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The epiplankton community in the southern Adriatic: Multiple trophic levels along the south - north and inshore-offshore gradients

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The epiplankton community was investigated during Meduza cruises along south - north and offshore – inshore transects in the middle and southern Adriatic in spring 2002. The diel and vertical distribution of heterotrophic bacteria, phytoplankton pigment composition, micro- and mesozooplankton were assessed. At most stations we observed a thermocline at approximately 20 m and a prominent chlorophyll a peak at about 70 m depth. The integrated phytoplankton and bacterial biomass were lower at the station in the central part of the southern Adriatic, and increased gradually towards middle Adriatic and towards coastal stations. Vertical profiles of both bacterial abundance and production showed a distinct peak in the surface layer. Bacterial abundance was high also in the layer of the deep chlorophyll a maximum. Higher bacterial production was associated with elevated abundance of pico- and nanoplankton feeding zooplankton indicating that bacterial populations were generally controlled by predation.

Key words: heterotrophic bacteria, phytoplankton pigments, microzooplankton, mesozooplankton, Adriatic Sea

INTRODUCTION

Heterotrophic and autotrophic bacteria are recognized as an important component of the pelagic food web (AZAM & MALFATTI, 2007) and the variability of the flux of organic matter into the microbial food web, the sinking of the organic matter and the grazing food chain may determine overall plankton production (AZAM *et al.,* 1993). Bacterial abundance and growth rate is controlled by substrate availability (bottom-up control) and by predation or virus infection (top-down control). Predation has been identified as the main force that influences food web structure and species composition of the different trophic levels (BROOKS & DODSON, 1965). Direct and indirect effects of predation have been studied in the classical grazer food chain

– for example metazoan predation on protozoa (SANDERS & WIKHMAN, 1993) and predation on bacteria at various trophic levels. A number of investigations have dealt with pelagic communities in different hydrodynamic regimes, showing enhanced bottom-up control on bacteria from oligotrophic to eutrophic sites and top-down control on bacteria from surface to deeper layers (DUFOUR & TORRETON, 1996; TANAKA & RASSOULZADEGAN, 2002; 2004).

The significance of protozoa and their size/selective grazing on bacteria was studied in the laboratory (TURK & HAGSTRÖM, 1997) and during several field studies in the Adriatic Sea (ŠOLIĆ & KRSTULOVIĆ, 1991; ŠESTANOVIĆ, 2004; BOJANIĆ *et al.,* 2006; ŠOLIĆ *et al*., 2009). The distribution and productivity of planktonic bacteria have been mainly investigated in the northern and middle Adriatic basins. Studies of seasonal dynamics showed a bottom-up control on bacteria with an increasing abundance as a consequence of eutrophication (ŠOLIĆ & KRSTULOVIĆ 1991; 1994; KRSTULOVIĆ *et al.,* 1995; ŠOLIĆ *et al*., 1998, ŠOLIĆ *et al*., 2009), while grazing strongly influenced the microbial food web in the oligotrophic open sea (ŠOLIĆ & KRSTULOVIĆ, 1994; ŠESTANOVIĆ *et al,.* 2004; BOJANIĆ *et al*., 2006). Long-term data indicate also the importance of changes in water mass dynamics affecting nutrient availability and biological parameters (ŠOLIĆ *et al*., 2008).

Middle and south Adriatic biogeochemical parameters are influenced by different water masses. The general circulation pattern features an incoming northward current along the eastern Adriatic coast comprised of Ionian surface water and Levantine intermediate water (LIW), while a southward outflow prevails along the western coast (ORLIĆ *et al.,* 1992). The surface circulation in the south Adriatic forms a gyre that isolates the middle Adriatic from open Mediterranean waters. The Bimodal Oscillating System (BiOS) was proposed to explain the water exchange between the Adriatic and northern Ionian Seas across the Otranto Strait (CIVITARESE *et al.*, 2010). Analyses of a 20 year time-series of salinity and nutrients in the southern Adriatic indicated that the distribution of nutrients is related to variations in the Ionian Sea that well up or down the nitracline in the Adriatic (CIVITARESE *et al.,* 2010).

Primary production in the southern Adriatic appears to be controlled by changes in winter climatic conditions that determine convective mixing and the amount of nutrients available for autotrophic consumption in relation to changes in oceanographic mechanisms (GAČIĆ *et al.,* 2002; CIVITARESE *et al.,* 2010). The maximum phytoplankton biomass was recorded in spring (ANTOINE *et al*., 1995; NINČEVIĆ *et al*., 2002; SANTOLERI *et al*., 2003; MOROVIĆ *et al*., 2004). An offshore high pigment core in the southern Adriatic was reported as a rare phenomenon of short to medium term duration in March and April. A highly variable spring phytoplankton bloom influenced population density which can change by an order of magnitude from year to year (VILIČIĆ *et al*., 1989). Moreover, several publications suggested the possible impact of circulation on bacterioplankton and zooplankton abundance and community structure in the eastern part of the Adriatic Sea and the open waters of the southern Adriatic (DULČIĆ & GRBEC, 2000; KRŠINIĆ & GRBEC, 2002, 2006; BATISTIĆ *et al.*, 2004; BENOVIĆ *et al*., 2005; LUČIĆ *et al*., 2005; ŠOLIĆ *et al.,* 2009; NINČEVIĆ GLADAN *et al*., 2010).

