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ORIGINAL ARTICLE

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Seasonal and vertical distribution of planktonic bacteria and heterotrophic nanoflagellates in the middle Adriatic Sea

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Abstract Temporal and spatial patterns of bacteria and heterotrophic nanoflagellates (HNF) were studied monthly from January 1997 to December 1998 in the middle Adriatic Sea. Bacterial and HNF relationships with phytoplankton biomass and temperature were analyzed to examine how the relative importance of bottom-up and top-down factors may shift over seasons and locations. For the coastal area, an inconsistent relationship between bacterial abundance and chlorophyll *a* and a stronger relationship between bacterial abundance and bacterial production suggest that other substrates than those of phytoplankton origin are important for bacteria. The analysis of simultaneous effects of temperature and bacterial production on bacterial abundance showed that the effect of temperature obscured the effects of bacterial production, suggesting that bacterial growth itself is highly temperature-dependent. The relationship between HNF abundance and bacterial abundance was slightly improved by the inclusion of in situ temperature, bacterial production or both parameters, as additional independent variables. About 60% of the variability in HNF abundance can be explained by bacterial abundance, bacterial production and temperature. In the open sea, tight coupling of bacterial abundance with chlorophyll *a* concentrations implied that phytoplankton-derived substrates have a dominant role in controlling bacterial abundance. During the colder months, bacterial abundance was high enough to support higher HNF abundance than observed, suggesting that predation exerted a minor depressing influence on bacterial abundance during that period. During the spring-summer period, HNF controlled bacterial standing stocks by direct cropping of bacterial production.

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Introduction

The distribution and dynamics of microbial organisms are the result of complex interactions between environmental variables and interspecific relationships. Previous studies have provided considerable empirical evidence that resource availability, predation, viral lysis and temperature affect the components of the microbial food web (Cole et al. 1988; Currie 1990; Sanders et al. 1992; Shiah and Ducklow 1994; Azam 1998; Ducklow 1999). Bacterioplankton growth is positively correlated with temperature up to a certain threshold (Hoch and Kirchman 1993; Shiah et al. 1999, 2003), above which other controlling processes occur (Ducklow 1992; Shiah et al. 1999, 2000, 2003). The relative importance of resources derived from phytoplankton was shown to be higher in the oligotrophic open sea than in coastal and estuarine areas, where allochtonous inputs of organic matter present the dominant source of substrates for microorganisms. Heterotrophic nanoflagellates (HNF) have been identified as a major source of bacterial mortality in aquatic ecosystems (Sherr and Sherr 1994, 2001; Šolić and Krstulović 1994; Christaki et al. 2001), but predation pressure was found to be dependent on temperature and the trophic state of the studied area (Shiah and Ducklow 1994; Vaque et al. 1994; Krstulović et al. 1997; Šolić et al. 1998, 2001; Gurung et al. 2000). The effects of these factors are not always clear, as they can act simultaneously, changing their relative importance over space and time.

The aim of this study was to gain a better understanding of temporal (seasonal) and spatial (vertical; coastal sea vs. open sea) patterns of bacterial and HNF abundances. Bacterial and HNF distribution were analyzed in relation to phytoplankton biomass and temperature in order to examine how the relative importance of bottom-up and top-down factors may shift over seasons and locations.

Methods

Study area

This study was conducted at one coastal station (Kaštela Bay) and one station located in the open sea of the middle Adriatic (Island of Vis).

The coastal station (Station A) was located in an enclosed, shallow basin, Kaštela Bay (43°31′N; 16°22′E). The bay, with a surface area of 61 km^2 and an average depth of 23 m, communicates with the adjacent channel through an inlet that is 1.8 km wide and 40 m deep. The river Jadro, which discharges into the eastern part of the Bay, is the most important freshwater source (average annual inflow of 10 m^3 s^{-1}). Its waters are characterized by a very high nitrogen to phosphorus (N/P) ratio. This part of the Bay also receives domestic and industrial sewage. Water circulation and exchange with the open sea is generated mostly by the local wind, which is related to the passage of mid-latitude cyclones over the area (Gačić 1989). Cyclones are more frequent during the winter, and therefore water circulation and exchange with the open sea are more intense during that period of the year. The strong terrestrial influence results in wide oscillations of chemical and physical parameters (Zore-Armanda 1980).

The open sea station (Station B) was located 4 km southeast of Cape Stončica on Vis Island (43°00′N; 16°20′E) where water depth is about 100 m. Because of its distance from the mainland (50 km), oscillations of all hydrographic parameters are smaller than in the coastal waters (Buljan and Zore-Armanda 1979). Fluctuations of thermohaline properties of the surface layers are subject to direct atmospheric conditions, while the fluctuations in deeper layers are more influenced by advection and diffusion (Grbec and Morović 1997). This station is also exposed to advection of Mediterranean waters (Grbec et al. 1998).

Sampling

Sampling was conducted monthly, from January 1997 to December 1998 at depths of 0, 5, 10, 20 and 35 m at Station A, and 0, 5, 10, 20, 30, 50, 75 and 100 m at Station B. Samples for chlorophyll *a* (chl *a*), bacterial and HNF counts were collected using 5 l Niskin bottles, while an STD system was used for the measurement of temperature, salinity and depth.

