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Seasonal variation of particulate organic carbon, dissolved organic carbon and the contribution of microbial communities to the live particulate organic carbon in a shallow near-bottom ecosystem at the Northwestern Mediterranean Sea

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Abstract. Microbial planktonic communities (i.e. bacteria and protozoa), phytoplankton, dissolved organic carbon (DOC) and particulate organic carbon (POC) were seasonally examined at Medes Islands (Northwestern Mediterranean) to assess their variation in abundance and composition throughout the year in a near-bottom littoral ecosystem. From October 1995 to November 1996, samples were collected between two and six times per month at 0.5 m above the bottom. Mean DOC and POC values throughout the year were 2560 ± 180 (SE) and 387 ± 35 μg C l^{-1}, respectively. All year, detrital organic carbon (detrital = total POC – live carbon) represented the main POC fraction, and mean live carbon was 24 ± 9 μg C l^{-1}. Winter and spring had maximum values of POC, and spring and summer had maximum values of DOC. Heterotrophic bacteria, with a mean abundance of 5.16 ± 0.08 × 10^5 cells ml^{-1}, were the main contributor to live carbon (26 ± 7%). During winter, heterotrophic bacterial biomass decreased 40% due to a decrease in mean biovolume per cell. *Synechococcus* sp. and *Prochlorococcus* sp. abundance were 2.24 ± 0.09 × 10^4 and 1.05 ± 0.07 × 10^4 cells ml^{-1}, respectively. However, while *Synechococcus* sp. were present all year, *Prochlorococcus* sp. were not observed from April to July. Mean phytoplankton (i.e. diatoms and dinoflagellates) abundance was 2.06 ± 0.40 × 10^4 cells l^{-1} with biomass at a maximum during the winter months, the period with the lowest temperature and the highest nutrient concentration. The size composition of live carbon showed two clearly distinct periods: from December to March, live carbon was dominated in biomass by microplankton, while from April to November, pico- and nanoplankton cells were dominant. Overall, the dynamics of the near-bottom planktonic communities was characterized by a low biomass of heterotrophic and autotrophic bacteria, phytoplankton and ciliates in contrast to previous water column studies. This pattern and the high temporal heterogeneity of the different planktonic communities are discussed in relation to the physical and chemical characteristics of the environment, as well as to the potential role that benthic communities may be exerting in the control of the near-bottom planktonic communities.

Introduction

Planktonic communities show a high spatio-temporal heterogeneity along the water column both at mesoscale (Denman and Powell, 1984) and small scale (Owen, 1989). Physical processes influence plankton distribution, enhancing community development in high-energy layers where the different species adapt to special conditions of mixing and turbulence (e.g. Mackas *et al*., 1993). This phenomenon is well known in the plankton communities along the water column, especially throughout or in hydrographic structures such as the haloclines, but little work has been carried out in near-bottom layers. This spatial structure consists of multiple sublayers which allow habitat partitioning by planktonic organisms. The small-scale distribution enables species to concentrate and exploit a turbulent, high-energy habitat such as the thermocline (Longhurst, 1985). A similar phenomenon may also occur in near-bottom layers where topography strongly affects currents and the dynamics of local water masses (Holloway, 1992).

In littoral areas, the vertical structure of plankton communities could be more homogeneous due to continuous water mixing. However, near the bottom, the environmental and biological conditions for the development of plankton communities are strongly modified by substratum–current interactions (Riedl, 1971) and by the supply of nutrients by benthic organisms (Graf and Rosenberg, 1997). In extensive shallow marine ecosystems such as coral reefs, planktonic communities are strongly affected by structure (space and volume) and activity (predation and food supply) of benthic communities (Sorokin, 1994). Indeed, planktonic communities are actively exploited by benthic suspension feeders, which partially return the organic matter captured from the water column, through detrital and dissolved forms or through meroplanktonic larvae (Graf, 1992). Although quantitative data on suspension feeder diet and capture rates under natural conditions are still scarce, suspension feeders can capture important amounts of planktonic prey and, therefore, the grazing pressure on the water column planktonic communities by macroinvertebrates appears to be much greater than previously thought (Reiswig, 1990; Coma *et al.*, 1995; Pile *et al.*, 1996; Ribes *et al*., 1998, 1999, in press).

During the last decade, it has been shown that picoplankton (cells < 2 μm) and nanoplankton (cells 2–20 μm) dominate the pelagic planktonic community in terms of biomass (Stockner and Antia, 1986) and production (Platt *et al.*, 1983; Burkill *et al.*, 1993). Pico- and nanoplankton communities include prokaryotic (heterotrophic bacteria, cyanobacteria and prochlorophytes) and eukaryotic organisms (autotrophic and heterotrophic flagellates). As a consequence of this relevance, an important amount of research has been conducted to study the dynamics of these planktonic communities in the water column and their trophic interactions with other groups of plankters (Sherr and Sherr, 1991; Van Wambeke *et al.*, 1996).

Despite research on the dynamics of the impact of the benthos on the associated planktonic microbial and algal communities (Stuart and Klumpp, 1984; Fielding and Davis, 1989; Velimirov and Walenta-Simon, 1993), little is known about the seasonal changes in the whole particulate organic matter pool, including microbes, phytoplankton, and dissolved and detrital organic carbon in shallow littoral ecosystems. Moreover, little is known about their variation in relation to the seasonal changes in the physical and chemical characteristics of the water.

The coastal waters of the Western Mediterranean, like those of other temperate seas, are characterized by two peaks of plankton production and biomass during the year, related to mesoscale hydrographic structures. An autumn peak develops after the disappearance of the summer thermocline, and a late winter–early spring peak develops with the onset of water column stability. In both situations, nutrient supplies enhance phytoplankton development (Estrada *et al*., 1985). The production dynamics of the near-bottom planktonic communities should not be the same as those from the water column. First, the sublittoral zone receives a major input of detrital and dissolved organic matter (DOM) from run-off and from benthic organisms such as algae and invertebrates; these coastal and benthic inputs represent more substrates for bacterial activity (Mann, 1982; Delille *et al.*, 1997). Second, near-bottom planktonic communities are

subject to higher and more variable turbulence due to the bottom effect; this turbulence may directly or indirectly affect the dynamics of microbes and phytoplankton through the resuspension process (Wainright, 1990). Third, in coastal zones during episodes of high primary production (i.e. phytoplankton blooms), a small percentage of this production is consumed by zooplankton with the main fraction being transferred directly to the benthos (Kiørboe, 1993). Finally, near-bottom planktonic communities are actively preyed on by benthic suspension feeder groups such as bivalves, sponges, ascidians and cnidarians. These benthic macroinvertebrates can prey on micro-, pico- and/or nanoplankton including prokaryotic and eukaryotic organisms (Stuart and Klumpp, 1984; Reiswig, 1990; Pile *et al.*, 1996; Ribes *et al*., 1998, 1999, in press) and, thus, they could directly control the abundance of these planktonic populations.

In this study, we analysed the composition, abundance and seasonal variations of dissolved and particulate organic matter in a Northwestern Mediterranean near-bottom ecosystem as an example of a temperate sea. We wanted to examine whether the particular environmental and biological conditions of this ecosystem cause the dynamics of their planktonic communities to differ from those observed in planktonic communities studied in the water column. For this purpose, seasonal changes in abundance and biomass of the near-bottom phytoplankton and microbial communities, as well as the concentration of dissolved organic carbon (DOC) and particulate organic carbon (POC), were determined in relation to physical and chemical characteristics of the water. The role of benthic organisms as a potential source of influence on the composition and dynamics of the near-bottom planktonic communities was also considered.

Method

Sampling was conducted at a coastal station (15 m depth) in the Medes Islands Marine Reserve (Northwestern Mediterranean Sea, 42º3′N, 3º13′E; Figure 1) between October 1995 and November 1996. The islands are uninhabited and located ~1 mile from the mainland and 4 miles from the Ter River mouth. Sampling took place between two (every 2 weeks) and six (every 5 days) times per month, for a total of 48 sampling days distributed throughout the year. Samples were collected by scuba divers at 0.5 m above the bottom using six 500-ml replicate plastic bags. In order not to stir up the water, divers swam upstream and collected immediately before anything else was done. Water used for the analysis of DOC, POC, pico- and nanoplankton was screened through a 100 µm net to avoid larger plankters. Temperature was measured *in situ* using an electrode (EOT 196 WTW) at the same time that the samples were collected. Samples were processed in the laboratory 20 min after sampling. Vertical profiles of the seawater temperature from a permanent station located about 100 m from the study site and the Ter River run-off (Figure 1) were provided by the Medes Islands meteorological station (Pascual, 1996). Vertical profiles of the water temperature were used to estimate the 'stratification coefficient', defined as the variance around the mean temperature along a depth gradient (0.5, 5, 10 and 15 m). High values of the stratification coefficient indicate a high temperature

Fig. 1. Map of the study area (Medes Islands, NW Mediterranean Sea). The arrow and asterisk show the sampling site and the temperature monitoring site, respectively.

difference from the top to the bottom of the thermocline and, therefore, stratification of the water column. Low values of the stratification coefficient indicate a small temperature difference over the 15 m depth interval and, therefore, mixing of the water column.

