

Bacterial biomass and production rates in the central Adriatic

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Study of bacterioplankton biomass and production as well as of the relationship between bacterioplankton biomass and total microbial biomass were carried out in the coastal and open middle Adriatic on a monthly basis from January 1980 to September 1982.

Bacterioplankton biomass ranged from 1.8 to 24.6 mg C m⁻³ in Kaštela Bay and from 2.18 to 9.88 mg C m⁻³ in the open sea. The highest bacterioplankton biomass values in the open sea were twice lower than the highest values in the Bay. The proportion of bacterioplankton biomass in total microbial biomass is significant, on the average 14.7% in Kaštela Bay and twice that (26.3%) in the open sea. The peak bacterioplankton production was recorded from both study areas in summer. However, the Kaštela Bay may be assigned among very productive areas with the values which are highly in excess of the values in the open sea. The ratio of bacterioplankton production in Kaštela Bay to that in the open sea was 1.3 in winter to 6.3 in summer. This shows an explosive growth of bacterioplankton population in Kaštela Bay in summer (on the average 59.17 mg C m⁻³ day⁻¹) persisting over a long period (from July to October)

INTRODUCTION

Bacteria are increasingly recognized as a large and active component of marine ecosystem (SIEBURTH, 1979).

Bacterial biomass may equal that of all other organisms except phytoplankton in oceanic systems (WILLIAMS, 1981). However, our understanding of the roles bacteria play in these systems and of the environmental factors regulating the size and growth of bacterial populations has been severely limited. Until quite recently this was due in large part to a lack of suitable methods for collecting data on bacterial abundance and rate processes which could be compared to similar data on phytoplankton and zooplankton. With the introduction of epiflores-

cence microscopy for enumerating bacteria (HOBBIE *et al.*, 1977; FERGUSON and PALUMBO, 1979) and several techniques for assessing bacterial growth and production rates (FUHRMAN and AZAM, 1980; FUHRMAN *et al.*, 1980; CUHEL *et al.*, 1982; BURNEY *et al.*, 1981; NEWELL and CHRISTIAN, 1981; KARL *et al.*, 1981), bacterial ecologists are now better equipped to measure the structure and function of planktonic bacterial populations in marine ecosystem. However, present knowledge points that heterotrophic bacteria are an important component of planktonic communities and represent a major pathway for the flux of organic matter in marine and limnic pelagic ecosystems (COLE *et al.*, 1988).

Our to date knowledge of the bacterioplankton biomass in the Adriatic has been mainly based on the studies of heterotrophic bacteria by a method of culture in nutrient media. Since this method gives a very low percentages of total quantity of bacteria in the sea (0.04 to 8%), the aim of this paper is to establish the total bacterioplankton biomass and production in the Adriatic and to obtain the proportion of bacterioplankton biomass in the total microbial biomass.

METHODS

Samples were collected on monthly basis at depths of 0, 10, 20 and 35 m at the coastal sea station, and 0, 10, 20, 30, 50, 75 and 100 m at the open sea station from January 1980 to September 1982.

Total bacterial abundance was estimated with acridine orange direct counts (AODC) (HOBBIE *et al.* 1977) using a Zeiss epifluorescent microscope. For cell counting and measuring a New Porton G12 graticule (Graticules, LTD, UK) was used. Cell volumes and conversion to carbon contents were estimated after WATSON *et al.*, (1977).

Bacterial production was estimated by the increase in cell number - bacteria are separated substantially from bacteriovores by filtering the seawater sample through 3 μm filters. Increase in bacterial abundance is then followed microscopically with time (3 and 6 hours in situ conditions). Bacterial abundance (and also average cell volume) is measured to compute the rate of increase of bacterial biomass (MAYER-REIL, 1977; FUHRMAN and AZAM, 1980).

ATP was extracted and analysed in samples after HOLM-HANSEN and BOOTH'S method (1966). ATP values were transformed in total planktonic carbon by factor 250 (HOLM-HANSEN, 1973).

STUDY AREA

Samples were taken at two stations: at a coastal sea station (Kastela Bay - 1) and at an open sea station (Stoncica - 2) both in the middle Adriatic (Fig. 1)

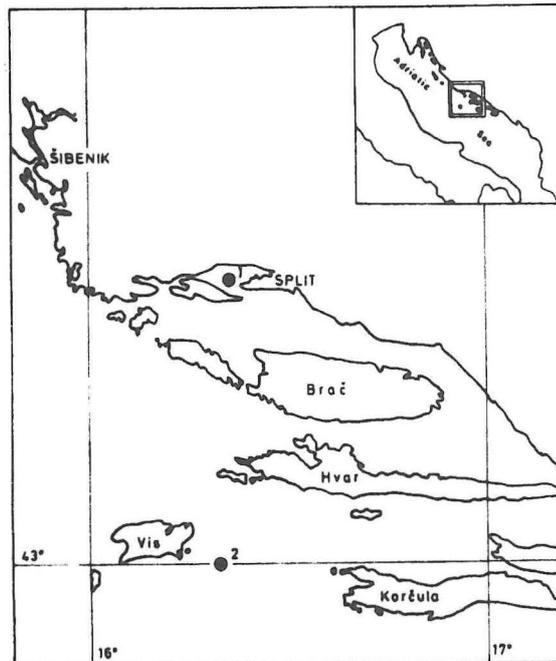


Fig.1. Study area with sampling locations: 1-coastal sea station (Kastela Bay); 2-open sea station (Stoncica)

Station Kaštela Bay is closed shallow area with an average depth of 23 m. It is characterized by great oscillations of biological, chemical and physical parameters as a result of direct land influence (ZORE-ARMANDA, 1980). The Bay is also under the influence of the city and associated industry concentrated in the area.

Station Stoncica is located south-east of cape Stoncica on the Island of Vis where the depth is about 100 m. Because of its distance from land influences, oscillations of all parameters are smaller than at the former station (BULJAN and ZORE-ARMANDA, 1979), hence this station is typical of the open middle Adriatic.

RESULTS AND DISCUSSION

Volume of bacterial cells

Size of >4000 bacterial cells was measured from the Kaštela Bay samples. They were grouped in five categories after their size (Table 1). Specimens of very tiny bacterial cells ("minibacteria") were best represented. "Minibacte-

ria" (cocci of diameter smaller than $0.6 \mu\text{m}$ and coccoid rods less than $0.6 \mu\text{m}$ long) constituted 68% of measured cells. They were followed by the rods of the size $0.6\text{-}1.2 \times 0.38\text{-}0.44 \mu\text{m}$ (24.2%), then rods of $1.2\text{-}1.8 \times 0.44\text{-}0.50 \mu\text{m}$ (5.5%) rods of $1.8\text{-}3.0 \times 0.54\text{-}0.63 \mu\text{m}$ (1.5%). Cocci of the $0.5\text{-}1.2 \mu\text{m}$ diameter occurred in smallest numbers, not more than 0.7%. The average volume of bacterial cells was μm^3 .