This study is an extension of the results published by BENOVIĆ *et al.* (2005) on the multidisciplinary investigation of plankton performed during MEDUZA cruises by the research vessel "Naše more" but focuses more on microbial variations. Two transects starting from the central part of the southern Adriatic were studied: a south - north transect from the south Adriatic Pit towards the middle Adriatic (south Adriatic Pit - Palagruža - Jabuka pit) and an offshore - inshore transect from the south Adriatic Pit towards coastal stations (from > 1000 m depth to < 300 m depth).

The aim of this paper is to evaluate the bacterial abundance and production in the euphotic layer in the oligotrophic south Adriatic Pit in relation to phytoplankton and zooplankton distribution. Phytoplankton composition was assessed in terms of chemotaxonomic pigment analysis while zooplankton organisms were grouped according to their trophic role into pico-, nano-, and microplankton feeders.

MATERIAL AND METHODS

Study area and sampling

The southern Adriatic is circular, app. 1,200 m deep depression which is bounded by a 250 m Palagruža sill to the north and an 800 m sill at the Otranto Straits to the south (Fig. 1). Sampling for bacterio-, phytoplankton, meso- and microzooplankton was carried out in the southern Adriatic during the MEDUZA I cruises by R/V "Naše more", from 25th of May to 6th of June 2002 (a detailed description of the cruise was presented in publication BENOVIĆ *et al.* (2005)). Sampling was performed at a transect from the station in the central part of the southern Adriatic (P1000) towards the middle Adriatic, the station at Palagruža Sill (Palagruža) and about 280 m deep Jabuka Pit (Jabuka) (Table 1, Fig. 1). A second set of sampling was performed along offshore - inshore transect, from station P1000 towards stations P800 and P300 (Table 1, Fig. 1).

Each time the temperature, salinity, oxygen and fluorescence profiles were assessed at each station from the layers from 0 to 200 m depth using a CTD multiprobe (SBE25 CTD SeaBird, Inc., Westar Fluorometer, Wetlabs, Inc. and a Cstar Transmissometer Wethlabs, Inc.).

Seawater samples for bacterioplankton and phytoplankton analyses were taken using Niskin bottles (5L volume) at different depths according to thermocline and fluorescence profiles (Table 1). Two samplings were performed at the stations P1000, P800 and Jabuka one during daylight and one during the night, at other station sampling was carried out only during the day.

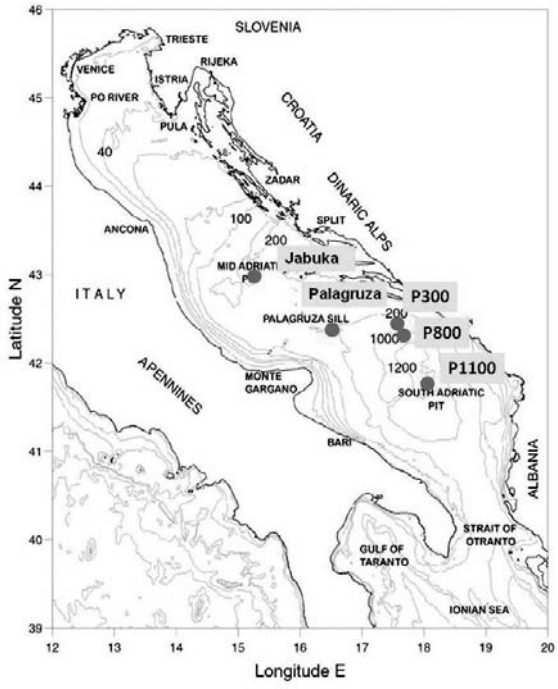


Fig. 1. Sampling locations during the MEDUZA 1 cruise in the middle and south Adriatic Sea in May - June 2002

During the MEDUZA II cruises, sampling was performed on 25th and 27th of May 2005 at the station in the central part of the southern Adriatic (P1000). Seawater was collected in the upper layer at following depths: 0.5, 2, 30, 54, 100 m in late afternoon, night, midnight, morning and midday.

All zooplankton samples were collected by vertical hauls with a Nansen opening-closing net

Table 1. Station codes, locations with depth to bottom and geographic position; depths and date of sampling during the MEDUZA 1 cruise in the middle and south Adriatic in May - June 2002

Code	*Location*	*Depth (m)*	*Geographic position*	*Sampling depth (m)*	*Date*
P1000	Southern Adriatic Pit	1100	42°11'N, 17°42'E	0.5, 10, 20, 70, 150	31 May - 1 June
Palagruža	Palagruža Sill	184	42°28'N, 16°21'E	0.5, 10, 20, 70, 150	31 May
Jabuka	Jabuka Pit	270	43°06'N, 15°07'E	0.5, 10, 30, 50, 70, 150	30 - 31 May
P800	Southern Adriatic Pit	850	42°22'N, 17°50'E	0.5, 10, 30, 70, 100, 150	4 June
P300	Southern Adriatic Pit	330	42°27'N, 17°57'E	0.5, 20, 30, 70, 150	3 June

at the following depth intervals: 0–50, 50–100, 100–200 (250) m. The same intervals were applied, within the limits of the bottom depth, at all stations. Microzooplankton samples were taken only during the day, with a 53-µm mesh (280 cm long, 57-cm diameter); mesozooplankton were sampled during both day and night at four deep stations using a 200-µm mesh net (470 m long, 113-cm diameter). Average hauling speed was 0.5 m s^{-1}. Samples were preserved in a 2.5% formaldehyde-seawater solution buffered with $CaCO_3$.

