Biological evidence of a winter convection event in the South Adriatic: A phytoplankton maximum in the aphotic zone

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ABSTRACT

An unusual phenomenon was recorded in the deep South Adriatic in February 2008: phytoplankton reached their maximum abundance in the aphotic zone. This was associated with strong downward flow induced by (1) surface cooling during *bura* (the region's cold, dry north wind) events and (2) ingression of more saline Eastern Mediterranean Water. Maximum abundance of microphytoplankton (MICRO) and nanophytoplankton (NANO), 1.4×10^4 and 6.8×10^5 cells L^{-1}, respectively, was at 400 m in the South Adriatic Pit. Diatoms dominated deep microphytoplankton samples. Atypically, autotrophic picoflagellates were found throughout the water column, with high abundance in the aphotic layers. Zooplankton did not show such dramatic deviations from their usual vertical distribution, but the abundance and relative contribution of some species between 200 and 800 m layer were markedly different.

1. Introduction

The Adriatic Sea is a semi-enclosed basin in the Northeastern Mediterranean with a shelf that extends from its northernmost extent to the Split-Gargano transect. Its deeper southern part is characterized by the circular, 1243-m-deep South Adriatic Pit (SAP).

Adriatic ecosystems are influenced by the regular exchange of water with the Eastern Mediterranean through the Strait of Otranto. Levantine Intermediate Water (LIW) and Ionian Surface Water (ISW) flow into the Adriatic along the sea's eastern border. The volume of this flow is greater in winter but, depending on climatic oscillations that occur from the Atlantic to the Southeast Mediterranean, varies year-to-year (Grbec et al., 2002).

The more saline LIW is entrained in the semi-permanent SAP cyclonic gyre. When this saltier water is exposed to winter episodes of cold, dry northerly winds, conditions are favorable for deep convection and generation of Adriatic dense water (AdDW) (Manca et al., 2002). The water so formed contributes to the Eastern Mediterranean's deep thermohaline cell (Malanotte-Rizzoli et al., 1996).

Winter convective mixing also transports nutrients from the deep reservoir to the surface, thus making them available for authotrophs (Williams and Follows, 1998; Marra et al., 1990; Civitarese and Gačić, 2001; Gačić et al., 2002). Conversely, convection transports living and non-refractory organic matter produced in the surface to depth (van Haren et al., 2006). Episodic changes in the abundance and composition of mesozooplankton in the deep Eastern Mediterranean (Weikert et al., 2001) and the unusual spring vertical distribution of the cyanobacterium *Synecococcus* in the SAP (Vilibić and Šantić, 2008) may be the evidence of this latter process.

The vertical distribution of zooplankton in the deep South Adriatic (SA) is well documented (e.g. Hure, 1980; Kršinić, 1998; Batistić et al., 2003, 2004; Benović et al., 2005; Lučić et al., 2005, 2009; Kršinić and Grbec, 2006). Phytoplankton data for the open SA, however, are not so numerous and have been collected mainly during the more productive spring period (Viličić, 1985; Viličić et al., 1989; Jasprica et al., 2001). With the exception of data on the spring–summer vertical distribution of the cyanobacterium *Synecococcus* (Vilibić and Šantić, 2008), the distribution of picoplankton in the open SA has not yet been investigated.

The vertical distribution of phytoplankton generally is limited by light penetration, with peaks of primary production recorded in the epipelagic layer between 0 and 100 m (e.g. Viličić et al., 1989; Totti et al., 2000; Viličić, 2003). Under certain conditions, i.e. transported by herbivorous fecal pellets, in form of cell aggregates or by mesoscale eddies, phytoplankton can be found in the aphotic zone (Smayda, 1971; Platt et al., 1983; van Haren et al., 2006). The presence of the maximum abundance of viable

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phytoplankton in the deep aphotic zone, reported for the first time in the present study, was discovered by chance when the winter sampling program happened to coincide with a wind-induced convection event.

The present study analyzes data collected during convection event to shed light on the role of such winter circulation processes of short duration on the structure and production of South Adriatic plankton communities, with particular attention paid to the effect on vertical distribution.

2. Material and methods

This study was conducted at four stations: P-100, P-150, P-300 on 18 February 2008, P-1200 on 19 February 2008 along the central transect of the South Adriatic (Fig. 1) with R/V Naše More.

Temperature and salinity profiles (0–800 m, averaged over 1-m intervals) were taken with a CTD multiparametric sonde (SEA Bird Electronics Inc., USA). Potential temperature and the potential density (sigma-θ, referenced to 0 dbar) were calculated. A white Secchi disk (30-cm diameter) was used to estimate transparency. Euphotic zone depth was calculated as 2.5 times the Secchi depth (Strickland, 1958).

Water samples were taken with 5-L Niskin bottles at 0, 5, 10, 20, 50, 75, 100, 200, 300, 400, 600, and 800 m. Dissolved oxygen was determined by the Winkler method and oxygen saturation (O_2/O_2') was calculated from the solubility of oxygen in seawater as a function of temperature and salinity (Weiss, 1970; UNESCO, 1973). Nutrients were analyzed by standard oceanographic methods (Strickland and Parsons, 1972).

Meteorological data for the Dubrovnik area for February 2008 were provided by the Croatian Meteorological and Hydrological Service.

Samples for determination of bacteria, cyanobacteria, and picoflagellate abundance were taken by 5-L Niskin bottles and preserved with formalin (4% final concentration). Bacteria were quantified by the acridine orange staining technique (Hobbie et al., 1977). Sub-samples of 10 mL were filtered onto 25-mm diameter, 0.2 μm pore sized polycarbonate black filters. At least 200 cells were counted on each filter using a Zeiss JENALUMAR epifluorescence microscope. Abundance of autotrophic (APF) and heterotrophic (HPF) picoflagellates and cyanobacteria was determined by epifluorescence microscopy on preparations stained with proflavine hemisulfate (Haas, 1982). Sub-samples of 20 mL were filtered onto 25-mm diameter, 0.8 μm pore size polycarbonate filters. Abundance was based on the size cell range ≤ 2 μm.
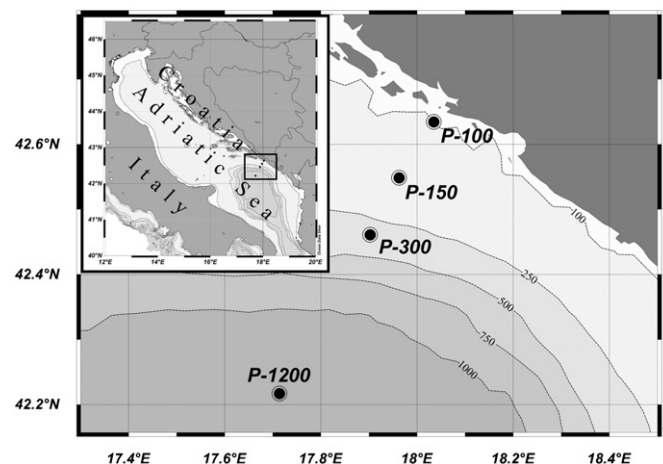

Fig. 1. Sampling stations in the Southern Adriatic.

Nano- and microphytoplankton was collected with 5-L Niskin bottles and with a 53-μm mesh Nansen open-closing net, and then preserved in 2% neutralized formalin. Net samples were used for qualitative analysis of phytoplankton at magnifications of 100 × and 600 ×. Owing to the green color of deep net samples we decided to analyze whole water column (0 to max. 800 m). Because we have dealt with no sparse phytoplankton populations, even in the open sea deep samples, we used sub-samples of 50 mL for phytoplankton counting as recommended by Hasle (1978). According to this method, minimum abundance of 20 cells L^{-1} can be determined (Utermöhl, 1958). Abundance was determined with an inverted microscope (Olympus IX 71) equipped with phase contrast. Microphytoplankton (> 20 μm, MICRO) were counted at a magnification of 200 × in 2–3 transects of the central chamber and at 100 × in transects along the rest of the base-plate. Nanophytoplankton (2–20 μm, NANO) were counted in 30 randomly selected fields along the chamber bottom base-plate at 400 ×. Whenever possible, phytoplankton were identified to the level of species or genus using standard keys, monographs, and taxonomic guides.

Zooplankton were sampled with vertical hauls of two Nansen opening–closing nets, one with a 53-μm mesh (51-cm diameter, 250 cm length) and one with a 250-μm mesh (114-cm diameter, 380 cm length). Average hauling speed was 1 m s^{-1}. As station depth permitted, the following intervals were sampled: 0–50, 50–100, 100–200, 200–300, 300–400, 400–600, and 600–800 m. Samples were preserved in a 2.5% formalin–seawater solution buffered with CaCO$_3$.

Counting and taxonomic identification of microzooplankton from the 53-μm mesh net were performed with an Olympus inverted microscope at 100 × and 400 ×. Sub-samples of 1/32 of the samples were analyzed for common species, while the entire catch was examined for rare species. Species were determined only for tintinnids.

Mesozooplankton from the 250-μm samples were counted and identified with an Olympus stereomicroscope SZX9 at 25 × and 40 ×. For crustacean mesozooplankton, sub-samples from 1/16 to 1/64 of the original sample volume were counted for the richer surface layers (0–50 and 50–100 m). Aliquots were determined according to the maximum appropriate density for the analyses. The entire catch was examined for all deeper collections and rare species. Samples were completely analyzed for non-crustacean mesozooplankton. The abundance of all zooplankton groups is presented as the number of specimens per cubic meter (ind m^{-3}).

Hydrographic, biological, and chemical data profiles were interpolated along the offshore section perpendicular to the coast using the nearest-neighbor gridding as implemented by Surfer software (Golden Software, Inc.). For high resolution hydrographic data (temperature, salinity, and density), horizontal and vertical steps were set to 5 km and 5 m, respectively. For the coarser-grained biological and chemical data, equivalent steps were 10 km and 10–50 m. The search ellipse radii were set to 10 km on the horizontal axis; the vertical radii depended on the data set: 5 m for the hydrographic, and either 50 or 100 m for the biological and chemical data.

