compensatory increase in cell size when abundance declined (Tables 4 & 5). Differences among years had a modest contribution (16% of the variance) to the temporal variation in ciliate abundance. We found that the dominant time scale for ciliate abundance variability was about 50 d, similar to that of chl *a* concentration in the Bay of Blanes (Prairie & Duarte 1996). In contrast, the variation in ciliate biomass was independent of the time scale, with as much variance in ciliate biomass at short sampling intervals as at the interannual scale (Fig. 7b).

In summary, the results presented provide additional information on the temporal variability of ciliate abundance, biomass and composition in an oligotrophic coastal area. Oligotrich ciliates dominated the community throughout the study period, during which no simple seasonal or annual pattern for ciliate abundance and biomass was observed. The abundance of ciliates showed a dominant time scale of variation of about 50 d, while the variation in biomass was similar across the time scales resolved in this study. These results suggest a complex control of ciliate abundance and, particularly, biomass by the interaction of environmental (e.g. rainfall and temperature) and biological (e.g. prey and predator abundance) processes. The net result of this complex regulation is a complex pattern of change in ciliate abundance, and a uniform biomass, only weakly related to the underlying forcing factors.

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