Vol. 9: 41-45, 1995 | AQUATIC MICROBIAL ECOLOGY Aquat microb Ecol | Published April 28

The relation between bacterioplankton and phytoplankton production in the mid Adriatic Sea

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ABSTRACT: The ratio of bacterioplankton: phytoplankton production was studied on a monthly basis from January 1980 to September 1982 in the area of the coastal and open mid Adriatic Sea. Bacterial production constituted significant percentages of phytoplankton production at both sites. Bacterioplankton production amounted to, on average, 9 to 28% of phytoplankton production in the coastal sea upper layers, and 10 to 40% in the open sea. On some occasions, bacterioplankton production exceeded phytoplankton production. This occurred during the summer when bacterioplankton production was maximal and the phytoplankton bloom was declining in the surface as well as in deeper layers where primary production was very low due to poor light penetration. Our results suggest that bacterial biomass could be a significant source of carbon for higher trophic levels in the Adriatic, particularly in the oligotrophic open area.

KEY WORDS: Bacterioplankton · Phytoplankton · Production · Adriatic Sea

INTRODUCTION

Productivity and biomass estimates indicate that phytoplankton and free-living heterotrophic bacterioplankton mediate most of the flow of carbon and associated nutrients from dissolved inorganic and organic biomass available to particle grazers in the water column (Pomeroy 1974, Fuhrman et al. 1980). Large-scale geographic and vertical distributions of phytoplankton and bacterioplankton suggest a general dependence of bacteria on phytoplankton production (Bird & Kalff 1984). The amount of bacterial production in relation to primary production is the subject of many recent investigations. Cole et al. (1988) found that bacterial production, estimated with a wide variety of methods, was significantly correlated with primary production and that bacterial production was about 30% of net primary production across a wide range of trophic states.

So far, the knowledge about the production of organic matter in the Adriatic mainly refers to primary production, estimated in the Adriatic since 1962 (Pucher-Petković et al. 1988). However, the role of bacteria in the production of organic matter in the Adriatic is totally unknown and the aim of this research is to evaluate the role of bacteria as a producer of organic matter in relation to the primary production. The investigation was carried out in 2 different areas of the Adriatic: in the oligotrophic open sea and in the coastal area which is under the process of eutrophication.

STUDY AREA

Samples were taken at 2 stations: at a coastal sea station (Kašela Bay, Stn 1) and at an open sea station (Stončica, Stn 2) both in the mid Adriatic (Fig. 1).

Kaštela Bay is a closed shallow area with an average depth of 23 m. The Bay communicates with the adjacent channel through an inlet of 1.8 km width and 40 m depth. The river Jadro, which discharges into the eastern part of the Bay, is an important freshwater source. The eastern part of the Bay also receives large quantities of untreated municipal and industrial effluents. Significant changes of some parameters in the last decade indicate that eutrophication has taken place in this area, as a result of direct land influence. Primary production increased from 150 g C m^{-2} in 1970 to 240 g C m^{-2} in 1985 (Pucher-Petković & Marasović 1989). The same authors also recorded an increasing

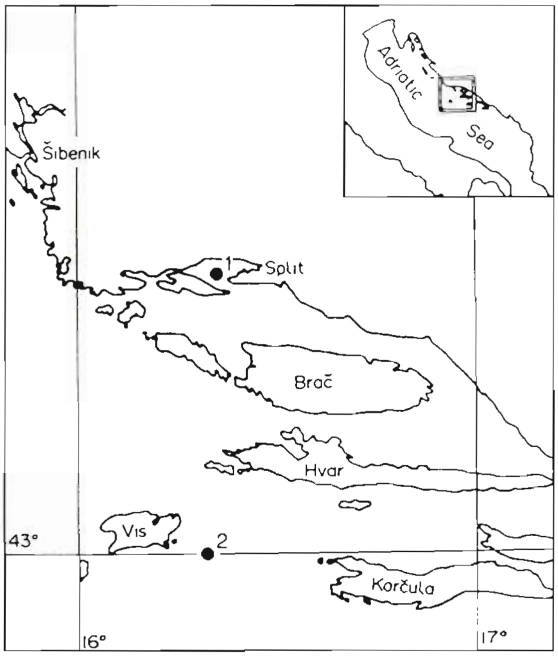

Fig. 1. Study area with sampling locations: Stn 1, coastal sea station (Kaštela Bay); Stn 2, open sea station (Stončica)