Phytoplankton biomass was estimated from chl *a* concentrations using fluorimetric methods (Strickland and Parsons 1972). Bacterial abundance was determined in fixed samples (2% formalin, final concentration) using acridine orange direct counts (Hobbie et al. 1977). At least 300 bacteria per filter were counted under 1,000× magnification using an Olympus epifluorescence microscope. For HNF counts, preserved samples (2% formalin, final concentration) were filtered at low pressure through a 0.8-μm pore size black-stained Millipore filter. The preparations were stained with proflavine (Haas 1982) and phototrophic organisms differentiated by chlorophyll autofluorescence. The samples were counted the same day after preparation, and at least 100 fields per filter were counted.

Bacterial cell production was inferred from DNA synthesis measured as incorporation rate of ^{3}H-thymidine (Fuhrman and Azam 1982). (Methyl-^{3}H)-thymidine was added to 10 ml seawater to a final concentration of 10 nM (specific activity 86 Ci $mmol^{-1}$, Amersham Ltd, UK). Incubations were run in triplicate, plus a formalin-killed control (final concentration 0.5%), in the dark for 1 h at in situ temperature. Formalin addition (final concentration 0.5%) stopped the incorporation. The fixed samples and the control were passed through a 0.2-μm pore size cellulose nitrate filter and rinsed seven times with 1 ml ice-cold TCA (5% weight/volume). The filters were dried, dissolved in 10 ml Filter-Count (Packard scintillation cocktail) and counted, after 24 h storage, in a scintillation counter (Packard Tricarb 2500). The conversion factors for estimating bacterial cell production were calculated from bacterial cell abundances and ^{3}H-thymidine incorporations in the <1-μm fractions (Riemann et al. 1987) as: $CF=(N_2-N_1)/{}^3H_{inc}$, where N_1 and N_2 are the abundances at the beginning and at the end of the experiment; $^3H_{inc}$ is the integrated ^{3}H-thymidine incorporation rate during the experiment.

Results

Hydrographical parameters

Temperature and salinity at the investigated stations are shown in Fig. 1. At Station A, temperature varied from 10.9°C in February 1997 to 26.0°C in June 1998. The highest variations were recorded in the surface layers. Until April, there were no significant temperature differences between surface and bottom layers. A thermal stratification started to develop in June and lasted until September. The vertical thermal gradient disappeared in October. Water salinity fluctuated between 30.62 and 38.30 psu. The greatest vertical salinity gradient was recorded in January 1997. During winter and spring, salinity of the surface layers dropped as a result of higher precipitation, while bottom waters were characterized by increased salinities in summer and autumn.

At Station B, temperature ranged from 13.0°C to 26.1°C. A thermocline developed in July between 20 and 30 m depth, attaining its maximum in August. The stratified conditions remained until September, when a strong mixing occurred. The whole period from November until April was characterized by homothermy. Salinity values fluctuated between 37.60 and 38.78 psu. During the winter months, the water column was characterized by almost uniform salinity values. With the beginning of the spring heating, a halocline started to develop. The highest salinity gradient was recorded during the summer months.

Bacteria and heterotrophic nanoflagellates

At Station A, bacterial abundance varied from 0.44×10^6 to 2.50×10^6 cells ml^{-1}, with a mean value of 1.13×10^6 cells ml^{-1}. During the whole study period, bacteria were most abundant in the surface layers above 20 m depth, and their abundance peaked during summer at 0 and 5 m depth. The greatest variations of bacterial abundances with depth were observed during thermal stratification of the water column.

Bacterial production varied from 2.25 to 45.34 μg C l^{-1} day^{-1} (mean value=28.23 μg C l^{-1} day^{-1}), with maximum values in the surface layers. Below 10 m depth, bacterial production showed little variation, with no clear seasonal patterns.

The seasonal fluctuations of bacterial abundance, bacterial production and temperature showed similar patterns in the surface layers (0–5 m) (Fig. 2). Bacterial abundance was positively correlated with temperature (r=0.55; P<0.001), while the correlation with bacterial production was statistically significant but relatively low (r=0.289; P<0.05) (Table 1). On the other hand, bacterial abundance was not related to chl *a* concentration, a value that represents the measure of substrate supply. A possible

