

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

Valentina TURK^{1*}, Davor LUČIĆ², Jakica NJIRE², Senka TERZIĆ³, Tinkara TINTA¹, Adam BENOVIĆ² and Alenka MALEJ¹

¹ National Institute of Biology, Marine Biology Station, , Fornace 41, 6330 Piran, Slovenia

² Institute for Marine and Coastal Research, University of Dubrovnik, D. Jude 12, 20000 Dubrovnik, Croatia

³ Center for Marine and Environmental Studies, RBošković Institute, Zagreb, Croatia

*Corresponding author, e-mail: turk@mbss.org

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 dur-

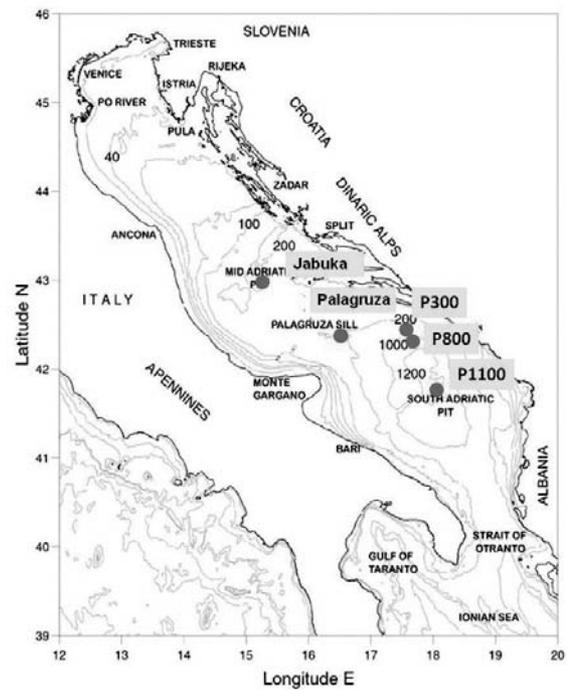


Fig. 1. Sampling locations during the MEDUZA I cruise in the middle and south Adriatic Sea in May - June 2002

ing daylight and one during the night, at other station sampling was carried out only during the day.

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 I 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 CaCO₃.

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 $\mu\text{g mL}^{-1}$ 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 ³H-leucine incorporation method by employing the centrifugation protocol described by SMITH & AZAM (1992). For each sample, three replicates of seawater sample were incubated with ³H-leucine (20 nM final concentration, PerkinElmer) for 2 hours in the dark and *in situ* temperature. Incubation was stopped by adding trichloroacetic acid (TCA, 5% final concentration). In addition, two replicates were treated with TCA (5% final concentration) before addition of ³H-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 Å). 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: $X = K (C_{\text{pig}}/C_{\text{chl}a})$ (where *X* is the relative contribution of different phytoplankton groups to the total biomass, *K* is the chlorophyll *a*/biomarker pigment characteristic for a certain phytoplankton group, *C*_{pig} is the concentration of biomarker pigment characteristic for a certain phytoplankton group and *C*_{chl*a*} 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	Microzooplankton (> 53 μm)	Mesozooplankton (> 200 μm)
Picoplankton feeders	tintinnids appendicularians-juvenile	Appendicularians (<i>Oicopleura longicauda</i> , <i>O. fusiformis</i> and <i>Fritillaria boreali</i>) Pteropods (<i>Limacina inflata</i> , <i>L. trochyformis</i>)
Nanoplankton feeders	copepod nauplii, copepodites	Cladocerans (<i>Evadne spinifera</i> -shallow) small adult calanoids (<i>Paracalanus parvus</i> – shallow), copepodites of <i>Clausocalanus</i> spp. (<i>Clausocalanus pergens</i> , <i>Clausocalanus paululus</i>), ostracods-deep
Microplankton feeders	Adult calanoid copepods	<i>Ctenocalanus vanus</i> , <i>Centropages typicus</i> , <i>Acartia clausi</i> -shallow, <i>Euchaeta hebes</i> , <i>Clausocalanus jobei</i> , <i>Cl. arcuicornis</i> , <i>Lucicutia flavicornis</i> & <i>Mecynocera clausi</i> , <i>Calanus helgolandicus</i> Doliolids (<i>Dolioletta gegenbauri</i> dominated P800, P1000),
Omnivores	cyclopoida-oithonids cyclopoida-oncaeids furciliae	<i>Oithona plumifera</i> , <i>O. similis</i> , <i>Oncaea</i> spp. <i>Nematoscelis megalops</i> - night Chaetognats (<i>Sagitta minima</i> , <i>S. decipiens</i> & <i>S.lyra</i> – deep), Hydromedusae (<i>Rhopalonema velatum</i> , <i>Aglaura hemistoma</i> , <i>Solmissus albescens</i> -deep/night,) Syphonophorae (<i>Lensia subtilis</i> & <i>Eudoxoides spiralis</i> -deep), Hyperids
Carnivores		