3. Results

3.1. Meteorological conditions

Meteorological conditions in February 2008 were characterized by several episodes of the *bura*, the region's cold, dry northeasterly wind (Fig. 2). On 5, 8, and 16 February, wind speed exceeded 10 m s^{-1}. The maximum speed (13 m s^{-1}) from 15–18 February was accompanied by a marked drop in air temperature,
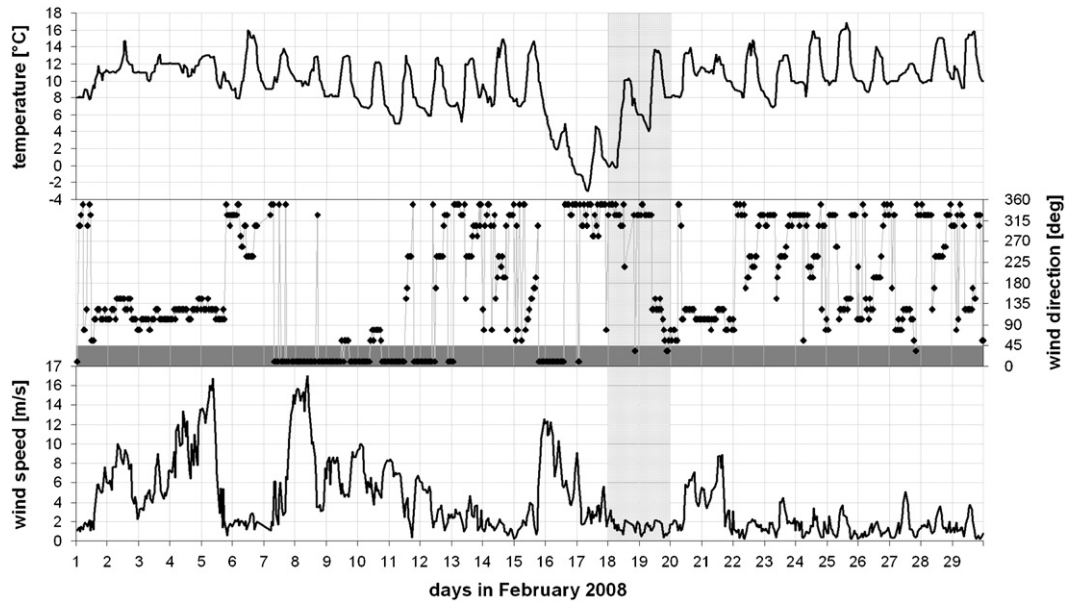
Fig. 2. Air temperature, wind speed, and direction (clockwise, from north) at Dubrovnik meteorological station. Gray strip indicates the *bura* wind sector. Shaded portion indicates the cruise dates.
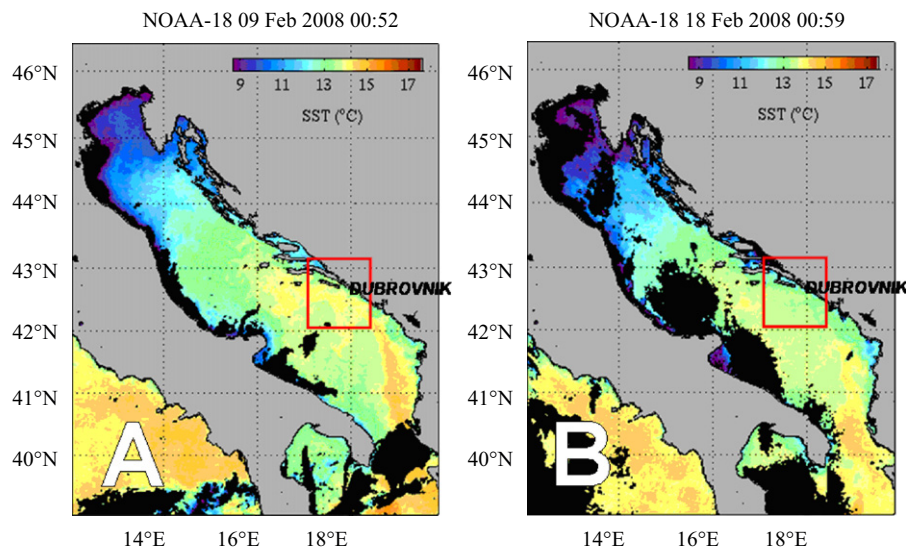

Fig. 3. Sea-surface temperature of the Adriatic Sea on 9 February 2008, prior to the cooling event (A); and on 18 February 2008, during the cooling event (B). Red rectangular area indicates the study region near Dubrovnik.

which fell from 14.7 to −3.0 °C in less than 48 h. These conditions naturally favor cooling of surface water and can be expected to have triggered, or perhaps intensified, vertical convection in the South Adriatic Pit.

3.2. Physical–chemical parameters and chl a

Surface thermal conditions in the Southern Adriatic (SA) prior to the cruise, captured by satellite imagery of the SST (Fig. 3A), reveal a continuous tongue of warm water extending north-westward from the Ionian Sea along the eastern flank of the Adriatic. It meandered between cooler coastal waters and those of the open sea. The imagery also shows a warm filament extending offshore of Dubrovnik, while, further north, warm surface water tended to circulate in a cyclonic sense around the South Adriatic

Pit (SAP). Subsequently, a decrease in SST was observed within the study area as a consequence of the sudden onset of the cooling event (Fig. 3B). Moreover, when the tongue of warm Ionian surface water was disrupted in the central part of the SAP, the warm filament disappeared.

Physical properties of the east South Adriatic (SA) along the 57-km cross-shore section (stations P-100, P-150, P-300, and P-1200) had noteworthy features (Fig. 4). The lowest transparency (20 m) was in P-100 and the highest (22 m) in P-1200. The euphotic zone was at least 55 m deep.

The vertical distribution of thermal properties in the upper layer shows that slightly cooler waters were evident at P-300 (13.6 °C). A subsurface temperature increase at 100 m (14.1 °C) is owed to LIW intrusion. Relatively uniform thermal conditions were present at the offshore deep station P-1200. The surface and coastal waters were less saline (38.4–38.45), while there was a
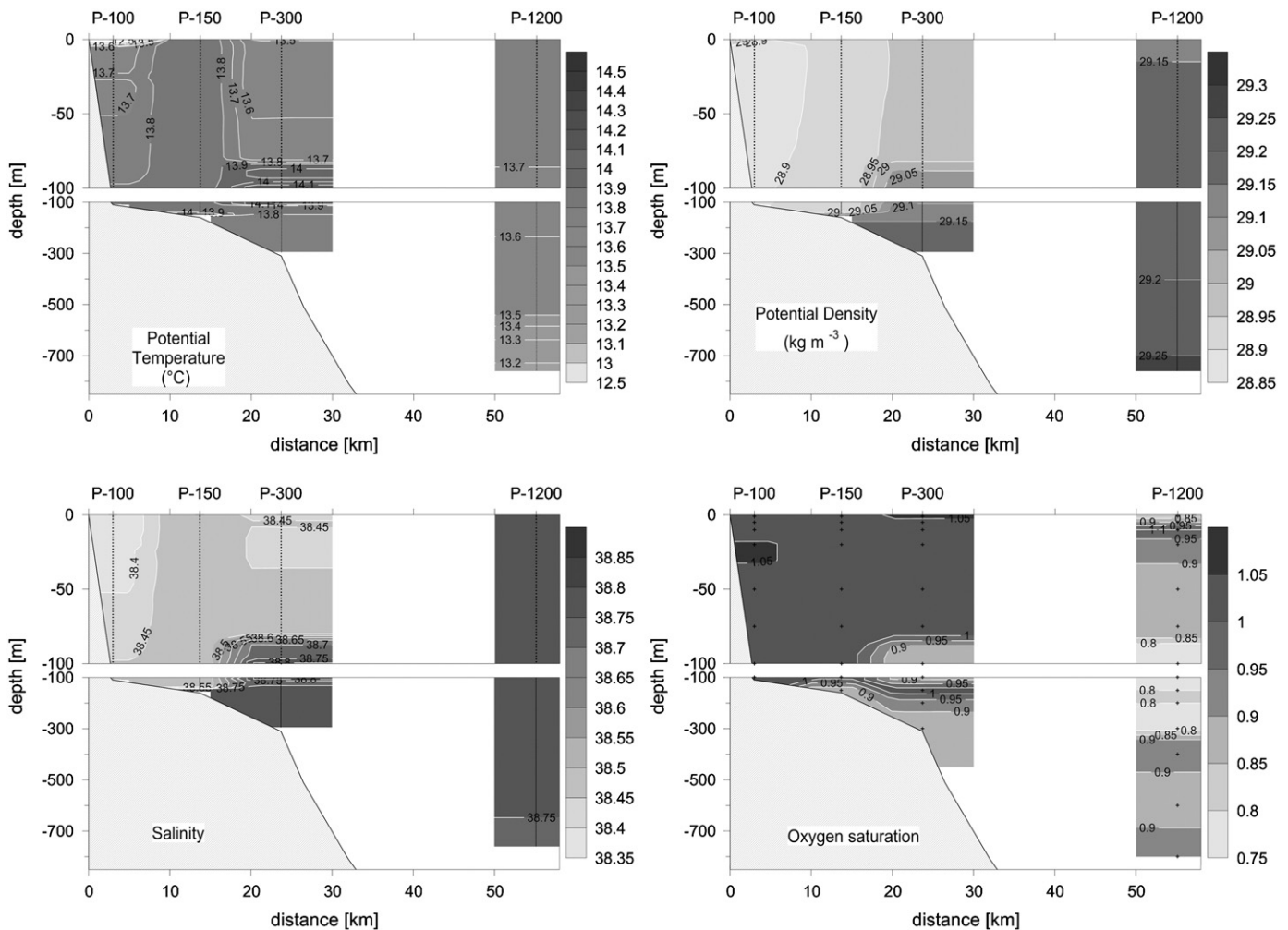
Fig. 4. Vertical distribution of potential temperature (°C), salinity, potential density (kg m^{-3}), and oxygen saturation in the Southern Adriatic along the cross-shore section. Note the vertical scale change: the surface layer (0–100 m) is stretched compared to the deep one.

salinity maximum at 100 m (> 38.8) at P-300, an indication of the influence of the more saline LIW water. Salinity was rather uniform at P-1200, a consequence of the vertical mixing.