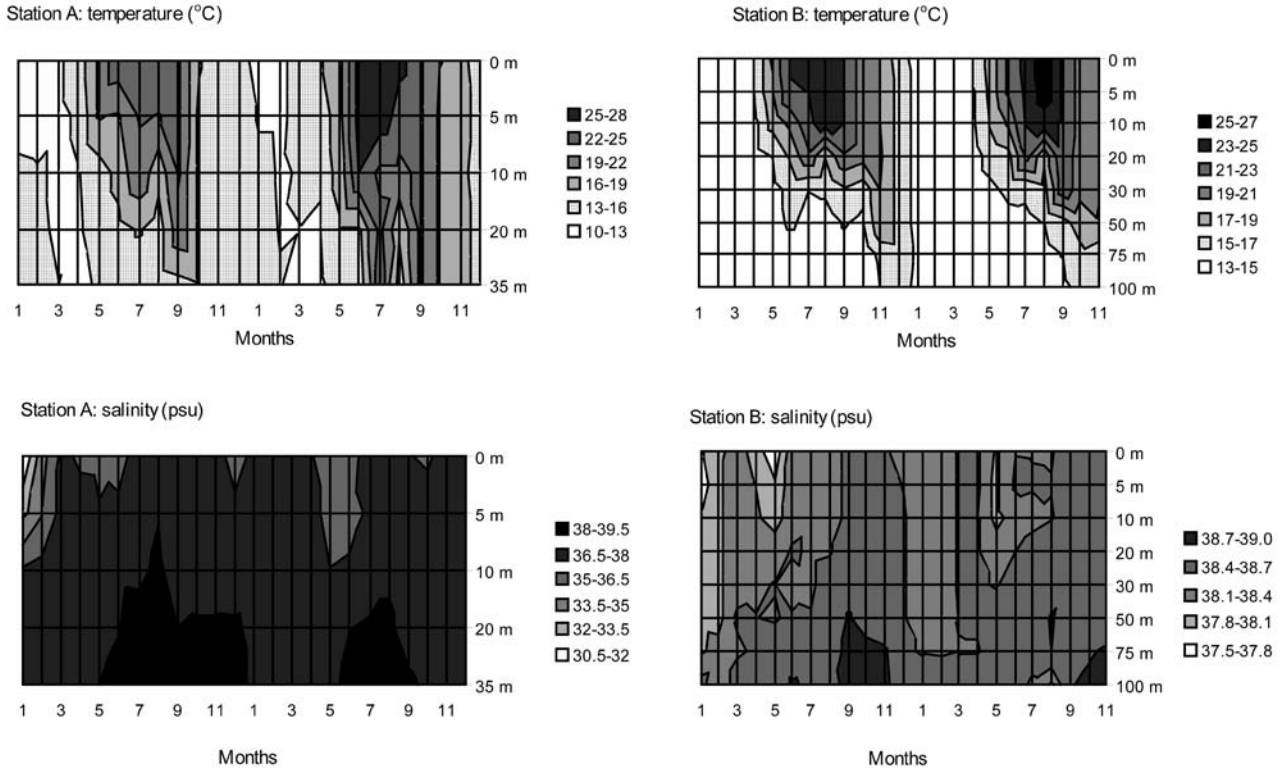

Fig. 1 Hydrographic parameters at the investigated stations

Table 1 Simultaneous effects of temperature, chl *a* and bacterial production on bacterial abundance in the surface layers (0–5 m) of Kaštela Bay. *R* coefficient of correlation; r_p coefficient of partial correlation; *a*, *b* coefficients of multiple linear regression (*a* intercept; *b* slope; *n*=24); β (beta coefficient) regression coefficient *b* stated in terms of its standard deviation; *R* coefficient of multiple regression; R^2 *(%)* coefficient of multiple determination, i.e. measure of the proportion (percentage) of variance explained; ** $P<0.01$; * $P<0.05$

Variable	*r*	r_p	*a*	*b*	β	*R*	R^2 (%)
Temperature	0.549**	0.589**	215,806.1	54,247.7	0.615	0.591**	35.00
Chl *a*	0.055	0.254		68,628.3	0.230		
Temperature	0.549**	0.523**	264,166.4	45,843.7	0.519	0.565**	31.94
Bacterial production	0.249	0.160		6,348.5	0.137		
Chl *a*	0.055	0.041	914,320.3	12,060.9	0.040	0.304*	6.35
Bacterial production	0.289*	0.286*		11,415.1	0.247		
Temperature	0.549**	0.564**	116,788.3	51,797.2	0.587	0.601**	36.12
Chl *a*	0.055	0.249		64,341.7	0.216		
Bacterial production	0.249	0.132		5,088.10	0.110		

explanation for this is that bacterial abundance in Kaštela Bay is not limited by substrate supply. It seems that temperature was the main factor determining maximal bacterial abundance.

HNF abundance at Station A varied from 0.07×10^3 to 23.51×10^3 cells ml^{-1} (mean value=2.84×10^3 cells ml^{-1}) showing relatively lower values (<2.5×10^3 cells ml^{-1}) during the cold period of the year (from December until April) and higher values (>8×10^3 cells ml^{-1}) during summer (July and August). Pronounced summer maxima in the surface layers (0–10 m) were found during both years of observation. During 1997, the HNF abundance summer peak was also present at 20 and 35 m depth, while in 1998 this peak disappeared below 10 m depth (Fig. 3).

The seasonal fluctuations of HNF abundance showed a similar pattern as the fluctuations of bacterial abundance, temperature and bacterial production in the surface layers (Figs. 3a and 3b). In the layers down to 10 m, HNF abundance was positively correlated with temperature, bacterial abundance and bacterial production (Table 2). The strongest correlation (r=0.754; $P<0.001$) was found with bacterial abundance. The analysis of the relationship between HNF abundance and bacterial abundance was slightly improved by the inclusion of in situ temperature, bacterial production or both parameters as additional