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 19.6°C at offshore stations, 19.8°C at station P800, and 21.0°C at the near shore station P300. The thermocline was weak, the average temperatures were 19.3 \pm 0.2°C at 10 m, 17.3 \pm 0.4°C at 20 m and 16.1 °C at 30 m depth. In the layers between 50 and 100 m, average temperatures were 15.3 \pm 0.2°C and below 100 m, 13.3 \pm 1.2°C. A minimum of 11.1°C was recorded at the 200 m depth at Jabuka Pit. Salinity ranged from 38.04 to 38.80, and averaged 38.77 \pm 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

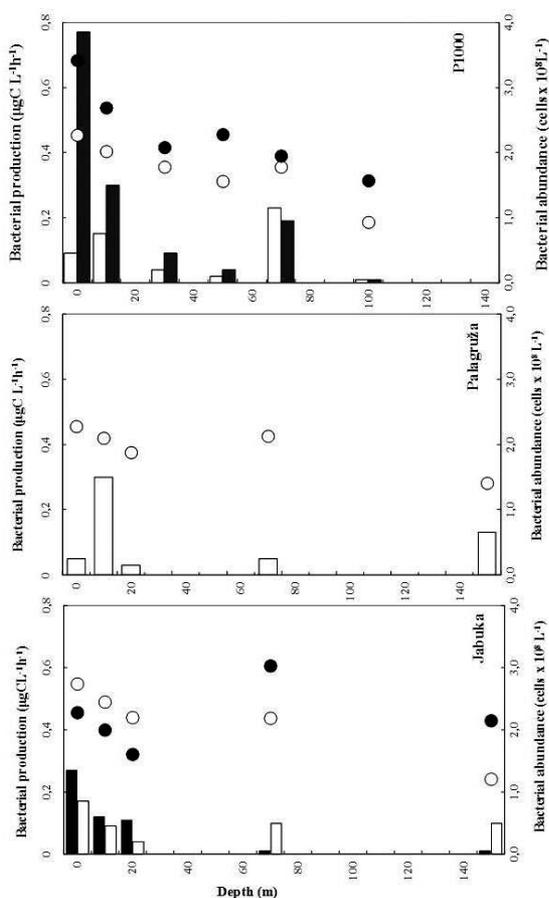


Fig. 2. Vertical distribution of chlorophyll *a* concentration at stations along the north-south and offshore-inshore transects in the Adriatic Sea in May-June 2002 with the pigment composition in the layer of the chlorophyll peak. Values for day samplings - white diamond; night sampling - black diamond

differences in phytoplankton concentrations along the south-north and offshore-inshore transects (Fig. 2). Chlorophyll *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

