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Composition and dynamics of the phytoplankton of the Ionian Sea (eastern Mediterranean)

R. Casotti, A. Landolfi,¹ C. Brunet, F. D'Ortenzio, O. Mangoni,² and M. Ribera d'Alcalà
 Stazione Zoologica "A. Dohrn" di Napoli, Naples, Italy

M. Denis

Laboratoire d'Océanographie et de Biogéochimie, Marseille, France

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[1] The relationship between phytoplankton distribution and dynamics, and the resident water masses in the Ionian Sea was investigated in the spring of 1999 by flow cytometry, HPLC, microscopy, ¹⁴C incorporation, and serial dilutions. More than 50% of total biomass was represented by ultraphytoplankton, with proportions increasing with depth (up to 80%) and eastward (up to 60%). *Synechococcus* sp. cyanobacteria dominated ultraphytoplankton numbers and biomass. Hydrological stability explained the relative vertical distribution of *Synechococcus* sp. and *Prochlorococcus* sp. cyanobacteria and their degree of photoacclimation. The northwestern area ("Italian Side") was in a transition from bloom to oligotrophic conditions, reflected in high biological instability in terms of phytoplankton composition, photoacclimative properties, and photosynthetic efficiency (P/B of 11.40 mg C mg chl⁻¹ h⁻¹). The influence of the Adriatic Surface Water, carrying a trace of the spring bloom was visible from satellite imagery (SeaWiFS). The eastern part of the sampled area ("Greek Side," GS) was hydrologically more stable (low estimated vertical velocities), resulting in higher photosynthetic efficiency (P/B of 20.47 mg C mg chl⁻¹ h⁻¹) and phytoplankton photoacclimative properties. The Atlantic Water (AW) was the most oligotrophic in terms of nutrient concentration, *chl a*, and productivity (208.0 mg C m⁻² d⁻¹), but also the most variable in terms of mesoscale features. Growth of *Synechococcus* sp. and *Prochlorococcus* sp. was slow (0.36 d⁻¹ at max), while picoeukaryotes grew well in the deep chlorophyll maximum (DCM) of the GS (0.67 d⁻¹). Picoeukaryote growth was tightly coupled with grazing (0.80 d⁻¹), indicating efficient biomass recycling. Biological characterization and DCM dynamics in the three areas are discussed in relation to physical features present at the time of sampling. **INDEX TERMS:** 4803 Oceanography: Biological and Chemical: Bacteria; 4815 Oceanography: Biological and Chemical: Ecosystems, structure and dynamics; 4817 Oceanography: Biological and Chemical: Food chains; 4855 Oceanography: Biological and Chemical: Plankton; **KEYWORDS:** ultraplankton, flow cytometry, primary productivity, Mediterranean Sea, mixing, photoacclimation

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1. Introduction

[2] The Ionian Sea has been the focus of oceanographic cruises over the last decade, due to its key role in the interaction between the Adriatic Sea and the eastern Mediterranean Sea, the former being the main source of deep water for the Levantine Basin [Malanotte-Rizzoli *et al.*, 1997]. In the last 15 years, a new source of dense deep

water has been observed in the eastern Mediterranean originating from the Aegean Sea, challenging the previous dominance of the Adriatic Deep Water [ADW; Roether *et al.*, 1996; Klein *et al.*, 1999; Lascaratos *et al.*, 1999; Malanotte-Rizzoli *et al.*, 1999]. The Ionian Sea plays a crucial role in this process and it has been the object of several investigations aimed at assessing the impact of the water mass redistribution (denominated Eastern Mediterranean Transient) on the general functioning of the area. In fact, the generation of deep water from the Aegean Sea, should lead to a rise in the intermediate layer and consequent rise of the nutricline [Klein *et al.*, 1999] and strongly alters the nutrient distribution in the southern Adriatic Sea [Civitaresse and Gacic, 2001; Manca *et al.*, 2002]. The effect of the change on the biological activity of the

¹Now at School of Ocean and Earth Science, University of Southampton, Southampton Oceanography Centre, Southampton, UK.

²Now at University of Naples "Federico II", Dipartimento di Zoologia, Naples, Italy.

