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Discussions

Autotrophic and heterotrophic metabolism of microbial planktonic communities in an oligotrophic coastal marine ecosystem: seasonal dynamics and episodic events

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Abstract

A 18 month study was performed in the Bay of Villefranche to assess the episodic and seasonal variation of autotrophic and heterotrophic ecosystem processes. A typical spring bloom was encountered, where maximum of gross primary production (GPP) was followed by maxima of bacterial respiration (BR) and production (BP). The trophic balance (heterotrophy vs. autotrophy) of the system did not exhibit any seasonal trend although a strong intra-annual variability was observed. On average, the community tended to be net heterotrophic with a GPP threshold for a balanced metabolism of 2.8 µmol O_2 l^{-1} d^{-1}. Extended forest fires in summer 2003 and a local episodic upwelling in July 2003 likely supplied orthophosphate and nitrate into the system. These events were associated with an enhanced bacterioplankton production (up to 2.4-fold), respiration (up to 4.5-fold) and growth efficiency (up to 2.9-fold) but had no effect on GPP. A Sahara dust wet deposition event in February 2004 stimulated bacterial abundance, production and growth efficiency but not GPP. Our study suggests that short-term disturbances such as wind-driven upwelling, forest fires and Sahara dust depositions can have a significant but previously not sufficiently considered influence on phytoplankton- and bacterioplankton-mediated ecosystem functions and can modify or even mask the seasonal dynamics. The study also indicates that atmospheric deposition of nutrients and particles not only impacts phytoplankton but also bacterioplankton and could, at times, also shift systems stronger towards net heterotrophy.

1 Introduction

Bacteria take up a significant fraction of dissolved organic carbon (DOC) produced by phytoplankton and remineralize up to 50% of primary production (Azam et al., 1983). Radiolabeled substrates have been used to assess bacterial carbon production and oxygen consumption to measure respiration (Fuhrman and Azam, 1982; Kirchman et al., 1985). Measurement of bacterial respiration (BR) is difficult but pivotal, since it is needed to estimate growth efficiency, a fundamental attribute largely determining the ecological and biogeochemical role of bacteria in aquatic microbial food webs (Del Giorgio and Cole, 1998). Over the last years, a renewed interest has been put into determining BR, in order to better understand the role of bacterioplankton in the carbon fluxes (Del Giorgio and Williams, 2005).

Measurements of gross primary production (GPP) and community respiration (R) have been used to assess the metabolic balance of marine ecosystems. Particularly in the late 1990ies a debate took place on the predominance of heterotrophy in the most oligotrophic regions and the biogeochemical consequences of the metabolic balance in the ocean (Del Giorgio et al., 1997; Duarte and Agusti, 1998; Williams 1998). This idea seemed counter intuitive because the isolated location of those areas make them the least likely candidates for external organic inputs (Williams and Bowers, 1999). However, a series of subsequent studies have lent support to the initially surprising reports of net heterotrophy in low latitude oligotrophic areas (Serret et al., 2001; Robinson et al., 2002). Nevertheless, much of the data published to date have been derived from oceanographic transects and the number of coastal studies performed over longer time scales remains scarce (Smith and Kemp, 2001; Duarte et al., 2004; Williams et al., 2004; Gazeau et al., 2005; Regaudie-de-Gioux et al., 2009). Bacterial production and respiration play a crucial role in these processes.

In temperate systems, a spring phytoplankton bloom is typically followed by an increase in bacterial production as a consequence of increased dissolved primary production. Often, a phytoplankton bloom also occurs in fall, however, this bloom is typically less pronounced than in spring but also followed by an increase in bacterial production. The spring bloom is typically accompanied by an accumulation of DOC. This has been attributed to accumulation of refractory organic material (Legendre and Le Fèvre, 1995). However, it has also been explained by a "malfunctioning" of the microbial loop in the sense that the bacterial growth rate is kept low by competition between phytoplankton and bacteria for limiting nutrients and by control of bacterial biomass by predators (Thingstad et al., 1997). These two explanations are not mutually exclusive. Recent studies also suggest that atmospheric deposition could influence bacteria-mediated carbon cycling stronger than previously thought. For example, carbon and P input by dry deposition of Sahara dust was shown to stimulate carbon mineralization in the NW Mediterranean Sea (Pulido-Villena et al., 2008; Lekunberri et al., 2010).

To increase our knowledge on ecosystem functions, we assessed ecosystem processes such as bacterial production, bacterial and community respiration, and primary production during a seasonal cycle in the NW Mediterranean Sea. As short-term events can be considered as disturbances potentially affecting ecosystem functions, we investigated shorter time scales such as phytoplankton blooms, an upwelling event, rainfall, forest fires and Sahara dust deposition.

2 Methods

2.1 Study site and sample collection

The study was conducted from November 2002 to April 2004 in the Bay of Villefranche located in the northwestern Mediterranean Sea. This study sites is considered as an oligotrophic coastal system (Sheldon et al., 1992). Sampling was performed before sunrise at a permanent coastal station (Point B: 43°51′10″ N, 07°19′00″ E; bottom depth: >90 m) at the entrance of the Bay. Samples were collected in 0.5, 10, 20 and 30 m depth with a 20 l Niskin bottle every month. Additional sampling was carried out during phytoplankton blooms or after specific events such as heavy rain, forest fires or Sahara dust deposition. For these additional samples GPP, NCP and CR (see below) were not measured.

Temperature, salinity and conductivity were obtained from the weekly sampling program (SOMLIT) and also using a Seabird SBE25 CTD at the time of sampling. Daily data on wind direction, wind speed and rain frequencies were obtained from the meteorological station at Cap-Ferrat, close to Point B (distance, ca. 1 km). Daily data on irradiance were obtained from the airport Nice (distance from Point B, ca. 5 km). Data on forest fires were obtained for the Var Department, which stretches to the West from the study site, i.e. in the main wind direction (Prométhée, French Mediterranean forest fire data base: http://www.promethee.com/prom/home.do).