Picoplankton and nanoplankton

For analysis of heterotrophic bacteria, *Prochlorococcus* sp., *Synechococcus* sp., autotrophic picoeukaryotes and nanoeukaryotes, 2 ml subsamples were withdrawn from each of six replicates and preserved with paraformaldehyde (1.0% final concentration), kept cold and dark for <30 min, and frozen in liquid nitrogen (Campbell *et al.*, 1994). Afterwards, they were stored at –80ºC or in dry ice. Samples were analysed using a Coulter EPICS 753 flow cytometer (Coulter

Electronics Corporation, Hialeah, FL) equipped with two 5 W argon lasers and a Micro-Sampler-Delivery-System. The flow cytometer was set up for UV (220 mW) and 488 nm (1 W) colinear analysis. Hoechst 33342 (DNA-specific fluorochrome) was used to stain DNA according to Monger and Landry (1993). Five parameters were collected in list mode and analysed with custom-designed software (CYTOPC by Daniel Vaulot): red fluorescence (from chlorophyll *a*), orange fluorescence (from phycoerythrin), blue fluorescence (from DNA stained with Hoechst 33342), forward- and right-angle light scatter signals (FALS and RALS). For statistical purposes, sample size for analysis was chosen to provide >10 000 events per sample; therefore, 1 ml of each sample was analysed for picoeukaryotes and nanoeukaryotes, and 100 µl for heterotrophic bacteria, *Prochlorococcus* sp. and *Synechococcus* sp.

For the quantification of heterotrophic nanoflagellates, 50 ml of water from four replicates were preserved with formaldehyde (0.5% final solution). Subsamples of 20 ml were stained with DAPI, filtered onto 0.2 µm filters, and heterotrophic nanoflagellates were counted by epifluorescence microscopy (Porter and Feig, 1980). The same subsamples stained with DAPI were used to measure cell size (length and width) of heterotrophic bacteria, *Synechococcus* sp., pico- and nanoeukaryotes, and heterotrophic nanoflagellates. For heterotrophic bacterial size, over 100 cells were measured using framegrabber and software for image analysis [NIH (National Institute of Health)-Image)] as described in Massana *et al*. (1997). For *Synechococcus* sp., pico- and nanoeukaryotes, and heterotrophic nanoflagellates, we used an ocular micrometer to measure cell length and width. Cells smaller than 2 µm were attributed to picoeukaryotes and the cells larger than 2 µm to nanoeukaryotes. Autotrophic nanoeukaryotes and heterotrophic nanoflagellates were measured together, and a common mean biovolume per month was calculated. It was not possible to measure *Prochlorococcus* sp. due to the difficulty of observing the cells with epifluorescence microscopy; we used a mean size of 0.7 µm calculated for the Mediterranean by Vaulot *et al*. (1990).

Cell biovolume was calculated from length and width by approximation to the nearest geometric figures. Carbon content was then estimated from literature conversion factors as follows: heterotrophic bacteria, 0.22 pg C μm^{-3} (Fry, 1988); *Prochlorococcus* sp., 0.133 pg C μm^{-3} (Simon and Azam, 1989); *Synechococcus* sp., 0.357 pg C μm^{-3} [mean value of Björnsen (1986), Kana and Glibert (1987) and Verity *et al*. (1992)]; pico- and nanoeukaryotes, pg C = $0.433 \times (\mu m^3)^{0.863}$ (Verity *et al*., 1992).

Flow cytometer counts were compared to epifluorescence microscopy counts. Thirty-two samples stained with DAPI were used to count heterotrophic bacteria, *Synechococcus* sp. and autotrophic nanoflagellates by both epifluorescence microscopy (Porter and Feig, 1980) and flow cytometry as described above.

Phytoplankton and ciliates

For analysis of phytoplankton and ciliates, two replicate 350 ml water samples were preserved with acid Lugol's (1% final concentration). For each sample, 100 ml subsamples were allowed to settle and were observed with an inverted

microscope using the Utermöhl technique. Dominant groups of diatoms and dinoflagellates were quantified in this study. The microscope was provided with a colour CCD video camera connected to a video recorder. Images of the organisms for measurement were recorded and digitized, and sizing was performed using image-analysis software (NIH-Image). For each sampling day, 20 individuals of the most common groups were measured; the volumes were estimated from the length and width measurements assuming ellipsoidal, cylindrical or conical shapes (Edler, 1979; Sebens and Koehl, 1984). Carbon content was then estimated from literature conversion factors: phytoplankton, pg C $cell^{-1} = 0.109 \times (\mu m^3)^{0.991}$ (Montagnes *et al*., 1994); ciliates, 0.19 pg C μm^{-3} (Putt and Stoecker, 1989).

Total particulate organic carbon

POC was measured by filtering 60 ml (four replicates) on pre-combusted GF/F glass fibre filters. Filters were then frozen in liquid nitrogen and kept at –80ºC until analysis. Prior to analysis, filters were dried at 60ºC for 24 h and exposed to hydrochloric acid vapours for 48 h to destroy inorganic material. Then filters were dried again and analysed with a C:H:N autoanalyser (Perkin-Elmer 240).

Dissolved organic carbon

For DOC, 20 ml water samples (four replicates) were filtered through pre-combusted GF/F glass fibre filters. The filtered water was stored in glass tubes at –20ºC until analysis. Analysis was conducted by high-temperature catalytic oxidation with an autoanalyser (Shimadzu TOC-5000).

A multiple regression analysis was used to establish the relationship between DOC and the different POC groups with environmental and biological variables such as water temperature, stratification coefficient, irradiance, nutrients, run-off and macroalgal production. Macroalgal production includes the production of the most abundant benthic algae throughout the year (i.e. *Rissoella*, *Cystoseira* and *Halimeda* species; data from Ballesteros, 1991). Nutrient concentration and irradiance values throughout the year come from Garrabou (1997). A backward stepwise procedure was used to exclude non-relevant variables (Sokal and Rohlf, 1995). Variables were square root transformed when normality (Kolmogorov–Smirnov test) and/or the heteroscedasticity (Levene's test) requirements were not fulfilled.

Results

Methodological considerations

Distinct microbial populations were identified by flow cytometry (Figure 2). Comparison between flow cytometer counts (FCT) and epifluorescence microscope counts (EMC) showed a good correlation for all cell types (Table I). For heterotrophic bacteria and for autotrophic nanoflagellates, the slope of the regression line was not significantly different from 1.0 (Table I). However, the high value of the nanoflagellate intercept indicates that, for low abundance, flow

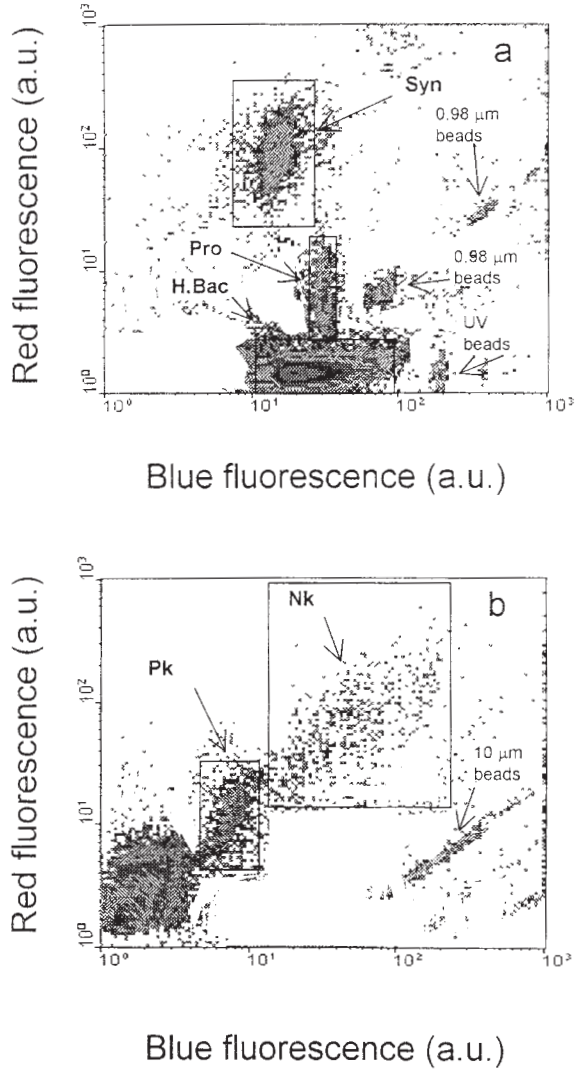

Fig. 2. Pico- and nanoplankton populations identified by flow cytometry. Red fluorescence results from chlorophyll *a* excitation and blue fluorescence from DNA stained with Hoechst 33342. (**a**) Picoplankton: H. Bac, heterotrophic bacteria; Pro, *Prochlorococcus* sp.; Syn, *Synechococcus* sp.-type cyanobacteria. (**b**) Pico- and nanoeukaryotes: Pk, autotrophic picoeukaryotes; Nk, autotrophic nanoeukaryotes. a.u., arbitrary units.

cytometry was counting more cells than microscopy was. For *Synechococcus* sp., the slope was significantly different from 1.0 (Table I), showing that flow cytometry was counting ~6% more cells than epifluorescence microscopy. Regarding picoeukaryotes, we were not able to quantify them by epifluorescence microscopy to check the flow cytometer counts, but other authors have reported a good correlation between both methods (Buck *et al*., 1996).

Table I. Parameters for the regression equation between flow cytometer counts (FCT) and epifluorescence microscope counts (EMC), and *t*-test analysis testing whether the slope of the regression line was significantly different from one

FCT-EMC	Intercept	Slope	r^2	*P*	*t*-test		
					t	d.f.	*P*
Heterotrophic bacteria	-1.60×10^4	1.11	0.87	<0.0001	1.25	30	0.221
Synechococcus sp.	162	1.16	0.91	<0.0001	2.39	30	0.023
Autotrophic nanoflagellates	179	0.89	0.43	<0.005	0.58	30	0.567

Physical and chemical variables

Water temperature showed minimal values (12–14ºC) from December to March and maximal values during the summer months (20–23ºC; Figure 3a). Autumn and winter had the lowest stratification coefficients (i.e. mixing was occurring in the water column). During the spring season, the water column gradually became stratified until the summer when the maximal stratification coefficient values were observed (Figure 3a). The highest nutrient concentrations were present in autumn and winter. Nutrient concentrations decreased during spring, and the minimal values were recorded in the summer months (Figure 3b). River run-off was highest during the winter months, while minimal values were recorded during the summer period (Figure 3c). The variations in nutrient concentrations along the year correlated positively with river run-off ($r^2 = 0.65$, $P < 0.0001$), but they did not show a significant correlation with the stratification coefficient.

