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Seasonal dynamics of planktonic microbial communities on the coast of the northwest Mediterranean Sea

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ABSTRACT

Changes in microbial communities (abundance, biomass and structure) were followed during one year in an oligotrophic coastal area in the northwest Mediterranean Sea (Blanes Bay). Bacterial abundance reached maximum values after phytoplankton blooms (early spring-summer), and maxima in bacterial abundance were followed by peaks of nanoflagellates and ciliates. Variability of bacterial abundance was lower than that of nanoflagellates and ciliates, as expected from prey-predator models. Different assemblages of ciliates were present during the year: the orders of Oligotrichida, Choreotrichida, Haptorida, Pleurostomatida, and Scuticociliatida changed in importance over the course of the season. Most of these ciliate groups are considered to be phagotrophics (heterotrophics or/and mixotrophics), except for Haptorida, in which *Mesodinium* sp., the main genus, is autotrophic. The most representative group during the whole studied period was Oligotrichida, although other orders, such as Choreotrichida or Pleurostomatida, reached higher biomass per cell. Because Oligotrichida was the most abundant group and can ingest a wide range of particles, from bacteria to nanoflagellates and small algae, they could play an important role in changing the abundance of bacteria and nanoflagellates. Heterotrophic carbon content calculated for bacteria, heterotrophic nanoflagellates and ciliates showed that bacterioplankton dominated the microheterotrophic biomass. Carbon content of phagotrophic ciliates was moderate and that of heterotrophic nanoflagellates was much lower in comparison to bacteria. Ciliate assemblages could be important in channelling carbon (from bacteria and nanoplankton) to higher trophic levels.

Key words: Microheterotrophs, bacteria, nanoflagellates, ciliate biomass.

RESUMEN

Dinámica estacional de las comunidades microbianas planctónicas de la costa del Mediterráneo noroccidental

Durante un año se siguieron los cambios en las comunidades microbianas (abundancia, biomasa y composición) de una zona costera oligotrófica en el Mediterráneo noroccidental (bahía de Blanes, Girona). La abundancia bacteriana alcanzó valores máximos después de blooms *de fitoplancton (principios de primavera y verano). Estos máximos en abundancia bacteriana fueron seguidos por incrementos en nanoflagelados y ciliados. La variabilidad de la abundancia bacteriana era menor que la de nanoflagelados y ciliados, como era de esperar para modelos de presa-depredador. Se observaron distintos grupos de ciliados a lo largo de un año: así los órdenes Oligotrichida, Choreotrichida, Haptorida, Scuticociliatida, o Pleurostomatida cambiaron en importancia en las distintas estaciones del año. La mayoría de estos grupos de ciliados son considerados fagotróficos (heterotróficos o mixotróficos), excepto el orden Haptorida, donde* Mesodinium *sp., que era el género predominante, es autotrófico. El grupo más representativo de todo el periodo de estudio fue el orden Oligotrichida, aunque otros órdenes tales como Choreotrichida o Pleurostomátida alcanzaron un mayor biovolumen por célula. Debido a que el orden Oligotrichida era el más abundante y tiene la capacidad de ingerir un amplio rango de tamaño de partículas, desde bacterias, nanoflagelados y algas de pequeño tamaño, puede jugar un papel importante en cuanto a los cambios del número de bacterias y nanoflagelados. El con-*

tenido en carbono estimados para bacterias, nanoflagelados heterotróficos y ciliados fagotróficos mostraba que el bacterioplancton dominaba la biomasa microheterotrófica. El contenido en carbono de los ciliados fagotróficos era moderado mientras que el de los nanoflagelados heterotróficos era mucho menor en comparación con el del bacterioplancton. Este conjunto de grupos de ciliados podría ser importante en el flujo de carbono (desde bacterias y nanoplancton), a niveles tróficos superiores.

Palabras clave: *Microheterótrofos, bacterias, nanoflagelados, biomasa de ciliodos.*

INTRODUCTION

Primary producers exert an important control on the microheterotrophic community (production and abundance) in the euphotic zone of oligotrophic oceans (Bird and Kalff, 1984; Cole, Findlay and Pace, 1988). Growth and abundance of planktonic microheterotrophs may be enhanced in coastal waters, where they can use allochthonous carbon in addition to dissolved organic carbon released from phytoplankton. Microheterotrophs, therefore, would act as the entry point of this organic carbon into planktonic food webs.

