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ORIGINAL ARTICLE

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Relationship between bacterial and primary production in a newly filled reservoir: temporal variability over 2 consecutive years

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Abstract Seasonal and spatial variations in bacterial abundance, biomass and production in a recently flooded reservoir were followed for 2 consecutive years, in conjunction with phytoplankton biomass (chlorophyll *a*) and activity (primary production). Between the 2 years of the study, the mean value of primary production remained constant, while those of the chlorophyll *a* concentration, bacterial abundance (BA), bacterial biomass (BB) and bacterial production (BP) decreased. The observed trends of the bacterial variables were linked to changes in the relative importance of allochthonous dissolved organic matter. Moreover, this factor would explain discrepancies observed between the slope of the model II regression equations established from results of the present study and those of the predictive models from the literature, relating to bacterial and phytoplankton variables. An estimate of the carbon budget indicated that 22 and 5% of the ambient primary production in the Sep Reservoir might be channeled through the microbial loop via BP during the 1st and 2nd year of the study, respectively. We conclude that heterotrophic BP in the Sep Reservoir may, on occasion, represent a significant source of carbon for higher order consumers.

Keywords Bacterioplankton · Bacterial production · Chlorophyll *a* · Primary production · New reservoir

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Introduction

The role of bacterioplankton in cycling carbon and nutrients is increasingly recognized in pelagic systems. Indeed, heterotrophic planktonic bacteria are not only the major decomposers of organic matter in aquatic ecosystems, but they also mediate a significant fraction of poor-quality dissolved organic carbon into high-quality particulate organic carbon available for higher trophic levels. Therefore, they occupy a pivotal position in the aquatic trophic structure (Azam et al. 1983) and contribute significantly to microbial food web cycles in pelagic ecosystems.

It is evident that a thorough assessment of the role of bacterioplankton in aquatic systems requires knowledge as to what controls their composition, abundance, biomass and productivity. Among the panoply of environmental factors that have been identified, the physical environment (mainly temperature) and dissolved organic matter (DOM) supply are usually listed. Other researches have described broad scale empirical relationships between bacterial abundance and algal biomass (Bird and Kalff 1984; Cole et al. 1988), between bacterial production (BP) and bacterial abundance (BA) (White et al. 1991), as well as between BP and net primary production (Cole et al. 1988). Empirical relations such as these can help to develop hypotheses regarding which parameters are important regulators of bacterial growth and production and are extremely useful in directing future research efforts.

The seasonal and inter-annual variations in bacterial parameters, especially when compared with phytoplankton parameters, are essential in assessing the importance of heterotrophic bacteria in consuming primary production and in providing organic matter and energy for higher trophic levels in pelagic ecosystems (Cole et al. 1988; Ducklow 1992). Most of the information on bacterial processes in aquatic systems comes from studies performed in marine systems and in natural or stabilized artificial lakes. Little or no such informa-

tion is available on recently flooded reservoirs since biologists have rarely had the opportunity to conduct studies in such environments. Recently flooded reservoirs are expected to contain large quantities of allochtonous DOM, which can affect bacterial activity (Lennon and Pfaff 2005; Paterson et al. 1997; Tranvik 1992).

This study was designed to analyze temporal fluctuations in bacteria abundance and production in relation to phytoplankton biomass (chlorophyll *a*) and activity (primary production) in a model system represented here by the recently flooded Sep Reservoir. We hypothesized that in this system, bacterioplankton as well as sources of organic matter other than from the phytoplankton compartment may play important roles within the microbial loop.

Materials and methods

Site description and sampling

The study was carried out in the recently formed oligo-mesotrophic Sep Reservoir. This man-made lake resulted from a dam built across the Sep Stream and was completed in 1994 as a water supply scheme for summertime irrigation of the agricultural zone of the Haute Morge, "Massif Central," France (ca. 46°N, 3°E). The Sep Reservoir was built in 1994 and completely filled for the first time in January 1995. However, it was emptied progressively during the summer, usually from July to September, in 1995 and 1996 to prevent deoxygenation in the deep water. At its full supply level, the reservoir contains 4.7×10^6 m^3 of water and has a surface area of 33 ha, with mean and maximum depths of 14 and 37 m, respectively. This reservoir has a catchment of 27 km^2 whose vegetation consists of oak and beech forests and grasslands. The Sep Reservoir is generally classified as an oligo- to mesotrophic lake, based on the annual pigment and nutrient concentrations, following the Organization for Economic Cooperation and Development (OECD) recommendations (OECD 1982). Between the 2 years of the study, important physico-chemical variables such as the temperature, oxygen concentration, total phosphorus and total nitrogen did not vary significantly. However, the concentrations of nutrients such as orthophosphates and nitrates used for the growth of planktonic organisms increased between 1996 and 1997 (Thouvenot et al. 2000).

The sampling point was chosen at the deepest part of the reservoir, and samples were collected with a Van-Dorn-type bottle. In 1996, samples were taken monthly from January to April, biweekly in May and weekly from June to September. In 1997, samples were collected biweekly. Sampled depths were at 1, 7 and 15 m under the surface and at 1 m above the sediment for bacterial counts and production measurements. Chlorophyll *a* concentrations were determined at 1, 7, 15 and 1 m above the sediment, and primary production measured at 0, 1, 4, and 7 m.