From the open sea samples (Stončica) the size of >4000 cells was also measured. The percentage of "minibacteria" was slightly higher (71.4%), whereas the percentage of bigger rods was lower (Table 1). The average volume of measured bacteria was $0.086 \mu\text{m}^3$.

Table 1. Procentual proportion of bacterial cells in different volume categories

Station	Volume (μm^3)				
	0.065	0.110	0.320	0.254	0.574
Kaštela Bay	68.1%	24.2%	0.7%	5.5%	1.5%
Stončica	71.4%	24.1%	0.0%	3.8%	0.7%

PALUMBO *et al.*, (1984) found coccoid rods smaller than $0.6 \mu\text{m}$ in 85% of the total of measured bacteria, FERGUSON and RUBLEE (1976) in 80%, and PAINTING *et al.*, (1985) in 87% of measured bacterial cells.

Present data on the average volume of bacterial cells are mainly comparable to those from the literature where bacterial cells were measured by fluorescence microscopy (Table 2).

Table 2. An average bacterial volume as reported for some other marine environments (μm^3)

Area	Volume (μm^3)	Author
Central Pacific	0.15	SOROKIN, 1971
Coastal area of North Caroline	0.09	FERGUSON and RUBLEE, 1976
Baltic Sea	0.06	ZIMMERMAN, 1977
Closed experimental pond	0.1	LAAKE <i>et al.</i> , 1983
Gulf of Mexico	0.078-0.096	PALUMBO <i>et al.</i> , 1984
English Channel	0.038-0.11	HOLLIGAN <i>et al.</i> , 1984
Golf Current Area	0.024-0.098	DUCKLOW, 1986

Some earlier investigations of bacterial cell volume in the middle Adriatic came to considerably higher values than recorded by our study. RISTIĆ and ŠOBOT (1972) found the average volume of coccoid forms of $0.86 \mu\text{m}^3$ in the coastal area and that of rod forms of $1.12 \mu\text{m}^3$. They recorded slightly smaller volume in the open sea ($0.65 \mu\text{m}^3$ for cocci and $0.78 \mu\text{m}^3$ for rods. CVIĆ (1963) calculated the average volume of bacterial cells of $0.25 \mu\text{m}^3$.

The differences between these and our data are considerable, presumably due to different methods applied for bacterial cell measurements. Earlier researchers used larger pore size filters ($0.45 \mu\text{m}$), through which all "minibacteria" leaked as well as light microscopy (dyeing by erythrosine) by which the distinction between detritus and bacteria could hardly be done.

Density and distribution of bacterioplankton

Bacterial numbers ranged from 1.8 to $21.4 \times 10^8 \text{ dm}^{-3}$ in Kaštela Bay samples. This recalculated to biomass is $2.07\text{-}24.60 \text{ mg C m}^{-3}$ (Fig.2)

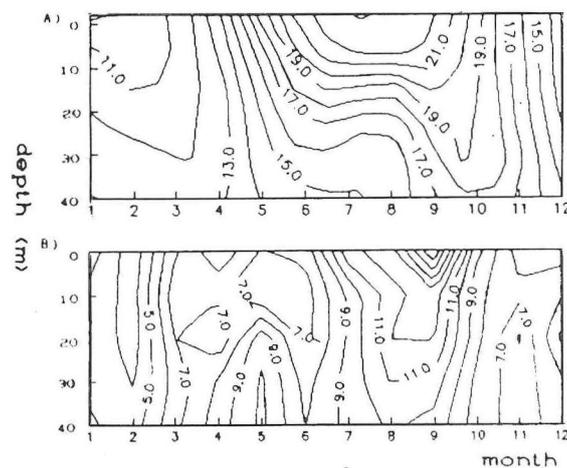


Fig.2 Vertical and temporal variations of temperature ($^{\circ}\text{C}$) (A) and bacterioplankton biomass (mg C m^{-3}) (B) in Kaštela Bay (means by depths and months for the period 1980-1982 period)

Vertical distribution of bacterioplankton showed a defined regular pattern in the coastal

area (Fig.2). In winter, when the water column is homogeneous from surface to bottom, bacterioplankton distribution is uniform throughout it. Greater oscillations of bacterial numbers by layers were recorded during stronger thermal stratification of the water column that is during summer. Their density maximum in that period occurred in the surface down to the thermocline depth (10 m). Larger quantities of bacteria in the bottom layer (May) is presumably related to the resuspension from the bottom where organic matter and bacterial quantities are larger. Earlier studies showed that the number of bacteria in Kaštela Bay and Stoničica sediment were for two orders of magnitudes greater than in the water of these areas (KRSTULOVIĆ, 1980). The relationship between temporary bottom maxima and sediment resuspension was already mentioned by ZIMMERMAN (1977) and SOROKIN (1971). These maxima very likely result from intensified currents in the bottom layer.

The observation of monthly mean bacterioplankton density for the entire period of our research show particularly marked seasonal oscillations (Fig.3). Increase in bacterioplankton density occurs in spring, even though maxima were, as a rule, recorded in summer and minima in winter. It should be emphasized that rather high values persist all summer round (from July to October).

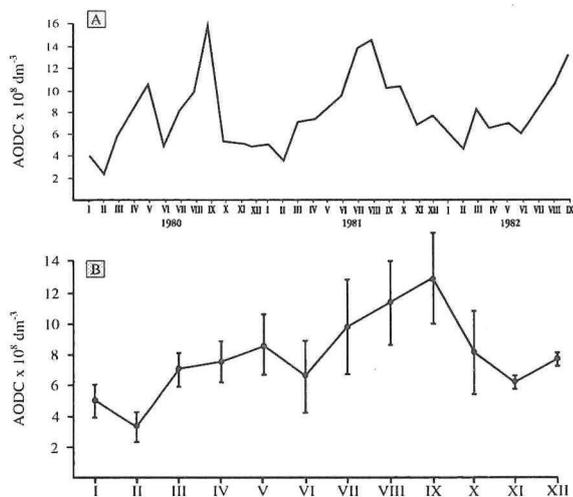


Fig. 3. Total number of bacteria in the Kaštela Bay
A) Monthly mean values
B) Monthly mean values with standard deviations for the 1980-1982 period

The number of bacteria ranged from 2.1. to 9.5 x 10⁸ dm⁻³ in the open sea (Stoničica). Recalculated to biomass this is 2.18 to 9.88 mg C m⁻³. Maximum bacterioplankton density in the area of Stonica was two times lower than the maximum values recorded from Kaštela Bay (Fig.4). Similar results were obtained by the long-term research of heterotrophic bacteria (KRSTULOVIĆ and ŠOLIĆ, 1990).