Density gradually increased from 28.9 to 29.15 kg m^{-3} in the offshore direction. Stratification at about 100 m is accounted for by the warmer but more saline LIW water at P-300. Relatively dense surface waters at P-1200 (29.15 kg m^{-3}), where density increased with depth and salinity was almost constant (38.76), was a result of lower temperature. Temperature and salinity decreased more markedly only below 500 m; as a result, the density anomaly rose to 29.26 kg m^{-3} at 800 m.

Vertical mixing and homogenization were more evident at station P-1200. Doming and upwelling of isopycnal in the center of the gyre, close to P-1200, caused the increase of upper-layer density. Convective mixing, owing to surface cooling and buoyancy loss, was thereby facilitated. Further evidence for vertical mixing comes from the uniform distribution of low (avg. 0.86) oxygen saturation. The sole exception is the subsurface minimum (0.75) from 100 to 300 m associated with the typically lower oxygenated LIW.

The nutrient distribution is presented in Fig. 5. Nitrate and silicate in the upper layer (0–75 m) increased from the coast (P-100: about 2.15 and 2.5 μM, respectively) to the open sea (P-1200: about 4 and 4.5 μM, respectively). Nitrite, however, decreased offshore from 0.13 to 0.05 μM. Ammonia and phosphate had different distributions at each station.

Vertical profiles of nutrients at P-100, the most nearshore station, and P-1200, the most offshore station, were relatively homogeneous. P-150 and P-300 showed different patterns. Maxima were at P-300 at 100 m: nitrate (5.53 μM), phosphate (0.22 μM), and silicate (6.54 μM).

The evolution of convective event was also captured by a series of surface chlorophyll maps taken by the MODIS satellite (Fig. 6). These indicate (1) medium-high Chl-*a* concentration at the beginning of February (Fig. 6A); (2) a subsequent Chl-*a* minimum extending over a wide area of the Southern Adriatic in mid-February, corresponding with the cooling event (Fig. 6B); and (3) a significant increase over the following two weeks, from 0.5 to ≥ 1 mg m^{-3} (Fig. 6C). This winter bloom likely was a consequence of upwelled nutrients that fertilized the photic zone.

3.3. Plankton community

3.3.1. Bacterioplankton and heterotrophic picoflagellates

Bacterial abundance was highest at the open-sea deep station (P-1200). The maximum, 2.53×10^5 cells mL^{-1}, was at 20 m (Fig. 7). This decreased slightly from 75 to 600 m and again increased at 800 m (Fig. 7). The maximum was deeper (between 50 and 75 m) at shallower stations (P-100 and P-150). Values at P-300 were very uniform throughout the water column (average:
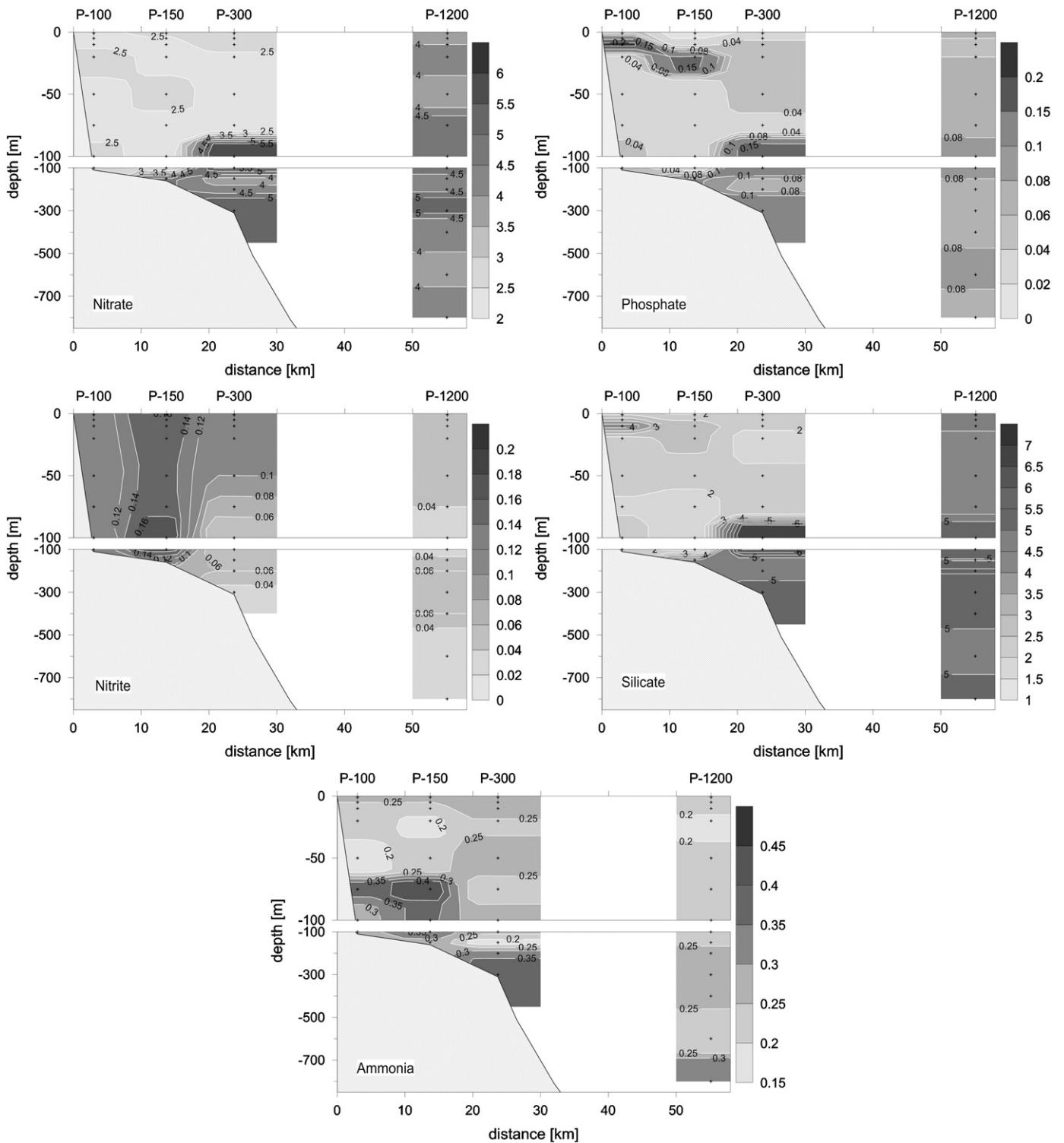
Fig. 5. Nutrients (μM) distribution along the study transect.

1.4×10^5 cells mL^{-1}). Unusually large (5–15 μm), elongated rods were found at all stations except P-150. They occurred from 50 to 100 m at P-100 and P-300, while at P-1200 they were found almost throughout the water column (5–800 m). Their maximum density, 0.70×10^5 cells mL^{-1}, was at 300 m (P-1200). Almost throughout the water column a high concentration of detritus (food source for bacteria) was observed.

Heterotrophic picoflagellates (HPF) were most abundant above 75 m and increased toward the open sea (Fig. 7). The maximum at

P-1200 (11.02×10^3 cells mL^{-1}) was at the surface and decreased to less than 4×10^3 cells mL^{-1} from 5 down to 800 m.

3.3.2. Phytoplankton

Cyanobacteria abundance showed a clear trend of decreasing abundance from the coast to the open sea (Fig. 7). Maximum abundance (74.12×10^4 cells mL^{-1}) was at 5 m at P-100. High means were found throughout the water column at this station
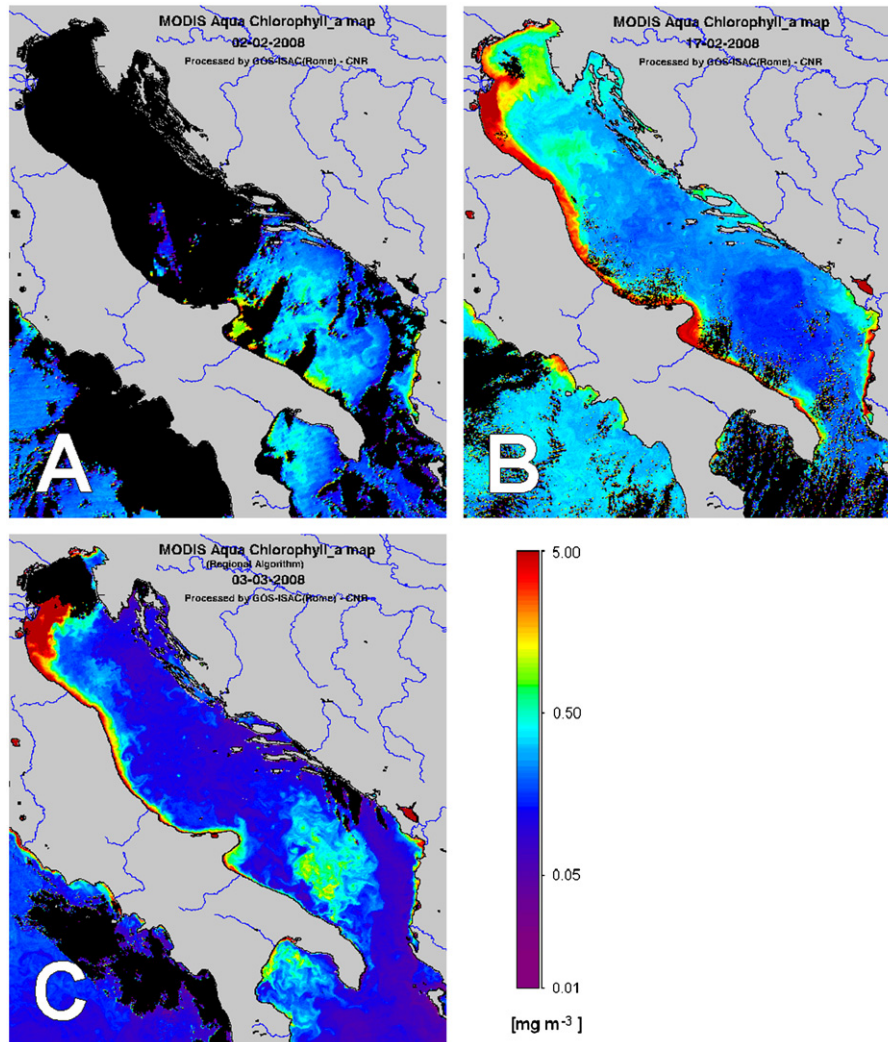
Fig. 6. Surface Chl-*a* concentration on 2 February 2008 (A), 17 February 2008 (B), and 3 March 2008 (C) showing patterns in the Southern Adriatic connected to the evolution of the convection event: irregular distribution before the main cooling (A), depletion owing to convection (B), and enrichment owing to the nutrient increase after convection.