The highest values of irradiance throughout the year occurred during the summer months. Irradiance values decreased during autumn and winter. During spring, irradiance values gradually increased towards the summer months (Figure 3c).

Heterotrophic bacteria

Heterotrophic bacterial abundance throughout the year ranged between 3 and 9×10^5 bacteria ml^{-1}. Abundances were similar throughout the year, except for May, August and November 1996 when lower values were observed [ANOVA, $F_{(13,316)} = 4.68$, $P < 0.0001$; Turkey's post hoc test; Figure 4a]. The size range found for heterotrophic bacteria was from 0.2 to 2.3 μm length (0.5 ± 0.3 SD). Heterotrophic bacteria were smaller from January to April than for the rest of the period sampled [ANOVA, $F_{(9,4078)} = 28.91$, $P < 0.0001$; Turkey's post hoc test]. Therefore, biomass was 40% lower during the latter 3 months (Figure 4b and c). Mean values for cell abundance, biovolume and carbon per litre are given in Table II. The variation of the heterotrophic bacterial biomass along the year correlated positively with water temperature and negatively with irradiance. Heterotrophic bacterial biomass did not show a significant relationship with either dissolved or detrital organic carbon (Table III).

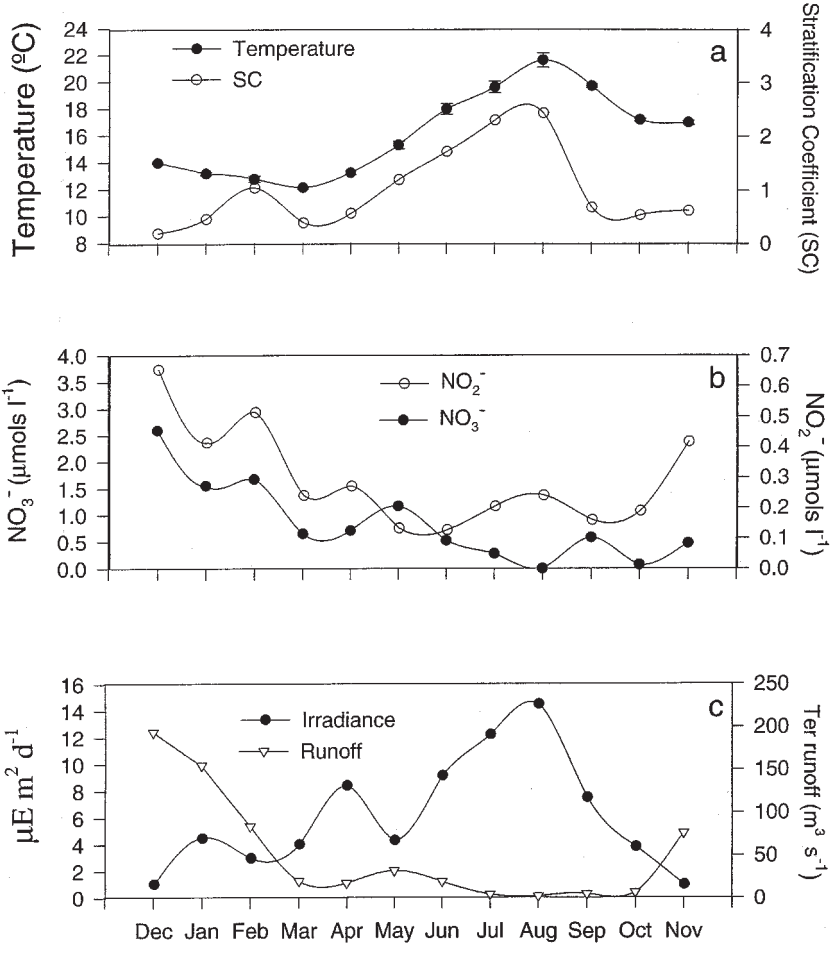

Fig. 3. (**a**) Average temperature monthly values ± SE at the sampling site (15 m) and stratification coefficient for the area. Monthly values of (**b**) nutrients, (**c**) irradiance and Ter River run-off.

Table II. Annual mean (± SE) abundance for the different groups of cells expressed as cell number (cells ml^{-1}), biovolume ($\mu m^3\ l^{-1}$) and biomass in carbon units ($\mu g\ C\ l^{-1}$)

	Cell number (cells ml^{-1})	Biovolume ($\mu m^3\ l^{-1}$)	Carbon ($\mu g\ C\ l^{-1}$)
Heterotrophic bacteria	$5.16 \pm 0.08 \times 10^5$	$2.14 \pm 0.04 \times 10^7$	4.72 ± 0.09
Prochlorococcus sp.	$1.05 \pm 0.07 \times 10^4$	$1.87 \pm 0.14 \times 10^6$	0.55 ± 0.04
Synechococcus sp.	$2.24 \pm 0.09 \times 10^4$	$9.96 \pm 0.39 \times 10^6$	3.56 ± 0.14
Picoeukaryotes	1640 ± 72	$2.75 \pm 0.14 \times 10^6$	1.10 ± 0.05
Autotrophic nanoeukaryotes	657 ± 24	$1.46 \pm 0.05 \times 10^7$	4.14 ± 0.14
Heterotrophic nanoeukaryotes	633 ± 36	$1.39 \pm 0.07 \times 10^7$	3.07 ± 0.17

Table III. Multiple regression analysis to estimate the variance in the variables (HBac, heterotrophic bacteria; Syn, *Synechococcus*; Pro, *Prochlorococcus*; Pk, picoeukaryotes; Nk, nanoeukaryotes; Diat, diatoms; Din, dinoflagellates; Cil, ciliates; POC, detrital particulate organic carbon; DOC, dissolved organic carbon) explained by temperature, stratification coefficient (SC), irradiance, nutrient concentration, Ter River run-off, macroalgal production (P), POC and DOC. All variables are in biomass units (μg C l^{-1}). $N = 12$. (a) Slopes (± SE) for the different variables, intercept (A), adjusted squared r (Adj R^2). (b) Standardized partial regression coefficients

(a)

Variable	HBac	Syn	Pro	Pk	Nk	Diat	Din	Cil	POC	DOC
Temperature (°C)	0.39 ± 1.33	0.55 ± 0.07	ns	ns	ns	–0.43 ± 0.14	ns	ns	–	–
SC	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Irradiance (μE m^2 day^{-1})	–0.21 ± 0.09	ns	–0.05 ± 0.02	ns	ns	ns	ns	ns	–	–
Nutrients (μmol l^{-1})	ns	ns	0.27 ± 0.12	0.59 ± 0.17	ns	5.32 ± 2.69	ns	ns	–	–
Ter River run-off (m^3 s^{-1})	ns	ns	ns	ns	ns	ns	ns	ns	3.54 ± 0.76	ns
Macroalgae P (g C m^{-1} day^{-1})	–	–	–	–	–	–	–	–	61.95 ± 15.40	1708 ± 622
POC	ns	ns	ns	ns	ns	ns	ns	ns	–	ns
DOC	ns	ns	ns	ns	ns	ns	ns	ns	ns	–
Nk	–	–	–	–	–	–	–	–	ns	ns
Pk	–	–	–	–	–	–	–	–	ns	ns
Diat	–	–	–	–	–	–	–	–	ns	ns
Din	–	–	–	–	–	–	–	–	ns	ns
A	ns	–6.65**	0.84*	2.34*	–	ns	–	–	ns	ns
Adj R^2	0.37*	0.85***	ns	0.76*	–	0.37*	–	–	0.71**	0.37*

(b)

Variable	HBac	Syn	Pro	Pk	Nk	Diat	Din	Cil	POC	DOC
Temperature (°C)	0.96*	0.93***	ns	ns	ns	–1.15*	ns	ns	–	–
SC	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Irradiance (μE m^2 day^{-1})	–0.75*	ns	–0.75*	ns	ns	ns	ns	ns	–	–
Nutrients (μmol l^{-1})	ns	ns	0.73*	0.74*	ns	0.79*	ns	ns	–	–
Ter River run-off (m^3 s^{-1})	ns	ns	ns	ns	ns	ns	ns	ns	0.79**	ns
Macroalgae P (g C m^{-1} day^{-1})	–	–	–	–	–	–	–	–	0.68**	0.66*
POC	ns	ns	ns	ns	ns	ns	ns	ns	–	ns
DOC	ns	ns	ns	ns	ns	ns	ns	ns	ns	–
Nk	–	–	–	–	–	–	–	–	ns	ns
Pk	–	–	–	–	–	–	–	–	ns	ns
Diat	–	–	–	–	–	–	–	–	ns	ns
Din	–	–	–	–	–	–	–	–	ns	ns

Analysis not performed (–); not significant (ns); ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$.