Examination of the seasonal patterns of microheterotrophic communities' abundance, biomass, and composition (bacterioplankton, nanoflagellates and ciliates) in a coastal area may help to elucidate the importance of these communities in the plankton, and how they respond to allochthonous inputs (during the periods of freshwater discharge, which are discontinuous in Mediterranean coastal areas). For this purpose we conducted an intensive sampling programme in Blanes Bay (northwest Mediterranean) to permit a high temporal resolution of sequential communities' development and to gather some evidence for trophic coupling between the investigated groups.

MATERIAL AND METHODS

This study was conducted in Blanes Bay (northwest Mediterranean Sea, 42°18' 26" N, 3°18' 11" E, see map, first chapter of this volume) at a fixed station. Samples were collected from a boat approximately half a nautical mile from the shore. Subsurface (-0.5 m) water samples were collected twice a week, and sometimes daily from March 1992 to February 1993. Water samples were used to determine bacteria, nanoflagellate and ciliate abundance, composition and biomass.

The abundances of bacteria and nanoflagellates were determined by epifluorescence microscopy, and that of ciliates using an inverted microscope.

Duplicate water samples for bacteria and nanoflagellates were preserved with formaldehyde (0.5% final solution), and glutaraldehyde (1% final solution) respectively, and stained with 4.6-diamidino -2-phenylindole (DAPI, Porter and Feig, 1980). Nanoflagellates were counted separately in heterotrophic (colourless) and autotrophic (with pigments) groups, although myxotrophic nanoflagellates could be included in both groups. A 100 ml sample was preserved in a 1% final concentration of Lugol's solution for enumeration of ciliates. Ciliates were counted after settling, using an inverted microscope at 200 × magnification. Biomass of bacteria was calculated using an equivalence of 23.3 fg C · bacteria^{-1} (Simon and Azam, 1989). Bacterial biovolume was determined with an epifluorescence microscope, measuring the length and width of 20 cells from 10 samples, with a measured average of 0.09 μm^3 · bacteria^{-1}. Protist biovolume was calculated from cell length and width by approximation to the nearest geometric figures; for this purpose at least 20 cells per sample were measured. Carbon content was then estimated from published equivalences of 0.22 pg C · μm^{-3} for nanoflagellates (Børsheim and Bratbak, 1987), 0.15 pg C · μm^{-3} for ciliates (DeBiase, Sanders and Porter, 1990). Groups of ciliates were classified following Pierce and Turner (1992) and Aladro Martínez and Mayén (1990).

The seasonal pattern of heterotrophic microbes was described after averaging the data at monthly intervals. Statistical analyses, however, were made using the whole data set.

RESULTS

Bacteria presented two maxima, one in March and the other between June-July 1992 (figure 1), with a monthly abundance average ranging from 1.3×10^5 bacteria . ml^{-1} in September to 9.8×10^5 bacteria · ml^{-1} in March.

Nanoflagellate (autotrophic plus heterotrophic) abundance was highest in June and September