$(29.89 \times 10^4 \text{ cells mL}^{-1})$, as well as at P-150 and P-300 $(40.27 \times 10^4 \text{ and } 23.09 \times 10^4 \text{ cells mL}^{-1}$, respectively). Abundance at P-1200, however, was very low throughout the water column, with the lowest mean being $1.92 \times 10^4 \text{ cells mL}^{-1}$.

Autotrophic picoflagellates (APF) exhibited no clear trend in abundance either laterally or vertically (Fig. 7). The maximum, $6.65 \times 10^3 \text{ cells mL}^{-1}$, was at 100 m at P-100 (Fig. 7). An unusually high abundance was found in the aphotic zone at the deepest station P-1200 with maximum of $4.18 \times 10^3 \text{ cells mL}^{-1}$ at 200 m.

Nanophytoplankton (NANO) and microphytoplankton (MICRO) abundances varied from 9.8×10^4 to $6.8 \times 10^5 \text{ cells L}^{-1}$ for NANO and from 60 to $1.4 \times 10^4 \text{ cells L}^{-1}$ for MICRO (Fig. 7). The highest levels for both were found unexpectedly within the aphotic zone (400 m) of the deep-open station P-1200 (Fig. 7).

Seventy-nine taxa representing 45 genera of MICRO were identified. Mainly were diatoms (43 taxa), followed by dinoflagellates (26), coccolithophorids (9), and one silicoflagellate (Table 1). Samples from stations P-100, P-150, P-300 included two species previously unrecorded for the Adriatic Sea: neither *Ornithocercus splendidus* nor *Neoceratium paradoxides* are included in the recent literature or in check-lists of Adriatic phytoplankton (Totti et al., 2000; Viličić et al., 2002; Moscatello et al., 2004; Banchetti et al., 2006; Xhulay and Miho, 2008).

Diatoms dominated MICRO abundance along the transect (Fig. 8), except at P-150, at which they were out-numbered by coccolithophorids and silicoflagellates. The contribution of diatoms generally increased below 75 m.

Along the transect the most abundant MICRO were *Chaetoceros* spp. with maximum of $6.7 \times 10^3 \text{ cells L}^{-1}$ on P-1200 at 400 m depth. Other taxa that exceeded $10^3 \text{ cells L}^{-1}$ were the silicoflagellate *Dictyocha fibula*; the coccolithophorids *Rhabdosphaera tignifer*, *Syracosphaera pulchra*, and unidentified coccolithophorids $> 20 \text{ μm}$; and the diatoms *Bacteriastrum delicatulum*, *Cerataulina pelagica*, *Nitzschia* spp., *Pseudo-nitzschia* spp., *Thalassionema nitzschioides*, and unidentified diatoms.

The following diatoms (Fig. 9) were prominent below 150 m contributing $\geq 50\%$ of microphytoplankton abundance in each sample: *Pseudo-nitzschia* spp., *Chaetoceros* spp., *Nitzschia* spp., *Ditylum brightwellii*, and several unidentified pennate diatoms. Most of these taxa had their maximum abundance at 400 m, and all phytoplankton had clearly visible chloroplasts.

3.3.3. Zooplankton
3.3.3.1. Microzooplankton. The highest microzooplankton abundance was in the 0–50 m layer of all stations except P-1200, where
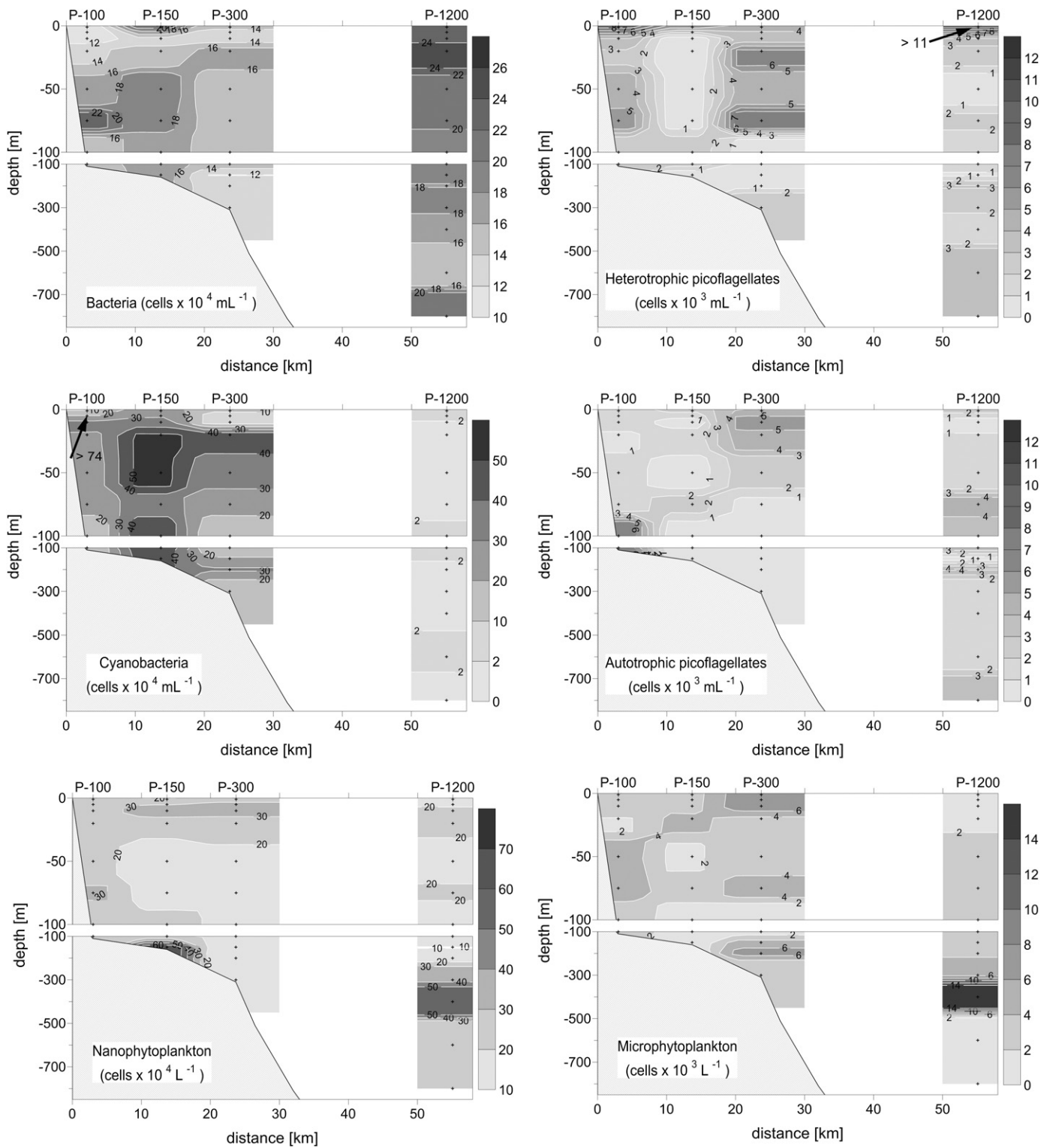
Fig. 7. Distribution of bacteria, cyanobacteria, autotrophic and heterotrophic picoflagellates, nano- and microphytoplankton abundance along the study transect in the South Adriatic.

it was in the 50–100 m layer. The maximum, 9678 ind m^{-3}, was at the nearshore station P-100. Abundance then generally decreased both offshore and with depth (Fig. 10).

Radiolarians contributed less than 2% of total microzooplankton abundance in the upper 100 m, and between 4% and 9% below 100 m. Radiolarian abundance was higher at the deeper stations,

P-300 and P-1200 (Fig. 10). The maximum of 152 ind m^{-3} were found from 300 to 400 m at station P-1200.

Tintinnids contributed 14–29% of the total microzooplankton abundance and were most abundant in the upper 100 m (Fig. 10). The maximum of tintinnids, 2304 ind m^{-3}, was in the surface layer (0–50 m) at the nearshore station P-100. Only at the

Table 1
List of microphytoplankton taxa found in the South Adriatic on 18–19 February 2008.