2.2 Nutrients, dissolved organic carbon, particles and Chl *a*

Total organic carbon (TOC) rather than dissolved organic carbon (DOC) was measured in order to avoid contamination during filtration. However, due to the low particle concentration, it is referred to in the following as DOC. DOC was determined by high temperature oxidation with a Shimadzu 5000A TOC Analyzer (Benner and Strom, 1993). Concentrations of chlorophyll *a* (Chl *a*) were measured fluorometrically, while nitrate (NO_3) and soluble reactive phosphorus (SRP) concentrations were determined using an Alliance-Instrument EV2 Autoanalyzer following standard methods (Lorenzen, 1966; Strickland and Parsons, 1972).

The concentration of particles in the water column was determined using a Coulter Counter Multisizer II within 2 h of sampling to avoid aggregation and denaturation of organic matter (Sheldon and Parsons, 1967). Counts were performed on triplicate sub-samples, ensuring that at least 10^4 particles were counted.

2.3 Bacterial abundance

Samples (2 ml) were fixed in glutaraldehyde (0.5% final concentration), kept in the dark for 30 min at 4 °C, flash frozen in liquid nitrogen and stored at −80 °C pending analysis. The abundance of heterotrophic bacteria was determined by flow cytometry (Becton Dickinson, FACSCalibur) upon staining with SYBRGreen I (Molecular Probes) as described previously (Gasol and Del Giorgio, 2000). Fluorescent 1 µm latex beads (10^5 beads ml^{-1}) were systematically added to the bacterial samples as an internal quality standard (Polyscience Inc., Europe). Although archaea are detectable by PCR in the Bay of Villefranche, their abundance is below the detection limit using single-cell analysis (unpublished data). Therefore, in accordance with other coastal studies

(Zhang et al., 2007) the community is considered bacterial in the following.

2.4 Bacterial and planktonic community metabolism

Water samples for community metabolism were carefully distributed into calibrated 60 ml borosilicate bottles. Five replicates were fixed immediately and used to determine the initial oxygen concentration at T0 and 10 others were used to estimate the rates of dark community respiration (R, "dark" bottles) and net production (NCP, "light" bottles), respectively. At sunrise, the bottles were suspended in situ at the depths of sampling using a rope tethered to a permanent buoy. Incubations lasted 24 h. Additional water was transferred directly from the Niskin bottle into 10 acid-washed carboys and transported immediately to the laboratory (<15 min). Subsamples were taken for measurements of BR and rates were determined in the laboratory, following the same procedures as for the estimation of R, after prefiltration of the water through a 0.8 µm pore size polycarbonate filter (diameter 142 mm, Millipore). Incubations were carried out in the dark at in situ temperature (±1 °C) for 24 and 48 h. Dissolved oxygen was fixed immediately at the beginning and end of the incubation and measured by the Winkler technique using a potentiometric end-point detector (Anderson et al., 1992) with an Orion redox electrode (9778SC) and a custom built titrator. Reagents and standardizations were otherwise similar to those described by Knap et al. (1996). Community and bacterial respiration (CR and BR) as well as net community production (NCP) were calculated from changes in oxygen concentration after incubation in the "dark" and "light" bottles, respectively, relative to their concentration at T0. Respiration rates ($[O_2]$T0 – $[O_2]$dark bottle), NCP ($[O_2]$light bottle – $[O_2]$T0), and gross primary production (GPP=NCP+R) were expressed in µmol $O_2\ l^{-1}\ d^{-1}$. Changes in the trophic conditions were characterized by the GPP/R ratio, where GPP/$R>1$ represents net autotrophy, GPP/$R=1$ represents metabolic balance and GPP/$R<1$ represents net heterotrophy.

BP was measured using the ^{3}H-leucine incorporation method described by Smith and Azam (1992). Four replicates from each depth were spiked with 12 nM of ^{3}H-leucine and either 0, 40 or 80 nM of "cold" leucine, in order to check for saturation conditions, and incubated in the dark at in situ temperature for 1 h. We used the conversion factor of 1.545 kg C mol Leu^{-1} (Kirchman and Ducklow, 1993) and assumed a carbon content of 20 fg C cell^{-1} (Lee and Fuhrman, 1987). Bacterial growth efficiency was calculated as BGE=BP/(BP+BR), assuming a respiratory quotient of 1. Bacterial carbon demand (BCD) was calculated as BP+BR.

2.5 Statistics

Spearman correlation coefficients (r) were calculated to test the relationship between parameters. GPP and R relationships were analysed using the reduced major axis (r.m.a.) regression model. The results of statistical analyses were considered significant at p values$<$0.05.

3 Results

3.1 Environmental conditions

The increase of atmospheric irradiance with time was faster in spring 2003 than in spring 2004 (Fig. 1a). The water column was well mixed from autumn to early spring. In 2003, stratification started in April, was well established in May 2003 (thermocline at 20 m) and broke down in the following October (Fig. 2a). In 2004, stratification did not occur before the end of the sampling period (on 6 April).

Several episodic events were observed during the study period. A local episodic upwelling event occurred in the first week of July as indicated by a change in wind direction from westerly to easterly winds with daily maximum wind speed of 11–16 m s^{-1} between 2 and 4 July (Fig. 1b). Wind speeds above 10 m s^{-1} from SW or W winds can cause a change in the water circulation in the Bay and cause upwelling and intrusion of colder and nutrient-rich deep water into the Bay (Nival, 1976). Water temperature dropped from 26 °C to 18 °C (Fig. 2a).