Analytic methods

Temperature and oxygen were measured in situ with a YSI-GRANT/3000 multiparametric probe. Transparency of the water column was determined with a Secchi disk. Chlorophyll *a* concentrations (Chl) were estimated spectrophotometrically from samples (500 ml) collected on GF/F Whatman glass–fiber filters. Pigments were extracted in 90% acetone overnight in the dark at 4°C, and concentrations were calculated from SCOR-UNESCO (1966) equations. Primary production (PP) was measured from ^{14}C incorporation according to Steemann Nielsen (1952). Sub-samples (125 ml) from each of the sampled depths were collected before local noon and drawn into two transparent and one dark (control) Pyrex glass bottles. Each bottle was inoculated with 0.5 μCi $NaH^{14}CO_3$ and incubated in situ for 3 h. Radioactive samples were filtered onto 0.45-µm pore size acetate membrane filters (Sartorius). Filters were then rinsed twice with 2 ml of 1% HCl-acidified distilled water and stored in a scintillation cocktail until counting of radioactivity with a LKB liquid scintillation counter. Hourly primary production in µg C l^{-1} h^{-1} (averaged over the incubation period) was calculated according to Strickland and Parsons (1972). Daily primary production (DPP) was calculated using the depth-integrated values from the euphotic zone (PPZ_{eu}) and the relationship $DPP = PPZ_{eu} \times (I_J/I_{inc})$, where I_J is the total daily irradiance and I_{inc} the irradiance recorded during the incubation period. Z_{eu} determined from Secchi depth measurements (using the relationship Z_{eu} = Secchi×2) was the depth in the water column at which only 1% of the incident light penetrated.

For the determination of bacterial abundance (BA) and biomass (BB), 30-ml samples were fixed with buffered, alkaline formalin (final concentration 2% v/v, from 37% w/v commercial formaldehyde). Sub-samples (1–5 ml) were treated with 4′,6-diamidino-2-phenylindole (DAPI) (Porter and Feig 1980) and filtered onto 0.2-µm pore-size black polycarbonate filters. Filters were mounted between a slide and glass cover slip with a non-fluorescent oil prior to examination by epifluorescent microscopy. At least 500 bacterial cells were counted and sized with a micrometer in 20–50 fields as previously described (Sime-Ngando et al. 1991). A blank was routinely examined to control for contamination of the equipment and reagents. Bacterial biomass was calculated with the established equation $Y = 88.6\ X^{0.59}$, where X denotes mean cell volume (µm^3) per sample and Y denotes cell protein (fg), with the C:protein ratio being 0.86 (Simon and Azam 1989).

Bacterial production was determined by the mean of [^{3}H-methyl] thymidine (Tdr) incorporation (Fuhrman and Azam 1982; Wicks and Robarts 1987). Duplicate aliquots (10 ml) of freshly collected water

and one 0.5 N NaOH-killed control were inoculated with [^{3}H-methyl] thymidine (specific activity = 80 Ci/mmol; final concentration 20 nM) in Pyrex glass bottles and incubated in situ and in the dark for 45–60 min. Preliminary tests indicated that Tdr uptake rates in Sep plankton were linear for at least 90 min, and saturation occurred at a final concentration of 15 nM. Tdr incorporation was stopped by adding 5 N NaOH to a final concentration of 0.5 N NaOH. Radioactive samples were then passed through 0.2 µm cellulose nitrate filters, and rinsed twice with 3 ml ice-cold 5% trichloroacetic acid. Labeled bacterial DNA was extracted using the phenol–chloroform method of Wicks and Robarts (1987). Filters were placed in vials, allowed to dry and solubilized with 0.5 ml of ethyl acetate. After adding 5 ml of a scintillation cocktail, radioactivity was counted with the LKB counter and BP, calculated in moles of Tdr incorporated into DNA, was converted into the number of bacteria cells produced by using an empirical conversion factor ($1.67\times1{,}0^{18}$ cells per pM of Tdr incorporated) determined by regressing bacterial numbers against Tdr incorporation rates, from a dilution-growth experiment, i.e., the derivative method (cf. Robarts and Zohary 1993). Briefly, triplicate grazer-free (i.e., < 1 µm filtered) bacterial samples from the different sampling depths were diluted at the ratio of 1:9 with sterile (i.e., 0.22 µm filtered) lake water, amended with Tdr and incubated in the dark at the in situ temperature. Sub-samples were then taken at 1–2 h intervals over 24 h for the measurement of bacterial abundance and Tdr incorporation. To convert bacterial cell production into carbon biomass production, the equations of Simon and Azam (1989) were used (see above).

Statistical treatments consisted of regression equations to relate bacterial and phytoplankton variables. The differences between the first and second year values of the variables under study were tested for significance ($P < 0.05$) using the Student's *t*-test.

Results

Physico-chemical environnement

The temperature of the water ranged from 4.2 to 24.4°C (mean ± SD = 10.7 ± 6.4°C) and 5–25.4°C (mean ± SD = 14.8 ± 4.6°C) in 1996 and 1997, respectively. As in many temperate lakes, the water column was homothermous during winter and early spring, and stratified during summer (Fig. 1). However, both in 1996 and 1997, this thermal stratification disappeared early by the end of summer, because of the drawdown of the reservoir for agricultural needs (Fig. 1). Secchi disk transparency was low in 1996 (mean ± SD = 2.49 ± 1.2 m) compared to 1997 (mean ± SD = 4.63 ± 1.19 m), but did not exceed 7 m throughout the 2 years of the study. Seasonal variations in Secchi depth transparency differed between 1996 and 1997 in that, unlike the unimodal pattern observed in 1996 with the highest value recorded in May, the pattern in 1997 was bimodal with maxima registered in May and July (Fig. 1).