trend of oxygen saturation in the layer of intensive photosynthesis and a decreasing trend in the near-bottom layer. It was further observed that the ratio of nitrogen to phosphorus salt (the Redfield ratio) decreased over the last 15 yr. The average decrease of sea-water transparency, measured by Secchi disc, was 3 m in the period 1971 to 1988.

Station Stončica is located southeast of Cape Stončica 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 & Zore-Armanda 1979), hence this station is typical of the open mid Adriatic.

METHODS

Samples were collected on a monthly basis from January 1980 to September 1982 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 each sample bacterial counts and production as well as primary production were measured.

Enumeration of bacteria was made by epifluorescence microscopy using the standard AODC technique (Hobbie et al. 1977). For biovolume estimates, length and width of bacterial cells were measured with an eyepiece graticule (New Porton G12; Graticules, Ltd, England). Volumes were calculated as $0.785\,W^2(L - W/3)$, where W is width and L is length (Bratbak 1985). The average volume of bacterial cells was 0.095 μm^3 in Kaštela Bay and 0.086 μm^3 at Stončica (>4000 cells were measured for each station).

Bacterial production was assessed by bottle incubation experiments using 300 ml glass bottles (Meyer-Reil 1977, Fuhrman & Azam 1980). Bacteria were separated substantially from bacteriovores by filtering the seawater sample through 3 μm filters. Increase in bacterial number was than followed microscopically with time (after 3 and 6 h at *in situ* conditions). Bacterial abundance (and also average cell volume) is measured to compute the rate of increase of bacterial biomass (Meyer-Reil 1977, Fuhrman & Azam 1980).

Phytoplankton production was measured by the ^{14}C method (Steeman-Nielsen 1952). Samples (125 ml) were incubated at *in situ* conditions for 6 h. After incubation the samples were filtered through membrane filters (pore size 0.20 μm). Activity on the filters was counted by the International ^{14}C Agency. Production per day was calculated using the ratio of irradiance per day/irradiance per incubation time.

RESULTS AND DISCUSSION

Bacterial numbers ranged from 1.8×10^8 to 21.4×10^8 l^{-1} in Kastela Bay samples, and from 2.1×10^8 to 9.5×10^8 l^{-1} in the open sea (Stončica). Recalculated to biomass this represents 1.8 to 24.6 mg C m^{-3} in Kaštela Bay and 2.18 to 9.88 mg C m^{-3} in the open sea. Maximum values of bacterioplankton biomass in Kaštela Bay were twice those in the open sea. This difference is due to the different characteristics of the study areas. Average Secchi depths in the period 1980 to 1982 were 10 m in Kaštela Bay and 24 m at Stončica. The (NO_3 + NO_2 + NH_4)-N/PO_4-P atomic ratio ranged most frequently from 16 to 24 in Kaštela Bay while the open sea was characterized by relatively frequent values <36 (Viličić & Stojanoski 1987). Average salinity values for the same period were 36.80‰ in Kaštela Bay and 38.39‰ at Stončica. Mean concentrations of chlorophyll *a* for the period 1980 to 1982 were 1.35 mg m^{-3} in Kaštela Bay and 0.20 mg m^{-3} at Stončica (Pucher-Petković et al. 1988).