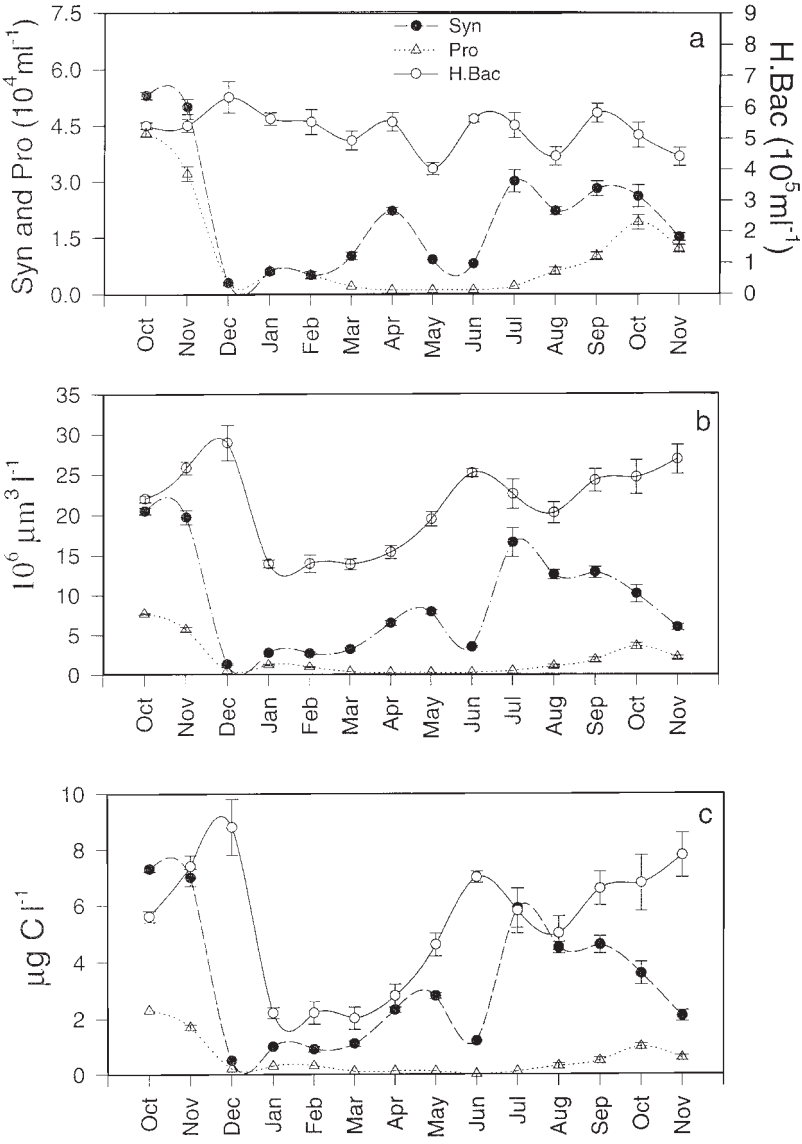

Fig. 4. Monthly averages (± SE) for heterotrophic bacteria, *Synechococcus* sp. and *Prochlorococcus* sp. abundance expressed as (**a**) cells ml^{-1}, (**b**) biovolume in µm^3 l^{-1} and (**c**) carbon biomass in µg C l^{-1}.

Prochlorococcus sp., Synechococcus sp.

A *Prochlorococcus* sp. population was detectable in the water from August to March (Figure 4a). The highest abundance and biomass values were found from September to November and minimal values were observed from December to March (Figure 4b and c). From April to July, it was not possible to distinguish a clear population of *Prochlorococcus* sp. using flow cytometry because of the few

cells present in the samples (<300 cells ml^{-1}; Figure 4a). The size range of *Synechococcus* sp. (cyanobacteria) cells found was from 0.4 to 2.4 μm length (1.3 ± 0.5 SD). *Synechococcus* sp. cells were present in the water throughout the year. They were most abundant from August to November (Figure 4a), and a low abundance of cyanobacteria was observed during winter and spring. This temporal pattern was clearer in biovolume and carbon terms (Figure 4b and c). Mean annual values of abundance, biovolume and biomass for *Prochlorococcus* sp. and *Synechococcus* sp. are shown in Table II. *Prochlorococcus* sp. and *Synechococcus* sp. abundance showed a good correlation during the period in which there was a clear *Prochlorococcus* sp. population [August–March; Pro ml^{-1} = –1719 + 0.7 (Syn ml^{-1}); Pro = *Prochlorococcus* sp., Syn = *Synechococcus* sp., $n = 97$, $r^2 = 0.74$; $P < 0.0001$]. *Synechococcus* sp. biomass correlated positively with water temperature (Table III). *Prochlorococcus* sp. biomass showed a positive correlation with nutrient concentrations and a negative correlation with irradiance (Table III).

Picoeukaryotes, nanoeukaryotes, phytoplankton and ciliates

Autotrophic pico- and nanoeukaryotes and heterotrophic flagellates were always present in the samples (Figure 5a). Except in spring, picoeukaryotes were more abundant than nanoeukaryotes and heterotrophic nanoflagellates all year round. Mean annual values of abundance, biovolume and biomass for each group are shown in Table II. The size range found for picoeukaryotes was from 0.80 to 1.60 μm length (1.2 ± 0.3 SD), and for nanoeukaryotes and heterotrophic flagellates it was from 2.40 to 9.60 μm length (3.79 ± 1.39 SD). In biomass units, autotrophic nanoeukaryotes and heterotrophic nanoflagellates were always dominant over picoeukaryotes. Nanoeukaryotes and heterotrophic nanoflagellates were especially abundant in spring (Figures 5b and 6a). Picoeukaryotes biomass showed a positive correlation with nutrients (Table III). The biomass of nanoeukaryotes did not correlate significantly with any of the examined variables (Table III).

Phytoplankton abundance throughout the year varied from 1.1×10^3 to 170×10^3 cells l^{-1} [$20.6 \pm 4.1\ 10^3$ (SE)]. Ciliates were much less abundant, with mean values of 358 ± 30 cells l^{-1} (between 80 and 990 cells l^{-1}; Figure 5c and e). Phytoplankton size ranges varied for each group and were: pennate diatoms from 6.1 to 348 μm length (70 ± 22 SD); centric diatoms from 8.6 to 288 μm length (65 ± 27 SD); dinoflagellates from 8.4 to 49 μm length (28 ± 4 SD); ciliates from 10 to 72 μm length (38 ± 12 SD). The general trend of phytoplankton cell abundance and biomass showed two distinct periods: from December to June, clearly dominated by diatoms, and from July to November, dominated by dinoflagellates (Figure 5c and e). During the period dominated by diatoms, it was possible to distinguish two peaks of high phytoplankton abundance: one during March (late winter bloom) and another one from late May to early June (spring bloom; Figure 5c). The late winter and spring blooms were dominated in biomass, as in number of cells, by pennate diatoms of the genus *Nitzschia* and centric diatoms of the genus *Chaetoceros*, respectively. Phytoplankton biomass was about three times higher during the winter period (from December to February; Figures 5d and 6b), mainly due to the centric diatoms of genus *Ditylum*. In September, it

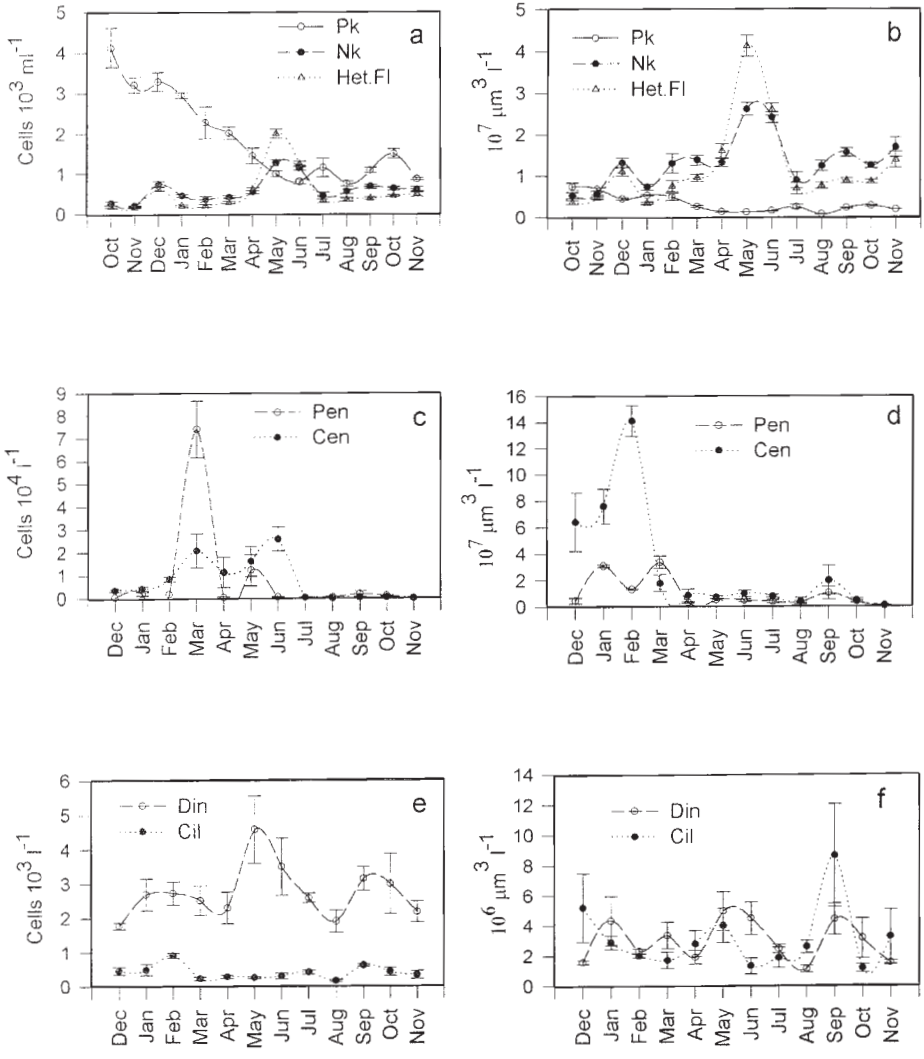

Fig. 5. Monthly averages (± SE) of pico- and nanoplankton abundance expressed as (**a**) cells ml^{-1}, (**c**, **e**) cells l^{-1} and (**b**, **d**, **f**) biovolume expressed as μm^3 l^{-1}. Pk, picoeukaryotes; Nk, autotrophic nanoeukaryotes; Het.Fl, heterotrophic flagellates; Pen, pennate diatoms; Cen, centric diatoms; Din, dinoflagellates; Cil, ciliates.

was possible to distinguish a short-term peak dominated in cell number by diatoms, mainly of the genus *Thalassionema*, and in terms of biomass by the centric diatoms of genus *Rhizosolenia*. Dinoflagellates were present throughout the year, but it was from July to November when their relative contribution in number of cells was most important (Figure 5e). However, even during this period, the biomass of diatoms and ciliates was as important as the dinoflagellate biomass (Figures 5f and 6c).