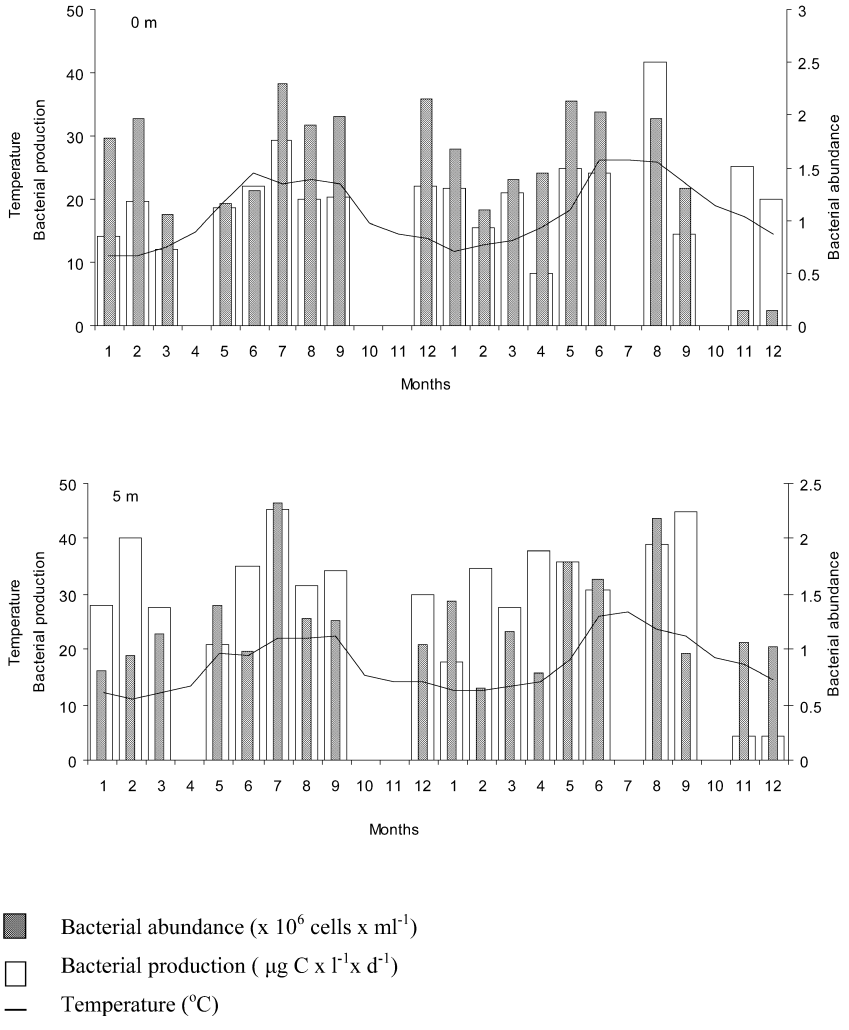

Fig. 2 Distribution of temperature, bacterial abundance and bacterial production at Station A in the surface layers (0 m and 5 m)

Table 2 Simultaneous effects of bacterial abundance, bacterial production and temperature on HNF abundance in the surface layers (0–10 m) of Kaštela Bay. *R* coefficient of correlation, r_p coefficient of partial correlation; *a*, *b* coefficients of multiple linear regression (*a* intercept; *b* slope; *n*=36); β (beta coefficient) regression coefficient *b* stated in terms of its standard deviation; *R* coefficient of multiple regression; R^2 *(%)* coefficient of multiple determination, i.e. measure of the proportion (percentage) of variance explained; ** $P<0.01$; * $P<0.05$

Variable	*r*	r_p	*a*	*b*	β	*R*	R^2 (%)
Bacterial abundance	0.754**	0.665**	–4,901.48	0.010	0.693	0.760**	57.76
Temperature	0.493**	0.141		79.12	0.111		
Bacterial abundance	0.754**	0.745**	–5,290.96	0.010	0.722	0.773**	59.69
Bacterial production	0.306*	0.255		51.68	0.170		
Temperature	0.493**	0.454**	–3,982.12	84.526	0.445	0.530**	28.06
Bacterial production	0.306*	0.224		36.080	0.201		
Bacterial abundance	0.754**	0.668**	–5,775.60	0.010	0.680	0.775**	60.13
Temperature	0.493**	0.105		74.906	0.080		
Bacterial production	0.306*	0.237		27.181	0.159		

independent variables. The coefficient of multiple determination (R^2), which measures the overall degree of association between HNF abundance and independent variables, varied from 0.58 to 0.60. That means that about 60% of the variability in HNF abundance can be explained by bacterial abundance, bacterial production and temperature. The particularly high relative importance of bacterial abundance in controlling HNF abundance is shown by the coefficients of partial correlation (r_p) and the beta coefficients (β). The partial correlation between HNF abundance and bacterial abundance (i.e. the correlation when the individual effects of temperature and/or bacterial production were excluded) was higher than the partial correlation of HNF abundance with