Taxa/stations	P-100	P-150	P-300	P-1200	Taxa/stations	P-100	P-150	P-300	P-1200
Dictyochophyceae					Nitzschia spp.	+	+	+	+
Dictyocha fibula Ehrenberg	+	+	+	+	Pleurosigma angulatum (Quekett) W. Smith	+	+	+	+
Prymnesiophyceae					Pleurosigma elongatum W. Smith				+
Calciosolenia brasiliensis (Lohmann) J.R. Young	+	+	+	+	Pleurosigma sp.		+	+	+
Calciosolenia murrayi Gran				+	Pseudo-nitzschia seriata (Cleve) Peragallo			+	+
Calyprtosphaera oblonga Lohmann	+				Pseudo-nitzschia spp.				+
Michaelsarsia adriaticus (Schiller) Manton, Bremer et Oates		+	+		Pseudosolenia calcar-avis (Schultze) Sundström				+
Ophiaster hydroideus (Lohmann) Lohmann		+			Rhizosolenia imbricata Brightwel				+
Rhabdosphaera clavigera Murray et Blackman		+			Skeletonema costatum (Greville) Cleve				+
Rhabdosphaera tignifer Schiller	+	+	+		Surirella sp.		+	+	
Scyphosphaera apsteinii Lohmann	+		+		Synedra spp.	+		+	
Syracosphaera pulchra Lohmann	+	+	+		Thalassionema nitzschioides (Grunow) Mereschkowsky	+	+	+	+
Unidentified coccolithophorids > 20 μm	+	+	+		Thalassiosira spp.			+	+
Bacillariophyceae					Unidentified centric diatoms	+	+	+	+
Amphiprora sulcata O'Meara	+		+	+	Unidentified pennate diatoms	+	+	+	+
Bacteriastrum delicatulum Cleve		+			**Dinophyceae**				
Cerataulina pelagica (Cleve) Hendey			+	+	Alexandrium tamarense (Lebour) E. Balech			+	
Chaetoceros affinis Lauder	+		+	+	Amphidinium sp.			+	
Chaetoceros brevis Schütt			+		Dinophysis ovum Schuüt	+			
Chaetoceros compressus Lauder			+		Dinophysis parva Schiller	+			
Chaetoceros costatus Pavillard				+	Dinophysis tripos Gourret			+	
Chaetoceros danicus Cleve				+	Dinophysis spp.	+	+		+
Chaetoceros decipiens Cleve			+	+	Diplopsalis—complex	+	+	+	
Chaetoceros rostratus Lauder				+	Gonyaulax polygramma Stein	+	+		
Chaetoceros socialis Lauder			+		Goniodoma polyedricum (Pouchet) Jörgensen	+			
Chaetoceros tenuisimus Meunier			+		Gymnodinium spp.	+			
Chaetoceros spp.	+		+	+	Kofoidinium velleloides Pavillard	+			
Cosinodiscus perforatus Ehrenberg		+			Neoceratium fusus (Ehrenberg) F. Gomez, D. Moreira et P. Lopez-Garcia	+		+	
Cosinodiscus thorii Pavillard			+		Neoceratium kofoidii (Jørgensen) F. Gomez, D. Moreira et P. Lopez-Garcia			+	
Coscinodiscus sp.			+	+	Neoceratium limulus (Gourret) F. Gomez, D. Moreira et P. Lopez-Garcia			+	
Cylindrotheca closterum (Ehrenberg) Reimann et Lewin	+	+	+	+	Neoceratium paradoxides (Cleve) F. Gomez, D. Moreira et P. Lopez-Garcia	+	+	+	
Dactyliosolen sp.			+		Neoceratium tripos (O.F. Müller) F. Gomez, D. Moreira et P. Lopez-Garcia			+	
Diploneis spp.	+	+	+	+	Ornithocercus heteroporus Kofoid	+			
Ditylum brightwellii (T. West) Grunow			+	+	Ornithocercus splendidus Schütt	+	+	+	
Guinardia striata (Stolterfoth) Hasle			+		Oxytoxum milneri Murray et Whitting		+		
Guinardia flaccida (Castracane) Peragallo			+		Oxytoxum scolopax Stein	+			
Hemuaulus hauckii Grunow ex Van Heurck			+	+	Oxytoxum variabile Schiller	+	+		
Leptocylindrus danicus Cleve			+		Pronoctiluca sp.				+
Leptocylindrus mediterraneus (H. Peragallo) Hasle	+				Prorocentrum micans Ehrenberg				+
Licmophora sp.			+		Protoperidinium brochi (Kofoid et Swezy) Balech			+	+
Navicula distans (W. Smith) Ralfs			+		Protoperidinium globulus (Stein) Balech			+	
Navicula spp.	+	+	+	+	Protoperidinium tubum (Schiller) Balech		+		
Nitzschia longissima (Brébisson in Kützing) Ralfs	+	+	+	+	Unidentified dinoflagellates	+	+	+	+
Nitzschia lorenziana Grunow			+						

deep-sea station (P-1200) was the maximum (2221 ind m^{-3}) in a subsurface layer (50–100 m). Relatively high abundance of tintinnids was registered from 200 to 300 m (403 ind m^{-3}) and from 200 to 400 m (248–280 ind m^{-3}) at P-300 and P-1200, respectively. A total of 37 tintinnid species were found (Table 2), all of which had been identified in previous investigations (Kršinić, 1998; Kršinić and Grbec, 2006). Of note, the coastal surface species Tintinnopsis campanula and Codonellopsis schabii were uncharacteristically found down to 800 m.

Copepod nauplii were the dominant micrometazoans in the entire water column, making up 43% to 66% of the microzooplankton population. They were most abundant in the upper 50 m (Fig. 10). Their maximum of 5267 ind m^{-3} was in the upper 50 m of P-300. Abundance decreased with depth, with the lowest values below 400 m. Calanoid copepodites and cyclopoids contributed less than 9% and 6% to total microzooplankton, respectively, with the highest abundance in the upper 100 m (Fig. 10).

Poecilostomatoids accounted from 8% to 29% of total microzooplankton. Highest abundance was recorded in the upper 100 m, but the highest contribution to total microzooplankton was in deeper layers, from 100 to 300 m (20–25%) at station P-300 and from 400 to 600 m (29%) at station P-1200 (Fig. 10).

3.3.3.2. Mesozooplankton. Mesozooplankton along the transect were most abundant in the 0–50 m layer and decreased with depth. There was an increase toward the open sea, with higher values at P-300 and P-1200 (657 and 624 ind m^{-3}, respectively), Fig. 11.

Copepods dominated throughout the water column (> 89%). Although abundance decreased with depth (Fig. 11), their contribution to total mesozooplankton was very high down to 400 m depth (94–98%). Calanoids were the dominant group in all samples, particularly offshore (55–97%). Their abundance decreased with depth but was unusually high in the 300–400 m layer: 100 ind m^{-3} (Fig. 11). Calanoid copepodite stages dominated the entire water
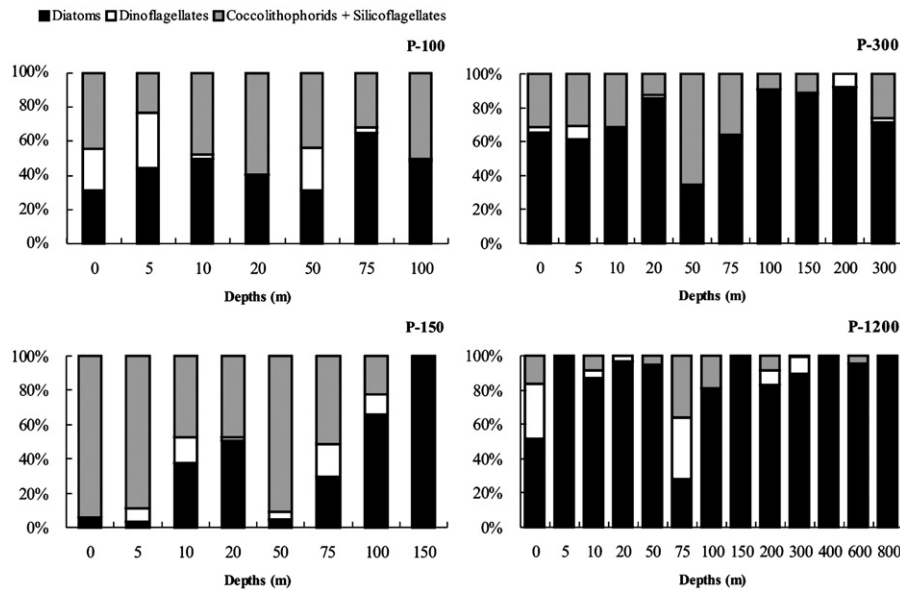
Fig. 8. Percentage contribution of taxonomic groups to microphytoplankton abundance in the water column.
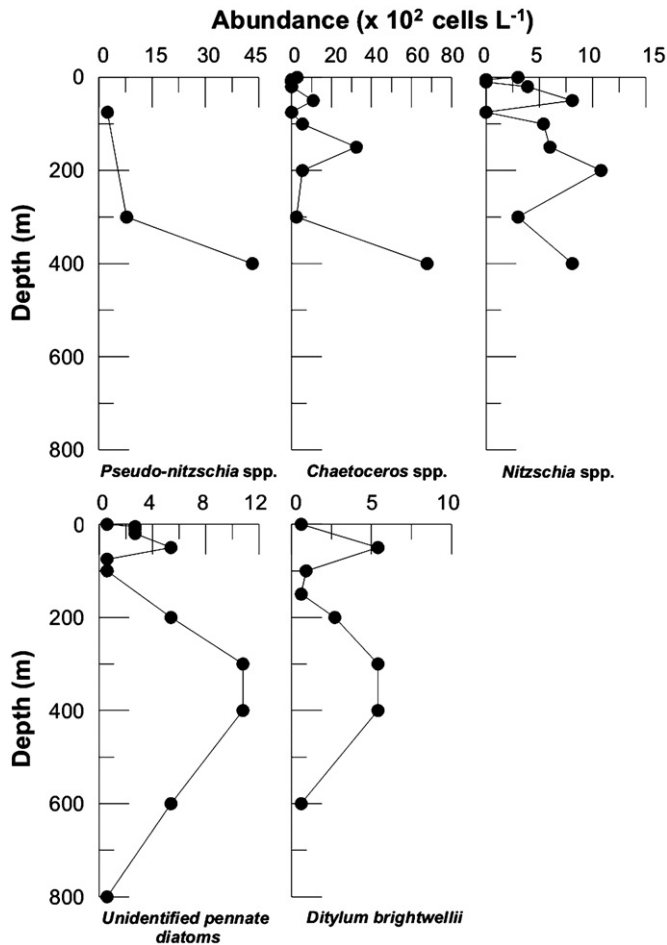
Fig. 9. Vertical distribution of dominant diatom taxa contributing ≥50% of microphytoplankton abundance in each sample below 150 m at P-1200.

column at P-1200, as well as the deeper layers of most other stations. The sole exception was P-100, where adults dominated.