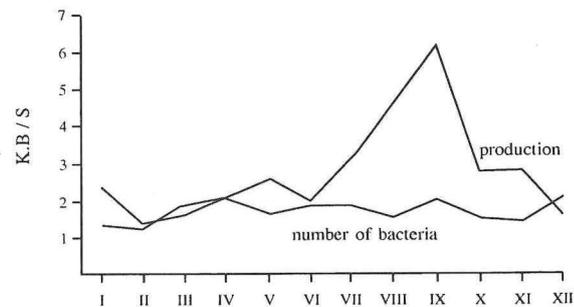


Fig. 4. The ratio of bacterioplankton density and production between the Kaštela Bay and Stoničica

Vertical distribution of bacterioplankton in the open sea is, like in the Kaštela Bay, presumably affected by temperature variations by layers (Fig. 5)

Seasonal oscillations of bacterioplankton density in the open sea are similar to those in the coastal area (Fig.6). However, the range of minimum and maximum values is far less broad. In addition, as shown by the comparison of the Fig. 3 to Fig. 6, standard deviations of monthly means are considerably greater in the coastal sea. This points to the fact that this parameter varies more in the coastal area than in the open waters. In general, all studied parameters were observed to vary more in Kaštela Bay.

Kaštela Bay is a natural area of relatively high primary production. On the one hand this is affected by a fertile Kaštela farmland, and the other by the pine wood on the Split Peninsula. In addition, the small Jadro River discharges in its eastern part, contributing to the nutrient input (BULJAN *et al.*, 1976; BARIĆ, 1989).

Man-made impacts have become progressively evident in this area for the past 20 years. Disposal of industrial and urban sewage effluents causes a further increase in biological pro-

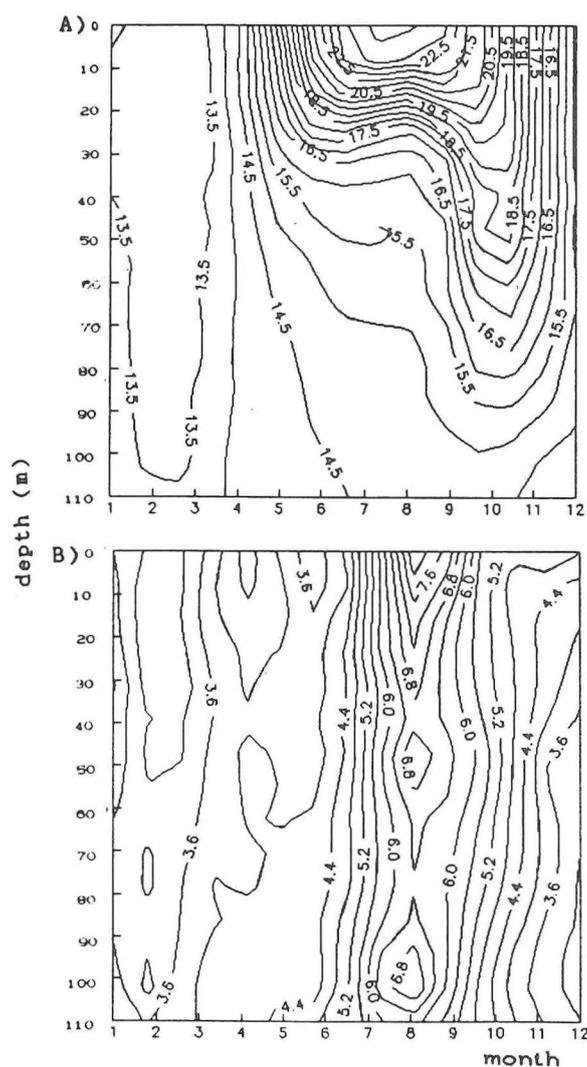


Fig. 5. Vertical and temporal variations of temperature (°C) (A) and bacterioplankton biomass (mg C m⁻³) (B) at Stončica (mean values by depths and months for the 1980-1982 period)

duction, which, at this point, should be taken adverse ecological factors. An increasing trend of gross primary production in the bay is clearly distinguished.

The value of daily gross primary production exceeded 640 mg C m⁻² for the past cycles of investigation, which meant a shift of Kaštela Bay into the most productive sea water category (PUCHER-PETKOVIĆ and MARASOVIĆ, 1989). Open Adriatic waters, far off the land influence, showed considerably lower values of primary production (about 150 mg m⁻² day⁻¹). Apart from mentioned factors the changes in Kaštela Bay (eutrophication) were estimated through

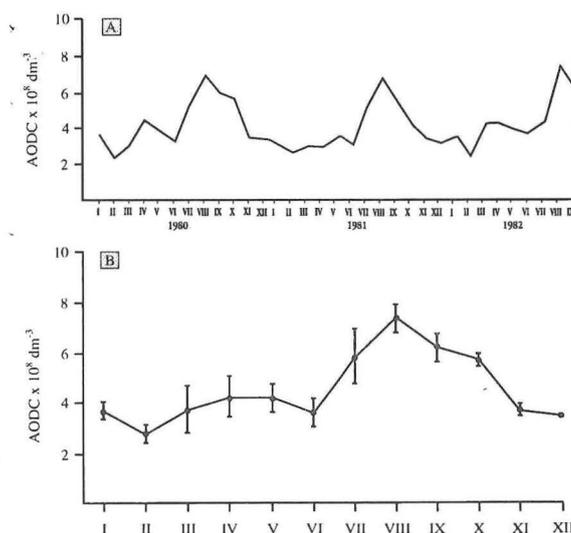


Fig. 6. Total number of bacteria at Stončica station
A) Monthly mean values
B) Monthly mean values with standard deviations for the 1980-1982 period

some chemical and physical indicators. It was observed that the ratio of nitrogen to phosphorus salts had been reduced for the past 15 years (PUCHER-PETKOVIĆ and MARASOVIĆ, 1989). This could be indicative of increased quantities in Kaštela Bay waters. As a rule, phosphorus salts confirms the fact that Kaštela Bay is a recipient of a large quantities of municipal wastewaters, the ratio of nitrogen to phosphorus of which is 5.

It was also found that the dissolved oxygen concentration increased in the upper layer of the bay and decreased in the bottom layer (BARIĆ, 1989). Such a divergence between the layers as to the oxygen content points to a long-term trend of phytoplankton photosynthetic activity intensification in the upper layer. Parallel to that the quantity of organic matter is increasing in the deeper layers. As known, organic matter is decomposed by bacteria consuming oxygen and reducing its concentrations.