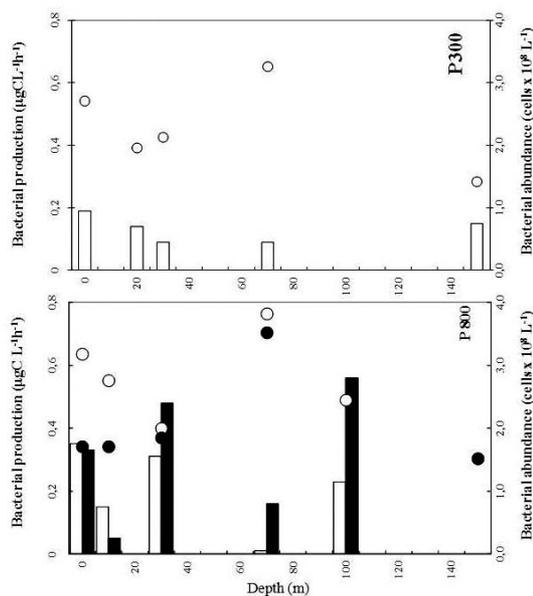


Fig. 3. Vertical distribution of bacterial abundance (circle) and bacterial production (bars) during the day (white symbol) and night sampling (black symbol) at the stations along the north-south and the offshore-inshore transects in the Adriatic Sea in May-June 2002

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

Station	Depth (m)	Microzooplankton				Mesozooplankton				
		Density (ind. m ⁻³)	Pico (%)	Nano (%)	Omnivors (%)	Density (ind. m ⁻³)	Pico (%)	Nano (%)	Micro- (%)	Omnivors (%)
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 3.8×10^8 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 10⁸ 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).

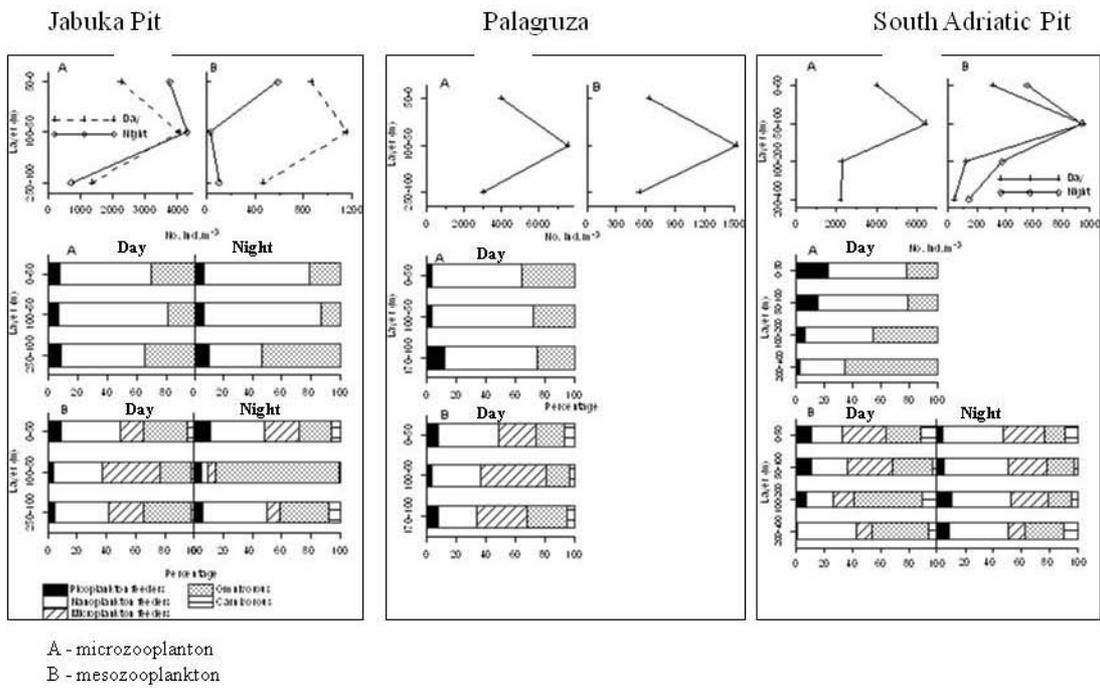


Fig. 5a. Vertical distribution of microzooplankton (Micro) and mesozooplankton (Meso) (individuals m^{-3}) with the percentage of different trophic groups along the north - south transect in the Adriatic Sea during the day and the night samplings in May - June 2002