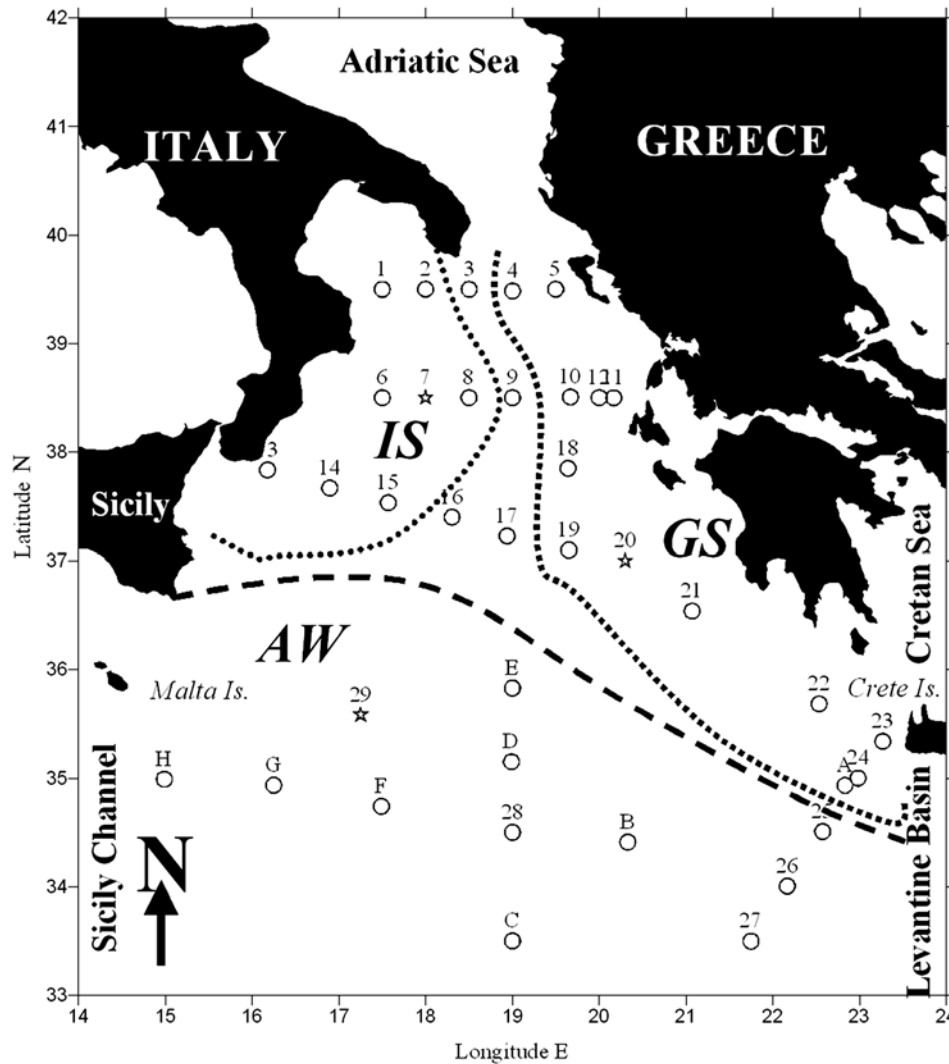


Figure 1. Map of the Ionian Sea with stations sampled from 20 April to 10 May 1999. Stations from 1 to 29 were sampled onboard the R/V *Urania* (EMTEC cruise), stations from A to H were sampled onboard the R/V *Meteor*, during a cruise covering the entire eastern Mediterranean (Leg 44). At the three stations indicated with a star, additional measurements of nutrients, ^{14}C incorporation, ultraphytoplankton growth and grazing rates, ciliate abundance, and phytoplankton microscopic counts were performed. Dotted lines delimit the different areas identified: Italian Side (IS), Greek Side (GS), and Atlantic Water (AW).

euphotic zone is still under debate, although both modeling exercises and in situ data suggest that the winter mixing may not reach the raised nutricline, and therefore would never allow injection of nutrients into the surface layer, fertilizing the area [Civitaresse and Gacic, 2001; D'Ortenzio *et al.*, this section]. Instead, mesoscale features may enhance photosynthetic capacity locally, as observed in many areas [Falkowski *et al.*, 1991; Estrada, 1996; Levy *et al.*, 1998; Morán *et al.*, 2001], yet, there is little evidence of large increases in biological production in the Ionian Sea at the basin scale [Stratford and Haines, 2002].