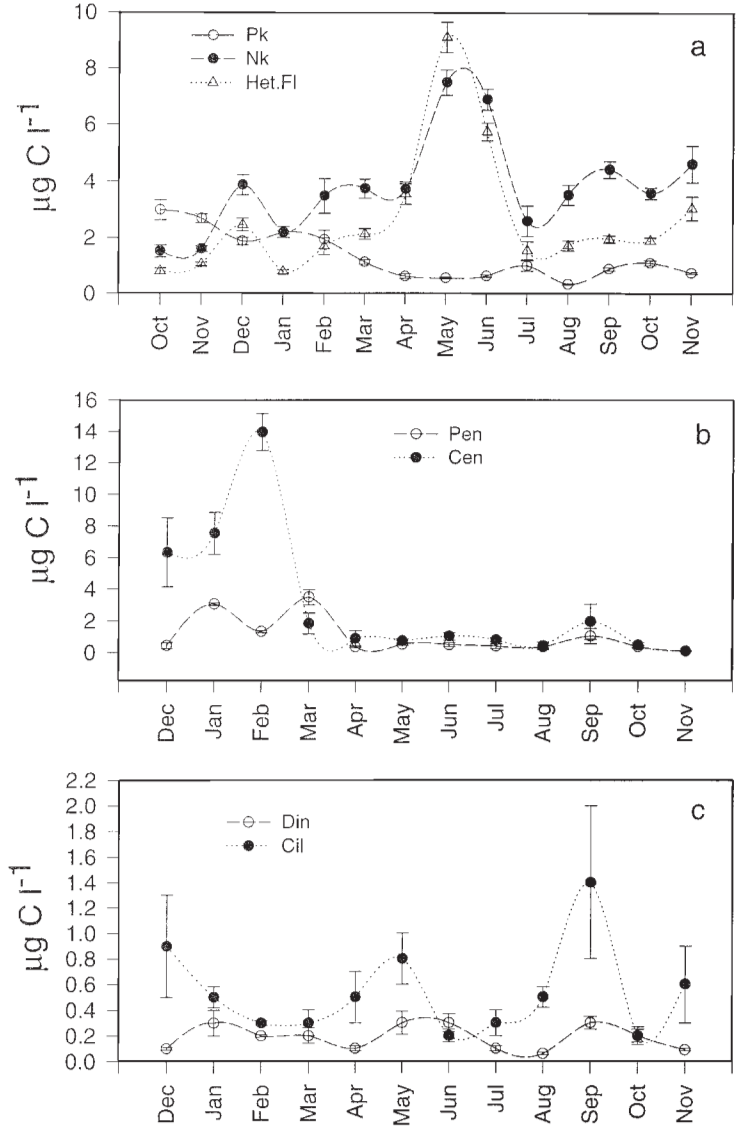

Fig. 6. Monthly biomass averages (± SE) in carbon units (µg C l^{-1}) for (**a**) picoeukaryotes (Pk), autotrophic nanoeukaryotes (Nk) and heterotrophic flagellates (Het.Fl); (**b**) pennate diatoms (Pen), centric diatoms (Cen), dinoflagellates (Din) and ciliates (Cil).

The biomass of diatoms correlated positively with nutrient concentration and negatively with water temperature (Table III). The biomass of dinoflagellates was relatively constant throughout the year (Figure 6c). The biomass of ciliates was rather variable throughout the year and did not exhibit a significant correlation with any of the examined variables. Ciliates biomass values were always lower than 2 µg C l^{-1} (Figure 6c).

Detrital and dissolved organic carbon

Total POC (from C:H:N analysis), including live carbon and detritus, showed an annual mean value of 387 ± 35 SE μg C l^{-1} (Figure 7a). Detrital organic carbon (hereafter detrital POC) throughout the year was, on average, 17 ± 3 SE times larger than live carbon. Winter and spring were the periods with the largest amount of detrital POC, which was, on average, 34 ± 4 SE times larger than live carbon, with a C/N relationship of 17 ± 4 SE. Summer and autumn had the lowest detrital organic carbon values, which were about 6 ± 2 SE times larger than live carbon and with a mean C/N relationship of 4 ± 2 SE. Detrital POC correlated positively with the Ter run-off and macroalgal production, mainly due to *Rissoella* and *Cystoceira* species. Detrital POC did not show any relationship with any phytoplankton group biomass (Table III).

DOC showed a mean annual value of 2560 ± 180 μg C l^{-1} (± SE). As a general pattern, two periods of high values of DOC can be distinguished: one in spring (May: mean ± SE 4240 ± 658 μg C l^{-1}) and one in summer (from late July to September: mean ± SE 3800 ± 309 μg C l^{-1}; Figure 7c). DOC correlated positively with macroalgal production (mainly due to *Halimeda* species). No significant relationship was observed between DOC and detrital POC concentration, or with any phytoplankton group biomass (Table III).

Live carbon composition

The overall contribution of the pico-, nano- and microplankton groups to the live carbon content of the water throughout the year showed that heterotrophic bacteria and the photosynthetic nanoeukaryotes were the groups with the highest and most constant contributions (mean ± SE: 26 ± 7% and 21 ± 7%, respectively) to the total carbon (Figure 7b). The contribution of the other groups was important in some periods. Diatoms contributed 37 ± 13 (SE)% of the total carbon from December to March, and *Synechococcus* sp. contributed 29 ± 6 (SE)% of the total carbon during summer (from July to September). The groups with minor annual contribution in terms of carbon were *Prochlorococcus* sp., picoeukaryotes, dinoflagellates and ciliates; overall, these groups contributed 2.4 ± 2.6 (SE)% of the total carbon (Figure 7b). Total live carbon estimated from cell counts showed an annual mean value of 24 ± 9 (SE) μg C l^{-1}. February was the month with the highest live carbon values and August was the period with the lowest values (Figure 7b).

Discussion

The seasonal variation of water temperature and nutrient concentrations were the environmental variables which better explained the changes observed in the contribution of the different planktonic groups to the pool of live carbon. During winter, a period of low temperature and high nutrient concentrations (Figure 3), large phytoplankton cells were dominant. During the winter months, diatoms contributed ~40% to the live carbon. In summer, a period of high temperature and low nutrients (Figure 3), small cells such as *Synechococcus* sp. and heterotrophic

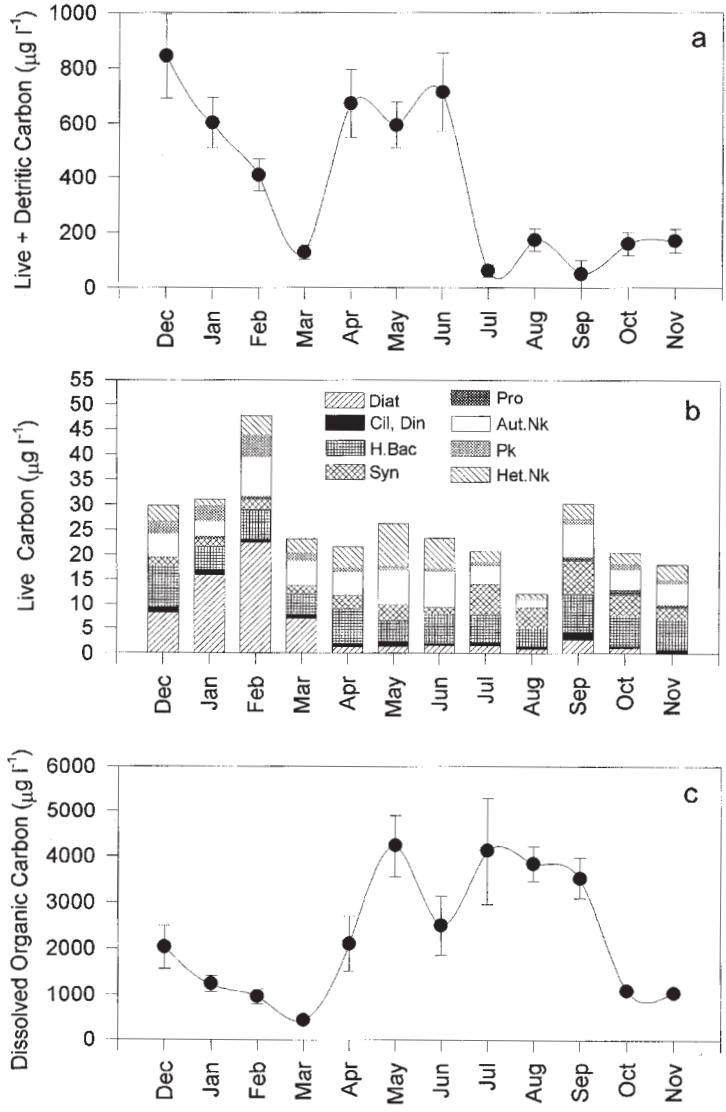

Fig. 7. Monthly averages (± SE) expressed as µg C l^{-1} of (**a**) live and detrital carbon from the C:H:N analysis, (**b**) live carbon from cell counts with the percentage composition (Het.Nk, heterotrophic nanoeukaryotes; Pk, picoeukaryotes; Aut.Nk, autotrophic nanoeukaryotes; Pro, *Prochlorococcus* sp.; Syn, *Synechococcus* sp.; H.Bac, heterotrophic bacteria; Din, dinoflagellates; Cil, ciliates; Diat, diatoms) and (**c**) dissolved organic carbon.

bacteria were the dominant groups. This fact appears to be related to the surface to volume ratio of the cells because the uptake of nutrients increases with the increase in this ratio (Kiørboe, 1993). Thus, under situations of low nutrients, such as the summer conditions in the Mediterranean, small cells may have an advantage in taking up nutrients.