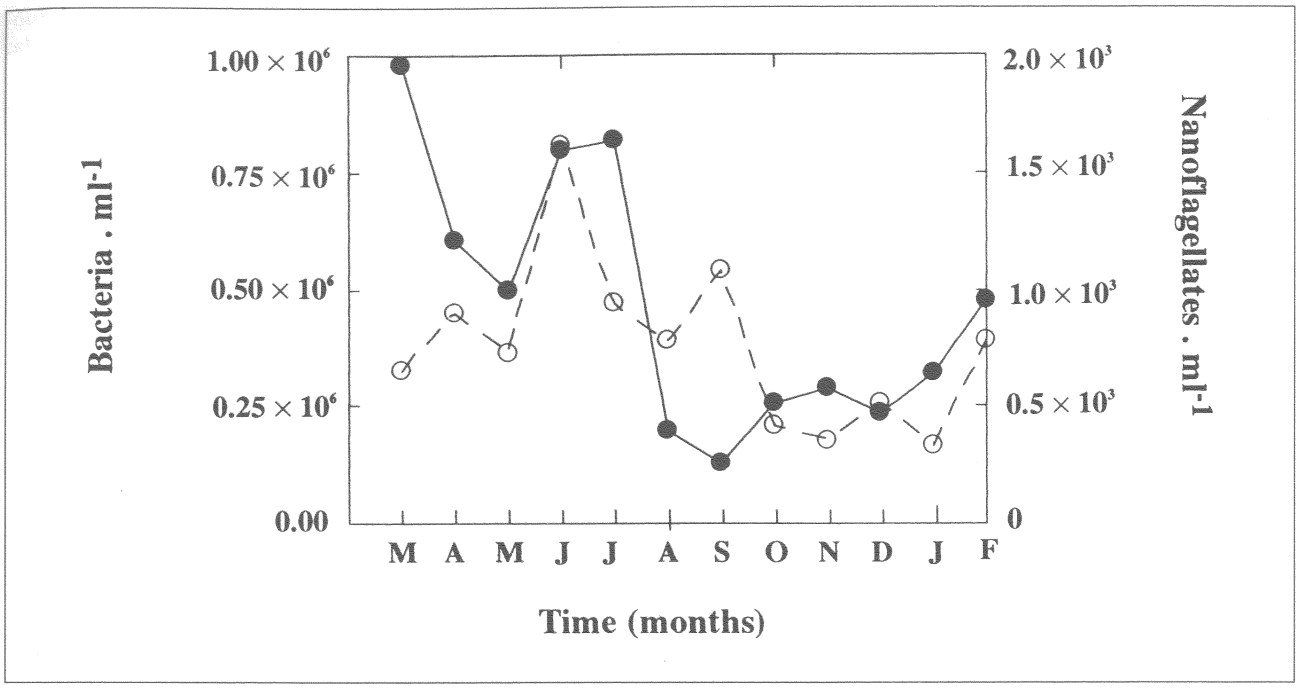

Figure 1. Averages on a monthly basis of abundance of bacteria (•) and nanoflagellates (o).

1992 (figure 1), ranging from 0.33×10^3 nanoflagellate . ml^{-1} in January to 1.6×10^3 nanoflagellates · ml^{-1} in June. Nanoflagellate abundance showed higher variability (CV = 83.4%) over the studied period than that of bacteria (CV = 67.4%, table I). Heterotrophic nanoflagellate abundance represented about 50.8% of the nanoflagellate community (autotrophic plus heterotrophic). Heterotrophic nanoflagellates were approximately spherical, and presented diameter sizes ranging from 2 to 6 µm for the whole sampling period.

There were important changes in the abundance (table I), biovolume, and community structure of ciliates (table II, figure 2) during the year. Monthly average abundance of ciliates ranged from 0.7×10^3 ciliates · l^{-1} in January 1993 to 1.1×10^4 ciliate · l^{-1} in March 1992. Hence, the variability in ciliate abundance observed across the sampling period was even higher (C V = 190.5%) than that for nanoflagellates.

The ciliate assemblage was dominated by a diverse group of organisms: Order Oligotrichida: *Halteria* sp., *Laboea* sp., *Strombidium* sp., and *Tontonia* sp.; Order Choreotrichida: tintinnids (loricate ciliates), and *Strobilidium* sp.; Order Haptorida: *Mesodinium* sp., and *Askenasia* sp.; Order Scuticociliatida : *Uronema* sp., and *Cyclidium* sp.; and Order Pleurostomatida: *Amphyleptus* sp. Except for *Mesodinium* sp., an autotrophic microorganism, all other ciliates found were phagotrophic (heterotrophic or/and mixotrophic, Andersen and Sørensen, 1986). Oligotrichida dominated the community over the year, reaching their highest abundance in May, July and August

Table I. Number of cases (N), range (minimum and maximum values), mean and coefficient of variation (CV %) of bacteria, nanoflagellate, and ciliate abundances determined during the annual cycle.

VARIABLES	N	MINIMUM	MAXIMUM	MEAN	CV (%)
Bacteria · ml^{-1}	102	73 000	1 445 962	501 924	67
Nanoflagellate · ml^{-1}	97	119	3 942	766	83
Ciliate · ml^{-1}	102	0.2	65	4	190
Oligotrichida · ml^{-1}	94	0.0	13	2	124
Tintinnids · ml^{-1}	94	0.0	2	0.2	241
Strobilidium sp. · ml^{-1}	94	0.0	6	0.4	157
Haptorida · ml^{-1}	94	0.0	4	0.3	212
Scuticociliatida · ml^{-1}	94	0.0	2	0.1	264
Pleurostomatida · ml^{-1}	94	0.0	2	0.1	223

Table II. Number of samples (N) range (minimum and maximum values), mean and coefficient of variation (CV %) of biovolume of ciliates ($\mu m^3 \cdot ciliate^{-1}$), and from each group of ciliates measured during the sampling period: Oligotrichida, Choreotrichida (tintinnids, *Strobilidium* sp.), Haptorida, Scuticociliatida and Pleurostomatida.