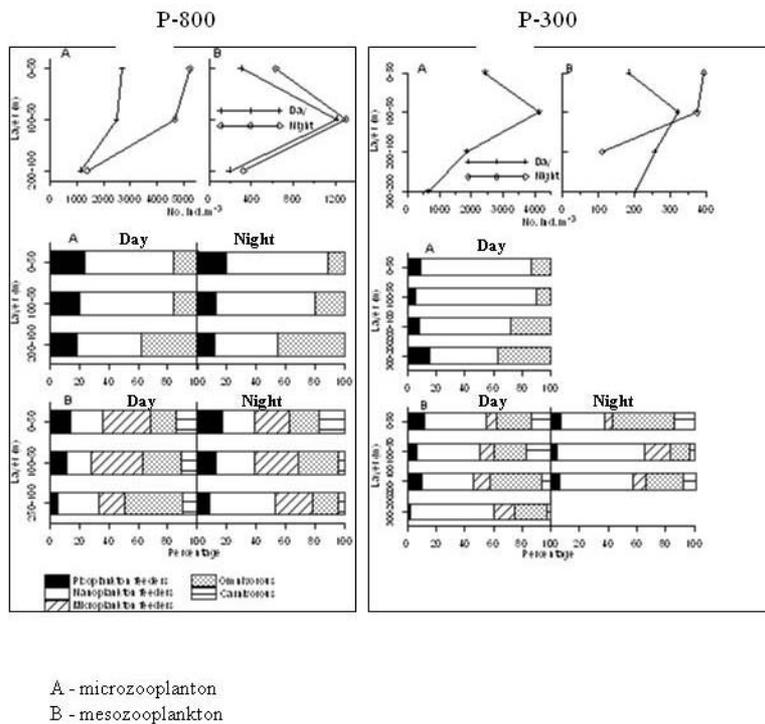


Fig. 5b. Vertical distribution of microzooplankton (Micro) and mesozooplankton (Meso) (individuals m^{-3}) with the percentage of different trophic groups along the offshore - inshore transect in the Adriatic Sea during the day and the night samplings in May - June 2002

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 19²-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 microzooplankton 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.

ACKNOWLEDGEMENTS

This research was supported by a grant from the Slovenian Research Agency, Ministry of Education, Science, Culture and Sport in Slovenia within the program Coastal Ocean Research (P1-0237), by the Ministry of Science, Education and Sport of the Republic of Croatia, by the University of Dubrovnik (Croatia) and by the support of the National Science Foundation (OCE-0116236). The authors would like to thank Dr. V. Onofri, Dr. A. Vuković, T. Makovec, J. Forte and “Naše more” crew for their help during the cruise. We are much indebted to two anonymous reviewers who helped to improve the manuscript.