The highest monthly rain frequencies were observed in spring (April–May 2003, ca. 11 days corresponding to 105 mm) and autumn (October 2003, 11 days and 83 mm; December 2003, 12 days and 114 mm). Daily precipitation is shown in Fig. 1c. In February 2004 a strong Sahara dust wet deposition event occurred, which was associated with a cold front and even reached central Europe (EUMETSAT data base; http://www.eumetsat.int/Home/index.htm). Rain occurred between 20 and 24 February with a daily precipitation ranging from 2.0 to 15.8 mm; total precipitation during these four days was 29 mm.

The summer period of 2003 was characterized by a high frequency of forest fires in the west of the sampling area (Fig. 3). The main wind direction during the forest fire period was westerly and deposition of fly ashes into the Bay of Villefranche could be observed on one occasion. The number of forest fires was 25 to 50% higher in 2003 than in 2002 or 2004 (Fig. 3). Moreover, the forest fires destroyed 20 to 100 times more forest area and large fires (>1km^2 destruction) were ≥7 times more frequent in 2003 than in 2002 and 2004.

3.2 Nutrients, DOC and concentration of particles

Nitrate and SRP concentrations ranged from undetectable levels to 3.75 µM and 0.14 µM, respectively (Fig. 2b, c). The highest values occurred in winter and dropped during the spring phytoplankton bloom. However, in summer, SRP concentrations were relatively high in the entire water column following a local upwelling event and the forest fire period; the maximum value (0.14 µM) was measured in July in surface water. Time and depth integrated SRP and nitrate values were ca. 1.4–4 fold higher in July–August (0.052 and 0.72 µM, respectively) than in June (≤0.001 and 0.16 µM, respectively) and September (0.025 and 0.26 µM, respectively) (Fig. 4).

DOC concentrations ranged from 56 to 108 µM (Fig. 2d). Following the low concentrations detected during winter 2002–2003, DOC increased from the spring bloom until the end of June when the highest value was measured in surface water. Afterwards, from summer 2003 to February 2004 DOC decreased throughout the water column and increased again during the phytoplankton bloom 2004 (for bloom conditions see below).

Particle concentrations showed the lowest values in autumn (811 particles ml^{-1}) at 20 and 30 m depth (data not shown). The highest values were measured throughout the water column during the phytoplankton bloom of 2003 (4090 particles ml^{-1}) and in early summer and February 2004 at 20 m. The specific peak at 20 m depth in February occurred after the Sahara dust wet deposition event and particle concentration integrated over depth was almost 2-fold higher than in January (Fig. 5a).

3.3 Phytoplankton and metabolic parameters

Chl *a* concentrations ranged from 0.04 to 0.80 $\mu g\,l^{-1}$ (Fig. 6a). The maximum concentration was measured between 10 m and 20 m depth in early spring 2003 marking the phytoplankton bloom and a second peak was observed in fall, with values up to 0.36 $\mu g\,l^{-1}$ in the surface. In 2004, Chl *a* concentrations were as high as 0.59 $\mu g\,l^{-1}$ in March. The spring bloom started with diatoms and was followed by autotrophic flagellates; after the proper bloom a period occurred with maximum abundances of *Synechococcus* (data not shown).

GPP values ranged from <0.01 to 5.85 $\mu mol\,O_2\,l^{-1}\,d^{-1}$ and was up to 3-fold higher in surface water than at the other depths, particularly in March and June 2003 when the highest rates were measured (Fig. 6b). The lowest GPP occurred in January and February 2004 at 30 m (<0.02 $\mu mol\,O_2\,l^{-1}\,d^{-1}$) but values were typically also low in summer and in autumn. Although slightly elevated values were observed in July/August, the time and depth integrated value (1.2 $\mu mol\,O_2\,l^{-1}\,d^{-1}$) was similar to the September value (0.96 $\mu mol\,O_2\,l^{-1}\,d^{-1}$) but clearly lower than in June (2.0 $\mu mol\,O_2\,l^{-1}\,d^{-1}$).

NCP ranged from −5.74 to 7.58 $\mu mol\,O_2\,l^{-1}\,d^{-1}$ and followed the same temporal trends in all depths with a slightly higher variability in the surface (Fig. 6c). Positive values were measured in the winter 2002 and early spring 2003 but rates were close to zero or negative throughout the summer and the rest of the study period. R ranged from 0.07 to 7.88 µmol O_2 l^{-1} d^{-1}, and was generally lower at the deeper stations than near the surface, particularly from June to October. The highest R occurred in early spring 2004 when it exceeded up to 7 times that measured during the same period in 2003 (Fig. 6d). The integrated R values in July and August (1.25 µmol O_2 l^{-1} d^{-1}) was lower than in in June (2.45 µmol O_2 l^{-1} d^{-1}) but similar to the September values (1.14 µmol O_2 l^{-1} d^{-1}).

Depth-integrated GPP and R ranged from 10.1 to 182.6 and from 28.7 to 180.9 µmol O_2 m^2 d^{-1}, respectively (Fig. 7a). Integrated GPP over the upper 30 m was up to ca. 3-fold higher than integrated R during winter 2002 and spring 2003, thus resulting in a net autotrophic balance, whereas from May 2003 to April 2004, R was about twice higher than GPP. Thus, metabolic balance in Villefranche Bay was net heterotrophic most of the studied period but a pronounced temporal variability was observed. The GPP:R volumetric ratio averaged from October 2002 to September 2003 was 1.2 and was about of 0.6 averaged from May 2003 to April 2004 (Fig. 7b). There was a positive relation between the GPP:R ratio and GPP (GRR:R=0.90 GPP$^{0.93}$; R_2=0.56; $P<0.0001$) as illustrated by the reduced major axis (r.m.a) regression model which explained 56% of the variance in the ratio. The threshold GPP to reach a balanced metabolism in Villefranche Bay was estimated at 2.8 µmol O_2 l^{-1} d^{-1} hence, exceeding by ca. 2.4 times the average measured GPP.