[3] In general, the Ionian Sea is considered an oligotrophic area, based both on low nutrient concentrations [Bregant *et al.*, 1992] and low primary production [Magazzù and Decembrini, 1995; Boldrin *et al.*, 2002; Moutin and Raimbault, 2002]. Primary production data

are scarce and from restricted areas [Viličić *et al.*, 1989; Magazzù and Decembrini, 1995; Turchetto *et al.*, 1998; Bianchi *et al.*, 1999; Moutin and Raimbault, 2002]. In general, biological data depict a very oligotrophic area, dominated by a microbial food web, where new production mostly derives from limited events in space and time which are mainly driven by climatological factors generating mesoscale instabilities [Civitaresse *et al.*, 1996; Boldrin *et al.*, 2002]. As for biology, the influence of the Adriatic water is mostly evident in the northern part of the subbasin in the form of higher phytoplankton biomass particularly diatoms [Socal *et al.*, 1999], while water of Atlantic origin makes up its southern part [Rabitti *et al.*, 1994], with the exception of the whole eastern side, where very oligotrophic water from the Cretan Sea dominates [Kerhervé *et al.*, 1999].

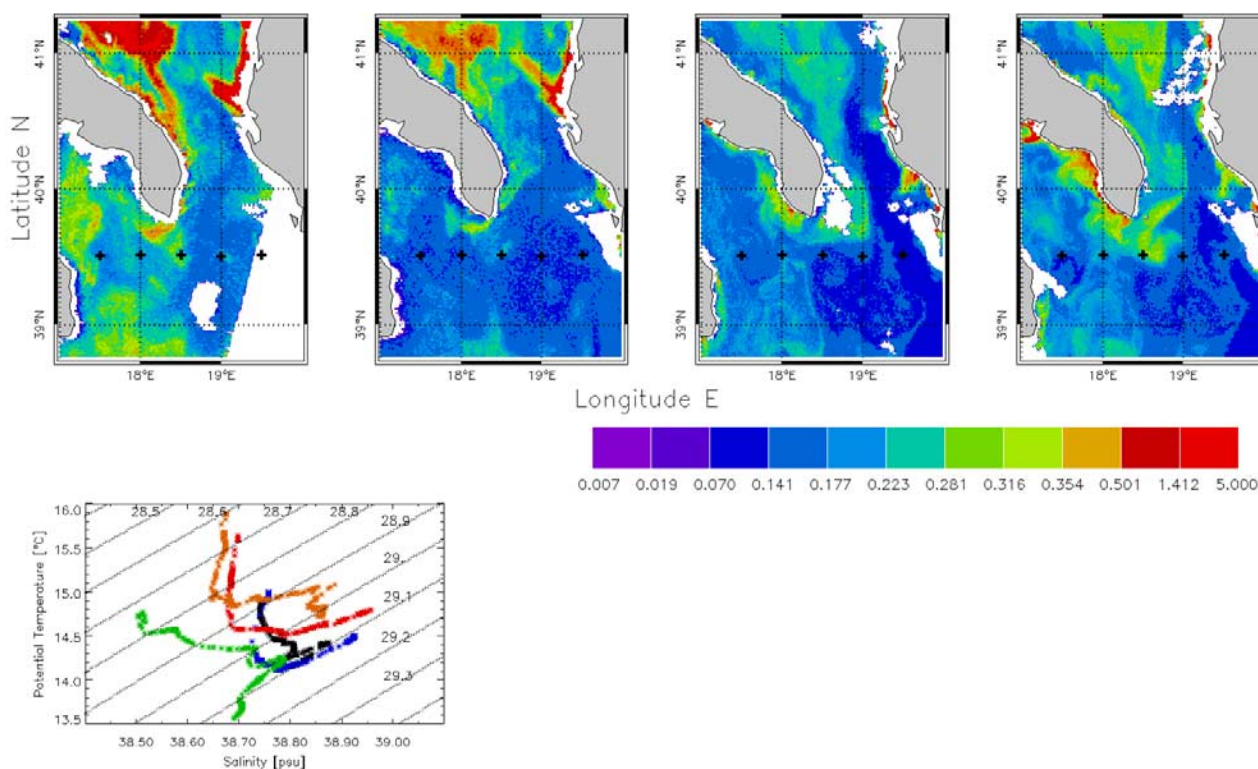


Figure 2. Satellite (SeaWiFS) estimates of chlorophyll concentrations ($\mu\text{g/L}$) in the Ionian Sea on (a) 4 April, (b) 7 April, (c) 14 April, and (d) 19 April (date of sampling of stations 1–5, dots on the figures, from left to right). (e) θ - S plots for the five stations of the transect: station 1 (black), station 2 (blue), station 3 (green), station 4 (red), and station 5 (brown).