REFERENCES

- AZAM, F., G. E. STEWARD & A. HAGSTROM. 1993. Bacteria - organic matter coupling and its significance for oceanic carbon cycling. *Microb. Ecol.*, 28: 167-179.
- AZAM, F. & F. MALFATTI. 2007. Microbial structuring of marine ecosystems. *Nat. Rev. Microbiol.*, 5: 782-791.
- ANTOINE, D., A. MOREL & J.M. ANDRE. 1995. Algal pigment distribution and primary production in the eastern Mediterranean as derived from Coastal Zone Color Scanner observations. *J. Geophys. Res.*, C, 100: 16193 -16209.
- BARLOW, R.G., R.F.C. MANTOURA, M.A. GOUGH & T.W. FILEMAN. 1993. Pigment signatures of the phytoplankton composition in the northeastern Atlantic. *Deep-Sea Res.*, 40: 2229-2242.
- BATISTIĆ, M., F. KRŠINIĆ, N. JASPRICA, M. CARIĆ, D. VILIČIĆ & D. LUČIĆ. 2004. Gelatinous invertebrate zooplankton of the South Adriatic: species composition and vertical distribution. *J. Plankton Res.*, 26: 459-474.
- BENOVIĆ, A., D. LUČIĆ, V. ONOFRI & M. BATISTIĆ. 2005. Bathymetric distribution of medusae in the open waters of the middle and south Adriatic Sea during spring 2002. *J. Plankton Res.*, 27: 79-89.
- BOJANIĆ, N., M. ŠOLIĆ, N. KRSTULOVIC, S. ŠESTANOVIĆ, Ž. NINČEVIĆ GLADAN, I. MARASOVIĆ & I. BRAUTOVIĆ. 2006. The role of ciliates within the microbial food web in the eutrophicated part of Kaštela Bay (middle Adriatic Sea). *Sci. Mar.*, 70: 431-442.
- BROOKS, J. L. & S. I. DODSON. 1965. Predation, body size and composition of plankton. *Science*, 150: 28-35.
- CIVITARESE, C., M. GAČIĆ, M. LIPIZER & G.L.E. BORZELLI. 2010. On the impact of the Bimo-

- dal Oscillating System (BiOS) on the biogeochemistry and biology of the Adriatic and Ionian Seas (Eastern Mediterranean). *Biogeosciences Discuss.*, 7: 6971-6995.
- DUFOUR, P. & J.P. TORRETON. 1996. Bottom-up control of bacterioplankton from eutrophic to oligotrophic sites in the North Eastern tropical Atlantic ocean. *Deep-Sea Res.*, 43: 1305-1320.
- DULČIĆ, J. & B. GRBEC. 2000. Climate change and Adriatic ichthyofauna. *Fish. Oceanogr.*, 9: 187-191.
- EVERITT, D. A., S. W. WRIGHT, J. K. VOLKMAN, D. P. THOMAS & E. J. LINDSTROM. 1990. Phytoplankton community compositions in the western equatorial Pacific determined from chlorophyll and carotenoid pigment distribution. *Deep-Sea Res.*, 37: 975-977.
- GAČIĆ, M., G. CIVITARESE, S. MISEROCCHI, V. CARDIN, A. CRISE & E. MAURI. 2002. The open-ocean convection in the Southern Adriatic: a controlling mechanisms of the spring phytoplankton bloom. *Cont. Shelf Res.*, 22: 1897-1908.
- GALLINA, A., M. CELUSSI, P. DEL NEGRO. 2011. Large-scale distribution and production of bacterioplankton in the Adriatic Sea. *J. Sea Res.*, 66: 1-8.