3.4 Bacterial parameters

Bacterial abundance ranged from 4.4×10^5 ml^{-1} to 12×10^5 ml^{-1} across the sampling period. Overall, the lowest abundance occurred in winter, whereas highest values were measured during the spring phytoplankton bloom, where small differences were observed between depths (coefficient of variation: C.V.<5%; Fig. 8a). In February 2004, sampling was performed 3 days after a strong Sahara dust deposition event associated with heavy rains. Bacterial abundance showed a temporary peak and was on average 57% higher than in the previous months (Fig. 5b).

BP ranged from 0.004 to 0.43 µmol C l^{-1} d^{-1}. Low rates were measured in autumn and winter, i.e. during the the downwelling and forest fire period, whereas the highest activity occurred after the spring phytoplankton bloom and in early summer (Fig. 8b). Additionally, BP peaked in May (following the *Synechococcus* bloom) and July 2003 (following a local upwelling). In July–August, the depth-integrated value was ca. 60% higher than in June and 2.4 fold higher than in September (Fig. 4). On 25 February, Sahara dust had reached 30 m as indicated by the particle profile. At this depth, the BP value was 2.1 to 2.3 fold higher than in shallower water (Fig. 5d). The depth-integrated value of BP at this sampling date was 2.9 fold higher than at 20 January 2004 and 2.7 fold higher than on 19 February 2003. Across the study period, BP represented between ca. 1% and 70% of GPP, and reached the highest values during the spring blooms of 2003 (up to 37%) and 2004 (up to 70%). Specific BP (BP $cell^{-1}$) varied in the same way as BP (data not shown).

BR ranged from 0.03 to 3.06 µmol O_2 l^{-1} d^{-1} and was lower than 0.047 µmol O_2 l^{-1} d^{-1} between 10 and 30 m during winter 2002. It increased starting from the spring 2003 phytoplankton bloom (Fig. 8c). The highest values occurred in association with a local upwelling event and the forest fire period. The June and July–August values were similar but 3.8 to 4.5 fold higher than in September. BR was low at all depths in autumn but increased again in winter 2003 when it reached the highest rates between 10 and 20 m. No consistent effects were found following the Sahara dust deposition event.

BGE ranged from 0.005 to 0.64, was high during the phytoplankton bloom and peaked in May at all depths (0.45 to 0.50; Fig. 8d). In July–August BGE was 2.9 fold higher than in June and 1.8 fold higher than in September (Fig. 4). After the Sahara dust event, BGE ranged from 0.02–0.24 (average: 0.10) across the water column with the highest value in 30 m, whereas before the event, BGE ranged from 0.004 to 0.02 (Fig. 5d). BCD ranged from 0.04 to 3.21 µmol C l^{-1} d^{-1}. Its distribution over time and depth is similar to that of BR (data not shown). BCD was higher at the beginning of the summer, and low in autumn and winter (data not shown). The strongest changes in BGE and in BCD occurred from March to early June 2003.

3.5 Co-variation between parameters

Many significant co-variations between parameters were found. In Table 1, only those co-variations were considered with correlation coefficients larger than 0.5 (which were all statistically significant). For example, BR decreased and BP increased with BGE. Positive correlations were found among Chl *a* concentrations, particle concentration and bacterial abundance. A positive correlation was also found between phosphate and nitrate. DOC increased with increasing temperature, specific BP increased with increasing BP and GGP increased with increasing CR.

4 Discussion

4.1 Evaluation of methods

It is well known that the used approaches to assess GPP, CR, BR and BR have inherent problems in the sense of measuring rates precisely. Therefore, the values of data such as GPP:R, BCD and BGE presented in this (and other) studies should be considered with caution. However, less problems should be expected, when data are used in a comparative way as in this study. In addition, GPP estimations based on the O_2 dark-light technique were not significantly different from ^{18}O-labelling based estimates carried out in parallel in the Bay of Villefranche (Gonzalez et al., 2008).

4.2 Trophic balance and planktonic metabolism

Large differences in the metabolic balance were observed with an initial autotrophic period in winter 2002 and spring 2003 followed by a shift towards equilibrium in summer and net heterotrophy from fall 2003 until April 2004. Coinciding with the autotrophic period and before the onset of the heterotrophic period, DOC accumulation was observed particularly in surface waters, while under heterotrophic conditions, total DOC consumption exceeded production rates. An accumulation of DOC during and after a phytoplankton bloom has been shown before in the northwest Mediterranean (Thingstad et al., 1997). This switch between autotrophy and heterotrophy, which has also been observed in other coastal regions and in the NW Mediterranean (Navarro et al., 2004), did not follow a seasonal pattern. Indeed, the maximum GPP rate was higher in 2003 than in 2004, whereas R exhibited an opposite trend. During the autotrophic period GPP and R rates were temporarily uncoupled with R remaining relatively stable compared to the strong increases observed in GPP thus, suggesting that changes in primary production were mainly driving the GPP:R ratio. The trend towards heterotrophy during most of the study period is consistent with other studies of NW Mediterranean coastal sites (Duarte et al., 2004; Navarro et al., 2004; Satta et al., 1996). The GPP threshold for a balanced metabolism (GPP:R=1) calculated from the regression in Fig. 6 was 2.8 µmol O_2 l^{-1} d^{-1}. This value was higher than the value for the global ocean (1.1 µmol O_2 l^{-1} d^{-1}) but similar or lower compared to values estimated for Palma Bay (Balearic Islands, 2.8 µmol O_2^{-1} d^{-1}) over an annual cycle (Navarro et al., 2004), a NW Mediterranean coastal site (Blanes Bay, 3.95 µmol O_2 l^{-1} d^{-1}) from a 6 years study period (Duarte et al., 2004) or from several cruises into offshore waters of the Western Mediterranean Sea (3.5 µmol O_2 l^{-1} d^{-1}) (Regaudie-de-Gioux, 2009).