VARIABLES	N	MINIMUM	MAXIMUM	MEAN	CV (%)
Ciliate ($\mu m^3 \cdot cell^{-1}$)	94	9.1×10^2	7.0×10^4	1.3×10^4	878
Oligotrichida	92	4.9×10^2	6.2×10^4	7.5×10^3	120
Tintinnids	55	8.9×10^2	6.2×10^5	5.8×10^4	212
Strobilidium sp.	84	4.9×10^2	1.6×10^4	4.4×10^3	70
Haptorida	66	4.3×10^2	4.6×10^4	6.0×10^3	137
Scuticociliatida	37	2.5×10^3	1.9×10^5	3.9×10^4	106
Pleurostomatida	44	2.7×10^3	1.8×10^5	4.0×10^4	96

(figures 2a, 2b). In contrast, Scuticociliatida were observed at rather low abundances over the year, reaching somewhat higher abundances in October and November (figure 2e).

Ciliate biomass ($\mu m^3 \cdot l^{-1}$) showed two maxima, one in May and the other in July (figure 2a). These ciliate blooms were attributed to Oligotrichida (56 % of the biomass in May, and 44 % in July, figures 2a, 2b), tintinnids (30 % in May, figures 2a, 2d), and Pleurostomatida (48 % in July, figures 2a, 2f). There were two secondary ciliate biomass maxima in November and February, due to proliferation of Oligotrichida (43 %) and Scuticociliatida (45 %) in November (figures 2a, 2b, 2e), and Haptorida (22 %), Pleurostomatida (20 %), and *Strobilidium* sp. (19 %) in February 1993 (figures 2a, 2c, 2f, 2g). The size ($\mu m^3 \cdot ciliate^{-1}$) of individual ciliates ranged over two orders of magnitude among groups, with *Strobilidium* sp., Haptoridae and Oligotrichida being substantially smaller than Scuticociliatida, Pleurostomatida and tintinnids (table II).

The seasonal pattern in the abundance of bacteria, nanoflagellates and ciliates reveals the existence of a succession of microheterotrophic assemblages. Bacterial maxima coincided with peaks of nanoflagellates and ciliates (figures 1, 2). Although bacterial abundance was weakly, but significantly correlated with nanoflagellates ($n = 102$; $r = 0.285$; $P < 0.005$), it was not significantly, correlated with the total number of ciliates. However, it was correlated with that of *Strobilidium* sp. (table III). In contrast, nanoflagellate abundances were correlated with ciliate abundance and specially with that of Oligotrichida and tintinnids. In particular, heterotrophic nanoflagellate abundance was correlated with that of Oligotrichida, Haptorida, and the genus *Strobilidium* sp. (table III). In summary, bacteria were better correlated with nanoflagellate abundance than with ciliate abundance, and the abundance of nanoflagellates was correlated with that of some groups of ciliates (table III).

Table III. Correlations between bacterial abundance (BN), and nanoflagellate, heterotrophic and autotrophic (TNF, HNF and ANF) abundance with that of total ciliates measured during the sampling period: Oligotrichida, Choreotrichida (tintinnids, *Strobilidium* sp.), Haptorida, Scuticociliatida and Pleurostomatida. n. s.: not significant; *: $P < 0.05$; **: $P < 0.005$; ***:$P < 0.0005$.

VARIABLES	BN	TNF	HNF	ANF
Ciliate	n. s.	0.253*	0.615***	n. s.
Oligotrichida	n. s.	0.235*	0.559**	n. s.
Tintinnids	n. s.	0.360*	0.543**	n. s.
Strobilidium sp.	0.317**	n. s.	n. s.	n. s.
Haptorida	n. s.	n. s.	0.525*	n. s.
Scuticociliatida	n. s.	n. s.	n. s.	n. s.
Pleurostomatida	0.270*	n. s.	n. s.	n. s.