[4] Data available suggest a relative homogeneity of the phytoplankton and bacterial populations, but no information is available on smaller autotrophic microbes, the picoplankton [Sieburth, 1979], and nanoplankton, despite their established importance [Rabitti et al., 1994]. These small algae include cyanobacteria belonging to the genera *Synechococcus* [Waterbury et al., 1979] and *Prochlorococcus* [Chisholm et al., 1988; Urbach et al., 1992], as well as a diversity of eukaryotic phytoplankton members of the Chlorophyceae, Pelagophyceae, Prymnesiophyceae, and other taxonomic groups [e.g., Andersen et al., 1993; Moon-van der Staay et al., 2001]. In the present study, we define as ultraphytoplankton, organisms $<5 \mu\text{m}$ in Equivalent Spherical Diameter (ESD), to account for cells commonly detected by flow cytometry [Li, 1997]. These organisms are very abundant in any environment, but dominate oligotrophic, nutrient poor, warm waters, where they can account for $\geq 50\%$ of total phytoplankton biomass and production [e.g., Agawin et al., 2000a]. The food web in these areas is based upon the production of these algae, and other organisms, notably the heterotrophic bacteria (also part of the ultraplankton), depend on dissolved organic molecules derived from phytoplankton.

[5] In the Mediterranean Sea, ultraphytoplankton has been shown to be abundant both in coastal and oceanic waters [e.g., Vaulot et al., 1990; Li et al., 1993; Casotti et al., 2000; Denis et al., 2000; Morán et al., 2001, and references therein]. The little available data from the open waters of the eastern Mediterranean basin point to a numerical and

biomass dominance of the ultraphytoplankton [Li et al., 1993; Yacobi et al., 1995; Siokou-Frangou et al., 2002], and a complex functioning of the microbial food web, with different pathways of carbon within and out of the microbial compartment [Zohari and Robarts, 1992; Robarts et al., 1996; Christaki et al., 2001]. The heterotrophic bacteria have received little attention, with the exception of a few papers [Zohari and Robarts, 1992; Robarts et al., 1996; La Ferla et al., 1999; La Ferla and Azzaro, 1996, 2001], all showing a tight coupling of the bacterial activity and respiratory processes with circulation patterns and water mass properties.

[6] In this paper, results of a cruise performed in April–May 1999 in the Ionian Sea, covering several stations at the subbasin scale, are reported and discussed. Shipboard flow cytometry was used to investigate vertical and spatial distributions and fluorescence characteristics of ultraplankton populations. During the cruise, different areas were identified based on their hydrological and biological characteristics, namely, the Italian Side (IS), the Greek Side (GS), and the Atlantic Water (AW), as marked in Figure 1. High heterogeneity was induced by mesoscale and basin-scale features in the surface layer, but similarities were observed between the GS and the Levantine Surface Water (LSW), and between the IS and the Ionian Surface Water (ISW), as previously defined by Malanotte-Rizzoli et al. [1999]. Sampling took place in the time following the spring bloom, as visible from satellite imagery in the IS [“Calabrian bloom,” D’Ortenzio et al., this section] or in the South Adriatic Sea (this paper, Figure 2). No such event was evident from remote sensing in the GS or the

AW, although we cannot exclude the occurrence of a relative increase in chlorophyll concentrations at depths not reached by the sensors.

[7] The aim of this study was to investigate the vertical and spatial distribution of phytoplankton, as well as their dynamics through measurements of growth and grazing of ultraphytoplankton, as related to hydrology at the scale of the subbasin. Results are discussed with respect to the biogeochemical features of the area and the factors influencing them.

2. Methods

2.1. Sampling and Hydrological Parameters

[8] In spring 1999 (20 April–10 May), the Italian EMTEC cruise (Eastern Mediterranean Transient Ecosystem) covered 29 stations in the Ionian Sea on board the Italian R/V *Urania* (Figure 1, stations 1–29). Additional samples for ultraplankton were also collected from eight stations sampled in the same period by the German R/V *Meteor* (Figure 1, stations A to H).