All the results point to the very apparent differences in hydrographic and biological characteristics between Kaštela Bay and open sea waters, which account for their different bacterioplankton density and distribution.

Some results of bacterioplankton density studies in some other marine environments by the use of the same methods are shown in Table 3.

Table 3. Some results of bacterioplankton density in some other marine environments

Area	Nº x 10 ⁸ dm ⁻³	Author
Estuaries		
English estuaries		
Humber	64	GOULDER, 1977
Tyne	264	
Newport Estuary	61.0	PALUMBO and FERGUSON, 1978
Estuary of the eastern U.S. coast	49.0	WRIGHT, 1978
Coastal areas		
Eastern U.S. coast	5.5 - 6.8	FERGUSON and RUBLEE, 1976
Coast of South Africa	63.0	HOBBIÉ <i>et al.</i> , 1977
Baltic Sea, Kiel F.	28.0	ZIMMERMANN, 1977
Baltic Sea, Kiel B.	14.0	ZIMMERMANN, 1977
Eastern U.S. coast	68.0	WRIGHT, 1978
Eastern U.S. coast	21.0	FERGUSON and PALUMBO, 1979
Eastern U.S. coast	18.0	JOHNSON and SIEBURTH, 1979
Baltic Sea	23 - 31	MEYER-REIL <i>et al.</i> , 1979
Australian coast (coral reefs)	2.0 - 5.0	MORIARTY, 1979
Southern California	7.0 - 19.0	FUHRMAN <i>et al.</i> , 1980
Eastern U.S. coast	78.0	WILSON and STEVENSON, 1980
Rosfiord	6.0 - 20.0	LAAKE <i>et al.</i> , 1983
Southern Benguela	2.1 - 26.8	LINLEY <i>et al.</i> , 1983
English Channel	4.0 - 17.0	HOLLIGAN <i>et al.</i> , 1984
Coastal area of Barcelona	42 - 83	VIVES-REGO <i>et al.</i> , 1988
Open sea waters		
North-eastern Pacific	1.4	CARLUCCI and WILLIAMS, 1978
Baltic Sea	4.3 - 8.4	DAWSON and GOCKE, 1979
Ice covered Antarctic waters	0.1	AZAM <i>et al.</i> , 1979
Northeastern Atlantic	6.7	FERGUSON and PALUMBO, 1979
Sargasso Sea	4.2	JOHNSON and SIEBURTH, 1979
Eastern Antarctic	6.5	FUHRMAN and AZAM, 1980
Western Antarctic	0.7	FUHRMAN and AZAM, 1980
Sargasso Sea	0.2 - 0.5	LIEBEZEIT <i>et al.</i> , 1980
Antarctic, Mc Murdo	0.6 - 6.5	HODSON <i>et al.</i> , 1981
Celtic Sea	2.0 - 5.8	LINLEY <i>et al.</i> , 1983

As seen from Table 3 the number of bacteria dropped by two orders of magnitude going from estuaries (>50 x 10⁸ dm⁻³) through the coastal zones towards the open and oceanic waters (0.5 - 10 x 10⁸ dm⁻³). Bacterioplankton den-

sity shows rather broad ranges in some areas, presumably related to their climatic and hydrographic characteristics.

A comparison of our results to some literature data shows that bacterioplankton density in

Kaštela Bay mostly complies with the values reported for coastal zones and that at Stončica with the values reported for the open sea. The dependence of bacterioplankton density on some abiotic factors proved temperature to affect mostly its oscillation (Table 4).

Table 4. Correlation between bacterioplankton density and some abiotic environmental factors

Parameter	Coastal area		Open sea	
	r	P	r	P
Temperature	0.64	<0.01	0.62	<0.01
Salinity	-0.28		-0.1	
Oxygen	0.21		0.24	
Phosphate	0.14		0.23	
Nitrate	0.06		0.03	
Ammonia	-0.28		-0.19	
Silicate	0.06		0.09	

Bacterioplankton component in the microbial community

Bacterioplankton component in plankton microbial community was studied through the relationship between bacterial biomass (B - C) and total microbial biomass (ATP - C), which includes phytoplankton, bacteria and micro - zooplankton.

The distribution of total microbial biomass (ATP - C) in Kaštela Bay is given in Fig. 7. Two its density maxima are pronounced in the upper layers in spring and summer. Since phytoplankton biomass constitutes the bulk of ATP-C the distribution of total microbial biomass mainly coincides with phytoplankton distribution.

However, apart from natural spring phytoplankton density maximum in Kaštela Bay a summer maximum occurs indicative of the changes in natural oscillations and eutrophication of this area (PUCHER-PETKOVIĆ and MARASOVIĆ, 1989).

The distribution of bacterial biomass, total microbial biomass and the percentage the bacterial biomass constitutes in total microbial biomass of the Kaštela bay are presented in Fig. 7 as well.

No correlation was established between bacterioplankton biomass and ATP-C quantity. However, the percentage the bacterioplankton biomass constitutes in the total microbial biomass follows a defined regular pattern. Minimum recorded percentage of B-C in ATP-C was 3.64% and the maximum one 43.76%. For the period of our study minimum was always recorded in the surface layer and maximum in the bottom layer. This was expected in the view of the fact that vertical phytoplankton variations were better pronounced than those of bacteria, so that phytoplankton made the bulk of microbial biomass in the upper euphotic layer. In deeper layers the phytoplankton quantity is reduced and bacterial biomass considerably increases in the total microbial biomass.

Similar was reported by PALUMBO and FERGUSON (1978) and FERGUSON and RUBLEE (1976) for the coastal area of North Caroline.

As to the seasonal distribution of microbial biomass, bacterioplankton percentages in the total Kaštela Bay plankton are highest during its greatest density (summer, autumn) and lowest in winter-spring. Expressed as monthly mean values it ranged from 4.2 to 27.5% (\bar{x} =14.75%).

It is quite obvious that bacterioplankton is complementary to phytoplankton as the producer of organic matter in the microbial community. Therefore it is highly significant in the aphotic zone and upon the termination of phytoplankton blooms.

The distribution of microbial biomass (ATP-C) in the open sea (Stončica) is given in Fig. 8, showing that the ATP-C quantities are considerably lower there than in the coastal sea. Monthly means ranged from 13.80 to 32.62 mg C m⁻², with a marked maximum in spring. As distinct from Kaštela Bay, summer maximum indicating eutrophication, was not recorded.

Bacterioplankton proportion in the microbial community of the open sea was twice as great as that in the coastal sea throughout the period of our study (Fig. 8). Minimum monthly value was 13.14% and maximum 44.59% (\bar{x} =26.29%). These results are consistent with the literature data reporting that bacteria constitute up to 50% of microbial biomass (LINLEY *et al.*, 1983).