Vertical and temporal distribution of temperature, biomass and production of bacterioplankton are shown in Figs. 2 & 3. Vertical distribution of bacterioplankton showed a defined regular pattern at both investigated areas. In winter, when the water column is homogeneous from surface to bottom, bacterioplankton density is likewise uniform. Great differences in bacterial numbers with depth were recorded during stronger stratification of the water column, that is during summer. Maximum density in that period occurred in the surface layer down to the thermocline depth. Proceed-

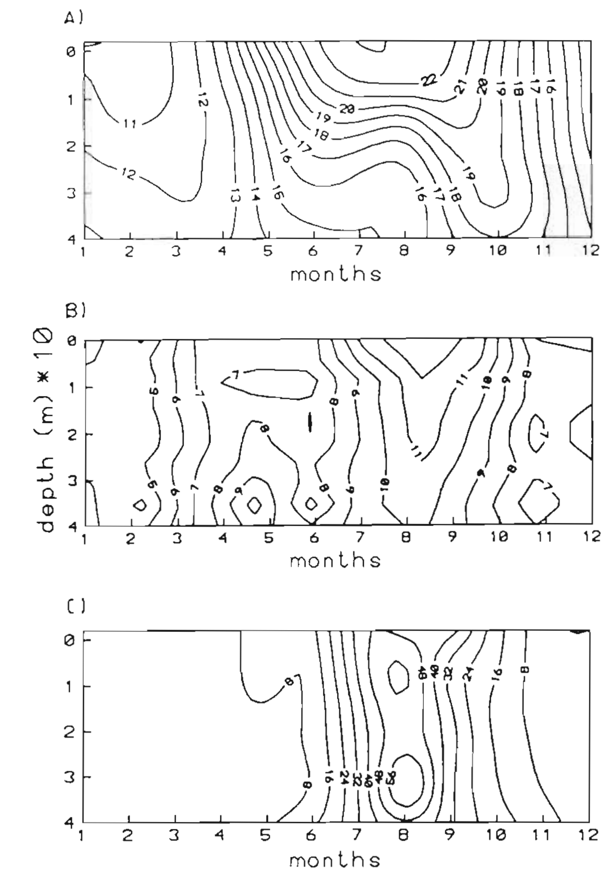

Fig. 2. Spatial and temporal distribution of (A) temperature (°C), (B) biomass of bacterioplankton (mg C m^{-3}), and (C) production of bacterioplankton (mg C m^{-3} d^{-1}) in Kaštela Bay (mean values for the period 1980 to 1982)

ing from autumn towards winter, the water column homogenizes again and bacterioplankton distribution gradually becomes uniform. The observations of monthly mean bacterioplankton density for the entire period of our research showed particularly marked month-to-month oscillations. An increase in bacterioplankton density occurred in spring (May, June), even though maxima were, as a rule, recorded in summer (July, August) and minima in winter (from December to March). It should be emphasized that rather high values persisted all summer (from July to September).

The production of bacterioplankton ranged from 1.41 to 59.17 mg C m^{-3} d^{-1} in Kaštela Bay and from 1 to 12.75 mg C m^{-3} d^{-1} in the open sea (Stončica) (Fig. 4). Seasonal variations in bacterioplankton production were very pronounced at both stations, but the maximum values were about 5 times lower at the open sea station. All the results point to the very apparent differences in hydrographic and biological characteristics between Kaštela Bay and the open sea station, which account for their different bacterioplankton density and production.