Among 39 adult copepods (Table 2) identified to the species level, thirty-one were calanoids representing fifteen families; nine were cyclopoids of five families; and one was an harpacticoid. All species had been recorded by earlier investigators (Hure and Kršinić, 1998).

The most dominant adult copepods in the upper 100 m were the calanoids *Paracalanus parvus*, *Mecynocera clausi*, *Clausocalanus arcuicornis*, *Clausocalanus pergens*, *Pseudocalanus elongatus*, and only at deep-sea station P-1200, *Calanus helgolandicus*.

A pelagic subsurface species, *Pleuromamma gracilis*, was observed in considerable numbers – up to 26 ind m^{-3} and 18% of total copepods – from 200 to 300 m at P-300. This species, along with *C. helgolandicus* also was found in relatively greater numbers (> 6 ind m^{-3}) between 300 and 400 m at P-1200. On the other hand, the deep-sea calanoid species *Eucalanus hyalinus*, *Monacilla typica*, and *Euchaeta acuta* were not present in significant numbers.

The most numerous adult cyclopoid was the epipelagic *Oithona similis*, with more than 90 ind m^{-3} in the 0–100 m layer of the study area. This species also was unusually abundant (12–17 ind m^{-3}) between 200 and 600 m, making up more than 30% of copepod abundance.

Other planktonic crustaceans (Ostracoda, Cladocera, Amphipoda, Euphausiacea, and Decapoda) combined for less than 12% of total mesozooplankton abundance, with most of their populations in the upper 100 m.

Similarly, the main populations of non-crustacean mesozooplankton, namely Hydromedusae, Calycophorae, Pteropoda, Heteropoda, Chaetognatha, Polychaeta, Thaliacea, and Appendicularia were in the upper 100 m, where they made up between 5% and 11% of all mesozooplankton. Their density generally decreased toward offshore and with depth (Fig. 11).

Of those species that were identified, there were 8 hydromedusae, 16 calycophores, 2 ctenophores, 1 heteropod, 9 pteropods, 11 polychaetes, 8 chaetognaths, 6 thaliaceans, and 20 appendicularians (Table 2). The polychaetes *Phalocrophorus pictus* and *Pontodora pelagica*, the ctenophore *Charistephane fugens*, the salp *Thalia orientalis*, and the appendicularian *Oikopleura villafrancae* were recorded for the first time in the Adriatic Sea. The other species had been recorded in previous investigations in the Adriatic and were vertically distributed as described earlier (see Batistić et al., 2004, 2007; Castelli et al., 2006; Licandro, 2006; Mills, 2006).

Among these groups, appendicularia were the most abundant (40–98% of non-crustacean mesozooplankton). The highest number of individuals (45 ind m^{-3}) were found in the 0–50 m layer at

Fig. 10. Distribution of microzooplankton along the study transect in the South Adriatic.

Table 2
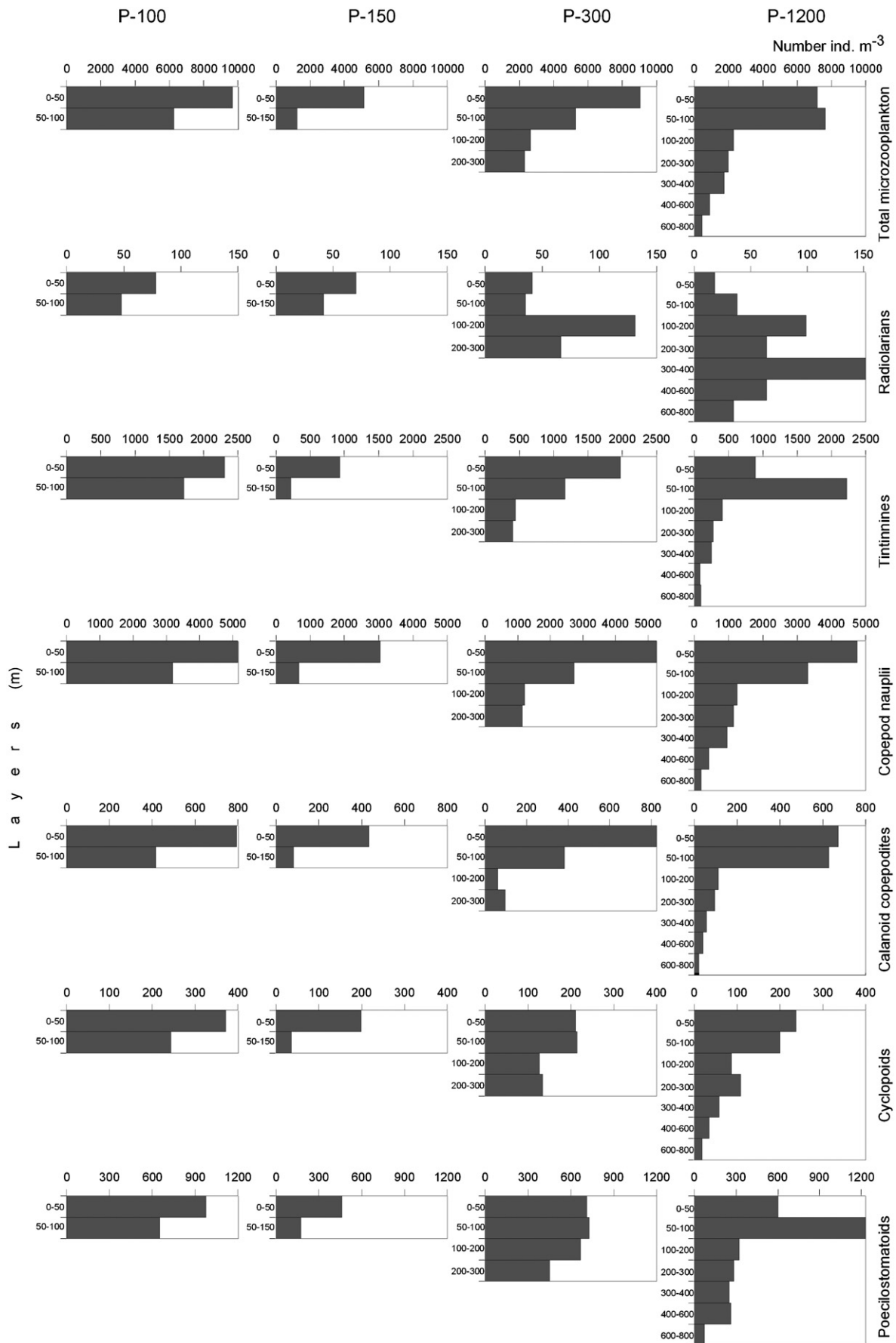List of zooplankton taxa found in the South Adriatic on 18–19 February 2008.

Taxa/stations	P-100	P-150	P-300	P-1200
PROTOZOA				
Tintininna				
Tintinnopsis campanula			+	+
Codonella aspera	+	+	+	+
Codonella amphorella				+
Codonella apicata			+	
Codonaria cistellula	+	+	+	+
Stenosemella nivalis				+
Codonellopsis orthoceras	+			
Codonellopsis schabii	+	+	+	+
Cyttarocylis eucecryphalus			+	+
Cyttarocylis cassis		+	+	
Epiplocylis acuminata	+	+	+	+
Epiplocylis undella				+
Rhabdonella spiralis	+	+	+	+
Parundella lohmanni		+	+	
Xystonella lohmanni				+
Xystonella treforti	+	+	+	+
Xystonellopsis paradoxa	+		+	+
Xystonellopsis scyphium		+	+	+
Xystonellopsis cymatica			+	+
Undella clevei	+		+	
Undella hyaline	+			+
Undella claparedei	+	+	+	+
Undella subcaudata	+	+	+	+
Amplectella tricollaria	+	+	+	
Undellopsis marsupialis	+	+	+	+
Dictyocysta elegans				+
Dictyocysta lepida	+	+	+	+
Dictyocysta mulleri		+	+	+
Dictyocysta mitra			+	
Stenstrupiella steenstrupii	+	+	+	+
Steenstrupiella intumescens	+			
Amphorella quadrilineata	+		+	+
Dadayiella ganymedes	+	+	+	
Eutintinnus fraknoi	+	+	+	+
Eutintinnus lusus-undae	+	+	+	+
Salpingella glockentoegeri	+	+	+	+
Salpingella rotundata				+
METAZOA				
Cnidaria				
Hydromedusae				
Leuckartiara octona			+	
Obelia sp.	+	+		
Aglaura hemistoma	+		+	+
Persa incolorata			+	+
Liriope tetraphylla	+	+	+	+
Rhopalonema velatum	+	+	+	+
Solmundella bitentaculata			+	+
Solmissus albescens			+	
Siphonophora (Calycophorae)				
Vogtia pentacantha				+
Hyppopodius hyppopus	+		+	
Lensia conoidea				+
Lensia subtilis	+	+	+	+
Lenisa meteori	+	+	+	+
Lensia campanella	+	+	+	
Lensia multicristata			+	+
Sulculeolaria turgida	+			