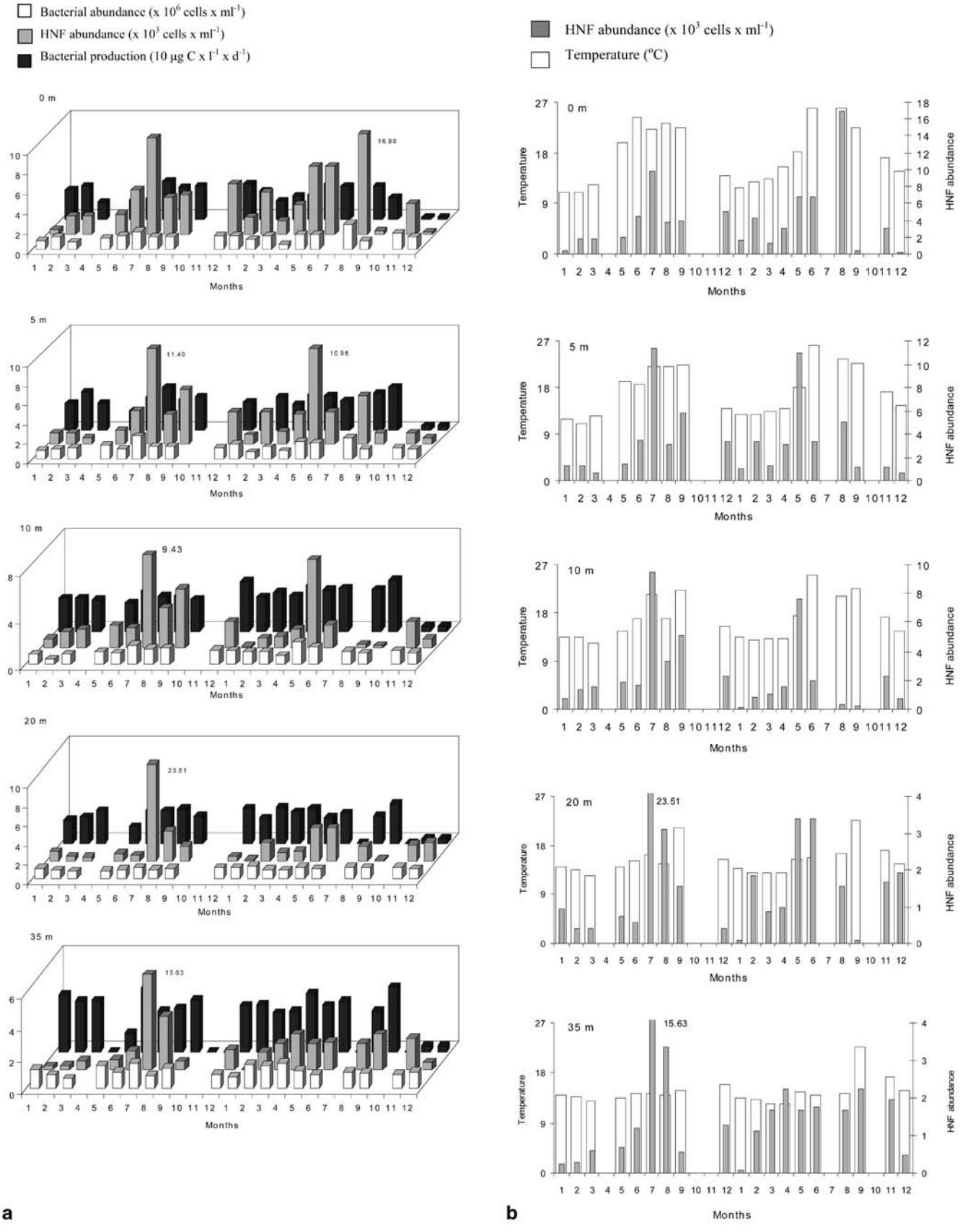

Fig. 3 **a** Distribution of bacterial abundance, bacterial production and HNF abundance at Station A. **b** Distribution of HNF abundance and temperature at Station A

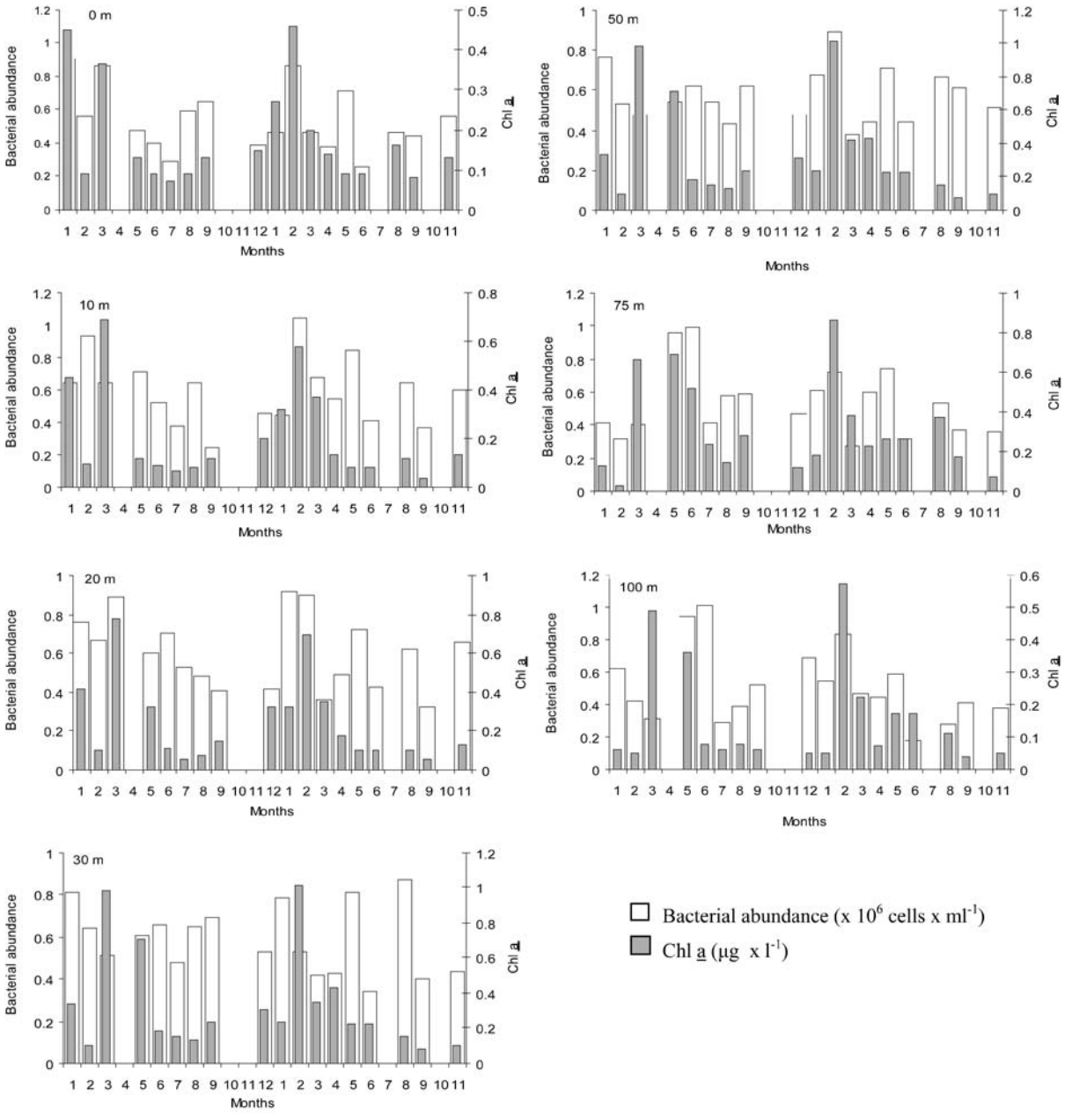

Fig. 4 Distribution of bacterial abundance and concentration of chl *a* at Station B