Chlorophyll *a* and primary production

With Chl, the range of values recorded in 1996 (0.47–22.5 µg l^{-1}) and 1997 (0–17.05 µg l^{-1}) were close, while the mean value decreased significantly by about 50% in 1997 (Table 1). In 1996, the spatial distribution of Chl through the water column was uniform from winter to early spring and variable during summer. This was not the case in 1997, since only minor vertical differences were observed throughout the study (Fig. 2). For the 2 years of the study, mean values of PP were almost identical (Table 1), and temporal fluctuations in this variable exhibited the same tendency, with low values during winter and spring that increased towards high values during summer (Fig. 2). This pattern was more pronounced at 0- and 1-m sampling depths.

Bacterioplankton standing stock and production

During the 2 years of the study, BA varied from 0.45×10^6 cells ml^{-1} (at 1 m above sediments in 1997) to 8.3×10^6 cells ml^{-1} (at 1 m below the surface in 1996), with the overall mean value being $2.4 \pm 1.5\times10^6$ cells ml^{-1}. As observed with Chl, bacterial density decreased significantly between 1996 and 1997 by 20% (Table 1). In both of these years, the peak in BA observed in April at all the sampled depths was reduced in May during the clear water phase characterized by high values of the Secchi depth transparency. Moreover, in 1996, BA exhibited similar low values at all the sampling depths during winter and spring, contrasting with high values and fluctuations observed during the summer period (Fig. 3). This was not the case in 1997, as regardless of the episodic peaks observed in April, June and August at 1, 7, and 15 m sampling depths, no important temporal fluctuations occurred in BA (Fig. 3). Bacterial cell volume ranged from 0.03 µm^3 (at 1 m under the surface in 1996) to 0.3 µm^3 (at 1 m above sediments in 1996), equivalent in terms of carbon to the resulting BB that varied between 6.1 and 235.4 µg C l^{-1}. Mean values of BB also decreased significantly by about 40% between the 2 years of the study (Table 1).

Bacterial production over the 2 years of the study varied from 0.01 µg C l^{-1} h^{-1} (in 1997 at 1 m above sediments) to 2.00 µg C l^{-1} h^{-1} (in 1996 at 1 m above the sediments). Similar to the observations made with Chl, BA and BB, BP also decreased significantly (approximately 80%) between 1996 and 1997 (Table 1). Fluctuations over time of the BP generally