MATERIAL AND METHODS

Bacterial abundance was determined in the formaldehyde fixed seawater samples (2% final concentration) according to the protocol by PORTER & FEIG (1980). From 5 to 8 mL of seawater sample was stained with 4', 6-diamino-2-phenylindole (DAPI, 1 µg mL^{-1} final concentration), and filtered on 0.2 µm black polycarbonate filters (Poretics). Bacterial cells were counted under epifluorescent microscope Olympus BX51 (30 counting fields per sample, magnification 2000 x). Bacterial biomass was calculated using 19.8 fg C $cell^{-1}$ as the conversion factor (LEE & FUHRMAN, 1987). Bacterial carbon production was measured using ^{3}H-leucine incorporation method by employing the centrifugation protocol described by SMITH & AZAM (1992). For each sample, three replicates of seawater sample were incubated with ^{3}H-leucine (20 nM final concentration, PerkinElmer) for 2 hours in the dark and *in situ* temperature. Incubation was stopped by adding trichloracetic acid (TCA, 5% final concentration). In addition, two replicates were treated with TCA (5% final concentration) before addition of ^{3}H-leucine, and served as blanks. All samples were centrifuged, aspirated, washed, and after addition of scintillation cocktail (Ultima Gold, Packard) were counted in a scintillation counter (TR2500, Packard). Bacterial carbon production was calculated as described by SIMON & AZAM (1989). Bacterial growth rate was calculated by dividing bacterial production with biomass and turnover time of biomass was calculated by dividing biomass with bacterial production.

For determination of photosynthetic pigments water samples (2 L) were filtered onboard (GF/F filters, 47 mm diameter, Whatman), afterwards filters were immediately preserved in liquid nitrogen until analyzed. Photosynthetic pigments were extracted in 4 mL of cold 90% acetone using sonication, centrifuged to clarify the extract and the chlorophylls and carotenoids separated by RP HPLC according to BARLOW *et al*. (1993). The extracts were mixed (1:1 v /v) with 1 M ammonium acetate and injected into an HPLC system incorporating a Hypersil MOS2-C-8 column (150 x 4.6 mm, 120 A). A binary linear gradient was used to separate the pigments. Solvent A consisted of 70:30 (v/v) methanol: 1 M ammonium acetate, while solvent B consisted of methanol. Chlorophyll and carotenoid pigments were detected by absorbance at 440 nm (Spectra Physics, Model UV 2000). Qualitative identification and quantitative determination of individual pigments was performed by external standard calibration using authentic pigment standards (VKI, Denmark). To estimate the contribution of various phytoplankton groups the concentrations of individual biomarker pigments were multiplied by published values of chlorophyll *a*/biomarker pigment ratios. The fucoxanthin was multiplied by 1.2 (TERZIĆ, 1996) for diatoms, 19'-hexanoyloxyfucoxanthin by 1.1 (TERZIĆ, 1996) for prymnesiophytes, peridinin by 1.5 (TERZIĆ, 1996) for dinoflagellates, zeaxanthin+lutein by 1.7 (STRANSKY & HAGER, 1970) for cyanophytes, 19'-butanoyloxyfucoxanthin by 1.6 (EVERITT *et al.,* 1990) for silicoflagellates, alloxanthin by 1.85 (STRANSKY & HAGER, 1970) for cryptophytes and chlorophyll *b* by 0.9 (TERZIĆ, 1996) for green algae. The relative contribution of different phytoplankton groups to total biomass (total chlorophyll *a*) was estimated with the following equation: $X = K (C_{pig}/C_{chla})$ (where X is the relative contribution of different phytoplankton groups to the total biomass, K is the chlorophyll *a*/biomarker pigment ratio characteristic for a certain phytoplankton group, C_{pig} is the concentration of biomarker pigment characteristic for a certain phytoplankton group and C_{chla} is the concentration of chlorophyll *a* in the sample).

Table 2. Grouping of the microzooplankton and mesozooplankton organisms into: pico-, nano-, microplankton feeders, omnivorous and carnivorous

FOOD SIZE	*Microzoplankton* *(> 53 μm)*	*Mesozooplankton* *(> 200 μm)*
Picoplankton feeders	tintinnids appendicularians-juvenile	Appendicularians (*Oicopleura longicauda*, *O. fusiformis* and *Fritillaria boreali*) Pteropods (*Limacina inflata*, *L. trochyformis)*
Nanoplankton feeders	copepod nauplii, copepodites	Cladocerans (*Evadne spinifera*-shallow) small adult calanoids (*Paracalanus parvus* – shallow), copepodites of *Clausocalanus* spp. (*Clausocalanus pergens*, *Clausocalanus paululus*), ostracods-deep
Microplankton feeders	Adult calanoid copepods	*Ctenocalanus vanus*, *Centropages typicus*, *Acartia clausi*-shallow, *Euchaeta hebes*, *Clausocalanus jobei*, *Cl. arcuicornis*, *Lucicutia flavicornis* & *Mecynocera claus*i, *Calanus helgolandicus*) Doliolids (*Dolioletta gegenbauri* dominated P800, P1000),
Omnivores	cyclopoida-oithonids cyclopoida-oncaeids furciliae	*Oithona plumifera*, *O. similis*, *Oncaea* spp. *Nematoscelis megalops* - night
Carnivores		Chaetognats (*Sagitta minima*, *S. decipiens* & *S.lyra* – deep), Hydromedusae (*Rhopalonema velatum*, *Aglaura hemistoma*, *Solmissus albescens*-deep/night,), Syphonophorae (*Lensia subtilis* & *Eudoxoides spiralis*-deep), Hyperids