DISCUSSION

The results obtained indicate that Blanes Bay is an oligotrophic coastal system. Comparison of the observed annual cycle of microheterotroph abundance with those reported for eutrophic coastal areas showed the bacterial abundance in Blanes Bay to be one order of magnitude lower than that in productive coastal areas. Nanoflagellate abundances also reached lower values than those observed in eutrophic coastal areas (table IV). Values observed in Blanes Bay were similar to those observed at another coastal northwestern Mediterranean site (Villefranche-sur-Mer, Ferrier-Pagés and Rassoulzadegan, 1994). Nevertheless, the highest ciliate abundance observed in Blanes Bay (64.5 ciliate $\cdot l^{-1}$, March 1992, table I), was much higher than other values for the northwest Mediterranean, although the most frequent highest values were around 5.0-7.0 ciliate $\cdot l^{-1}$, similar to those obtained by Ferrier-Pagés and Rassoulzadegan (1994). The seasonal patterns of ciliate abundance, biomass, and composition were similar to those described by Ferrier-Pagés

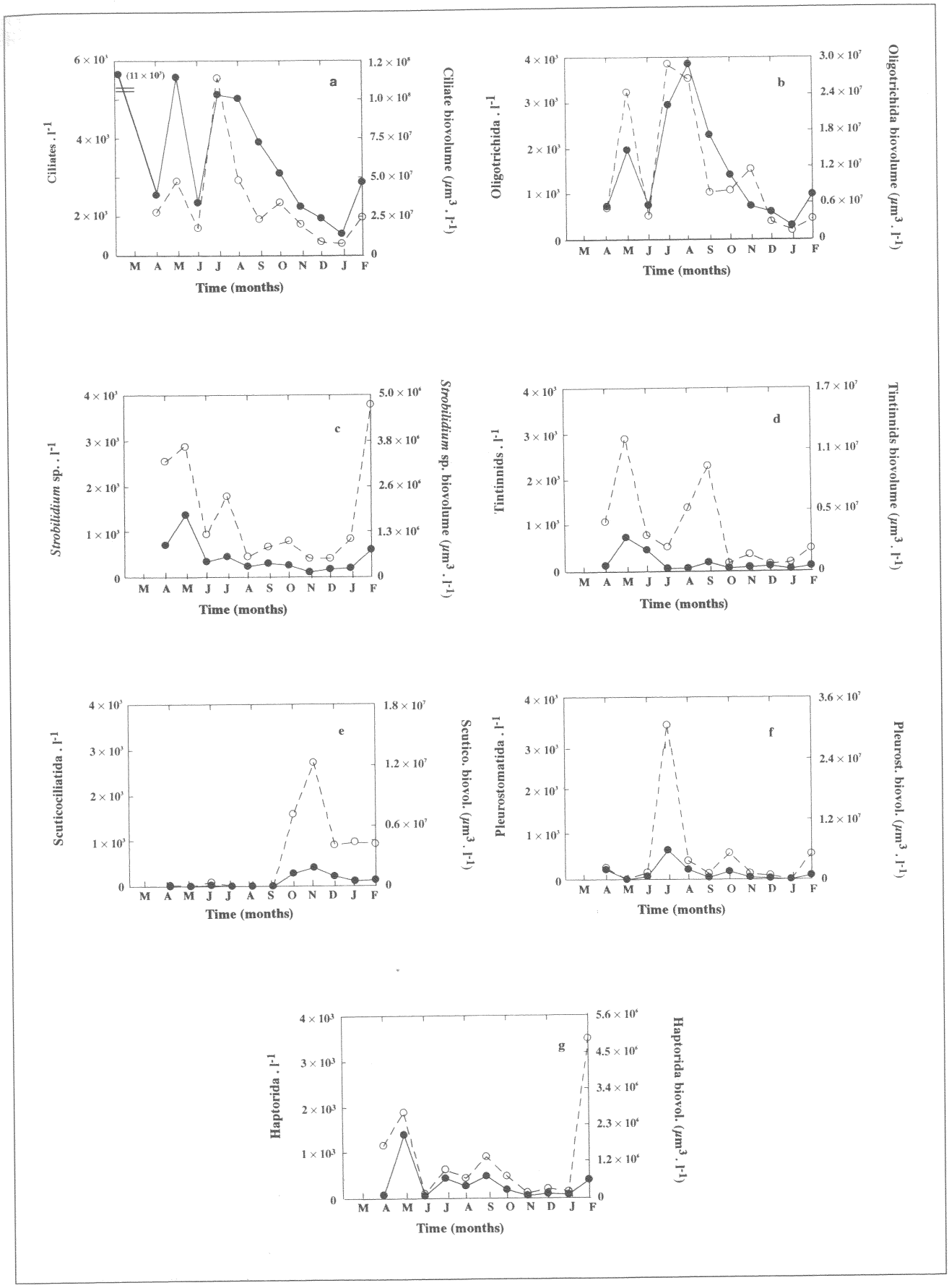