temperature and/or bacterial production. Beta coefficients (i.e. regression coefficients stated in terms of their standard deviations) point to the same conclusion. The increase of 1.0 standard deviations (SD) in the value of bacterial abundance is followed by an increase of about 0.7 SD in the value of HNF abundance, under the condition that bacterial production and/or temperature stay constant. On the other hand, an increase of 1.0 SD in the values of temperature and/or bacterial production is accompanied by an increase of between 0.11 and 0.17 SD in the values of HNF abundance. The relative importance of temperature and bacterial production in explaining variation in HNF abundance differed when their common influence was observed, isolated from the influence of bacterial abundance, and when the influence of all three factors was observed together. In the former case the influence of temperature was relative more important (P=0.445) than the influence of bacterial production (P=0.201). In the latter case, bacterial abundance obscured the effects of both other factors, particularly the effects of temperature. This result suggests that bacterial abundance itself was highly temperature-dependent, since temperature influences the variation in HNF abundance indirectly through the changes in bacterial abundance.

At Station B (open sea station), bacterial abundance varied from 0.18×10^6 to 1.04×10^6 cells ml^{-1} with a mean

Table 3 Simultaneous effects of chl *a* and temperature on bacterial abundance in the surface layers (0–20 m), and bacterial production and temperature on heterotrophic nanoflagellates (HNF) in the layers between 20 and 30 m depth at station Stončica. *R* coefficient of correlation; r_p coefficient of partial correlation; *a*, *b* coefficients of multiple linear regression (*a* intercept; *b* slope; *n*=36 for bacteria and *n*=24 for HNF); β (beta coefficient) regression coefficient *b* stated in terms of its standard deviation; *R* coefficient of multiple regression; R^2 *(%)* coefficient of multiple determination, i.e. measure of the proportion (percentage) of variance explained; ** $P<0.01$; * $P<0.05$

Variable		*r*	r_p	*a*	*b*	β	*R*	R^2 (%)
Bacterial abundance	Chl a	0.506**	0.424**	706,391.7	407,007.9	0.460	0.543**	29.44
	Temperature	−0.462**	−0.225		−12,069.9	−0.244		
HNF	Bacterial production	0.545**	0.560**	−100,923	52.68	0.558	0.565**	31.94
	Temperature	0.095	0.158		57.91	0.133		

value of 0.56×10^6 cells ml^{-1}. In both years of study, higher bacterial abundances were observed during winter and spring months. The winter peak in 1997 was present above 50 m depth, while the spring maximum was found near the bottom. In 1998, both winter and spring peaks of bacterial abundance were found throughout the water column.

At this station, bacterial abundance was closely related to chl *a* concentrations. The highest correlation was found in the surface layer (r=0.754; $P<0.001$). Pronounced bacterial abundance peaks that occurred at all depths in early spring (February–March) always coincided with the chl *a* maxima (Fig. 4). At other times, bacterial abundance followed chl *a* maxima sometimes with a time lag of 1–2 months. The fact that chl *a* maxima occurred during the colder part of the year could explain the statistically significant negative correlation between bacterial abundance and temperature (r=0.462; $P<0.01$). This is supported by the fact that the partial correlation between bacterial abundance and temperature ceased to be statistically significant when the effect of chl *a* was excluded (Table 3).

Bacterial production at Station B varied from 3.15 to 64.33 μg C l^{-1} day^{-1} (mean value=27.24 μg C l^{-1} day^{-1}), with maximum values in the surface layers, but with no clear seasonal pattern. In general, the values were much higher during 1998, with the maximum in April at 30 m (64.33 μg C l^{-1} day^{-1}), than in 1997 when the highest value was recorded at 10 m in June (54.66 μg C l^{-1} day^{-1}). The distribution of this parameter during spring, at depths of 10 to 50 m, followed the distribution of chl *a* and was lagging 2 months behind the peaks of algal biomass (Fig. 5).

HNF abundance at Station B varied from 0.07×10^3 to 4.22×10^3 cells ml^{-1}, with a mean value of 1.13×10^3 cells ml^{-1}. Seasonal fluctuations in HNF abundance differed between the years studied, with pronounced summer peaks in 1997 and spring peaks in 1998, at all depths. The rapid increase in bacterial production during summer 1997 and spring 1998 was followed by the increase in HNF abundances, and this pattern was particularly evident at depths from 10 to 50 m (Fig. 6). HNF abundance showed a stronger relationship with bacterial production than with bacterial abundance. HNF abundance was positively correlated with bacterial production in the layers from 20 to 30 m depth (r=0.545; $P<0.01$) (Table 3). At the same time, HNF abundance showed no correlation with bacterial abundance.