The overall predominance of heterotrophy indicates that the planktonic community relied on sources other than planktonic primary production to sustain the organic carbon demand. Macrophyte beds can play an important role as source of DOC to sustain excess respiration (Duarte and Cebrian, 1996; Duarte et al., 2005). Horizontal gradients between shallow-autotrophic and deep-heterotrophic areas were observed in the Bay of Palma (Gazeau et al., 2005). Although the Bay of Villefranche also harbourss extensive beds of the seagrass *Posidonia oceanica*, there is no seagrass bed at the Point B sampling station. In addition, the drop-off is much steeper than in the aforementioned bays and there is basically no shelf. Thus, while we cannot fully exclude the possibility that seagrass beds are a source of DOC sustaining the heterotrophic status of the bay, this influence should be relatively small.

The lack of seasonality and the low the GPP:R ratio in 2004 is more puzzling. It is possible that the phytoplankton bloom was short-lived. However, metabolic parameters were measured on a weekly basis in March 2004 until the end of the study period (6 April) during the onset of the spring bloom. Thus, it is unlikely that a low sampling frequency caused the observed heterotrophy. Another possible cause of the changes between the autotrophic and heterotrophic period could also be related to changes in the relative contribution of the different phytoplankton size classes to the total GPP rate (Smith and Kemp, 2001); however, no data is available to evaluate this hypothesis. The second part of the study period was also characterized by high nutrient concentrations in the the bay probably due to episodic events such as upwelling and forest fires (see below). This could have influenced the trophic balance. Nevertheless, it has to be pointed out that most studies report on a heterotrophic balance in the Mediterranean Sea (Duarte et al., 2004; Navarro et al., 2004; Regaudie-de-Gioux, 2009). Thus, our study supports the idea that the planktonic communities in the Mediterranean Sea act as CO_2 sources.

Using artificial neural networks, the GPP:R ratio could be modelled in three shallow European bays using sampling depth, DOC and temperature as input variables (Rochelle-Newall et al., 2007). However, this model did not produce satisfying data for the Bay of Villefranche (C. Winter, personal communication, 2006). One of the reasons could be the greater water depth (>90 m at Point B compared to a maximum depth of 37 m at the other study sites). In addition, the frequent episodic events encountered during the study could have masked potential relationships between parameters.

4.3 Co-variation between parameters

The co-variations between some parameters were significant, however, not very strong. Co-variations between parameters such as between GPP and BP are often more easily detected along trophic gradients than within systems during seasonal studies. A variety of mutually not exclusive factors can be the reasons for such an uncoupling between bacterioplankton and phytoplankton production. First, while BP and GPP are typically well related across systems (e.g. Baines and Pace, 1991; Cole et al., 1988), DOC consumption and BP can show a time lag during seasonal studies. This was also observed in our study (Figs. 6 and 8). Second, DOC utilization could be nutrient-limited (Thingstad et al., 1997). This hypothesis was actually developed using data from the Bay of Villefranche. Third, the use of allochthonous DOC could cause this uncoupling (Alonso-Saez et al., 2008). The significance of allochthonous carbon sources is poorly studied in the Bay of Villefranche. However, as discussed below, this uncoupling can be linked to episodic events introducing not only carbon but also nutrients into the system.

4.4 Seasonal and episodic variation of planktonic metabolism

In temperate marine ecosystems, the spring phytoplankton bloom is usually the period during which changes in biological activity are most prominent. This was also observed in the present study as bacterial production and respiration showed maxima following the GPP and Chl *a* maximum. A phytoplankton bloom was also observed in the fall together with a bacterial production maximum. Such fall phytoplankton blooms are also known from other NW Mediterranean bays (e.g. Alonso-Saez et al., 2008). In this sense, typical seasonal variability was detected. However, we also observed other potential sources of disturbance occurring on a different time scale and at less predictable frequencies such as heavy rain fall, wind driven upwelling, forest fires and a strong wet deposition event of Sahara dust. Precipitation events can introduce DOC and nutrients into the systems either directly from the atmosphere or indirectly with coastal run-off. Such events could not be clearly related to changes in autotrophic or heterotrophic processes in the present study, e.g. due to co-occurring events such as phytoplankton blooms or because the sampling was not frequent enough. Therefore, specific rain precipitation events are not discussed in the following.

Phosphate concentrations were higher during the summer period than in late spring and early fall. In July, a local wind-driven upwelling event occurred that brought cold and nutrient-rich deep water into the Bay. Upwelling events have been described before for this bay (Nival et al., 1975). In addition, the frequency of forest fires was high during summer 2003 and might have supplied nutrients. It is well known that forest fires contains inorganic nutrients (e.g. phosphorus, Schumann and Summer, 2000). While the upwelling event was a singular event, forest fires were more frequent and long lasting in summer 2003.