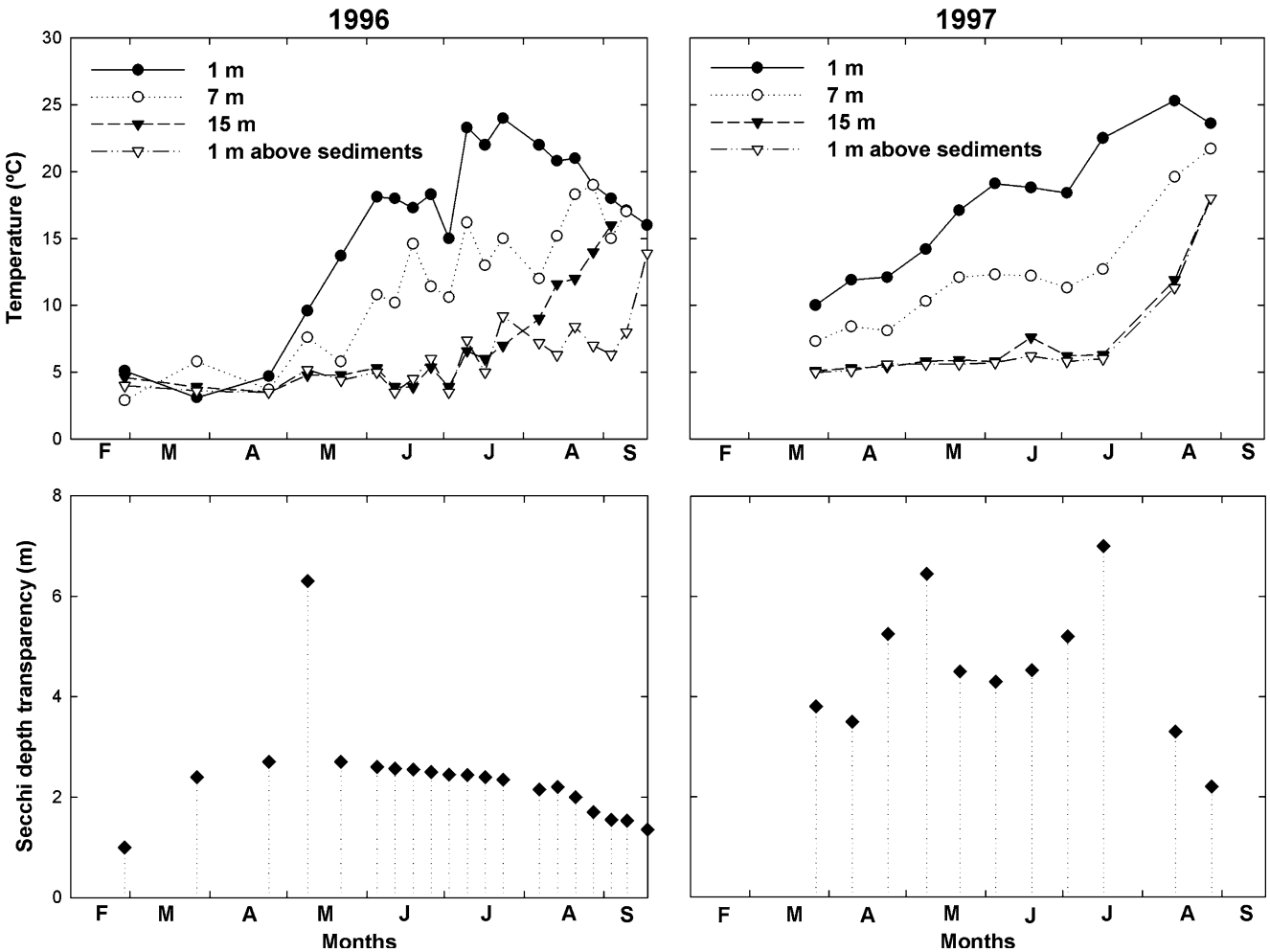

Fig. 1 Spatio–temporal variations of the temperature and Secchi disk transparency in the Sep Reservoir during the 2-year sampling period

Table 1 Mean values ± SD of the main biotic variables measured in the Sep Reservoir during the study and differences between the mean values registered in 1996 and 1997

Year	Chl (μg l^{-1})	PP (μg C l^{-1} d^{-1})	BA (×10^6 cells ml^{-1})	BB (μg C l^{-1})	BP (μg C l^{-1} d^{-1})
1996	7.09 ± 5.68	80.52 ± 75.44	2.67 ± 1.78	49.76 ± 41.89	13.60 ± 10.56
1997	3.43 ± 3.10	77.80 ± 65.68	2.14 ± 0.99	30.22 ± 17.23	2.74 ± 1.92
Difference *t*-test	4.03*	NS	2.85*	3.04*	6.89*

Chl Chlorophyll a, *PP* primary production, *BA* bacterial abundance, *BB* bacterial biomass and *BP* bacterial production
Data are from measurements through the water column
*$P < 0.05$; *NS* not significant

mimicked those of the BA and biomass (Figs. 3, 4), namely that by the end of the sampling in 1996, high values and variations were observed. In 1997, BP exhibited smooth variations with episodic peaks so that the importance decreased with the depth (Fig. 4). The relative importance of BP, expressed as a percentage of PP, ranged from 7.12 to 65.01% (mean = 22%) and from 2.06 to 20.16 (mean = 5%) in 1996 and 1997, respectively. In 1996, this importance changed with time, a pattern that did not occur in 1997 regardless of the single peak registered in July (Fig. 4).

Discussion

Bacterial standing stock and dynamics

Bacterial abundance and production from this study conducted during the 2 years following the flooding of