Heterotrophic bacterial abundance at Medes Islands throughout the year was similar to that documented for surface waters in other Mediterranean coastal waters (Villefranche-sur-mer: 2–7 $\times$ 10^5 cells ml^{-1}; Ferrier-Pagès and Rassoulzadegan, 1994), and agrees with values of abundance in offshore oligotrophic waters (Azam *et al*., 1983). Surface waters of Blanes Bay in the coastal Mediterranean showed similar annual mean values, but with a higher range of variation in bacterial abundance (annual mean 5.02 $\times$ 10^5 cells ml^{-1}; range 0.7–14 $\times$ 10^5 cells ml^{-1}; Vaqué *et al*., 1997). However, despite the agreement in bacterial abundance, the heterotrophic bacterial biomass that we observed was lower (mean annual value 5 μg C l^{-1}) than that documented in Blanes Bay (10 μg C l^{-1} in 1995, Vaqué, 1996; 8.56 μg C l^{-1} in 1996, E.Vazquez-Dominguez, personal communication). The differences were mainly because mean heterotrophic bacterial biovolume in the present study was lower than that of Blanes Bay.

Despite the high DOC values observed during spring and summer, similar to highly productive systems such as kelp beds (Fielding and Davies, 1989), the bacterial abundance reported during these periods was always one or two orders of magnitude lower than that reported in kelp bed ecosystems (Moriarty and Pollard, 1982). A similar fact had been reported previously by Velimirov (1986), who pointed out that despite the large amounts of DOC released by the *Posidonia oceanica* beds, the maximum bacterial abundance was never higher than 1.2 $\times$ 10^5 cells ml^{-1}. It remains unclear why there are not higher abundances of heterotrophic bacteria if POC and DOC are not limiting. One hypothesis would be that the high values of DOC observed, mainly of phytobenthic origin (see below), would have a higher refractory fraction than phytoplankton-produced DOC. Carbon consumption is restricted due to mechanisms controlling both growth and biomass of bacteria. Growth is kept low by bacteria–phytoplankton competition for nutrients, especially P which has been documented to be limiting production in the Northwest Mediterranean (Thingstad *et al.*, 1998). Heterotrophic bacterial biomass is also kept low by predators such as bacterivorous protozoa, but another factor could be the controlling effect of suspension feeders such as bivalves, sponges (Reiswig, 1990; Pile *et al.*, 1996; Ribes *et al*., 1999) and ascidians (Stuart and Klumpp, 1984; Ribes *et al.*, 1998), which are known to be active predators of microorganisms. In a similar way, the controlling effect of benthic suspension feeders has been suggested to explain patterns of variation of planktonic communities in certain lagoons and estuaries (e.g. Cloern, 1982).

The observed decrease in bacterial cell size in winter has also been documented for bacterial communities in seagrass beds (Velimirov and Walenta-Simon, 1992). These authors hypothesized that this decrease could be an adaptation to unfavourable low DOC. Our results point out that this effect could depend not only on DOC abundance, but also on temperature. The DOC abundance in autumn was as low as in winter and, nevertheless, the decrease in bacteria cell biovolume occurred only in winter. Furthermore, the positive relationship between bacterial biomass and water temperature suggests that the low temperature of the winter period may also be playing an important role in the growth process of bacteria, probably inhibiting it (Marrasé *et al.*, 1992).

Autotrophic bacterial (*Prochlorococcus* sp. and *Synechococcus* sp.) abundance

was within the low range of the abundance reported for the North Atlantic Ocean (Chisholm *et al*., 1988), but is in accord with the range of abundance observed in the Northwestern Mediterranean (Vaulot *et al*., 1990). Sampling throughout the euphotic zone, Vaulot and co-workers (1990) documented low *Prochlorococcus* sp. densities in the well-mixed nearshore water (8–12 $\times$ 10^3 cells ml^{-1}). These values were similar to those observed in the present work during the same months (December and January). However, those authors did not provide data on *Prochlorococcus* sp. abundance from late August to November, when we observed the highest abundance of these cells. A positive relationship between *Prochlorococcus* sp. biomass and nutrient concentration was observed, as has been previously reported by several authors (Chisholm *et al*., 1988; Ferrier-Pagès and Rassoulzadegan, 1994). Then, the absence of prochlorophytes in the near-bottom community from April to August could be related to the low nutrient abundance in the water during this period. During summer, as a general trend for the Mediterranean, the nitracline is close to the deep chlorophyll maximum at a depth between 40 and 100 m (Estrada *et al*., 1985). Therefore, the fact that the location of the study site was shallower than the summer nitracline position may be why prochlorophytes were not observed during this period. A similar displacement of the maximum occurrence of prochlorophytes following the nitracline position has been previously reported during late spring and summer in the North Atlantic (Olson *et al*., 1990).

Synechococcus sp. abundance showed a good correlation with *Prochlorococcus* sp. abundance during the period that *Prochlorococcus* sp. were present in the community, as has also been observed in offshore waters (Vaulot *et al*., 1990). The positive relationship between *Prochlorococcus* sp. biomass and nutrient concentration and the lack of relationship between *Synechococcus* sp. biomass and nutrient concentration suggest that the presence of *Synechococcus* sp. all year, even when *Prochlorococcus* sp. were absent, may be due to *Synechococcus* sp.'s higher adaptability to low nutrient levels, as has been observed by other authors (Olson *et al*., 1990; Vaulot *et al*., 1990). The positive correlation between *Synechococcus* sp. and temperature observed appears be related to the relationship between temperature and *Synechococcus* sp. growth rates (Agawin *et al.*, 1998). Vaulot and co-workers (1990) suggested that *Synechococcus* sp. and prochlorophytes may have a similar response to factors such as temperature, nutrients and light. However, our results, which include the whole year cycle, point out that, in shallow waters, the biomass of both groups exhibits a different response to nutrient, irradiance and water temperature changes.

Synechococcus sp. mean annual abundance was similar to that of the surface water at Villefranche-sur-mer (Northwestern Mediterranean; Ferrier-Pagès and Rassoulzadegan, 1994), and also to that of surface water values reported for Blanes Bay (Agawin *et al.*, 1998). The mean annual abundance of autotrophic nanoeukaryotes and heterotrophic nanoflagellates observed in the near-bottom planktonic community in Medes Islands agrees in abundance and biomass terms with previous values reported for surface oligotrophic waters of the Northwestern Mediterranean Sea (Ferrier-Pagès and Rassoulzadegan, 1994; Vaqué *et al*., 1997).

The abundance of phytoplankton cells (mean values of 2.1 $\times$ 10^4 cells l^{-1} with

a maximum of 1.2×10^5 cells l^{-1}, including diatoms and dinoflagellates) was lower for the Medes Islands near-bottom community than values reported for coastal waters (mean values for an integration of 100-m-depth shelf waters, maximum: 4×10^5 cells l^{-1}; Margalef and Castellví, 1967) and other nearby surface waters studied (two consecutive annual means: $>2 \times 10^5$ cells l^{-1}; Mura *et al*., 1996). In the same way, ciliate abundance throughout the year was one order of magnitude lower (in number and in biomass) at our study site than the values reported for Blanes Bay (Vaqué, 1996). The lack of an autumn phytoplankton peak of abundance (despite the sporadic peak of biomass in September) could be within the normal variability of the autumn peak.

As pointed out in the Introduction, there were several reasons to expect differential dynamics in the near-bottom planktonic community with respect to that of the water column. The expected effect of all but one of the reasons mentioned (see Introduction) would have produced an increase in the abundance of the various groups in the near-bottom planktonic community. In this sense, the constant contribution of detrital and dissolved organic material from the benthic organisms such as algae and invertebrates, and the increase in turbulence due to the bottom effect, should have enhanced production of the near-bottom planktonic communities. Also, the fact that, during episodes of high primary production, the main fraction of this production is directly transferred to the benthos (Kiørboe, 1993) should have enhanced production of the near-bottom planktonic communities. However, the main feature that distinguished the dynamics of the planktonic communities in the near-bottom site studied from those of the water column was the relatively low abundance of the different groups. This general low abundance of the different planktonic groups, together with (i) the high abundance of suspension feeders in the benthic communities of Medes Islands (suspension feeders account for >50% of the total benthic community; Gili and Ros, 1985), (ii) the recently estimated high rates of prey capture of certain suspension feeder groups (Coma *et al*., 1995; Ribes *et al*., 1998, 1999, in press), (iii) the high productivity of some benthic groups (Coma *et al*., 1998) and (iv) the release of larvae by the benthos which by predation modify the abundance and composition of planktonic communities (Graf, 1992), points out the interactions near-bottom planktonic and benthic communities might be exerting on one another, an important control on their dynamics. Benthic feeding activity might be exerting an important role in control of the dynamics of the near-bottom planktonic communities. On the other hand, the planktonic groups' size distribution is directly affecting the benthos. Because size is one of the major determinants of prey capture in suspension feeders, the pattern of variation in the size composition of the live carbon throughout the year may have important implications for food availability to the different suspension feeder groups.