As in other studies (Thingstad et al., 1997) we noted in the Bay of Villefranche an increase in DOC concentration following the spring bloom event. This is also supported by the finding that DOC concentration increased significantly with temperature. However, this accumulation phase of DOC ended earlier than in previous years (Thingstad et al., 1997), i.e. before the seasonal erosion of the thermocline due to storms (winter mixing), although the forest fires should have supplied additional organic carbon (e.g. in the form of black carbon) to the system. The Bay of Villefranche is typically P-limited in summer (Dolan et al., 1995; Thingstad et al., 1998). The phosphorus input by upwelling and forest fires could have relieved this P-limitation and stimulated GPP and BP, however, we found only a stimulation of BP. *Synechococcus* is a particularly strong competitor for P and among the most abundant phytoplankton in summer (Tanaka et al., 2004). Thus, we hypothesize that the higher supply of SRP by forest fires could have stimulated heterotrophic bacterial over photosynthetic process and resulted in the enhanced BP:GPP ratio in July–August. In addition, some organic P has likely been imported by atmospheric deposition originating from forest fires and used by heterotrophic bacteria. The consequence of the upwelling and, particularly, of the atmospheric input could have been the oxidation of the accumulated DOC by relieving the competition for phosphate between bacterio- and phytoplankton (Thingstad et al., 1997, 1998). Therefore, it is possible that less carbon was exported due to winter mixing in this year.

A particularly strong Sahara dust deposition event occurred in February 2004 and was associated with heavy rainfall. Sahara dust deposition events are frequently recorded in the NW Mediterranean; but they typically occur as dry deposition (Guerzoni et al., 1992; Ridame and Guieu, 2002). Aerosol deposition of Fe and Ca during the February 2004 event was ca. 7- and 3-fold higher than in the previous week, while wet deposition of phosphate and nitrate was 5- and 6-fold higher compared to the values usually recorded at that time of the year (C. Migon, personal communication, 2009). In addition, particle load measured a few days after the event was almost 2-fold higher than the month before. Although rain and Sahara dust can contain phosphorus and organic carbon (Migon and Sandroni, 1999; Pulido-Villena et al., 2008; Ridame and Guieu, 2002), we could not detect elevated SRP or DOC values the day after the end of the wet deposition event. Pulido-Villena et al. (2008) estimated that during a dry deposition event 0.01 µM phosphate and 2.6 µM DOC were added to the mixed water column. Such an import is likely too small to be detectable against the background values. GPP and Chl *a* were not affected by atmospheric depositions when data were compared to the previous sampling data. This suggests that phytoplankton (and bacterioplankton) was not limited by nutrients and this concurs with the idea that nutrients are regenerated in February. Thus, the limiting factor for phytoplankton was probably light.

In contrast, bacterial parameters such as abundance, production and growth efficiency increased after the wet deposition event. Bacterial abundance and production were ca. 1.4 and 1.3 times, respectively, higher than at the next sampling for bacterial parameters, when the phytoplankton bloom had already started. This supports other studies, who have found that the DOC input by a dry deposition event stimulated bacterial growth (Pulido-Villena et al., 2008). In addition, Sahara dust material collected during the deposition event in 2004 contained organic material and stimulated bacterial production in experiments (Lekunberri et al., 2010). The increase in BGE during the Sahara dust wet deposition event (Fig. 5) suggests that the DOC provided was labile. In addition, adsorption of organic matter in the water to the dust particles along with colonization of particles by bacteria and subsequent use of this concentrated organic material could have caused the increased production. Such an attachment could be the reason, why the lowest bacterial abundance (i.e. free-living bacteria) were found at the particle peak in 20 m depth, since attached bacteria are not detected by standard FCM analysis. While the detailed mechanisms remain unknown, our data suggest a stimulation of bacterial production and biomass due to the Sahara dust event. This increased bacterial activity might also influence the subsequent development of the phytoplankton bloom, e.g. by binding nutrients into bacterial biomass.

5 Conclusions

We found seasonal variability of planktonic auto- and heterotrophic processes in an oligotrophic coastal environment. The data also suggest that episodic short-term events such as forest fires and Sahara dust deposition can strongly modify the seasonal variability of phytoplankton and bacterioplankton-mediated ecosystem processes and the trophic balance. As climate modelling suggests that forest fires and Sahara dust events will increase in the future (Anderson et al., 2003; Ramanathan et al., 2007), the detected influence of episodic events could become more important, e.g. in terms of controlling plankton productivity and carbon export and shifting the trophic balance.

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Table 1. Spearman correlation matrix of all parameters for which significant ($P < 0.05$) and relevant ($r > 0.5$) correlation coefficients were found (in bold italics). Part, particles; sp. BP, cell-specific bacterial production.

	T	NO_3	SRP	DOC	Part.	Chl *a*	BA	sp. BP	BP	BR	BGE	GPP
NO_3	***−0.582***											
SRP	0.159	***0.641***										
DOC	***0.637***	***−0.582***	−0.298									
Part.	−0.342	0.114	−0.075	−0.085								
Chl *a*	***−0.712***	0.330	−0.029	−0.412	***0.521***							
BA	−0.401	0.,46	−0.124	−0.043	0.465	***0.505***						
sp. BP	0.432	−0.248	−0.212	0.249	−0.171	−0.288	−0.061					
BP	0.239	−0.444	−0.406	0.374	0.155	0.031	0.246	***0.592***				
BR	0.189	−0.061	−0.069	−0.206	−0.036	−0.131	−0.076	0.375	0.263			
BGE	0.084	−0.275	−0.253	0.231	0.144	0.052	0.194	0.209	***0.659***	***−0.508***		
GPP	0.027	0.088	0.105	−0.098	−0.073	0.135	0.065	0.275	0.256	0.172	0.009	
CR	0.239	−0.143	−0.155	0.075	0.080	−0.085	0.234	0.217	0.302	0.159	0.116	***0.541***