Discussion

The observed relationship between bacterial abundance and bacterial production, and a lack of correlation with chl *a* in the coastal area (Station A), suggest that the input from land is a more important source of substrate than phytoplankton. An uncoupling between bacteria and phytoplankton in coastal areas has been reported to be due to a response to alochtonous inputs at specific times of the year (Kepkay et al. 1993), seasonal changes (Pomeroy et al. 1991), and variations in hydrodynamic conditions (Cho et al. 1994). Since Kaštela Bay receives large quantities of nutrients throughout the year (Barić et al. 1996; Bogner et al. 1998), this location shows conditions in which substrate concentrations are almost always above the saturation level. Therefore, variation in bacterial abundance cannot be explained by variation in substrate concentrations, especially not by variation in substrate of phytoplankton origin.

The analysis of the simultaneous effects of temperature and bacterial production on bacterial abundance (Table 1) showed that the effect of temperature masked the effect of bacterial production. That is, the effect of bacterial production on bacterial abundance failed to occur when temperature stayed constant, suggesting that in Kaštela Bay bacterial growth itself is a highly temperature-dependent seasonal phenomenon (Šolić and Krstulović 1994).

The inconsistent relationship between bacterial abundance and productivity could also suggest a strong influence of mortality factors such as bacteriovory and viral lysis. It seems that, in Kaštela Bay, temperature controlled not only bacterial abundance but also the abundance of bacteriovorous protozoa, which in turn limited bacterial abundance by high grazing pressure. In these conditions, grazing was a factor controlling bacterial abundance, particularly during summer. This is consistent with the results of several other studies which showed that bacteriovory is highly dependent on water temperature, with a maximum in summer (Marrase et al. 1992; Shiah and Ducklow 1994; Vaque et al. 1994; Gurung et al. 2000). A marked increase in bacterial

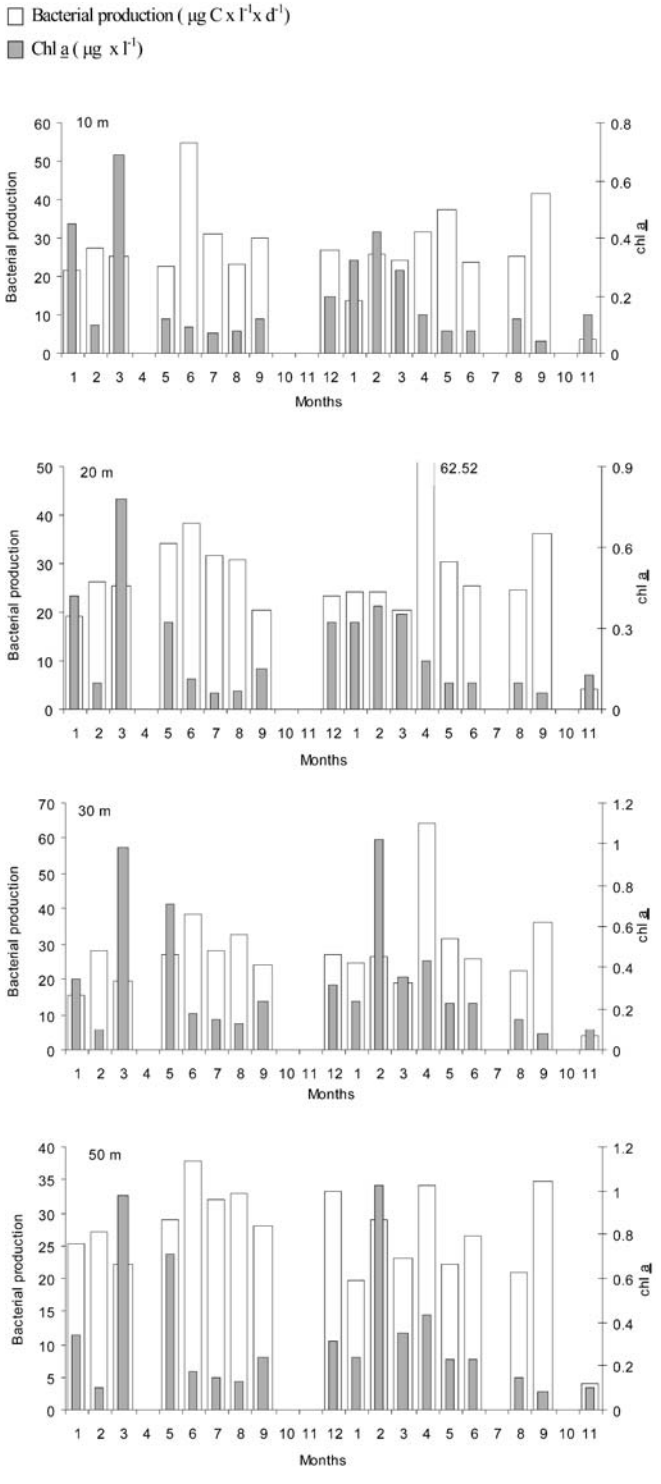

Fig. 5 Distribution of bacterial production and concentration of chl *a* at Station B