- KRŠINIĆ, F. & B. GRBEC. 2002. Some distribution characteristics of small zooplankton at two stations in the Otranto Strait (Eastern Mediterranean). *Hydrobiologia*, 482: 119-136.
- KRŠINIĆ, F. & B. GRBEC. 2006. Horizontal distribution of tintinnids in the open waters of the South Adriatic (Eastern Mediterranean). *Sci. Mar.*, 70: 77-88.
- KRSTULOVIĆ, N., T. PUCHER-PETKOVIĆ & M. ŠOLIĆ. 1995. The relationship between bacterioplankton and phytoplankton production in the middle Adriatic Sea. *Aquat. Microb. Ecol.*, 9: 41-45.
- LEE, S.H. & J.A. FUHRMAN. 1987. Relationships between biovolume and biomass of naturally derived bacterioplankton. *Appl. Environ. Microbiol.*, 53: 1298-1303.
- LUČIĆ, D., A. BENOVIĆ, M. BATISTIĆ, J. NJIRE & V. ONOFRI. 2005. Calyophorae (Siphonophora) in the open waters of the central and southern Adriatic Sea during spring 2002. *J. Mar. Biol. Ass. U. K.*, 85: 495-501.
- LUČIĆ, D., A. BENOVIĆ, M. BATISTIĆ, M. MOROVIĆ, I. ONOFRI, J.C. MOLINERO & M. MILOSLAVIĆ. 2011. A short-term investigation of diel vertical migrations of the calyophoran Siphonophora in the open south Adriatic Sea (July 2003). *Acta Adriat.*, 52(2): 159-172.
- MOROVIĆ, M., B. GRBEC & I. MARASOVIĆ. 2004. Changes patterns of remotely sensed chlorophyll *a* in the Adriatic - influence of meteorological conditions. *Gayana (Concepción)*, 68: 405-410.
- MOROVIĆ, M., V. FLANDER PUTRLE, D. LUČIĆ, B. GRBEC, B. GANGAI, A. MALEJ, F. MATIĆ. Signatures of pigments and processes in the south Adriatic Sea – project MEDUZA. *Acta Adriat.* 53 (2): 303-322.
- NINČEVIĆ, Ž., I. MARASOVIĆ & G. KUŠPILIĆ. 2002. Deep chlorophyll-*a* maximum at one station in the middle Adriatic Sea. *J. Mar. Biol. Ass. U. K.*, 82: 9-19.
- NINČEVIĆ GLADAN, Ž., I. MARASOVIĆ, B. GRBEC, S. SKEJIĆ, M. BIŽANIĆ, G. KUŠPILIĆ, S. MATIJEVIĆ & F. MATIĆ. 2010. Inter-decadal variability in phytoplankton community in the Middle Adriatic (Kaštela Bay) in relation to the Northern Atlantic oscillation. *Estuar. Coast.*, 33: 376-383.
- ORLIĆ, M., M. GAČIĆ & P.E. LA VIOLETTE. 1992. The currents and circulation of the Adriatic Sea. *Oceanol. Acta*, 15: 109-124.
- PORTER, K.G. & Y.S. FEIG. 1980. The use of DAPI for identifying and counting aquatic microflora. *Limnol. Oceanogr.*, 25: 943-948.
- SANDERS, R.W. & S.A. WIKHMAN, 1993. Planktonic protozoa and metazoa: predation, food quality and population control. *Mar. Microb. Food Webs*, 7: 197-223.
- SANTOLERI, R., V. BANZON, S. MARULLO, E. NAPOLETANO & F.D. D'ORTENZO. 2003. Year-to-year variability of the phytoplankton bloom in the southern Adriatic Sea (1998-2000): Sea-viewing Wide Field-of-view Sensor observations and modeling study. *J. Geophys. Res.*, C, 108 NO. C9, 8122, doi:10.1029/2002JC001636.
- SIMON, M. & F. AZAM. 1989. Protein content and