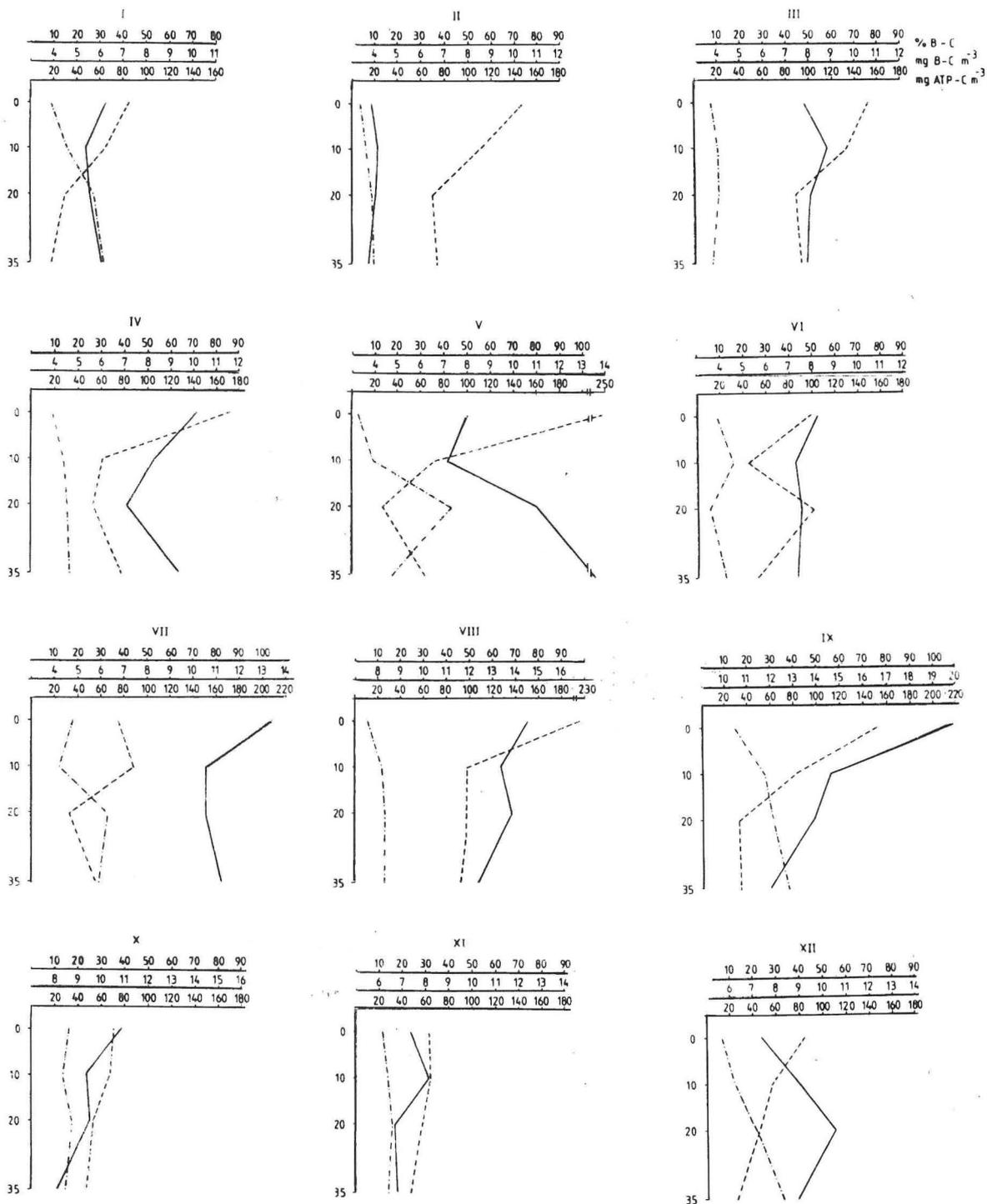


Fig. 7. Distribution of total microbial biomass - ATP-C (---), bacterioplankton biomass - B-C (—) and percentage proportion of B-C in ATP-C (-.-.-) in the Kaštela Bay

With respect to vertical distribution of B-C and ATP-C, the percentage proportion of bacterioplankton in the total microbial community shows a similar regularity as in the coastal sea. It is lowest in the surface layer where phyto-

plankton is most dense and highest in the bottom layers where phytoplankton density is lowest (Fig. 8). So, like in the coastal area, bacterioplankton contributes the bulk of organic matter production in deeper layers.