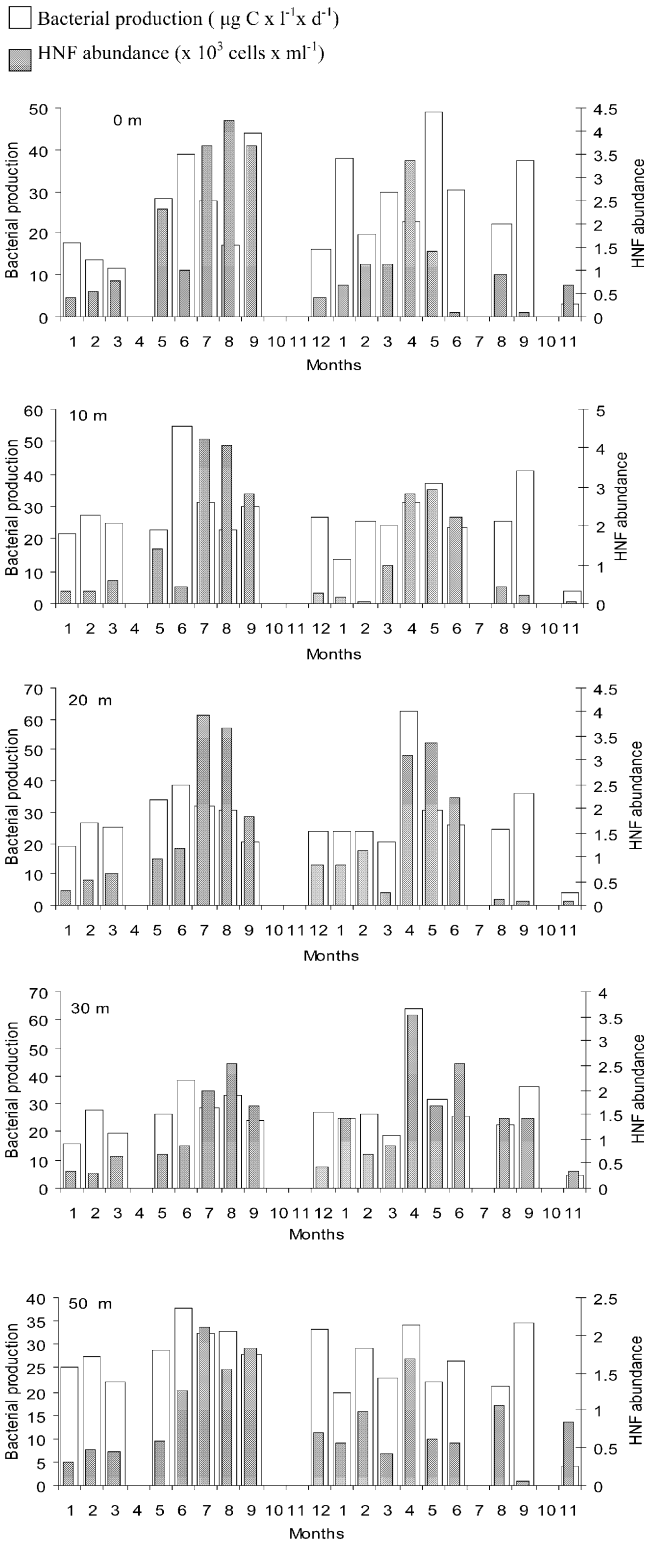

Fig. 6 Distribution of bacterial production and HNF abundance at Station B

abundance during the warm months, when temperature exceeded 20°C, resulted in an increase of HNF abundance. The weak relationship between bacteria and HNF during colder months could be a result of low grazing pressure on bacteria by HNF as found by Šolić and Krstulović (1994) and Šolić et al. (2001), as well as of

high grazing pressure on HNF by ciliates (Weisse et al. 1990) or zooplankton (Jürgens and Güde 1994; Sanders et al. 1994). Šolić et al. (1998) found very high abundances of ciliates in that same period and reported the importance of ciliates as HNF predators during winter. In addition, Bojanić (2001) reported that the low levels of ciliates found during the summer cannot have much effect on HNF at this time of year.

Contrary to the coastal area, at the open sea (Station B) bacterial abundance was closely related to chl *a* concentrations, suggesting that bacterial abundance was strongly controlled by substrate supply, and that phytoplankton was the most important source of substrate. Other studies also showed that, in systems that do not receive alochtonous inputs of substrates, bacteria are supported by the supply of organic carbon derived from phytoplankton (Carlson et al. 1996; Kirchman and Rich 1997). Previous investigations at this station have shown the presence of high concentrations of nutrients in the deep layers of chl *a* (from 30 to 100 m depth), which presumably stimulated the beginning of the phytoplankton bloom and bacterial activity (Ninčević et al. 2002). The dominant role of substrate supply in controlling bacterial abundance during the winter-spring period is supported by the fact that the coupling between bacteria and their predators (HNF) was very weak in that period. Bacterial abundance was high enough to support higher HNF abundance than was realized, suggesting that predation exerted a minor depressing influence on bacterial abundance during this period. Very low grazing on bacteria during the colder part of the year has been reported for the open middle Adriatic in several other studies as well (Šolić and Krstulović 1994; Šolić et al. 1998, 2001).

Bacterial production at Station B followed the distribution of chl *a* and was lagging 2 months behind the peaks of algal biomass. This lag between algal and bacterial seasonal development has also been observed by other authors (Coffin and Sharp 1987; Vaque 1996). Billen et al. (1990) suggested that the delayed development of bacterioplankton bloom with respect to phytoplankton might be explained by the fact that decaying phytoplankton release more dissolved organic matter, favoring the activity of bacteria.

HNF abundance at the open sea station (Station B) showed a stronger relationship with bacterial production than with bacterial abundance. This suggests that, at the open sea station, HNF controlled bacterial standing stocks by direct cropping of bacterial production, and that such control occurred only during the warmer spring-summer period. This finding is supported by the results of Gonzalez et al. (1993) and Sherr et al. (1992) who suggested that, because of a higher grazing pressure on more actively growing and dividing cells, bacterivores crop the production rather than simply the standing stocks of bacteria. Although HNF abundance was not correlated with temperature, temperature may explain a small part of HNF abundance variance because its inclusion as an additional independent variable slightly improved the regression model (coefficient of multiple correlation R=0.565; Table 3).

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