Microzooplankton was analyzed using a LEICA DMLB inverted microscope at magnifications of 100x and 400x. Mesozooplankton identifications were performed using an Olympus SZX 9 stereomicroscope at x 25 and x 40 magnification. The organisms of both zooplankton size fractions were grouped according to their trophic role into: pico-, nano-, microplankton feeders, omnivorous and carnivorous (Table 2).

RESULTS

The diel vertical distribution of heterotrophic bacteria, phytoplankton pigment composition as well as micro- and mesozooplankton were assessed along south - north and offshore - inshore transects during late May – early June 2002. At most stations we observed a shallow thermocline at approximately 20 m depth. The temperature was higher in the surface layer (0-5 m) with a range of 19.6ºC at offshore stations, 19.8ºC at station P800, and 21.0ºC at the near shore station P300. The thermocline was weak, the average temperatures were 19.3 ± 0.2ºC at 10 m, 17.3 ± 0.4ºC at 20 m and 16.1 ºC at 30 m depth. In the layers between 50 and 100 m, average temperatures were 15.3 ± 0.2ºC and below 100 m, 13.3 ± 1.2ºC. A minimum of 11.1ºC was recorded at the 200 m depth at Jabuka Pit. Salinity ranged from 38.04 to 38.80, and averaged 38.77 ± 0.11 for all depths in the studied area (in BENOVIĆ *et al.,* 2005).

A prominent fluorescence peak was recorded at 50 - 70 m depth at all stations, showing some

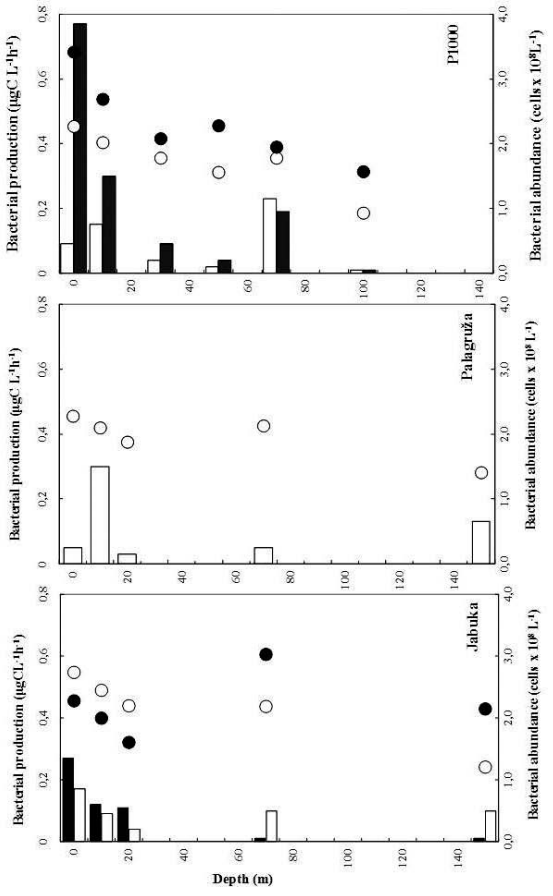


Fig. 2. Vertical distribution of chlorophyll a *concentration at stations along the north- south and offshore - inshore transects in the Adriatic Sea in May –June 2002 with the pigment composition in the layer of the chlorophyll peak. Values for day samplings - white diamond; night sampling - black diamond*

differences in phytoplankton concentrations along the south - north and offshore - inshore transects (Fig. 2). Chlorophill *a* concentrations were generally low, in a range from 6 to 290 ng L^{-1} with the highest value determined at Jabuka station (Fig. 2). Phytoplankton composition assessed in terms of chemotaxonomic pigments was dominated by 19'-hexanoyloxyfucoxanthin – containing phytoplankton (prymnesiophytes) in the upper 150 m layer. Lower concentrations were measured during night samplings, with a distinct reduction of the 19'-hexanoyloxyfucoxanthin – containing phytoplankton fraction. At station Palagruža the maximum concentration of chlorophyll *a* was 210 ng Chl *a* L^{-1} and among phytoplankton pigments the chlorophyll *b* (green