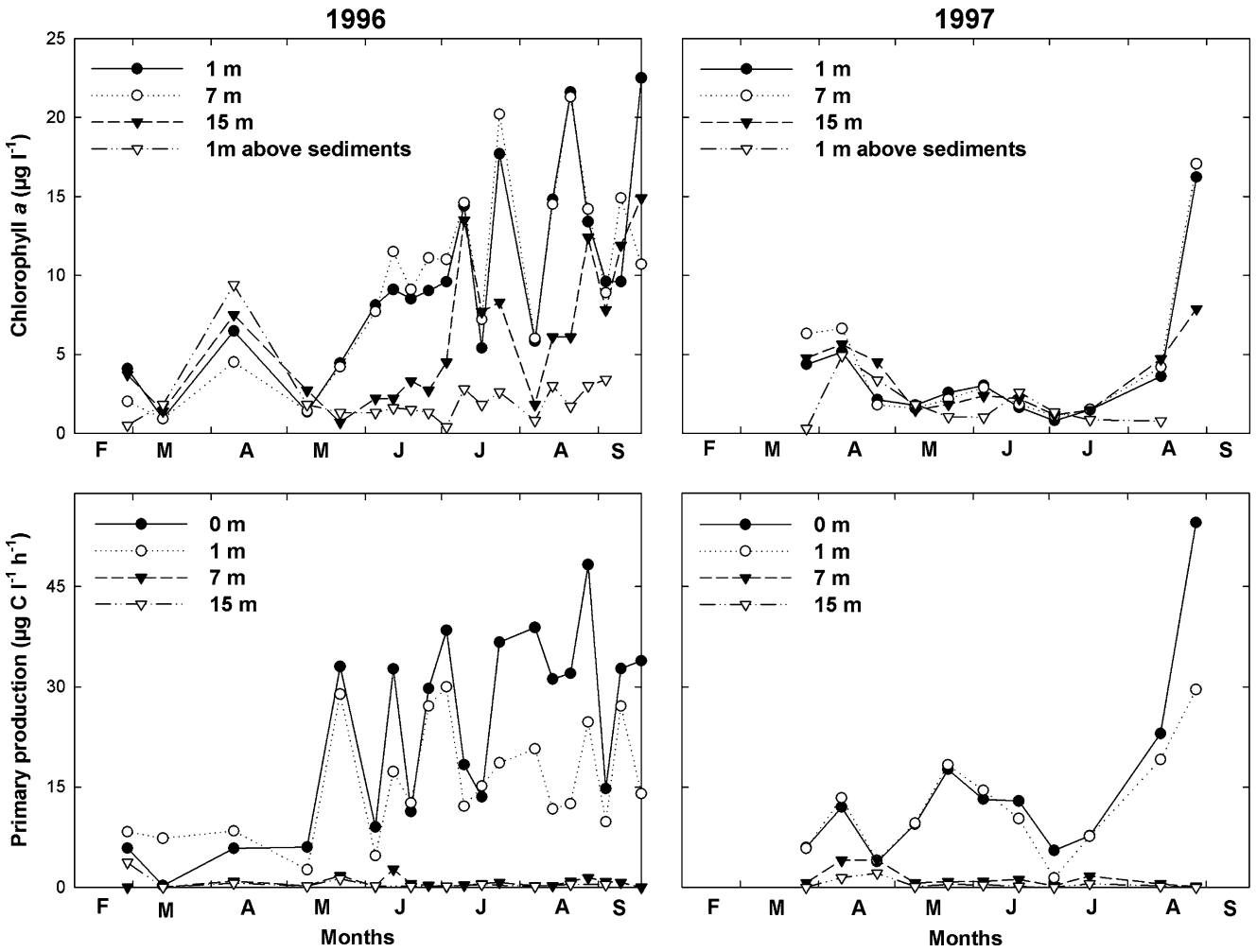

Fig. 2 Spatio–temporal variations of the phytoplankton biomass (chlorophyll *a* concentrations) and activity (primary production) in the Sep Reservoir during the 2-year sampling period

the Sep Reservoir fall within the range of values reported from oligo-mesotrophic systems (Chrzanowski and Simek 1993; Ochs et al. 1995; Simon et al. 1998; Tumber et al. 1993; Wetzel 1983). Likewise, bacterial cell volume encountered in the Sep Reservoir was typical of those from other pelagic systems, including temperate lakes of different trophic levels (Jugnia et al. 1998; Wetzel 1983). Between the two consecutive years under study, the decrease in the bacterial mean cell volume and the resulting biomass matched the tendency observed with the Chl, but not with PP (Table 1). This agrees with the observation by Thouvenot et al. (2000) in the Sep Reservoir, who explained the importance of the between-year decrease in the bacterial plankton as a consequence of the reduction in the allochthonous fraction of DOM.

Of interest, DOM concentrations, particularly those recorded 1 year after the Sep Reservoir flooding (in 1996) were higher than those measured in other lakes of similar trophic status, i.e., oligotrophic to oligo-mesotrophic, and decreased considerably in 1997 (Richardot et al.1999, 2000). However, both in 1996 and 1997, no relationship appeared between the DOM and phytoplankton biomass estimated from Chl (Richardot et al. 2000), as would have been the case if the DOM input were of autochthonous photosynthetic origin (Hanisch et al. 1996; Münster and Chróst 1990). The decrease in allochthonous DOM concentrations between 1996 and 1997 proved important as evidenced by observed changes in the structure of the plankton communities. This shifts from a high proportion of mixotrophic organisms (typical of environments rich in allochthonous organic matter) to a high proportion of strictly autotrophic organisms between 1996 and 1997 (Thouvenot et al. 2000).

Bacterial metabolism depends on the quality and quantity of supplied DOM (Eiler et al. 2003; Kramer et al. 2005; Perez et al. 2003), and in addition to algal carbon, there is a wide variety of organic substrates found in aquatic systems, which include terrestrial-derived DOM that bacteria can use for growth (Lennon and Pfaff 2005; Paterson et al. 1997; Tranvik 1992). Moreover, it is well established that in pelagic waters, dissolved carbohydrate inputs from sources other than the phytoplankton compartment can support bacterial