Taxa/stations	P-100	P-150	P-300	P-1200
Muggiaea atlantica	+	+	+	
Muggiaea kochi	+	+	+	
Chelophyes appendiculata	+		+	+
Sphaeronectes irregularis	+	+	+	
Sphaeronectes gracilis	+	+	+	
Abylopsis tetragonal	+		+	
Bassia bassensis	+		+	
Eudoxoides spiralis	+	+	+	+
Ctenophora				
Pleurobrachia pileus	+			+
Charistephane fugiens			+	+
Mollusca				
Heteropoda				
Firoloida desmaresti	+			
Pteropoda				
Limacina inflata	+	+	+	+
Limacina trochiformis	+	+	+	+
Styliola subula	+		+	
Hyalocylix striata	+			+
Creseis virgula	+	+	+	
Creseis acicula	+		+	
Clio pyramidata			+	+
Peracilis reticulata	+			
Cymbulia peroni	+	+	+	
Annelida				
Polychaeta				
Tomopteris elegans	+	+	+	+
Calizzonela lepidota	+	+	+	
Callizona nasuta				+
Vanadis crystalina	+	+	+	
Vanadis formosa	+		+	
Pelagobia longicirrata		+	+	+
Sagitella kowalevskii	+		+	
Travisiopsis lanceolata			+	
Phalacrophorus pictus		+	+	+
Pontodora pelagica			+	+
Maupsia coeca				+
Chaetognatha				
Sagitta enflata	+	+	+	+
Sagitta minima	+	+	+	+
Sagitta setosa	+	+		+
Sagitta serratodentata	+	+	+	+
Sagitta bipunctata		+		+
Sagitta lyra	+	+	+	+
Sagitta decipiens		+	+	+
Khronita subtilis			+	+
Crustacea				
Copepoda				
Calanus helgolandicus	+	+	+	+
Calanus tenuicornis		+	+	+
Eucalanus elongatus		+	+	+
Paracalanus parvus	+	+	+	+
Calocalanus pavo			+	
Calocalanus contractus			+	
Mecynocera clausi	+	+	+	+
Clausocalanus arcuicornis	+	+	+	+
Clausocalanus pergens	+		+	+
Ctenocalanus vanus				+
Pseudocalanus elongatus	+	+	+	+

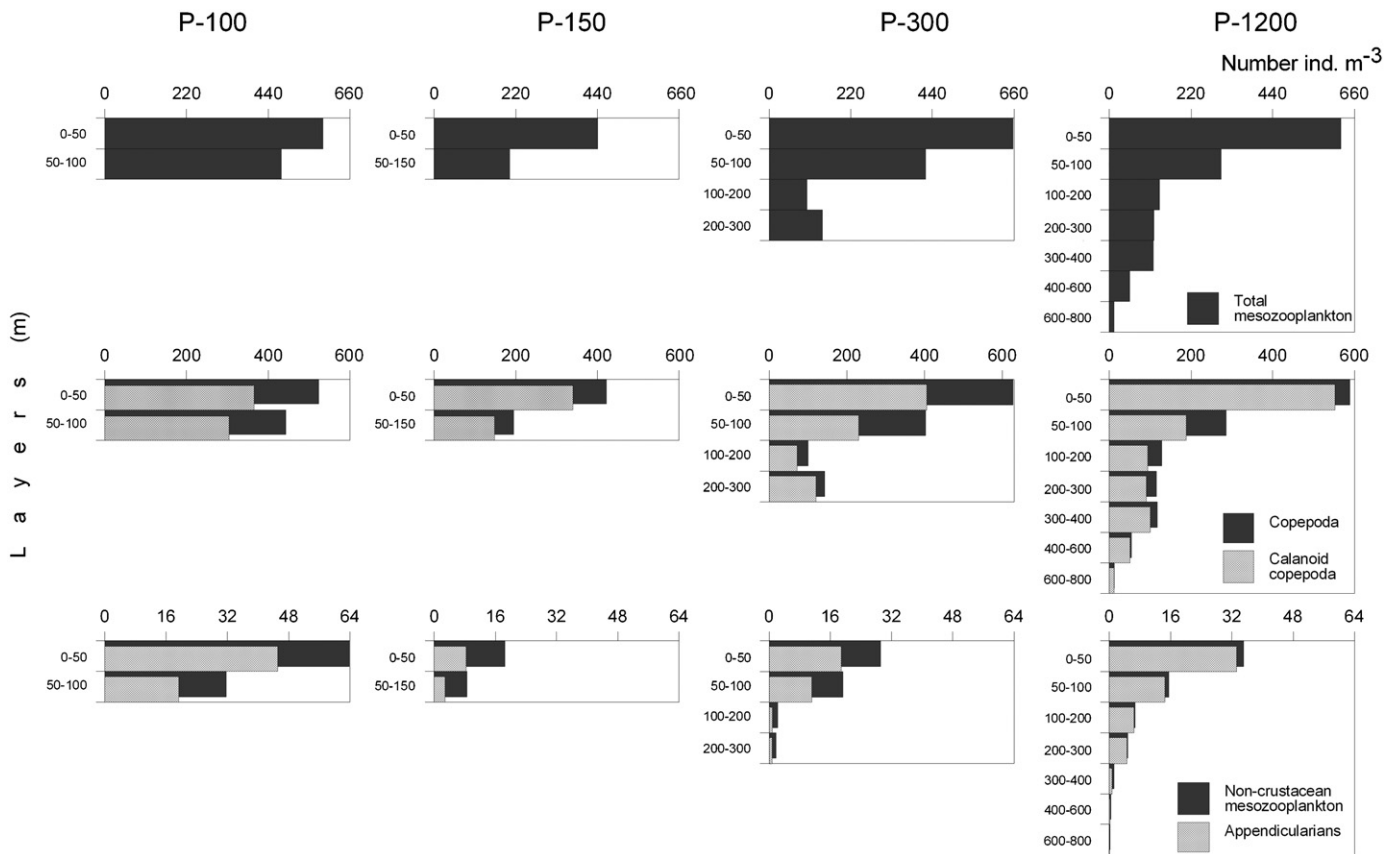| Taxa/stations	P-100	P-150	P-300	P-1200
Aetideus armatus			+	+
Monacilla typica			+	
Euchaeta acuta	+			+
Scolecitrix brady				+
Scolecithricella dentate			+	+
Scaphocalanus brevicornis				+
Scaphocalanus curtus			+	+
Centropages typicus			+	+
Temora stylifera			+	
Pleuromamma abdominalis				+
Pleuromamma gracilis	+	+	+	+
Lucicutia flavicornis		+	+	+
Lucicutia longicornis	+			+
Lucicutia clausi				+
Haloptilus longicornis			+	+
Haloptilus acutifrons			+	
Candacia armata	+			+
Candacia longimana	+	+		+
Candacia simplex			+	
Candacia varicans			+	
Oithona similis	+	+	+	+
Oithona plumifera	+		+	
Microsetella norvegica				+
Oncaea media	+	+	+	+
Oncaea mediterranea	+		+	+
Sapphirina sp.	+	+	+	+
Corycaeus sp.	+	+	+	+
Lubbockia sp.				+
Tunicata				
Thaliacea				
Doliolina mülleri	+		+	+
Doliolum nationalis	+		+	
Dolioletta gegenbauri		+		
Salpa fusiformis	+	+		
Thalia democratica		+	+	
Thalia orientalis		+	+	+
Appendicularia				
Oikopleura longicauda	+	+	+	+
Oikopleura cophocerca	+	+	+	+
Oikopleura albicans	+	+	+	+
Oikopleura parva			+	+
Oikopleura fusiformis	+	+	+	+
Oikopleura villafrancae			+	+
Oikopleura gracilis	+			
Oikopleura intermedia	+	+	+	
Folia mediterranea			+	
Stegosoma magnum	+		+	
Fritillaria pellucida	+	+	+	+
Fritillaria haplostoma			+	
Fritillaria borealis	+		+	+
Fritillaria formica tuberculata	+		+	+
Fritillaria gracilis			+	+
Fritillaria venusta			+	
Fritillaria tenella		+	+	+
Fritillaria urticans			+	
Fritillaria fraudax			+	
Fritillaria messanensis	+		+	

Fig. 11. Distribution of mesozooplankton along the study transect in the South Adriatic.

P-100 (Fig. 11). Abundance decreased with depth, the lowest values being found below 300 m (< 1 ind m^{-3}).

The most abundant appendicularians at all stations – *Oikopleura longicauda*, *Fritillaria pellucida*, and *O. cophocerca* – made up more than 90% of appendicularians collected in the upper 100 m. Station P-300 had characteristic deep species below 100 m, but these were mostly absent at P-1200. In fact, in comparison with P-300, the deeper layers of P-1200 had a very low abundance of *Oikopleura parva*, *O. villafrancae*, and *Fritillaria tenella*, while *F. fraudax*, *F. urticans*, *F. gracilis*, and *F. venusta* were completely missing. On the contrary – and unusual for these deeper layers – the dominant species bellow 100 m were *F. pellucida* and *O. longicauda*.

4. Discussion

4.1. Hydrography

The thermohaline data suggest one or more convection events in the southern Adriatic Sea study area during February 2008. The cruise took place during the coldest period of the month when there was substantial winter heat loss at the air-sea interface. This produced dense surface water and consequent convective mixing that, at offshore station P-1200, extended to 400 m. The ensuing vertical movements homogenized the properties of the upper water column. Salinity in particular was rather uniform from the surface to 400 m. The time evolution of this event was confirmed by the thermohaline properties of the SESAME (project, Southern European Seas: Assessing and Modeling of the Ecosystem Changes) oceanographic campaign. Those data, collected about a week later, proved that the mixed layer depth reached about 700 m near P-1200 (not shown).

The subsurface temperature and salinity maxima at 100 m (14.22 °C, 38.82) at station P-300 seem to be a signature of LIW (Malanotte-Rizzoli et al., 1997; Manca and Scarazzato, 2001). This water type is characterized by low dissolved oxygen and high nutrient concentrations, likely results of biologically mediated remineralization.

Similar features of LIW have been observed in the past (Gačić et al., 2002), but with the LIW core at 300 m. LIW thus is a possible source of nutrients for the basin (Zavatarelli et al., 1998). The LIW signal at P-1200 is attenuated by mixing with surface water that is poorer in nutrients. The lowest oxygen saturation, 0.75–0.80 (concentrations of 192–205 μM), are at 100–300 m, probably because of the combined effect of LIW intrusion, vertical convection, and biological processes.

The phenomenon of the open sea vertical convection is well known for the Southern Adriatic Pit (Manca et al., 2002, and references therein). There, favorable conditions for the winter convection occur, like in the Gulf of Lions (Leaman and Schott, 1991). The sub-basin cyclonic circulation of the Southern Adriatic gyre wells up denser waters in its center. Thus, the water column away from the coast, like station P-1200, has less buoyancy content at its surface than in the coastal zone. Hence, it is easier to trigger the vertical mixing due to the additional buoyancy loss at the air-sea interface due to the strong cooling during intense bora events. The borders, especially the surface layers along the eastern flank of the SAP remain relatively more stratified, owing mostly to the fresher coastal waters. Therefore, the effects of the cooling and mixing in the coastal region do not persist like in the open sea area.