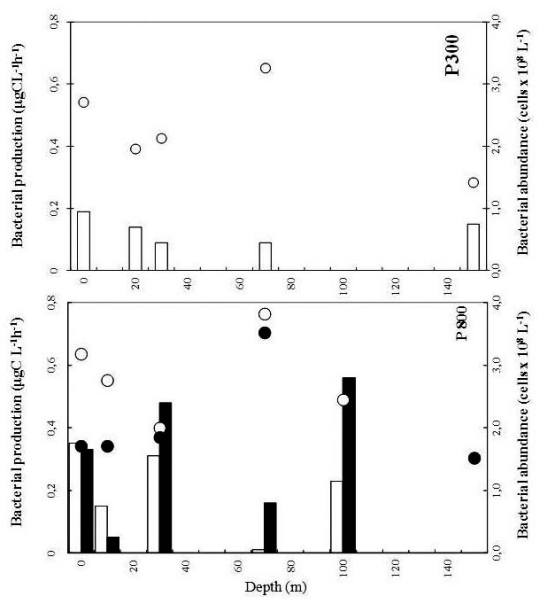


Fig. 3. Vertical distribution of bacterial abundance (circle) and bacterial production (bars) during the day (white symbol) and night sampling (black symbol) at the stations along the north - south and the offshore - inshore transects in the Adriatic Sea in May –June 2002

algae) and the 19'-hexanoyloxyfucoxanthin prevailed. Deep subsurface chlorophyll *a* maxima were also measured in the south Adriatic Pit (P1000) with concentrations of 140 ng Chl *a* L^{-1} at 50 m during the day and 131 ng Chl *a* L^{-1} at 70 m during the night. At this location more diverse pigment compositions were detected: in addition to prymnesiophytes (19'-hexanoyloxyfucoxanthin), phytoplankton containing divinyl chlorophyll *a* (prochlorophytes), 19'-butanoyloxyfucoxanthin (silicoflagellates) and alloxanthin (cryptophytes) were present. Similar pigment composition was detected at station P800 where the maximum chlorophyll *a* concentration was 182 ng Chl *a* L^{-1}. Here, the chlorophyll *a* peak coincided with peaks of 19'-hexanoyloxyfucoxanthin (prymnesiophytes), divinyl chlorophyll *a* (prochlorophytes) and chlorophyll *b* (green algae). Along the offshore - inshore transect from central station P1000 (Fig. 2) chlorophyll biomass slightly increased along with a reduction of zeaxanthin - containing phytoplankton.

Heterotrophic bacterial abundance in the water column for each station along the south - north and offshore - inshore transect are shown in Fig. 3. The bacterial abundance varied from

Table 3. Density and the percentages of the microzooplankton and mesozooplankton pico-, nano-, microplankton feeders, omnivorous and carnivorous at each station during the MEDUZA cruise in the middle and south Adriatic in May-June 2002

		Microzooplankton				*Mesozooplankton*				
Station	*Depth*	*Density*	*Pico*	*Nano*	*Omnivors*	*Density*	*Pico*	*Nano*	*Micro-*	*Omnivors*
	(m)	*(ind. m^{-3})*	*(%)*	*(%)*	*(%)*	*(ind. m^{-3})*	*(%)*	*(%)*	*(%)*	*(%)*
Jabuka	50-0	2263	8	62	31	317	11	37	24	22
	100-50	4032	7	74	19	953	5	4	6	84
	250-100	1379	9	57	34	123	6	44	9	33
Palagruža	50-0	4014	3	61	36	640	8	41	25	19
	100-50	7578	3	69	28	1519	3	33	45	16
	170-100	3045	12	63	26	541	8	26	34	27
P1000	50-0	4035	23	55	22	317	11	22	31	24
	100-50	6431	15	64	21	953	11	26	32	28
	200-100	2294	6	49	45	123	7	20	14	48
P800	50-0	2703	23	61	17	305	14	22	32	18
	100-50	2499	20	64	16	1218	11	17	35	26
	200-100	1167	18	44	39	195	5	28	18	39
P300	50-0	2437	9	77	13	186	12	43	7	24
	100-50	4140	5	85	10	322	6	45	9	23
	200-100	1867	8	64	28	257	10	36	12	36

0.9 to 3.8 x 10^8 cells L^{-1} and distribution along the water column displayed a vertical gradient, with higher numbers in the surface layer (0.5 - 2 m) and in the layer of the deep chlorophyll *a* maximum (70 m) (Fig. 3). In addition to the vertical gradient, a latitudinal increase in bacterial abundance was recorded with an increase toward north and towards the coast. Integrated values of the bacterial biomass for the studied layer (between 0.5 m and 150 m depth) showed the lowest value at the station in the central part of the southern Adriatic (3.24 mg C m^{-2}), then increased gradually towards the north (Palagruža and Jabuka Sill 3.75 and 4.81 mg C m^{-2}, respectively), and towards the coastal stations (Table 4). Bacterial carbon production ranged from 0.77 µg C L^{-1} h^{-1} to 0.01 µg C L^{-1} h^{-1} diminishing significantly with depth. The highest production rate was measured at station P1000 at the surface layer during the night (0.77 µg C L^{-1} h^{-1}) followed by a slightly lower rate at station P800 at 100 m depth (0.56 µg C L^{-1} h^{-1}). Growth rates ranged from 0.02 to 5.1 day $^{-1}$ and were lower below 70 m depth. The recalculated turnover for the bacterial population was high - about one day in the upper layer - compared to a slow growing bacterial population below 100 m (19 days). In contrast to bacterial abundance, integrated bacterial production showed a decreasing trend along the south - north transect (Table 4).

The bacterial distribution throughout the water column at the southern Adriatic station P1000 was also evaluated during the second MEDUZA II cruise at the end of May 2005. The vertical profile showed a diminution in abundance from the surface to the bottom (1100 m) with a clear stratification in the upper 200 m. Heterotrophic bacteria abundance varied between 4.3 and 0.6 x 10^8 cells L^{-1} showing the subsurface bacterial peak and the second one at a depth of 200 m (Fig. 4). The abundance then decreases to 1100 m depth. In the upper 100 m layer, similar numbers of heterotrophic bacteria were recorded in 24 hour measurements but dynamic changes in abundances were observed between day and night at 54 m depth (data not presented), where chlorophyll *a* and fluorescence peaks were recorded (MOROVIĆ *et al.,* this volume).