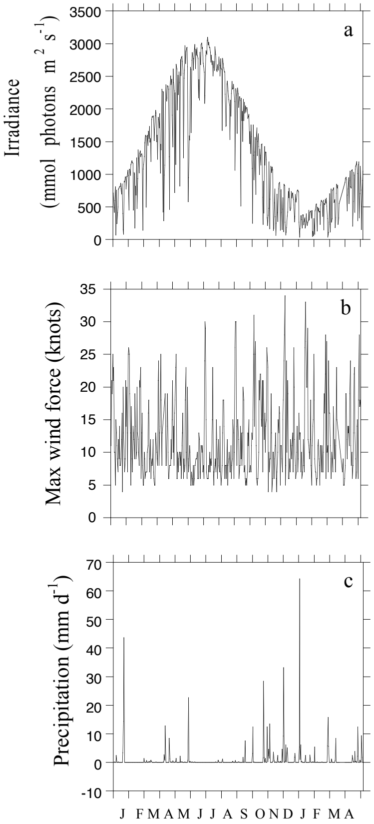

Fig. 1. Meteorological parameters during the study period. Data were collected on a daily basis. **(a)** Irradiance, **(b)** wind intensity and **(c)** precipitation.

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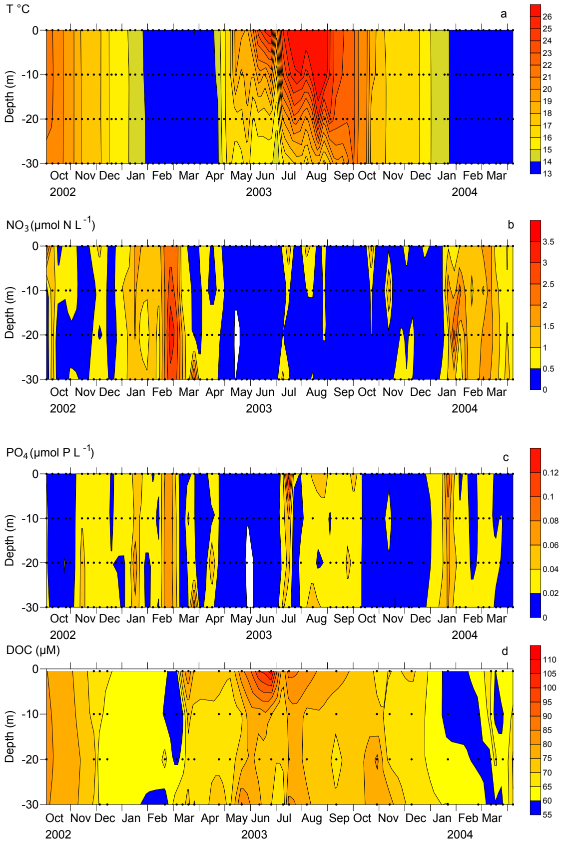

Fig. 2. Physical and chemical characteristics during the study period for the upper 30 m of the water column. Data (except for DOC) were typically collected on a weekly basis. The dots represent sampling datesr. **(a)** Temperature, **(b)** nitrate ($N0_3$), **(c)** SRP (PO_4) and **(d)** dissolved organic carbon (DOC).

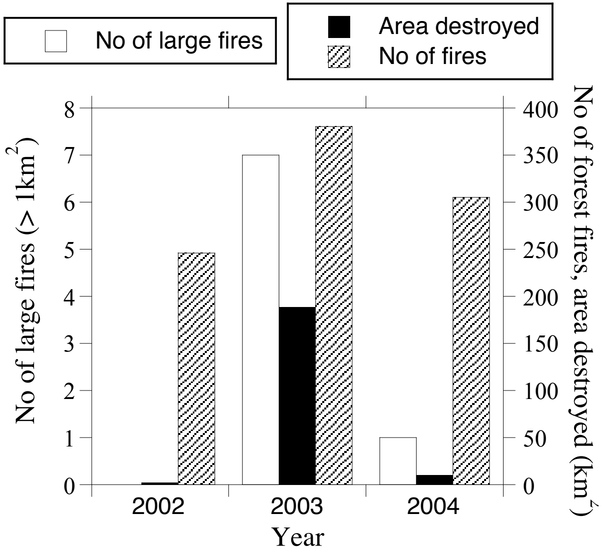

Fig. 3. Frequency of forest fires in the Var Department. The Var Department is in the West of the study site. In summer mainly westerly winds occur.

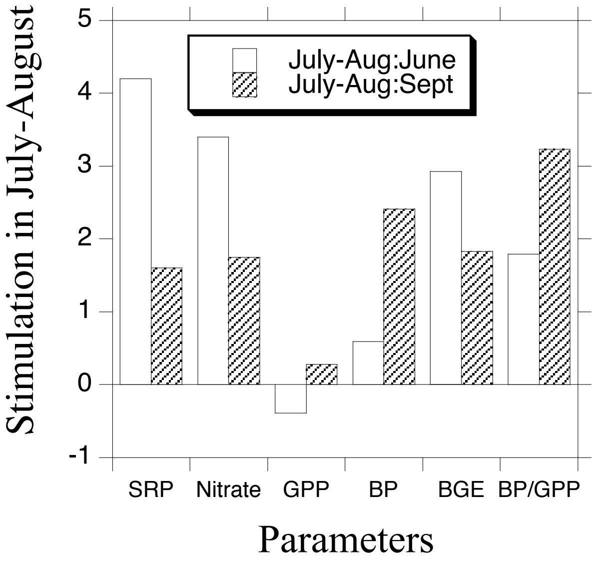

Fig. 4. Stimulation of nutrients and biological parameters during the forest fire period.