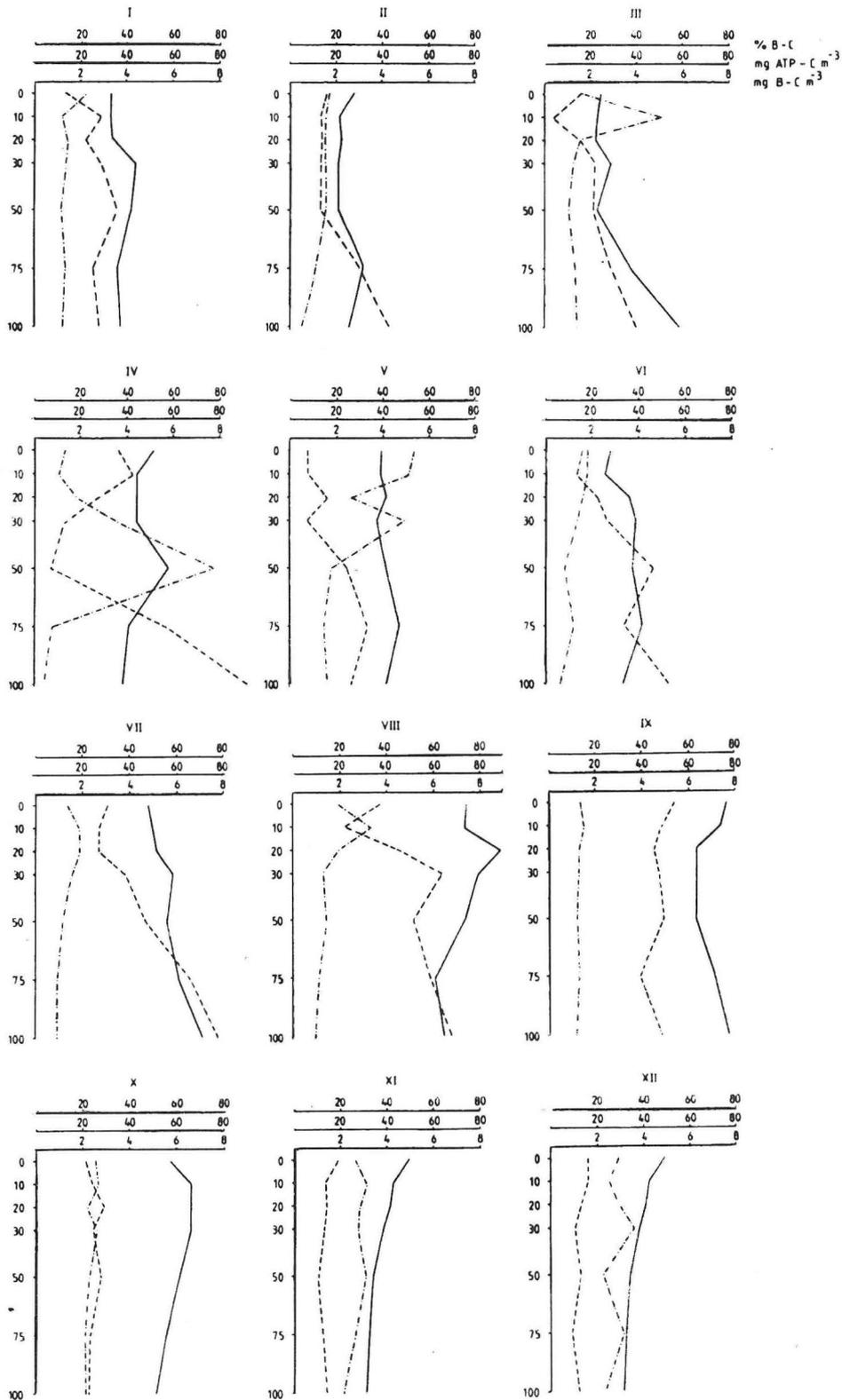


Fig. 8. Distribution of total microbial biomass - ATP-C (---), bacterioplankton biomass - B-C (—) and percentage proportion of B-C in ATP-C (-.-.) at Stončica

As shown by the literature data the proportion of bacterioplankton in the total microbial biomass ranges, on the average, between 10 and 50% (FERGUSON and RUBLEE, 1976; PALUMBO and FERGUSON, 1978; SIEBURTH *et al.*, 1976; SIEBURTH *et al.*, 1978; WILSON *et al.*, 1981; DUCKLOW, 1983), which agrees with our results.

Bacterioplankton production

Bacterioplankton production in Kaštela Bay varied from 0 to 70.48×10^8 cells $\text{dm}^{-3} \text{day}^{-1}$, what recalculated to biomass was 0 to $70.48 \text{ mg C m}^{-3} \text{day}^{-1}$.

Seasonal variations in bacterioplankton production are very marked (Fig. 9). The range between monthly minimum recorded in winter ($1.41 \text{ mg C m}^{-3} \text{day}^{-1}$) and maximum values recorded in summer ($59.17 \text{ mg C m}^{-3} \text{day}^{-1}$) was very broad pointing to an explosive development of bacterial population between July and September.

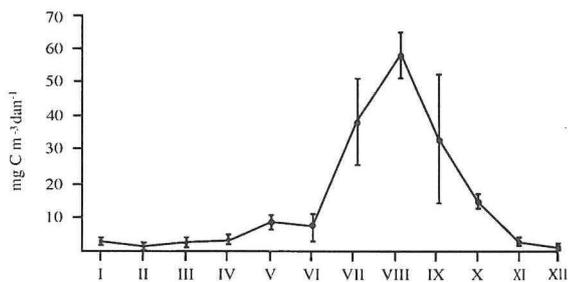


Fig 9. Seasonal oscillations of bacterioplankton production in the Kaštela Bay (monthly mean values with standard deviations for the 1980-1982 period)

The analysis of vertical and temporal variations of daily bacterial production is presented in Fig. 10.

In winter variations of daily bacterioplankton production are very small and almost uniform throughout the water column. Daily biomass increment is higher in spring mostly in the surface layer, spreading throughout the water column in June and reaching maximum in summer. Two maxima of bacterial biomass development were recorded in summer, the first one at 10 m, that is in the thermocline layer, and the second one in the bottom layer (com-

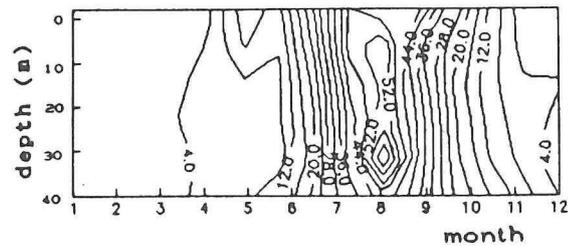


Fig. 10. Production of bacterioplankton ($\text{mg C m}^{-3} \text{day}^{-1}$) in the Kaštela Bay (means by depths and months for the 1980-1982 period)

pare the Figs. 2 and 10). The second maximum in the bottom layer (35 m) is probably due to the organic matter resuspension from the bottom layer which may stimulate the growth of bacteria (FERGUSON and PALUMBO, 1979). From September on towards winter bacterioplankton biomass values decrease. Since the water column becomes gradually homogenized the differences in bacterioplankton production between layers becoming negligible.

Bacterioplankton production is considerably lower in the open middle Adriatic than in the coastal sea. The lowest daily increment of the number of bacteria was measured to be 0 cells, that is $0 \text{ mg C m}^{-3} \text{day}^{-1}$. (at 0 m in December 1982) and the highest $15 \times 10^8 \text{ dm}^{-3} \text{day}^{-1}$, that is $15.60 \text{ mg C m}^{-3} \text{day}^{-1}$ (at 10 m in August 1982).

Seasonal variations in bacterioplankton production in the open sea are similar to those in Kaštela Bay. Minimum bacterioplankton production was recorded in winter ($1 \text{ mg C m}^{-3} \text{day}^{-1}$) and maximum in summer ($12.75 \text{ mg C m}^{-3} \text{day}^{-1}$) (Fig. 11).

Maximum values are about five times lower than in Kaštela Bay. The ratio of bacterio-

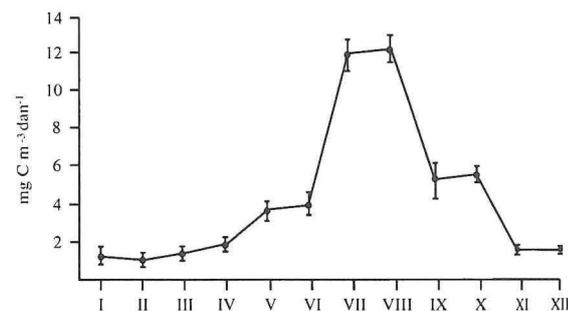


Fig. 11. Seasonal oscillations of bacterioplankton production at the Stončica (monthly mean values with standard deviations for the 1980-1982 period)

plankton production in Kaštela Bay to that at Stončica ranges from 1.35 to 6.27 (Fig. 4). If we recollect the data on bacterioplankton density where the ratio of Kaštela Bay to Stončica was from 1.23 to 2.09 it appears that within maximum production the bacterial counts do not proportionally follow the production. So, when the ratio for bacterioplankton production was 4-6 (July to September) the ratio for bacterioplankton density was not higher than 2. This is most likely due to the loss of bacteria by zooplankton elimination. Zooplankton "grazing" was found to be highest in Kaštela Bay just within the highest bacterioplankton production. It constituted 40% of the bacterioplankton production in Kaštela Bay and about 20% at Stončica. The same was established for phytoplankton grazing (HOMEN, 1979).