Figure 2. Averages on a monthly basis of abundances (•) and biomass (o) of ciliates (a), and the orders Oligotrichida (b), Choreotrichida (c, d), Scuticociliatida (e), Pleurostomatida (f) and Haptorida (g).

Table IV. Range of bacteria × 10^6 ml^{-1} (BN), nanoflagellate × 10^3 ml^{-1} (TNF), heterotrophic (HNF) and autotrophic (ANF) and ciliate × 10^3 l^{-1} abundances measured during an annual cycle in different coastal marine systems. (1): Ferrier-Pagés and Rassoulzadegan (1994), (2): Hoch and Kirchman (1993), (3): Coffin and Sharp (1987), (4): Andersen and Sørensen (1986), (5): Turner and Borkman (1993), (6): This study, and (n. d.): Not determined.

SITE	BN	TNF	HNF	ANF	CILIATES
NwMediterranean (Villefranche s.m.) (1)	0.2-0.7	0.4-1.7	0.1-0.8	0.1-1.2	1.0-5.0
Delaware Estuary (2)	0.7-12.7	n. d.	n. d.	n. d.	n. d.
Delaware Estuary (3)	1.0-8.0	n. d.	0.4-1.0	n. d.	n. d.
Limfjord Estuary (4)	0.5-15.2	n. d.	0.2-15.2	n. d.	1.4-162.0
Buzzards Bay (5)	0.3-10.9	0.05-0.4	n. d.	n. d.	n. d.
Blanes Bay (6)	0.07-1.4	0.01-3.9	0.05-0.8	0.03-0.7	0.2-64.6

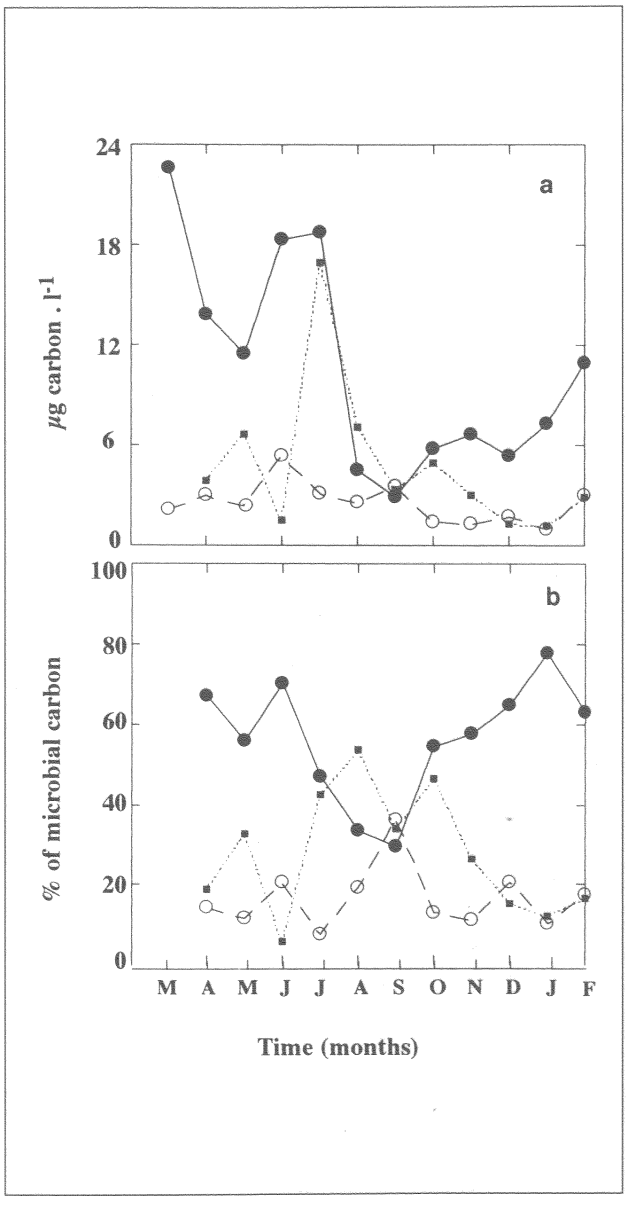

Figure 3. Averages on a monthly basis of carbon (a) and percentage from total microheterotrophic carbon (b) of bacteria (●), heterotrophic nanoflagellates (o) and ciliates (▪).