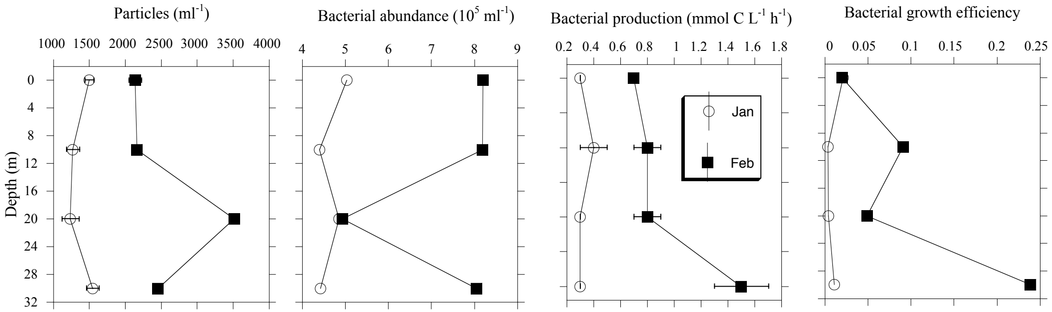

Fig. 5. Comparison of data collected after the Sahara dust event with data collected the month before.

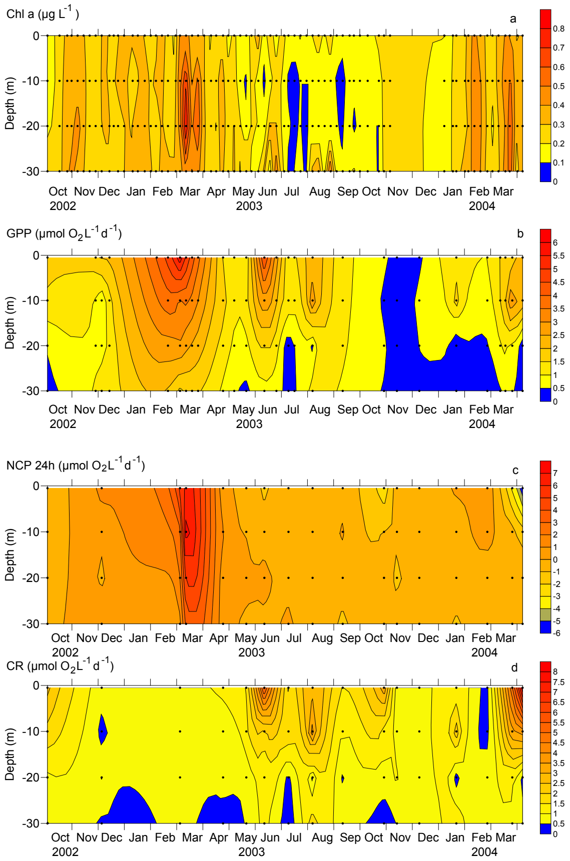

Fig. 6. Changes in phytoplankton and community parameters during the study period for the upper 30 m of the water column. **(a)** Chl *a*, **(b)** gross primary production (GPP), **(c)** net community production (NCP) and **(d)** community respiration (CR). Chl *a* data were collected on a weekly basis. The dots represent sampling dates.

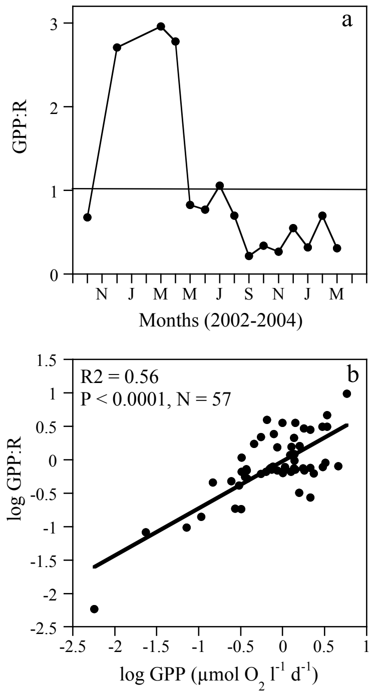

Fig. 7. Trophic balance and planktonic metabolism. **(a)** GPP:R and **(b)** relationship between GPP and GPP:R.

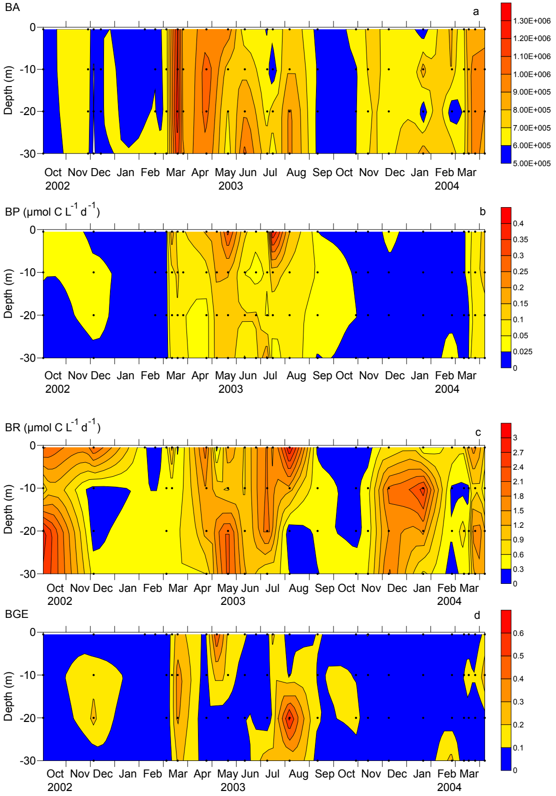

Fig. 8. Changes in bacterial parameters during the study period for the upper 30 m of the water column. **(a)** Bacterial abundance (BA), **(b)** production (BP), **(c)** respiration (BR) and **(d)** growth efficiency (BGE). The dots represent the sampling dates.