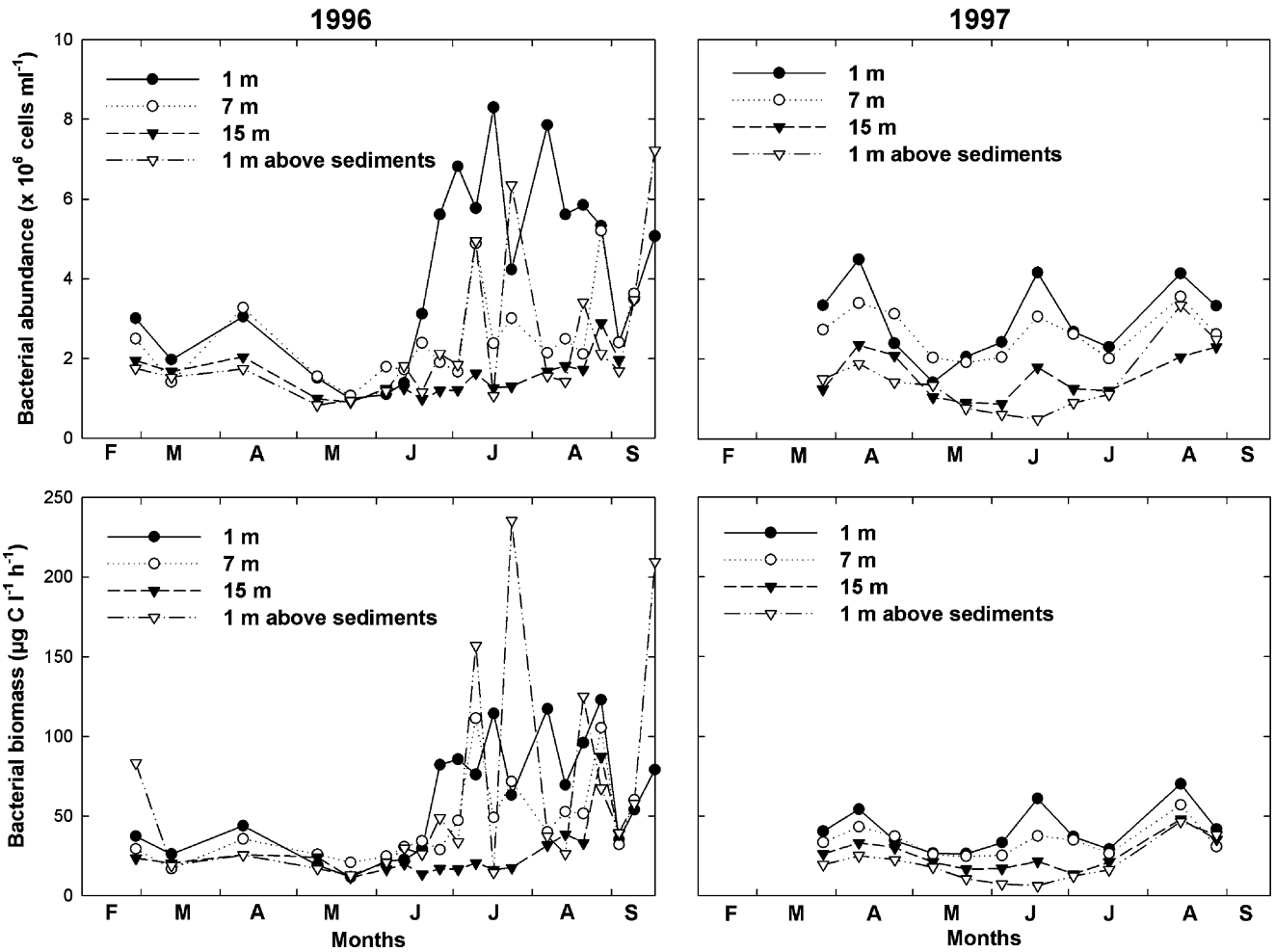

Fig. 3 Spatio–temporal variations in bacterial abundance and biomass in the Sep Reservoir during the 2-year sampling period

growth (Cherrier and Bauer 2004; Young et al. 2005). In the Sep Reservoir, BP was correlated to the dissolved free carbohydrate concentration in 1996 (Richardot et al. 2000), and the decrease in the allochthonous fraction of DOM in 1997, probably resulting from the successive reservoir emptyings, could explain the decrease in bacterial biomass causing BP also to decrease between the 2 years of the study.

Bacterial production: comparisons with published models

Following the study by Billen et al. (1990) and Ducklow (1992), the proposed theoretical values for the slope (a) of the regression of log (BB) versus log (BP) correspond to: strong ($a > 0.6$), intermediate ($0.4 < a < 0.6$), weak ($a < 0.4$), or no effect ($a < 0.2$) of substrate control. With data from the present study, this slope was 0.9 (Table 2), indicating that substrate control of BP was strong in our system. Further, since our estimations of BB and BP were subject to error, we judged it to be appropriate to interpret our regressions in terms of model II analyses (Laws and Archie 1981; Ricker 1973). In comparison to the slope of the regression equation of Billen et al. (1990) and Ducklow (1992), which remained lower than 1 and varied from one another, the slope associated with our regression equation was significantly higher than 1 (t-test, $P < 0.05$) (Table 2), suggesting that other factors may have interacted in our model. Likewise, the slope values of the model II regression equations established in the Sep Reservoir between BP and the PP was significantly higher than 1, although that between the BP and Chl was close to 1 (Table 2). This disparity between slope values indicates that in comparison to other lakes, a relative part of the BP in the Sep Reservoir depends on sources of substrates other than phytoplankton exudates, likely the above-reported allochthonous DOM in this new reservoir. Moreover, in Fig. 5 illustrating log–log graphs of BP versus BA, Chl and PP along with reference regression lines from Cole et al. (1988) for comparison, data were scattered with BA and Chl, while the BP versus PP points grouped well above the reference regression line. Previous studies reported bacterioplankton production in freshwater as affected