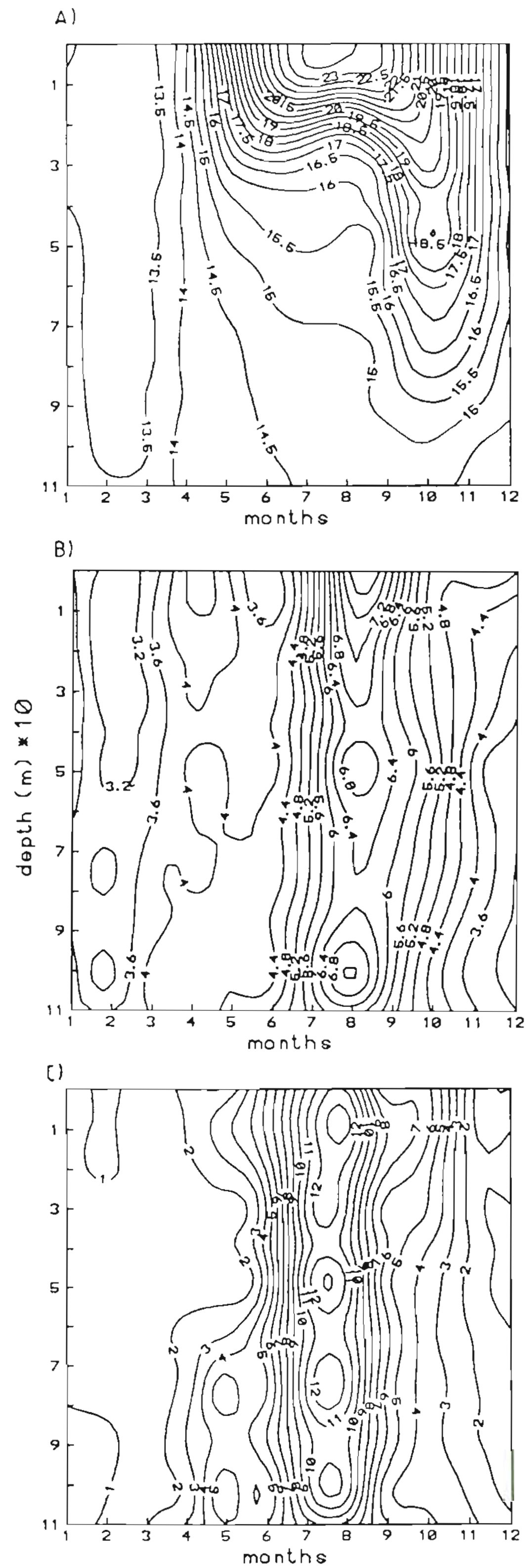

Fig. 3. Spatial and temporal distribution of (A) temperature (°C), (B) biomass of bacterioplankton (mg C m^{-3}), and (C) production of bacterioplankton (mg C m^{-3} d^{-1}) at Stončica (mean values for the period 1980 to 1982)

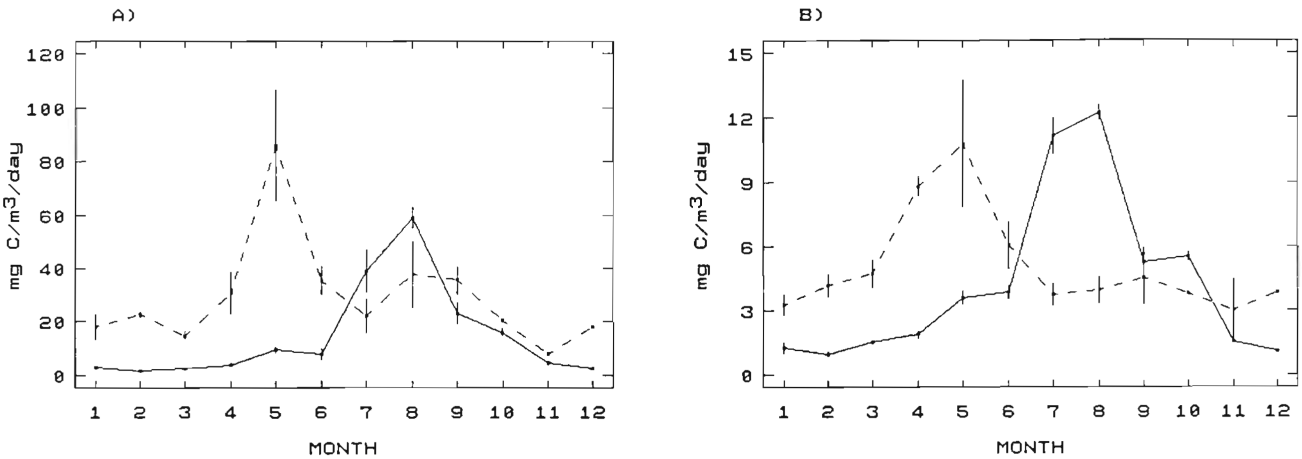

Fig. 4. Seasonal oscillations of bacterial (solid lines) and phytoplankton (dashed lines) production (mean values integrated for the entire water column) at (A) Kaštela Bay and (B) Stončica. All values are 3 yr means with 1 SE