Table 4. Integrated bacterial biomass, bacterial production, chlorophyll a *concentrations, microzooplankton and mesozooplankton abundance in the 0-200 m layer at the sampling stations in the middle and south Adriatic in May-June 2002*

Date	Station	Hour	Bacterial biomass (mg C m^{-2})	Bacterial production (mg C m^{-2} d^{-1})	Chlorophyll (mg Chl *a* m^{-2})	Microzooplankton (ind. m^{-2})	Mesozooplankton (ind. m^{-2})
30.5.2002	Jabuka	5:40	4.81	1.08	0.228	2927	587
30.5.2002	Jabuka	15:30	3.87	0.57	0.107	3260	706
31.5.2002	Palagruža	17:00	3.73	1.89	0.113	5553	1055
2.6.2002	P1000	11:20	2.39	0.92	0.043	4797	587
2.6.2002	P1000	22:10	3.57	1.61	0.039	888	706
3.6.2002	P300	11:15	5.06	2.83	0.105	3146	734
4.6.2002	P800	13:55	5.57	3.96	0.095	2217	888
4.6.2002	P800	19:15	4.77	7.88	0.077	3988	272

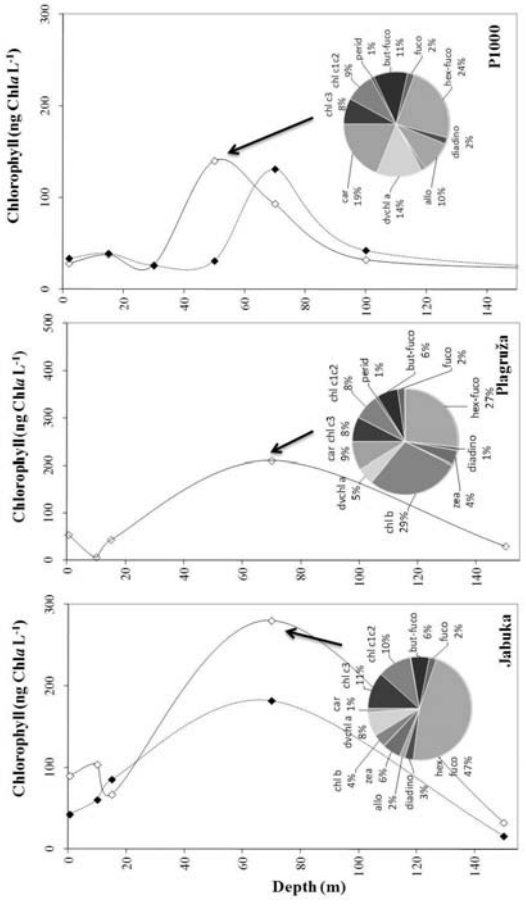
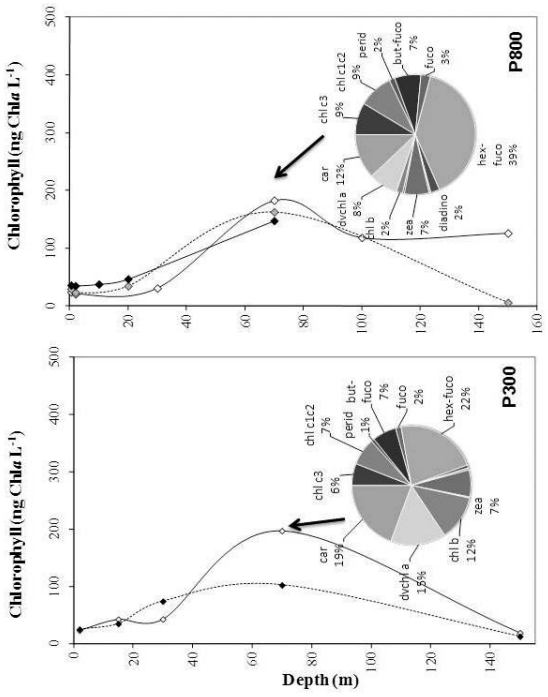
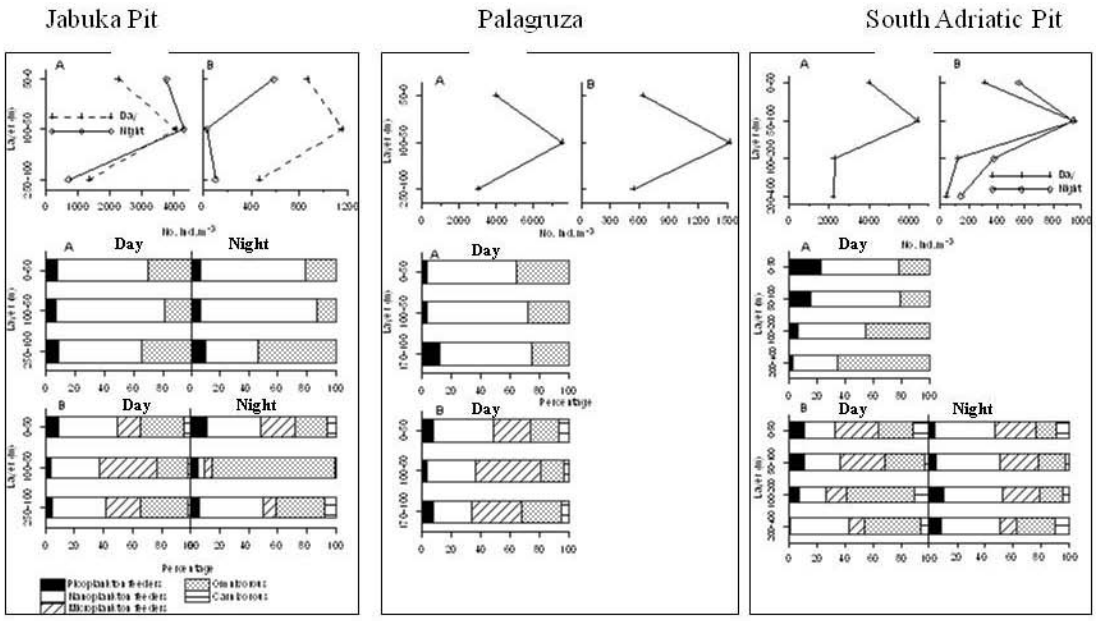