Mean annual POC values (387 μg C l^{-1}) for the near-bottom planktonic community studied were within the range of POC documented for coastal waters (200–2000 μg C l^{-1}; Mann, 1982), but close to the lowest values. However, POC abundances in winter and spring were within the range of values documented for near-bottom coastal systems of high productivity, such as kelp beds (533–762 μg C l^{-1} in summer and winter, respectively; Fielding and Davis, 1989). The annual

mean DOC abundance observed in this study (2560 μg C l^{-1}) was slightly higher than general values documented for coastal waters (i.e. 1000–2000 μg C l^{-1}; Fredericks and Sackett, 1970). The high DOC values observed during spring and summer were within the range documented for kelp beds (Delille *et al*., 1997), and within the range documented for a similar depth in Mediterranean seagrass systems (Velimirov, 1986). The seasonal variation of detrital POC was related to the run-off of the nearby Ter River, but it was also related to macroalgal production. The seasonal variation of DOC was related to the macroalgal production. Neither POC nor DOC variation were consistent with phytoplankton production peaks.

An approach to the POC composition was possible by the comparison between total POC (C:H:N analysis), which includes live carbon and dead organic carbon in detrital form, and live organic carbon (i.e. estimated from recognizable cells). All year round, organic carbon of detrital origin represented the main fraction of POC in the studied site and, in fact, mean total live carbon (24 μg C l^{-1}) was similar to values reported for oceanic waters (Mann, 1982), where the detrital organic carbon present is mainly lost by sedimentation. The relationship between total POC and live carbon showed a seasonal variation together with the C/N ratio. In this sense, during spring, total POC was ~34 times higher than live carbon with a high C/N ratio (C/N: 17); this value is consistent with the general atomic ratio of benthic marine macroalgae (C/N: 550/30; Atkinson and Smith, 1983). During summer and autumn, total POC was six times higher than live carbon with a low C/N value (C/N: 4) close to the Redfield ratio for marine plankton (C/N: 106/16; Atkinson and Smith, 1983), pointing out the relatively low detrital contribution of benthic macroalgae to POC during these periods in comparison to the spring period.

As for other temperate seas, sublittoral phytobenthic communities from the Western Mediterranean show seasonal fluctuations in biomass, diversity and production (Ballesteros, 1991). Sublittoral phytobenthic communities show biomass and production maxima in spring–summer (Ballesteros, 1991). In these communities, the input of organic matter from benthic macroalgal production is higher than that from phytoplankton production (Ballesteros, 1989). Then, DOC peaks observed during spring and summer in the near-bottom community may come from DOC released by macrophytobenthos which explain an important fraction of the large DOC variation along the year (almost 10-fold). DOC may also originate from microbial degradation of particulate organic matter, and accumulate due to limiting nutrients (P has been documented to be limiting bacterial and phytoplankton production in the Northwestern Mediterranean in summer; Thingstad *et al*., 1997, 1998). The POC spring peak may come from run-off, but also from the debris and decomposition of the sublittoral algae, mainly erect algae.

The differences in the DOC and POC variation along the year appear to be related to their sources, but also to the processes that allow their maintenance in the water column. The low POC values in summer could be due to the rapid sedimentation of the detrital material due to the low water mixing during this period (reflected by the stratification of the water column; Figure 4a). In the same sense, the increase in POC in winter appears to come from the run-off and its

maintenance in the water column may be favoured by the hydrodynamic conditions of the winter period (i.e. mixing of the water column). Then, the differences in the sources as well as the differential effect of sedimentation on POC and DOC may be among the main factors that influence and differentiate the variation in abundance of POC and DOC throughout the year. A similar pattern of DOC variation over the year has been documented in a water column study of the Northwestern Mediterranean in which DOC accumulates in the upper layer during summer and autumn until stratification is broken down by winter mixing (Copin-Montégut and Avril, 1993).

As a conclusion, we point out that the detrital fraction was the dominant component of the total organic carbon in the near-bottom planktonic community throughout the year. Microbial communities (autotrophic and heterotrophic bacteria) contributed a low percentage to the total organic carbon. This could point out the coastal origin (run-off and benthic macroalgae) of the high concentration of DOC and POC, which represent more substrate for microorganism activity, and is one of the features that differentiate near-bottom planktonic communities from those on the water column. However, the high DOC and POC values contrast with the relatively low abundance of the different live carbon groups. The low abundance and biomass of microbial organisms in the near-bottom community could be explained by the activity of benthic organisms, probably by the predation of suspension feeders. At the same time, in shallow waters, because near-bottom layers are mixed by waves and currents, the effects of benthic organisms could be extended to the water column by hydrographic processes. Then, a general approach of the results raised by this work could be to hypothesize that the structure and dynamics of the near-bottom planktonic communities might follow a pattern different from that exhibited by the water column planktonic communities. This pattern would be characterized by the low abundance and high temporal heterogeneity of the different planktonic communities in which the activity of benthic organisms may play an important role by seasonally releasing or removing organic components.

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References

Agawin,N.S.R., Duarte,C.M. and Agustí,S. (1998) Growth and abundance of *Synechococcus* sp. in a Mediterranean Bay: seasonality and relationship with temperature. *Mar. Ecol. Prog. Ser.*, **170**, 45–53.

Atkinson,M.J. and Smith,S.V. (1983) C:N:P ratios of benthic marine plants. *Limnol. Oceanogr.*, **28,** 568–574.

Azam,F., Fenchel,T., Field,J.G., Gray,J.S., Meyer-Reil,L.A. and Thingstad,F. (1983) The ecological role of water-column microbes in the sea. *Mar. Ecol. Prog. Ser.*, **10**, 257–263.

Ballesteros,E. (1989) Production of seaweeds in North-western Mediterranean marine communities: its relation with environmental factors. *Sci. Mar.*, **53**, 357–364.

Ballesteros,E. (1991) Structure and dynamics of North-Western Mediterranean phytobenthic communities: a conceptual model. In Ros,J. and Prat,N. (eds), *Homage to Ramon Margalef; or, Why There is Such Pleasure in Studying Nature. Oecol. Aquat.*, **10**, 223–242.

Björnsen,P.K. (1986) Automatic determination of bacterioplankton biomass by image analysis. *Appl. Environ. Microbiol.*, **51**, 1199–1204.

Buck,K.R., Chavez,F.P. and Campbell,L. (1996) Basin-wide distributions of living carbon components and the inverted trophic pyramid of the central gyre of the North Atlantic Ocean, summer 1993. *Aquat. Microb. Ecol.*, **10**, 283–298.

Burkill,P.H., Edwards,E.S., John,A.W.G. and Sleigh,M.A. (1993) Microzooplankton and their herbivorous activity in the northeastern Atlantic Ocean. *Deep-Sea Res. II*, **40**, 479–493.

Campbell,L., Nolla,H.A. and Vaulot,D. (1994) The importance of *Prochlorococcus* to community structure in the central North Pacific Ocean. *Limnol. Oceanogr.*, **39**, 954–961.

Chisholm,S.W., Olson,R.J., Zettler,E.R., Goericke,R., Waterbury,J.B. and Welschmeyer,N.A. (1988) A novel free-living prochlorophyte occurs at high cell abundance in the oceanic euphotic zone. *Nature*, **334**, 340–343.

Cloern,J.E. (1982) Does the benthos control phytoplankton biomass in south San Francisco bay? *Mar. Ecol. Prog. Ser.*, **9**, 191–202.

Coma,R., Gili,J.M. and Zabala,M. (1995) Trophic ecology of a benthic marine hydroid *Campanularia everta*. *Mar. Ecol. Prog. Ser.*, **119**, 211–220.

Coma,R., Ribes,M., Gili,J.M. and Zabala,M. (1998) An energetic approach to the study of life-history traits of two modular colonial benthic invertebrates. *Mar. Ecol. Prog. Ser.*, **162**, 89–103.

Copin-Montégut,G. and Avril,B. (1993) Vertical distribution and temporal variation of dissolved organic carbon in the North-Western Mediterranean Sea. *Deep-Sea Res. I*, **40**, 1963–1972.

Delille,D., Marty,G., Cansemi-Soullard,M. and Frankignoulle,M. (1997) Influence of subantarctic *Macrocystis* bed metabolism in diel changes of marine bacterioplankton and CO_2 fluxes. *J. Plankton Res.*, **19**, 1251–1264.

Denman,K.L. and Powell,T.M. (1984) Effects of physical processes on planktonic ecosystems in the coastal ocean. *Oceanogr. Mar. Biol. Annu. Rev.*, **22**, 125–168.

Edler,L. (ed.) (1979) Recommendations for marine biological studies in the Baltic sea. Phytoplankton and chlorophyl. *Baltic Mar. Biol.*, **5**, 5–38.

Estrada,M., Vives,F. and Alcaraz,M. (1985) Life and productivity of the open sea. In Margalef,R. (ed.), *Western Mediterranean*. Pergamon Press, Oxford, pp. 148–197.

Ferrier-Pagès,C. and 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.

Fielding,P.J. and Davis,C.L. (1989) Carbon and nitrogen resources available to kelp bed filter feeders in an upwelling environment. *Mar. Ecol. Prog. Ser.*, **55**, 181–189.

Fredericks,A.D. and Sackett,W.M. (1970) Organic carbon in the Gulf of Mexico. *J. Geophys. Res.*, **75**, 2199–2206.

Fry,J.C. (1988) Determination of biomass. In Austin,B. (ed.), *Methods in Aquatic Bacteriology*. Wiley and Sons, New York, pp. 27–72.

Garrabou,J. (1997) Structure and dynamics of north-western Mediterranean rocky benthic communities along a depth gradient: a Geographical Information System (GIS) approach. PhD Thesis, University of Barcelona, Barcelona, Spain.

Gili,J.M. and Ros,J. (1985) Study and cartography of the benthic communities of Medes Islands (NE Spain). *P.S.Z.N.I.: Mar. Ecol.*, **6**, 219–238.