The phytoplankton production ranged from 7.91 to 75.42 mg C m^{-3} d^{-1} in Kaštela Bay, and from 2.96 to 11.23 mg C m^{-3} d^{-1} at Stončica. Maximum phytoplankton production was recorded from both areas mainly in spring, and that of bacteria in summer (Fig. 4). This shows a time shift in their succession. However, it should be emphasized that bacterioplankton begins to increase intensively during maximum phytoplankton bloom, but its maximum occurs in summer under optimum temperature conditions. Presumably, during maximum phytoplankton production, algal metabolites stimulate the beginning of bacterioplankton population growth. However, its maximum occurs in summer under optimum temperature conditions in the presence of large quantities of dissolved organic matter produced by phytoplankton as well as an increased quantity of dead phytoplankton cells. It is obvious that after phytoplankton bloom, the quantity of dead cells, along with favorable temperature, contribute to optimum conditions for bacterioplankton growth in both Kaštela Bay and the open sea.

Bacterioplankton production constitutes a significant percentage of primary production values in both study areas. Thus, transforming a significant amount of organic carbon produced by phytoplankton, bacteria are an important source of carbon for higher trophic levels in microbial food web at the study areas. Bacterioplankton production amounted, on the average, 9 to 28% of phytoplankton production in the Kaštela Bay upper layers, and from 10 to 40% in the open sea. The contribution of bacterioplankton in the open sea is thus double that in the coastal area, suggesting that bacterioplankton plays a more important part as a vital link in the food web in the oligotrophic open sea area, than in the eutrophic Kaštela Bay. That is to say, in the oligotrophic open sea a significant part of primary production was channelled to higher trophic levels through the bacterial component. Thus, in this area, besides the classic food chain, the microbial loop could be an important link between primary production and higher trophic levels. The finding that bacterial carbon in oligotrophic waters is a substantial fraction of the total POC and biomass is implicit in several studies (Linley et al. 1983, Cho & Azam 1987, Fuhrman et al. 1989). However, the study of Cho & Azam (1990) has shown that bacterial biomass is commonly 2 to 3 times greater than phytoplankton biomass in oligotrophic waters.

The bacterial:primary production ratio throughout the water column followed a defined regular pattern. Minima of bacterioplankton production expressed as a percentage of primary production were always recorded in the surface layers where phytoplankton were most abundant and maxima in the bottom layers where phytoplankton density was very low. It should be emphasized that, on some occasions, bacterioplankton production exceeded phytoplankton production. This occurred during the summer when bacterioplankton production was maximal and phytoplankton bloom decayed, as well as in deeper layers where primary production was at a minimum due to poor light penetration.

Painting et al. (1985) also found that bacterial production exceeded phytoplankton production at the end of the bloom in Prydz Bay (Antarctica) by as much as an order of magnitude and even in deeper layers (142 and 3700 m). Similar was established by Lucas et al. (1986) at 2 Southern Benguela stations (SW Africa). However, on average, bacterial production in different marine environments does not exceed 30% of phytoplankton production (Table 1). Our results for the Adriatic Sea are very close to the results reported in Table 1

The results of our study show that bacterial production amounts to between 9 and 28% of primary pro-

Table 1 Bacterioplankton production:primary production ratio (%) in different marine environments

Area	%	Source
English Channel	2–23	Derenbach & Williams (1974)
Kiel Bight, Baltic	15–30	Meyer-Reil (1977)
S. California Bight	9–17	Fuhrman & Azam (1980)
Baltic Sea	18–24	Larson & Hagström (1992)
Georgian coast	5–25	Newell & Fallon (1982)
New York Bight	25	Ducklow & Kirchman (1983)
Rosfjord, Norway	12–15	Laake et al. (1983)
Chesapeake Bay	30	Malone & Ducklow (1990)
California Bight	10–25	Fuhrman et al. (1980)

duction in the eutrophic coastal area (Kastela Bay) and between 10 and 40% of primary production in the oligotrophic open sea area (Stončica), suggesting that the bacterial biomass produced could be a significant source of carbon for higher trophic levels particularly in the oligotrophic open Adriatic.

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