It is also shown in Fig. 11 that standard deviations from monthly means of bacterioplankton production at Stončica were considerably smaller than in Kaštela Bay (Fig. 9). This particularly applies to summer when large variations in bacterioplankton production were recorded from Kaštela Bay (for example the monthly means ranged from 18.42 to 64.87 mg Cm⁻³ day⁻¹ in September). These differences conform to earlier brought out differences in physico-chemical and biological characteristics of the study areas.

The analysis of vertical fluctuations during bacterioplankton production in the open middle Adriatic (Fig. 12) point to very small variations in daily bacterial biomass increment by depth in winter, when the values are, in general, very low and water column homogeneous from surface to bottom (Fig. 4). In spring an intensified production was observed in the layer from 70 m depth to bottom. This was most presumably due to the sedimentation of organic matter originating from the surface layers where phytoplankton production was particularly intensive. Deep chlorophyll maximum was recorded just from the 50 to 70 m layer (MARASOVIĆ and PUCHER-PETKOVIĆ, 1988). From June on bacterioplankton population gradually reached peak development in July and August at thermocline level. After summer maximum bacterioplankton values gradually decline approaching winter and are uniformly distributed throughout

the water column like they are in the coastal waters.

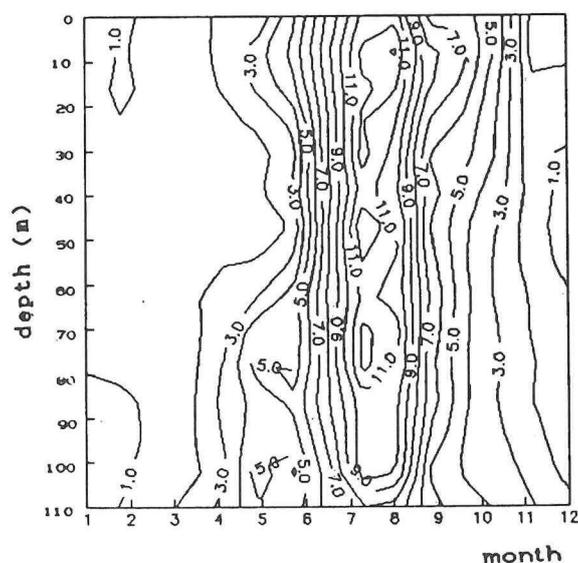


Fig. 12. Production of bacterioplankton (mg C m⁻³ day⁻¹) at Stončica (means by depths and months for the 1980-1982 period)

A comparison of the Figs 2 and 10 for Kaštela Bay and Figs 5 and 12 for the open sea revealed that the variations in bacterioplankton distribution and production coincided with the both vertical and temporal temperature variations. So, significant correlation was recorded between sea water temperature and bacterioplankton production in both study areas (Fig. 13).

Similar was reported by some other authors for some marine environments where

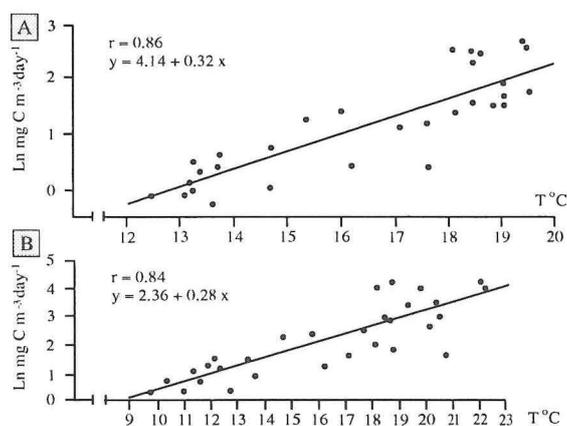


Fig. 13. Ratio of bacterioplankton production to temperature in the Kaštela Bay (A) and at Stončica (B)

temperature ranges were very large (HAGSTROM and LARSON, 1984; DUCKLOW, 1986).

The analysis of literature data on bacterioplankton production in different marine environments shows very wide value ranges (Table 5)

P/B values for Kaštela Bay are 0.27 to 4.50 (Table 6). This ratio varies very little in winter, ranging from 0.27 to 0.37. This means that daily variation of bacterioplankton biomass is very small, that is that daily increment in bacterial numbers or biomass is not more than 0.3 times

Table 5. Production of bacterioplankton in different marine environments

Area	N° x 10 ⁸ dm ⁻³	Author
Coastal area		
<i>Solomon sea</i>	0.3 - 46.0	SOROKIN, 1971
<i>Kiel-Fiord and Kiel-Bight</i>	0.0 - 78.0	MEYER-REIL, 1977
<i>Coastal area of Baltic</i>	2.0 - 10.0	HAGSTROM <i>et al.</i> , 1979
<i>North-western USA coast</i>	0.7 - 72.0	FUHRAM and AZAM, 1980
<i>Southern California</i>	10.0 - 35.0	FUHRAM and AZAM, 1980
<i>Coast of Georgia, USA</i>	19.22 - 177.6	NEWEL and CHRISTIAN, 1981
<i>Carribbean Sea</i>	15.0 - 40.0	BURNEY <i>et al.</i> , 1982
<i>Coastal area of Baltic</i>	0.0 - 32.0	LARSON and HANGSTROM, 1982
<i>Southeastern coast of USA</i>	4.0 - 12.0	NEWEL and FALLON, 1982
<i>English Channel</i>	55.8 - 84.0	LINEY <i>et al.</i> , 1983
<i>Antarctic, Prydz Bay</i>	0.08 - 0.40	PAINTING <i>et al.</i> , 1983
<i>Banguela</i>	17.8 - 138.4	LUCAS <i>et al.</i> , 1986
Open Sea		
<i>Carribbean Sea</i>	4.08	KARL, 1979
<i>Antarctic</i>	0.004 - 2.9	FUHRAM and AZAM, 1980
<i>Antarctic</i>	0.002 - 0.009	HANSON <i>et al.</i> , 1983
<i>Irish Sea</i>	3.0 - 12.7	LOCHTE and TURLEY, 1985

Comparing the values of bacterioplankton production we obtained to those shown in Table 5, Kaštela Bay appears to belong to very productive areas such as coastal area of Baltic, Solomon Sea and northwestern coast of USA. Open sea is less productive with the maximum of 15.6 mg C m⁻³ day⁻¹. However for the most part of the year these values range between only 1 and 4 mg C m⁻³ day⁻¹.