Fig. 4. Vertical distribution of bacterial abundance (with standard deviation) at station P1000 in the south Adriatic on 25 May (white circle) and 27 May 2005 (black circle)

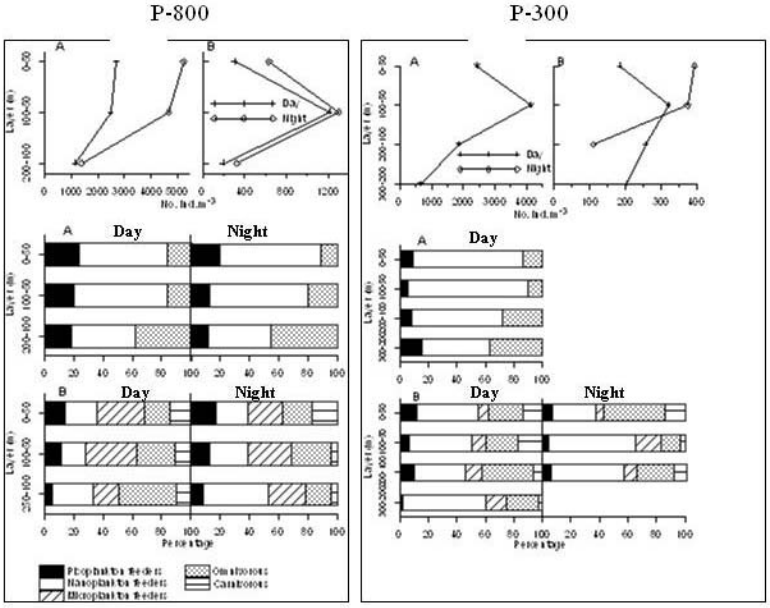


According to their trophic role herbivorous microzooplankton and mesozooplankton organisms were grouped into pico-, nano-, and microplankton feeders, while omnivorous and carnivorous organisms were grouped together (Table 2**)**. Within microzooplankton the most abundant picoplankton feeders were tintinnids (>75% of total tintinnid abundance was contributed by *Dictyocysta mitra, Codonella aspera, Undel-*



A - microzooplanton
B - mesozooplankton

Fig. 5a. Vertical distribution of microzooplankton (Micro) and mesozooplankton (Meso) (individuals m^{-3}) with the percentage of different trophic groups along the north - south transect in the Adriatic Sea during the day and the night samplings in May – June 2002



A - microzooplanton
B - mesozooplankton

Fig. 5b. Vertical distribution of microzooplankton (Micro) and mesozooplankton (Meso) (individuals m^{-3}) with the percentage of different trophic groups along the offshore - inshore transect in the Adriatic Sea during the day and night samplings in May – June 2002

la claparedei, Xystonella lohmanni) and juvenile appendicularians, while copepod nauplii and copepodites prevailed among nanoplankton feeders. Mesozooplanktonic picoplankton feeders comprised: pteropods, cladocerans and appendicularians. Among mesozooplankton organisms that formed the nanoplankton - feeding group, the most abundant were small adult calanoids and larger calanoid copepodites, and, in deeper layers, ostracods. Larger adult copepods, predominantly calanoids and doliolids were the main microplankton feeders. Cyclopoids (oithonids and oncaeids) and larval euphaisids were the main omnivorous organisms, while the carnivorous group consisted mostly of hydromedusae and siphonophores, chaetognaths and hyperids (Table 2).