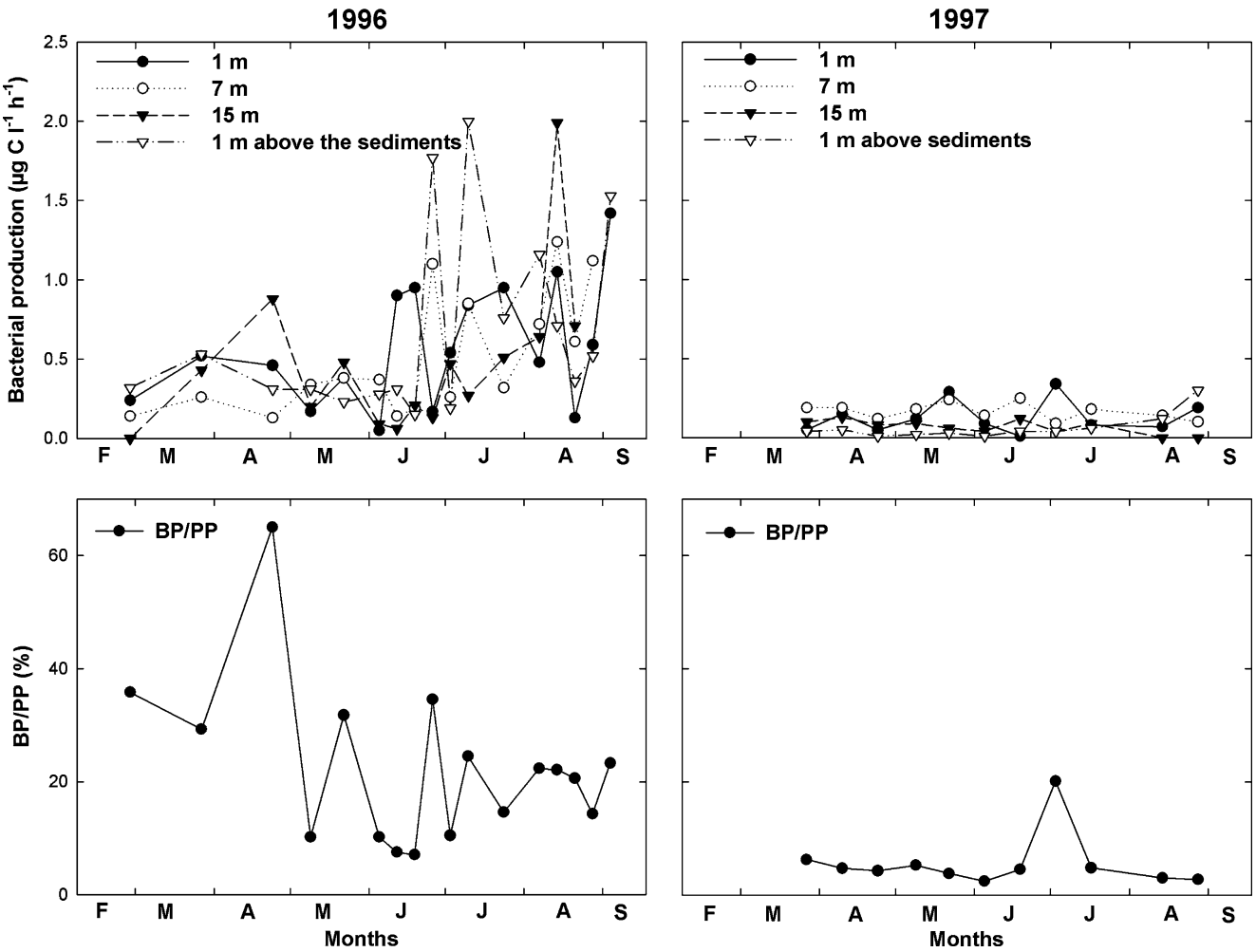

Fig. 4 Spatio–temporal variations in bacterial production and mean bacterial production expressed as a percentage of phytoplankton primary production in the Sep Reservoir during the 2-year sampling period

Table 2 Parameters from the literature of the linear regression between bacterial and selected biotic variables

Origin	*Y*, *X*	*n*	Slope(±SE)	*Y*-int (±SE)	r^2	Model II slope
Cole et al. (1988)	Log (BP), log (BA)	40	1.124	−6.08	0.627	1.42
White et al. (1991)	Log (BP), log (BA)	621	1.23	0.88	0.70	1.47
This study	Log (BP), log (BA)	104	0.86 (±0.17)	−2.14 (±1.6)	0.2	1.92
Billen et al. (1990)	Log (BP), log (BB)	298	0.7	1.67	0.828	0.77
Ducklow (1992)	Log (BP), log (BB)	210	0.43	1.67	0.803	0.48
This study	Log (BP), log (BB)	118	0.9 (±0.10)	−5.08 (±2.23)	0.4	1.42
Cole et al. (1988)	Log (BP), log (Chl)	41	0.618	0.346	0.618	0.79
White et al. (1991)	Log (BP), log (Chl)	346	0.76	0.86	0.39	1.22
This study	Log (BP), log (Chl)	87	0.48 (±0.22)	−2.07 (±1.86)	0.2	1.07
Cole et al. (1988)	Log (BP), log (PP)	31	0.787	−3.339	0.494	1.12
This study	Log (BP), log (PP)	31	0.71 (±0.13)	−3.15 (±2.71)	0.15	1.83

Regression equations from results obtained in the Sep Reservoir are also included for comparison
Y-int *Y*-Intercept, *BA* bacterial abundance (cells ml^{-1}), *BB* bacterial biomass (µg C l^{-1}), *Chl* chlorophyll *a* concentration (µg l^{-1}), *PP* primary production (µg C l^{-1} h^{-1}), *BP* bacterial production (µg C l^{-1} h^{-1}), *n* number of cases, and *SE* standard error
In all cases *P* values are <0.001. The model II slope is an estimate of the true relation between *X* and *Y* when they are subject to error

by inorganic nutrient limitation (Carlsson and Caron 2001; Cotner et al. 1997; Granéli et al. 2004; Le et al. 1994). However, concentrations of nutrients such as orthophosphates and nitrates used for the growth of planktonic organisms seem not to be limiting factors in Sep Reservoir (Thouvenot et al. 2000), and thus their role was mitigated as a contributing factor that could explain the disparity we observed between slopes.