4.2. Plankton community during convective event

The vertical distribution of the bacteria and heterotrophic picoflagellates (HPF) in the deep South Adriatic (SA) was similar to the heterotrophic component of the microbial community of the deep Northwestern Mediterranean in the February (Tanaka and Rassoulzadegan, 2002). Unusually large size of bacteria almost throughout the water column could be related to the high concentration of detritus (Jürgens and Sala, 2000) at the same depths.

Cyanobacteria were evenly distributed at very low abundance down to 800 m, which is consistent with their winter pattern in the Eastern Mediterranean (Zohary et al., 1998). Autotrophic picoflagellates (APF) were found throughout the water column (0–800 m) with a high abundance in the aphotic layers. This finding contrasts with the rapid decrease in abundance of autotrophic microbial community in the aphotic layers of the deep East and Northwest Mediterranean (Tanaka et al., 2007). Convective mixing owed to the buoyancy loss during the February *bura* events was responsible for aforementioned unusual finding and the dramatic change in the vertical distribution of nano- and microphytoplankton. According to previous investigations, nano- and microphytoplankton in the SA reach their peak abundance between 0 and 50 m throughout the year (Viličić et al., 1989; Viličić, 2003). The highest nano- and microphytoplankton abundance occurred in the aphotic layer on 19 February 2008 with a maximum at 400 m at P-1200. A necessary condition for such high phytoplankton abundance at depth is a high abundance of phytoplankton in the upper productive layers prior to the convective event. Indeed, before this event, in the beginning of February, an increase in surface Chl-*a* was evident in satellite imagery. This might be related to earlier convective mixing that increased the supply of nutrients to the surface layer, an important condition for bloom development. The upper layers were supplied with such higher nutrient concentrations during the 19 February event and, several weeks later, satellite imagery indicated high surface Chl-*a* (≥ 0.5 mg m^{-3}) in the open SA. A similar sequence was observed during spring in the SA (Gačić et al., 2002; Civitarese et al., 2005). On the other hand, convective mixing, by transporting phytoplankton below Sverdrup's critical depth, can lead to reduction of primary productivity (Dutkiewicz et al., 2001). This effect is probably present only during, and just after cessation of convective event. Additionally, sampling of phytoplankton exclusively in the euphotic layer, as is routinely done, can easily lead to under-estimation of primary production during the seasons of intensive convections due to exclusion of cells in the depth.

Diatoms were the dominant taxa in the aphotic layers. Of the diatoms in the aphotic layers, the most abundant were species of the highly diversified genus *Chaetoceros*, common in the surface SA (Jasprica and Carić, 2001; Jasprica et al., 2001). *Ditylum brightwellii*, a rather uncommon species in earlier investigations (Viličić et al., 1989; Viličić, 2002), was noticeably more abundant, especially at 50, 300, and 400 m. This species is very frequent in the coastal Aegean in autumn and winter (Balkis, 2009). Two newly recorded phytoplankton species for the Adriatic were found: *Ornithocercus splendidus* and *Neoceratium paradoxides*. Both are known from the northern Levantine Basin (Polat and Koray, 2007) so their occurrence altogether with *D. brightwelli* might be related to documented changes in Ionian Sea circulation that result in the flow of Aegean and Levantine waters into the Adriatic.

These changes in the Ionian Sea circulation consist of alteration of advection of saltier Aegean/Levantine water with less-salty water of Atlantic origin (MAW), which modify the thermohaline properties of the Adriatic Sea (Gačić et al., 2010). In years in which

Ionian circulation is cyclonic (after 1997), inflow of saltier Aegean/Levantine water should enhance the depth of convection. In years of Ionian anticyclonic circulation (1993–1997) lower salinity can lead to reduction or cessation of winter convection (Civitarese et al., 2010). In the latter case, there would be little or no downward transport of biological material. This difference in winter convection may partially explain year-to-year variability of the phytoplankton production in the open SA (Santoleri et al., 2003).

Zooplankton generally were distributed vertically as in previous investigations, with the main population in epipelagic layer and decreased in abundance with depth (e.g. Hure, 1980; Kršinić, 1998; Kršinić and Grbec, 2002; Batistić et al., 2003, 2004; Benović et al., 2005; Lučić et al., 2005). This suggests that zooplankton generally resisted downward convective transport. Experimental analyses of swimming behavior demonstrate that planktonic ciliates are able to maintain their vertical position even in turbulent water (Jonsson, 1989). Similar, swimming activity of copepods increases as they try to maintain their depth level during high wind speed and high turbulence (Lagadeuc et al., 1997).

However, even though tintinnids and copepods declined with increasing depth, their abundance during this study was several times higher in some layers below 200 m than in previous winter investigations in the deep SA (see Kršinić, 1998; Kršinić and Grbec, 2002; Batistić et al., 2003): tintinnid abundance was about 4 to 8 times higher at 200–400 m; copepod abundance was 3 to 4 times higher at 300–400 m; and 9–10 times higher at 400–600 m. In comparison with the East and West Mediterranean (Scotto di Carlo et al., 1984; Pancucci-Papadopoulou et al., 1992; Siokou-Frangou et al., 1997; Licandro and Icardi, 2009) copepod abundance was at least four times higher in the deep SA in corresponding layers.

The greater number of some herbivorous zooplankton (tintinnids, calanoid copepods) found in the deeper layers of the SA in February 2008 might be a consequence of the strong downward water flux, but also of their reaction to the supply of fresh phytoplankton related to earlier convective events. Taking into consideration that some diatoms can survive 20 to 30 days of darkness (Peters, 1996), it seems likely that they could be an important food source below the euphotic zone.

The occurrence and relative contribution of some zooplankton species from 100 to 800 m also was different compared with earlier studies (see Hure and Kršinić, 1998; Kršinić, 1998; Kršinić and Grbec, 2002). Neritic-coastal and surface tintinnid species, *Tintinnopsis campanula* and *Codonellopsis schabii* were uncharacteristically found down to 800 m. Typical deep-sea calanoid species were either absent or rare; the dominant species were the calanoids *Pleuromamma gracilis* and *Calanus helgolandicus* and the cyclopoid *Oithona similis*, particularly from 200 to 400 m. The vertical distribution of *P. gracilis* and *C. helgolandicus* in this study is consistent with their distribution in the East Mediterranean (EM), but their abundance in the EM is markedly lower, < 1.5 ind m^{-3} (Scotto di Carlo et al., 1984; Pancucci-Papadopoulou et al., 1992; Siokou-Frangou et al., 1997). *O. similis* as a typical epipelagic species in the Mediterranean Sea (Pancucci-Papadopoulou et al., 1992; Siokou-Frangou et al., 1997; Hure and Kršinić, 1998; Licandro and Icardi, 2009) was also uncharacteristically found down to 600 m. A similar pattern was found for Appendicularia: species heretofore characteristic of deeper layers were mostly absent (Fenaux, 1967). Instead, the dominant species in the 300–400 m and 400–600 m layers were the epipelagic species *Fritillaria pellucida* and *Oikopleura longicauda*. It seems that this difference in the vertical position of mentioned species was a consequence of the strong downward flux rather than an advection of Eastern Mediterranean Water.

All of these species are permanent inhabitants of the SA (Kršinić, 1998; Hure and Kršinić, 1998; Lučić, 1998), so neither their presence nor their abundance depends directly on advection of Eastern Mediterranean Water. The species newly recorded for the Adriatic can, on the other hand, be traced with higher confidence to Eastern Mediterranean Water inflow.

The most abundant zooplankton group, copepods, also deviated from their usual horizontal distribution. Instead of their characteristic decrease from nearshore to offshore (Hure and Kršinić, 1998; Batistić et al., 2003), mesozooplanktonic copepods abundance increases at the offshore stations. This correlated with higher offshore phytoplankton biomass documented by satellite imagery in this study and over the last decade (Morović et al., 2004) and could be an indirect consequence of the convective events.

5. Conclusions

Autotrophs, especially nano- and microphytoplankton can, as in the present case, provide strong evidence of convective events. This evidence may be direct, as when numerous viable phytoplankton are found well below the euphotic zone; or indirect, as manifests in a marked increase in primary production subsequent to such an event. This indirect sort of evidence was found few years ago during spring season in the Southern Adriatic (Gačić et al., 2002; Civitarese et al., 2005).

High phytoplankton abundance throughout the water column in the mid-February, combined with surface Chl-$a \geq 0.5$ mg m^{-3} (as judged by satellite imagery) in the beginning of February and March are evidence of a winter bloom in the open Southern Adriatic driven by convection. An important consequence of this increased phytoplankton biomass is that secondary production may have increased in both surface and deeper layers.

The strong convection responsible for the phytoplankton maximum in the aphotic layer observed in this study was induced by surface cooling during episodes of strong wind (the region's cold, dry north wind *bura*) at a time when saline Eastern Mediterranean Water had entered the Southern Adriatic. Those years in which the flow of less saline Atlantic water combines with a mild winter naturally should feature weaker – or perhaps even no significant – convection (Civitarese et al., 2010). Consequently, there should be considerably less living organic matter at depth. Therefore, year-to-year variability in the intensity of winter convection may have an important impact on the biogeochemical cycle and carbon storage in the deep South Adriatic.

The short duration of winter blooms (Legendre and Rassoulzadegan, 1996) suggests that they easily can be missed by typical ship-based sampling programs. In addition, phytoplankton abundance can be under-estimated due to convection-driven sinking of cells bellow standard phytoplankton sampling depths. If that is the case, then annual production for the South Adriatic has been under-estimated by an amount that yet is to be quantified.

This study has drawn attention to an aspect of the winter ecology of the open South Adriatic that heretofore has not been incorporated into explanations of the distribution and production of its planktonic communities. Future work that documents the frequency, magnitude, and impact of convective events such as that described herein will further enhance understanding of the structure and function of the South Adriatic ecosystem.

Acknowledgements

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