Both, microzooplankton and mesozooplankton were most abundant in the 50 - 100 m layer at all stations. Such vertical distribution seems to correlate well with peaks of phytoplankton biomass (Table 4, Fig. 5a,b). The only exceptions were microzooplankton samples at P800 and night mesozooplankton samples at Jabuka Pit that displayed surface peaks (Table 4, Fig. 5a,b). Within microzooplankton-sized organisms nanoplankton feeders dominated in all depth layers (57-74%). Picoplankton feeders were present in all layers too, but with low percentages (7-10%) and generally decreased towards the bottom in the majority of samples. Among mesozooplanktonic organisms the proportion of nanoplankton feeders was not so conspicuous and different trophic groups contributed to total abundance rather evenly (Fig. 5a,b). A fraction of nanoplankton feeding mesozooplankton organisms was larger in deeper layers and in night samples

DISCUSSION

The epiplankton community was investigated along south - north and offshore - inshore transects during MEDUZA cruises in the southern Adriatic in spring 2002 and 2005. Vertical and horizontal differences in bacterio-, phyto- and micro- and mesozooplankton distribution were evident during the one week cruise 2002. We detected an increasing gradient along both transects: from south towards north and from offshore towards coastal stations. Differences were also observed in vertical distribution during the diel cycle.

Our results for bacterioplankton were comparable to previous studies in the Middle Adriatic (ŠOLIĆ *et al*., 1998; 2008) and the South Adriatic Pit (GALLINA *et al*., 2011). Few data are available for the southern Adriatic, however, like us, GALLINA *et al*. (2011) observed an increase in bacterial abundance and production in the subsurface layer. A congruous rise in the subsurface layer was also reported for the eastern middle Adriatic in the period between 2002 and 2006, as a consequence of the ingression of LIW (ŠOLIĆ *et al*., 2008). In our study, bacteria were more abundant at greater depth during the day while higher production was recorded at the surface during the night. Since variations in bacterial abundances were small compared with those of bacterial production at the upper layer, it might be assumed that the loss rate was as great as the growth rate. Depth dependent decreases in abundance over 200-1100 m were detected in May 2005 with the deep bacterial peak at 200 m (Fig. 4). According to the log – log linear regression analysis of the logarithmic transformed data, the magnitude of the depth - dependent decrease ($N = 28$; $r = - 0.610$) of bacterial abundance in the south Adriatic in May 2005 was comparable to the previous studies reported in the Mediterranean Sea (TANAKA & RASSOULZADEGAN, 2004; GALLINA *et al*., 2011).

The chlorophyll *a* integrated values varied from 0.228 mg Chl *a* m^{-2} in the middle Adriatic (station Jabuka), to 0.068 mg Chl *a* m^{-2} at the station in the south Adriatic (Table 4). The prymnesiophytes dominated the phytoplankton biomass and the composition was more diverse at the offshore location than the inshore. In addition to the prevailing 19'-hexanoyloxyfucoxanthin pigment divinyl chl *a* (prochlorophytes) and chlorophyll *b* (green algae) were also important. As in our study, an increasing northward gradient of picocyanobacteria has been recorded before (ŠESTANOVIĆ *et al*., 2009; GALLINA *et al*., 2011), as well as the possible impact of the change in the

Ionian circulation on plankton abundance and community structure in the eastern part of the Adriatic sea and open waters in the southern Adriatic (BATISTIĆ *et al.,* 2004; LUČIĆ *et al*., 2005, 2011; KRŠINIĆ & GRBEC, 2006; NINČEVIĆ GLADAN *et al*., 2010).

Pico- and nanoplankton feeders dominated among microzooplanton organisms with consistent prevalence of prymnesiophytes, prochlorophytes and green algae. Also, both micro- and mesozooplankton organisms were most abundant in the layer of deep chlorophyll *a* maximum. Within mesozooplankton a consistent proportion of omnivorous organisms were present which became more prominent in deeper layers and during the night. Carnivorous mesozooplankton seemed to be less important during the studied season.

The effect of grazers plays an important role in selectivity at the lowest trophic levels and the productivity in marine systems. Our study indicated that bacterial populations were generally controlled by predation (top-down) in the upper layer, where a higher proportion of pico- and nanoplankton feeders were recorded which might control the bacterial grazers. This was especially evident during the night due to zooplankton vertical migration and bacterial response in a higher growth rate. On the other hand, in the deeper layers with a phytoplankton biomass maximum, bacterial abundance and production might be regulated more by the availability of resources than predation.

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Epiplanktonske zajednice u južnom Jadranu: višestruke trofičke razine na transektima jug – sjever i obala-otvoreno more

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SAŽETAK

Istraživanje površinskih zajednica planktona obavljena su u proljeće 2002. godine tijekom "Meduza" krstarenja srednjim i južnim Jadranom na transektima "jug-sjever" i "obala-otvoreno more". Utvrđena je dnevna vertikalna raspodjela heterotrofnih bakterija, sastava pigmenata fitoplanktona, te mikrozooplanktona i mezozooplanktona. Na glavnini postaja nađena je termoklina na oko 20 m i izraženo visoke vrijednosti klorofila *a* na oko 70 m dubine. Intergrirana bakterijska i fitoplanktonska biomasa bila je manja na središnjoj postaji južnoga Jadrana, a postupno se povećavala prema postajama Palagruža i Jabučka kotlina kao i prema obalnim postajama. Vertikalna raspodjela bakterijske brojnosti i produkcije pokazala je izraziti maksimum u površinskom sloju. Bakterijska brojnost bila je velika u sloju dubokog maksimuma klorofila *a*. Veća bakterijska produkcija bila je u svezi s povišenom brojnošću zooplanktona koji se hrani piko i nanoplanktonom, što ukazuje da su veličine bakterijskih populacija generalno kontrolirane predacijom.

Ključne riječi: heterotrofne bakterije, pigmenti fitoplanktona, mikrozooplankton, mezozooplankton, Jadransko more