P/B coefficient

P/B coefficient is the ratio of bacterioplankton production to bacterioplankton biomass which is good indicator of the enrichment of bacterioplankton standing stock.

greater than the standing stock. In summer, when the generation time is shortest and production at its peak, bacterioplankton standing stock is increased by 4.5 times.

In winter P/B ratio values in the open sea are almost the same as in Kaštela Bay (from 0.27 to 0.36). However, the difference in these values are considerable in summer. Maximum P/B value of 2.36 was recorded in July. This is twice less than found for Kaštela Bay in the same period.

The difference in P/B coefficient between different areas were reported by some other authors. SOROKIN (1971) found the P/B coefficient range of 0.7 to 2.8 for tropical oceanic waters (Solomon Sea) which is very close to the range we found for the open middle

Adriatic. VYSHKVARTEV (1980) reported the P/B coefficient range of 0.06 to 1.9 for the Japanese Sea.

Table 6. Monthly mean values of P/B coefficient

Month	STATION			
	Kaštela Bay		Stončica	
	x	sd	x	sd
January	0.35	0.07	0.33	0.13
February	0.38	0.13	0.35	0.08
March	0.27	0.06	0.36	0.04
April	0.47	0.09	0.55	0.31
May	1.04	0.34	0.83	0.07
June	1.01	0.22	1.01	0.09
July	3.88	1.98	2.36	0.38
August	4.50	1.35	1.57	0.04
September	2.48	1.64	0.81	0.23
October	2.10	0.95	1.02	0.22
November	0.62	0.15	0.37	0.01
December	0.27	0.08	0.30	0.04

The P/B coefficient values ranged from 0.06 to 1.9 in the English Channel (LINLEY *et al.*, 1983). Marine areas richer in organic matter showed higher values of P/B coefficient. MEYER-REIL (1977) performed similar research in Kiel Fiord in the Baltic Sea in summer and found that the P/B value was about 3. Benguela upwelling area was reported to have the P/B coefficient of 0.99 to 4.2 (LUCAS, 1986). So, the Kaštela Bay P/B coefficient is very similar to its values in the upwelling areas. This is indicative of considerable variations in biomass increment in this area. There is no doubt that this may be related to earlier described changes and properties of Kaštela Bay, which is a fairly changed marine environment.

CONCLUSIONS

Bacterioplankton biomass ranged from 1.8 to 25.6 mg C m⁻³ in Kaštela Bay and from 2.18 to 9.88 mg C m⁻³ in the open sea. The highest values in the open sea are two times lower than the highest values in Kaštela Bay. The differences between values for total microbial biomass,

which varied within a 26.5-246.6 mg C m⁻³ range in Kaštela Bay and within a 13.8-32.62 mg C m⁻³ range in the open sea, were still greater. Bacterioplankton biomass constitutes a significant part of the total microbial biomass. It forms on the average 14.7% in Kaštela Bay and almost twice that value (26.3%) in the open sea. Bacterioplankton appears to play a more significant part in the organic carbon enrichment of the open sea, which is oligotrophic, than of Kaštela Bay, which is almost quite eutrophized. A pattern of its seasonal and vertical distribution was found to be regularly related. This regular pattern is manifested as higher proportion of bacterio-plankton biomass in the total microbial biomass in bottom layers and during peak bacterioplankton density (summer, autumn) that is after the termination of phytoplankton blooms.

The highest bacterioplankton production was recorded from both study areas in summer. However, Kaštela Bay may be assigned among very productive areas with the values which are highly in excess of values in the open sea. The ratio of bacterioplankton production in Kaštela Bay to that at Stončica was 1.35 for winter and 6.27 in summer. This shows an explosive growth of bacterioplankton population in Kaštela Bay in summer (on the average 59.17 mg C m⁻³ day⁻¹) persisting over a longer period (from July to October).

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Raspodjela i proizvodnja bakterioplanktona u srednjem Jadranu

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KRATKI SARDŽAJ

Istraživanja biomase i proizvodnje bakterioplanktona, te studiranje odnosa biomase bakterioplanktona i ukupne mikrobne biomase vršena su mjesečno od januara 1980. do septembra 1982. godine u obalnom (Kaštelanski zaljev) i otvorenom (Stončica) području srednjeg Jadrana.

Biomasa bakterioplanktona na području Kaštelanskog zaljeva kretala se od 24.6 mg C m⁻³, na području otvorenog mora od 2.18 do 9.88 mg C m⁻³. Maksimalne vrijednosti biomase bakterioplanktona na području otvorenog mora za oko 2 puta su manje od maksimalnih vrijednosti iznijetih za Kaštelanski zaljev. Još veće razlike utvrđene su za vrijednosti ukupne mikrobne biomase koje su se u Kaštelanskom zaljevu kretale od 26.5 do 246.6 mg C m⁻³, na području otvorenog mora od 13.8 do 32.62 mg C m⁻³.

Učešće biomase bakterioplanktona u ukupnoj mikrobnj biomasu je značajno. U Kaštelanskom zaljevu iznosi u prosjeku 14.7%, na području otvorenog mora dvostruko više (26.3%). Proizlazi da bakterioplankton ima značajniju ulogu u obogaćivanju sredine organskim ugljikom na području otvorenog mora koje je oligotrofno područje nego u Kaštelanskom zaljevu gdje su ostali članovi lanca ishrane zastupljeni većim brojem.

Najveća aktivnost bakterioplanktona s obzirom na brzinu promjena biomase i na veličinu dnevnog prirasta biomase utvrđena je u ljetnom periodu na oba istraživana područja. Međutim Kaštelanski zaljev se po vrijednostima za proizvodnju bakterioplanktona može svrstati u vrlo produktivno područje s vrijednostima koje su znatno veće nego na području otvorenog mora.

Naime, u Kaštelanskom zaljevu vrijednosti za proizvodnju bakterioplanktona su se kretale u prosjeku od 1.41 do 59.17 mg C m⁻³ dan⁻¹, na Stončici od 1.3 do 12.75 mg C m⁻³ dan⁻¹. Treba naglasiti da se visoke vrijednosti za proizvodnju bakterioplanktona u Kaštelanskom zaljevu zadržavaju kroz duži vremenski period (od srpnja do listopada).