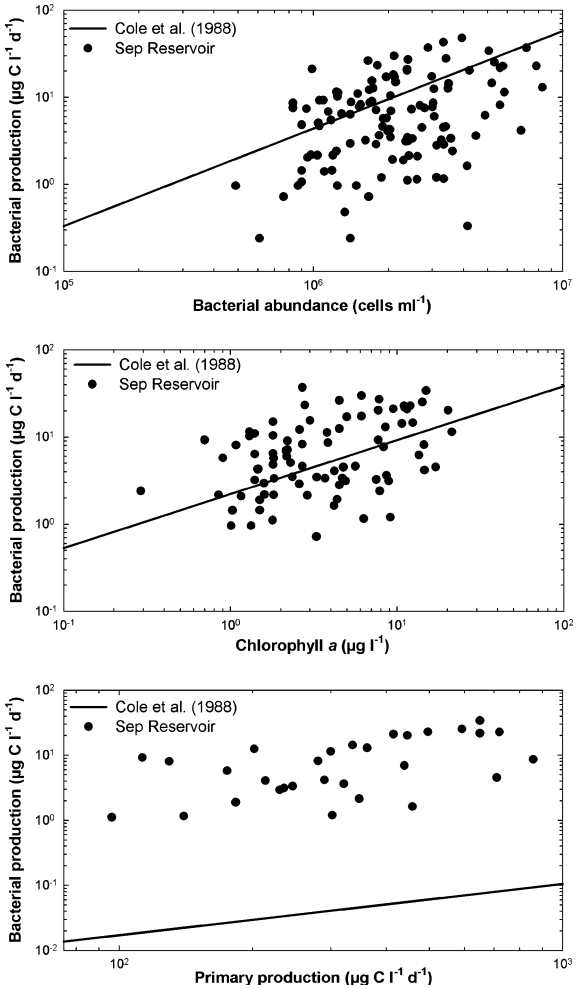

Fig. 5 Relationship between bacterial production and bacterial abundance, chlorophyll *a* and primary production in the Sep Reservoir. Reference regression lines from Cole et al. (1988) models are also included for comparison

Table 3 Measured and predicted mean values (1, 7, 15 and 1 m above sediments) of bacterial production (BP) in the Sep Reservoir

Years	Chlorophyll *a* (µg l^{-1})	BP measured (µg C l^{-1} h^{-1})	BP predicted (µg C l^{-1} h^{-1})
1996	7.10 (58)	0.56 (72)	7.45
1997	3.43 (36)	0.11 (46)	4.75

Predicted numbers were obtained from the equation log (bacterial production) $=0.618\times$ log (Chl) $+0.346$ (Cole et al. 1988). Chlorophyll *a* concentration was the mean for 1, 7 and 15 m. Data are given as mean and number of cases (in parentheses)

Cole et al. (1988) proposed a model that predicts BP from Chl. Applying this model to our data of Chl estimations from the Sep Reservoir, it appeared that values of BP measured during this study were low when compared to those computed from the predictive model by Cole et al. (1988) (Table 3). Of interest, the BP measured represented only 9 and 2% of the BP predicted by the model in 1996 and 1997, respectively. Besides the above-mentioned issues influencing BP, another factor exists that could explain this discrepancy. This is differences in conversion factors for the number of moles of Tdr incorporated into cells and probably the number of metabolically active cells involved in BP. Conversion factors for calculating cell production from Tdr incorporation vary greatly from <1 to 18×10^{18} cells mol^{-1} Tdr. Since our conversion factor of 1.67×10^{18} cells mol^{-1} Tdr was at the lower range of the factor used by authors, but within the realistic range of 1 to 2×10^{18} cells mol^{-1} Tdr, the overprediction by the model of Cole et al. (1988) (based on numerous literature data) might simply be due to this difference.

Bacteria phytoplankton relationship: carbon flux

Bacterial production over the 2 years of the study represents 22% of the daily PP in 1996 and 5% in 1997. In 1996, the mean percentage was comparable to that (mean $=20\%$) reported by Cole et al. (1988) for fresh and marine waters, while the 1997 mean was under this value. If using the assumption made by Calow (1977) and Cole et al. (1988) that pelagic bacterial growth yield is 50%, the mean carbon requirement of the bacterioplankton in this study would be 27.2 µg C l^{-1} d^{-1} in 1996 and 5.47 µg C l^{-1} d^{-1} in 1997. This represents 34 and 7% of the daily PP for 1996 and 1997, respectively. The growth yield of bacteria takes into account both the biomass production and the respiration of these microorganisms. Recent studies (Del Giorgio and Cole 1998; Del Giorgio et al. 1997) have shown that the yield in planktonic environments is in reality lower than the values ($>40\%$) that are commonly used (Calow 1977; Cole et al. 1988). In fact, it has recently been shown that this yield increases with the trophic status of the water from about $<10\%$ in oligotrophic environments to a plateau of about 40% in the most productive environments (Del Giorgio et al. 1997). According to the work of Del Giorgio et al. (1997), the median value of the bacterial growth yield in freshwaters, estimated using the model of White et al. (1991), which predicts BP from BA, would be 17%. As the relationship between abundance and BP in the Sep Reservoir is similar to that reported by White et al. (1991) for freshwaters (Table 3), we therefore chose a mean bacterial growth yield of 17% for estimating the mean carbon balance within the microbial food web in this study (Fig. 4). Using this value, the mean carbon requirement of the bacterioplankton in this study would be 80 µg C l^{-1} d^{-1} in 1996 and 15.53 µg C l^{-1} d^{-1} in 1997, i.e., about 100 and 20% of the DPP in 1996 and 1997, respectively. This calculation assumes that the primary production is entirely available for the bacterioplankton, which is unlikely. The BP in the Sep Reservoir is therefore probably partially dependent on substrates other than phytoplanktonic excreta, and most likely in 1996 on organic matter of allochthonous origin, which is also exploitable by the

bacterioplankton (Lennon and Pfaff 2005; Paterson et al. 1997; Tranvik 1992). Consequently, BP in the Sep Reservoir represents an important source of carbon for consumers, through the functioning of the microbial food web.

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