- protein synthesis rates of planktonic marine bacteria. *Mar. Ecol. Prog. Ser.*, 51: 201–213.
- SMITH, D. C. & F. AZAM. 1992. A simple, economical method for measuring bacterial protein synthesis rates in seawater using ^3H -leucine. *Mar. Microb. Food Webs*, 6: 107–114. (Ime časopisa *Marine Microbial Food Webs*)
- STRANSKY, H. & A. HAGER. 1970. The carotenoid pattern and the occurrence of the light induced xanthophyll cycle in various classes of algae. IV. Cyanophyceae and Rhodophyceae. *Arch. Microbiol.*, 72: 84–96.
- ŠESTANOVIĆ, S., M. ŠOLIĆ, N. KRSTULOVIĆ & Ž. NINČEVIĆ. 2004. Seasonal and vertical distribution of planktonic bacteria and heterotrophic nanoflagellates in the middle Adriatic Sea. *Helgol. Mar. Res.*, 58: 83–92.
- ŠESTANOVIĆ, S., Z. LJUBESIĆ, H. MIHANOVIĆ, G. OLUJIĆ, S. TERZIĆ, Z. JAKŠIĆ & D. VILIČIĆ. 2009. Picoplankton composition related to thermohaline circulation: The Albanian boundary zone (southern Adriatic) in late spring. *Est. Coast. Shelf Sci.*, 91: 519–525.
- ŠOLIĆ, M. & N. KRSTULOVIĆ. 1991. Time series of heterotrophic bacteria density in the central Adriatic Sea. *Cont. Shelf Res.*, 11: 397–407.
- ŠOLIĆ, M. & N. KRSTULOVIĆ. 1994. The role of predation in controlling bacterial and heterotrophic nanoflagellate standing stocks in the coastal Adriatic Sea: seasonal patterns. *Mar. Ecol. Prog. Ser.*, 114: 219–235.
- ŠOLIĆ, M., N. KRSTULOVIĆ, N. BOJANIĆ, I. MARASOVIĆ & Ž. NINČEVIĆ. 1998. Seasonal switching between relative importance of bottom-up and top-down control of bacterial and heterotrophic nanoflagellate abundance. *J. Mar. Biol. Ass. U. K.*, 78: 755–766.
- ŠOLIĆ, M., N. KRSTULOVIĆ, I. VILIBIĆ, G. KUPŠPILIĆ, S. ŠESTANOVIĆ, D. ŠANTIĆ & M. ORDULJ. 2008. The role of water mass dynamics in controlling bacterial abundance and production in the middle Adriatic Sea. *Mar. Environ. Res.*, 65: 388–404.
- ŠOLIĆ, M., N. KRSTULOVIĆ, I. VILIBIĆ, N. BOJANIĆ, G. KUPŠPILIĆ, S. ŠESTANOVIĆ, D. ŠANTIĆ, & M. ORDULJ. 2009. Variability in the bottom-up and top-down controls of bacteria on trophic and temporal scales in the middle Adriatic Sea. *Aquat. Microb. Ecol.*, 58: 15–29.
- TANAKA, T. & F. RASSOULZADEGAN. 2002. Full depth-profile (0–2000m) of bacteria, heterotrophic nanoflagellates and ciliates in the NW Mediterranean Sea: vertical partitioning of microbial trophic structures. *Deep-Sea Res. II*, 49: 388–404.
- TANAKA, T. & F. RASSOULZADEGAN. 2004. Vertical and seasonal variations of bacterial abundance and production in the mesopelagic layer of the NW Mediterranean Sea. *Deep-Sea Res.*, 51: 531–544.
- TERZIĆ, S. 1996. Biogeokemija autohtone organske tvari u neritičkim područjima Sredozemlja: fotosintetski pigmenti i ugljikohidrati. (Biogeochemistry of autochthonous organic matter in neritic areas of Mediterranean: photosynthetic pigments and carbohydrates) Ph.D. Thesis, University of Zagreb, Faculty of Science, Division of Biology, 177 p.
- TURK, V. & A. HAGSTRÖM. 1997. Seasonal distribution of nanoflagellates and bacterivory in the Gulf of Trieste (Northern Adriatic). *Period. Biol.*, 99: 205–208.
- VILIČIĆ, D., Z. VUČAK, A. SKRIVANIĆ & Z. GRZETIĆ. 1989. Phytoplankton Blooms in the Oligotrophic Open South Adriatic Waters. *Mar. Chem.*, 28: 89–107.

Received: 20 February 2012

Accepted: 5 October 2012

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

Valentina TURK^{1*}, Davor LUČIĆ², Jakica NJIRE², Senka TERZIĆ³, Tinkara TINTA¹,
Adam BENOVIĆ² i Alenka MALEJ¹

¹Nacionalni institut za biologiju, Morska biološka postaja, Fornače 41, 6330 Piran, Slovenija

²Institut za more i priobalje, Sveučilište u Dubrovniku, D. Jude 12, 20000 Dubrovnik, Hrvatska

³ Centar za morska istraživanja i zaštitu okoliša, R. Bošković Institut, Zagreb, Hrvatska

*Kontakt adresa, e-mail: turk@mbss.org

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