and Rassoulzadegan (1994), and Bernard and Rassoulzadegan (1994). Oligotrichida supported the highest biomass throughout the year, despite the fact that tintinnids, Pleurostomatida, and Scuticociliatida are larger in cell size (table II). These dominance patterns are similar to those found in other marine systems (Andersen and Sørensen, 1986; Jonsson, 1987).

Blanes Bay appears to be a heterotrophic system for long periods of the year, during which primary production exceeds respiration only during phytoplankton blooms (Satta *et al.*, 1996, in this volume). The highest bacterial abundance followed phytoplankton blooms with a lag of 8-15 days, as observed for other coastal systems (Coffin and Sharp, 1987).

Seasonal variability in the abundance of bacteria was moderate in comparison to that of nanoflagellates and ciliates (table I). Nanoflagellate and ciliate communities typically show more variability than bacteria (Wright, Coffin and Lebo, 1987; Vaqué and Pace, 1992), conforming to expectations of predator-prey models (Wright, 1988). Fluctuations in the microbial community (figures 1 and 2) initiated in March were apparently triggered by a combination of atmospheric changes (high atmospheric pressure and calm waters), a previous increase in primary production (Satta *et al.*, 1996; Cebrián, Duarte and Pascual, 1995, in this volume), and reduced zooplankton, particularly crustacean abundances (Andreu and Duarte 1995, in this volume). These conditions led to the dominance of plankton communities by bacteria, nanoplankton and microplankton. Coupling between bacteria (peak in March), nanoflagellates (small peak in April), and ciliates (peak in March and May), was clear in this first period of the cycle (figures 1, 2). The occurrence of torrential storms in June (loading allochthonous organic and inorganic nutrients into the bay) and a

phytoplankton bloom in summer (late July) led to increases in microbial biomass. Bacteria peaked in June and July, and dropped in August, while nanoflagellates only had a maximum in June, decreasing dramatically in July, when ciliate abundances increased. Oligotrichidae were the most abundant group of ciliates as observed in other planktonic communities, where they probably play an important role as predators on bacteria, and nanoflagellates and microflagellates (Rassoulzadegan, 1982; Jonsson, 1986; 1987; Bernard and Rassoulzadegan, 1990). This role is supported by the observation of a low abundance of bacteria and nanoflagellates after the abundance of Oligotrichida increased (i.e. August, figures 1, 2b).

Increased abundances of microbes were also expected in autumn when rainstorm events were important (loading allochthonous inputs), but less intensive than in summer; however, we observed the lowest values of chlorophyll *a* concentration found during the studied period (Mura *et al.*, 1996, in this volume), coinciding with our low values in microbial abundances and biomass, except for scuticociliate abundance and biomass (figures 1, 2, 3). Consequently, changes in abundance and biomass of autotrophic and heterotrophic communities were not necessarily associated with external inputs of nutrients.

Bacteria dominated the biomass ($\mu g\ C \cdot l^{-1}$) of microheterotrophs during the year (except in August-September, figure 3), followed by phagotrophic ciliates (excluding the autotrophic *Mesodinium* sp.). Heterotrophic nanoflagellates, which represented about 50.8% of the nanoflagellate community (autotrophic and heterotrophic), showed the lowest biomass.

The community structure of these microheterotrophs suggests bacterial carbon flowing through heterotrophic nanoflagellates and ciliates. Ciliates appear, therefore, as a keystone component of the plankton community in Blanes Bay, acting as links between microbial (both auto-and heterotrophic production) and metazoan production. The seasonal dynamics are, however, subject to complex control by autochthonous (i.e. phytoplankton blooms) and allochthonous (i.e. storms) inputs of organic matter, and by complex trophic interactions within the planktonic community.

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