Graf,G. (1992) Benthic-pelagic coupling: A benthic view. *Oceanogr. Mar. Biol. Annu. Rev.*, **30**, 149–190.

Graf,G. and Rosenberg,R. (1997) Bioresuspenion and biodeposition: a review. *J. Mar. Syst.*, **11**, 269–278.

Holloway,G. (1992) Representing topographic stress for large-scale ocean models. *J. Phys. Oceanogr.*, **22**, 1033–1046.
Kana,T. and Glibert,P.M. (1987) Effect of irradiances up to 2000 μE m^{-2} s^{-2} on marine *Synechococcus* WH 7803-I. Growth, pigmentation and cell composition. *Deep-Sea Res.*, **34**, 479–516.
Kiørboe,T. (1993) Turbulence, phytoplankton cell size and the structure of pelagic food webs. *Adv. Mar. Biol.*, **29**, 1–72.
Longhurst,A.R. (1985) Relationship between diversity and vertical structure of upper ocean. *Deep-Sea Res.*, **32**, 1535–1570.
Mackas,D.L., Sefton,H., Miller,C.B. and Raich,A. (1993) Vertical habitat partitioning by large calanoid copepods in the oceanic subartic Pacific during spring. *Prog. Oceanogr.*, **32**, 259–294.
Mann,K.H. (1982) *Ecology of Coastal Waters. A System Approach*. Blackwell Scientific, London.
Margalef,R. and Castellví,J. (1967) Fitoplancton y producción primaria de la costa catalana, de julio de 1966 a julio de 1967. *Invest. Pesq.*, **31**, 491–502.
Marrasé,C., Lim,E.A. and Caron,D.A. (1992) Seasonal and daily changes in bacterivory in a coastal plankton community. *Mar. Ecol. Prog. Ser.*, **82**, 281–289.
Massana,R., Gasol,J.M., Björnsen,P.K., Blackburn,N., Hagström,Å., Hietanen,S., Hygum,J., Kuparinen,B.H. and Pedrós-Alió,C. (1997) Measurement of bacterial size via image analysis of epifluorescence preparations: description of an inexpensive system and solutions to some of the most common problems. *Sci. Mar.*, **61**, 397–407.
Monger,B.M. and Landry,M.R. (1993) Flow cytometric analysis of marine bacteria with Hoechst 33342. *Appl. Environ. Microbiol.*, **59**, 905–911.
Montagnes,D.J., Berges,S.J.A., Harrison,P.J. and Taylor,F.J.R. (1994) Estimating carbon, nitrogen, protein and chlorophyll a from volume in marine phytoplankton. *Limnol. Oceanogr.*, **39**, 1044–1060.
Moriarty,D.I.W. and Pollard,P.C. (1982) Diel variation of bacterial productivity in seagrass (*Zostera capricorni*) beds measured by rate of thymidine incorporation into DNA. *Mar. Biol.*, **72**, 165–173.
Mura,M.P., Agustí,S., Cebrián,J. and Satta,M.P. (1996) Seasonal variability of phytoplankton biomass and community composition in Blanes Bay (1992–1994). *Publ. Espec. Inst. Esp. Oceanogr.*, **22**, 23–29.
Olson,R.J., Chisholm,S.W., Zettler,E.R., Altabet,M.A. and Dusenberry,J.A. (1990) Spatial and temporal distributions of prochlorophyte picoplankton in the North Atlantic Ocean. *Deep-Sea Res.*, **6**, 1033–1051.
Owen,R.W. (1989) Microscale and finescale variations of small plankton in coastal and pelagic environments. *J. Mar. Res.*, **47**, 197–240.
Pascual,J. (1996) Projecte de determinació de la circulació de les aigües de la reserva marina de les Illes Medes. Memòria de l'any 1996. Departament d'Ecologia. Universitat de Barcelona. Departament d'Agricultura Ramaderia i Pesca, Generalitat de Catalunya.
Pile,A.J., Patterson,M.R. and Witman,J.D. (1996) *In situ* grazing on plankton <10 μm by the boreal sponge *Mycale lingua*. *Mar. Ecol. Prog. Ser.*, **141**, 95–102.
Platt,T., Subba Rao,D.V. and Irwin,B. (1983) Photosynthesis of picoplankton in the oligotrophic ocean. *Nature*, **301**, 702–704.
Porter,K.G. and Feig,Y.S. (1980) The use of DAPI for identifying and counting aquatic microflora. *Limnol. Oceanogr.*, **25**, 943–948.
Putt,M. and Stoecker,D.K. (1989) An experimentally determined carbon volume ratio for marine 'oligotrichous' ciliates from estuarine and coastal waters. *Limnol. Oceanogr.*, **34**, 1097–1103.
Reiswig,H.M. (1990) *In situ* feeding in two shallow-water hexactinellid sponges. In Rützler,K. (ed.), *New Perspectives in Sponge Biology*. Smithsonian Institution Press, Washington, DC, pp. 504–510.
Ribes,M., Coma,R. and Gili,J.M. (1998) Seasonal variation of *in situ* feeding rates by the temperate ascidian *Halocynthia papillosa*. *Mar. Ecol. Prog. Ser.*, **175**, 201–213.
Ribes,M., Coma,R. and Gili,J.M. (1999) Natural diet and grazing rate of the temperate sponge *Dysidea avara* (Demospongiae, Dendroceratida) throughout an annual cycle. *Mar. Ecol. Prog. Ser.*, **176**, 179–190.
Ribes,M., Coma,R. and Gili,J.M. Heterogeneous feeding in benthic suspension feeders: the natural diet and grazing rate of the temperate gorgonian *Paramuricea clavata* (Cnidaria: Octocorallia) over a year cycle. *Mar. Ecol. Prog. Ser.*, in press.
Riedl,R. (1971) Water movement. Animals. *Mar. Ecol.*, **1**, 1123–1149.
Sebens,K.E. and Koehl,M.A.R. (1984) The feeding ecology of two subtidal rock wall zooplanktivores, *Alcyonium siderium* and *Metridium senile*. *Mar. Biol.*, **81**, 255–271.
Sherr,E.B. and Sherr,B.F. (1991) Planktonic microbes: Tiny cells at the base of the ocean's food webs. *Trends Ecol. Evol.*, **6**, 50–54.

Simon,M. and Azam,F. (1989) Protein content and protein synthesis rates of planktonic marine bacteria. *Mar. Ecol. Prog. Ser*., **51**, 201–213.
Sokal,R.R. and Rohlf,F.J. (1995) *Biometry. The Principles and Practice of Statistics in Biological Research*, 3rd edn. Freeman, New York.
Sorokin,Y.I. (1994) *Coral Reef Ecology. Ecological Studies*. Springer-Verlag, Berlin.
Stockner,J.G. and Antia,N.J. (1986) Algal picoplankton from marine and freshwater ecosystems: a multidisciplinary perspective. *Can. J. Fish. Aquat. Sci*., **43**, 2472–2503.
Stuart,V. and Klumpp,D.W. (1984) Evidence for food-resource partitioning by kelp-bed filter feeders. *Mar. Ecol. Prog. Ser*., **16**, 27–37.
Thingstad,T.F., Hagström,Å. and Rassoulzadegan,F. (1997) Accumulation of degradable DOC in surface waters: Is it caused by a malfunctioning microbial loop? *Limnol. Oceanogr.*, **42**, 398–404.
Thingstad,T.F., Zweifel,U.L. and Rassoulzadegan,F. (1998) P limitation of heterotrophic bacteria and phytoplankton in the northwest Mediterranean. *Limnol. Oceanogr.*, **43**, 88–94.
Van Wambeke,F., Christaki,U. and Gaudy,R. (1996) Carbon fluxes from the microbial food web to mesozooplakton. An approach in the surface layer of a pelagic area (NW Mediterranean Sea). *Oceanol. Acta*, **19**, 57–66.
Vaqué,D. (1996) Seasonal dynamics of planktonic microbial communities on the coast of the northwest Mediterranean Sea. *Publ. Espec. Inst. Esp. Oceanogr*., **22**, 39–46.
Vaqué,D., Blough,H.A. and Duarte,C.M. (1997) Dynamics of ciliate abundance, biomass and community composition in an oligotrophic coastal environment (NW Mediterranean). *Aquat. Microb. Ecol*., **12**, 71–83.
Vaulot,D., Partensky,F., Neveus,J., Mantoura,R.F.C. and Llewellyn,C. (1990) Winter presence of prochlorophytes in surface waters of the northwestern Mediterranean Sea. *Limnol. Oceanogr*., **35**, 1156–1164.
Velimirov,B. (1986) DOC dynamics in a Mediterranean seagrass system. *Mar. Ecol. Prog. Ser*., **28**, 21–41.
Velimirov,B. and Walenta-Simon,M. (1992) Seasonal changes in specific growth rates, production on biomass of a bacterial community in the water column above a Mediterranean seagrass system. *Mar. Ecol. Prog. Ser*., **80**, 237–248.
Velimirov,B. and Walenta-Simon,M. (1993) Bacterial growth rates and productivity within a seagrass system: seasonal varitions in a *Posidonia oceanica* bed. *Mar. Ecol. Prog. Ser*., **96**, 101–107.
Verity,P.G., Robertson,C.Y., Tronzo,C.R., Andrews,M.G., Nelson,J.R. and Sieracki,M.E. (1992) Relationships between cell volume and the carbon and nitrogen content of marine photosynthetic nanoplankton. *Limnol. Oceanogr*., **37**, 1434–1446.
Wainright,S.C. (1990) Sediment-to-water fluxes of particulate material and microbes by resuspension and their contribution to the planktonic food web. *Mar. Ecol. Prog. Ser*., **62**, 271–281.

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