[9] Water samples were collected using a CTD rosette sampler with 10 L Niskin bottles (General Oceanics, USA). The bottles were remotely triggered on the upcast at 10–12 depths together with the acquisition of hydrographic data (temperature, salinity, oxygen, and fluorescence). Sampling depth always included surface (5 m) and the DCM, the other depths being evenly distributed through the water column according to the fluorescence profile. Vertical profiles of light (PAR) were obtained at seven stations (3, 7, 17, 18, 20, 26, 29) by a spectroradiometer SPMR (Satlantic Inc., Canada) at 1200 LT on days when the sky was clear.

[10] Samples for Dissolved Inorganic Nitrogen ($\text{DIN} = \text{NO}_3^- + \text{NO}_2^-$) and phosphates were taken only at stations 7, 20, and 29. They were frozen and stored at -20°C until analysis. Concentrations were determined colorimetrically according to *Grasshof* [1983].

2.2. Pigment Analysis

[11] Samples for pigment analysis were taken at 13 stations at different depths, filtered onto Whatman GFF filters, frozen in liquid nitrogen and stored at -80°C for postcruise analysis. Once thawed, pigments were extracted in 90% acetone and analyzed using a Beckman Gold HPLC (Beckman, USA), according to *Mantoura and Llewellyn* [1983] as modified by *Brunet et al.* [1993]. Phytoplankton community composition was derived using marker pigments and conversion factors as in the work of *Casotti et al.* [2000] and reported in Table 2. The HPLC method used did not allow discrimination of divinyl chl *b* [which is contained in *Prochlorococcus*, *Goericke and Repeta*, 1992], from chl *b*, which is used as a marker pigment of chlorophyte algae (Table 2). Therefore the contribution of chlorophytes may have been overestimated when high concentrations of *Prochlorococcus* were present, such as, for example, at the DCM of the GS.

[12] The proportion of biomass attributed to new producers in the phytoplankton communities encountered was estimated using the F_p , which was defined as the ratio between the biomass of diatoms and dinoflagellates (in terms of chlorophyll) and the biomass of all groups present, identified through their diagnostic pigment markers [*Claustre*, 1994].

[13] In order to characterize phytoplankton biomass based on size distribution, additional samples were prefiltered onto Nuclepore filters of 2 or 10 μm pore size and successively filtered onto GFF filters, frozen, and analyzed spectrofluorometrically (mod. FluoroLog, SPEX Industries Inc., USA) according to *Neveux and Panouse* [1987].

2.3. Phytoplankton, Bacteria, and Carbon Estimates

[14] Samples for ultraplankton from all stations were collected in sterile 50 mL polycarbonate tubes (Nalgene Inc., USA) and maintained in the dark at 4°C for no more than 1 hour [*Jacquet et al.*, 1998]. Ultraphytoplankton from stations 1 to 29 (including those from the reference stations 7, 20, and 29) were counted onboard by flow cytometry using a Becton Dickinson FACScalibur (Becton Dickinson, USA), following standard procedures [*Partensky et al.*, 1996; *Marie et al.*, 1999]. Samples from stations A to H were fixed with a mix of glutaraldehyde 0.05% and paraformaldehyde 1% for 15–30 min [*Marie et al.*, 1999], frozen in liquid nitrogen and analyzed in the lab within 1 month. Beads (0.97 μm , Polysciences Inc., USA) were used as an internal standard, with all values for phytoplankton being expressed as units relative to the beads (r.u.). As in other studies [e.g., *Li*, 1997], we classified the fluorescing ultraphytoplankton into three groups: cyanobacteria belonging to the genera *Synechococcus* and *Prochlorococcus*, and picoeukaryotes, including small eukaryotic phytoplankton of composite taxonomic affiliation. Cell abundance, mean fluorescence, and light scatter per cell were extracted using CellQuest software (Becton Dickinson, USA).

[15] In order to assess the effects of fixation on ultraphytoplankton cell concentrations, duplicate samples from stations 7, 20, and 29 were analyzed both fresh and fixed (after 1 month storage). Mean cell concentrations were not significantly different ($p < 0.05$) and cell numbers of fresh samples were highly correlated to those of fixed samples ($p < 0.001$, $n = 15$ for *Synechococcus*, $n = 14$ for *Prochlorococcus*, $n = 12$ for picoeukaryotes). Based on the results, cell concentrations of fixed samples were corrected using a multiplication factor retrieved from the regression equation, i.e., 1.58 for *Synechococcus*, 1.32 for *Prochlorococcus*, and 1.00 for picoeukaryotes. In the case of extremely dim *Prochlorococcus* populations at the surface (not very frequent), the population was assumed to have a normal distribution, and the hidden portion was extrapolated, as indicated by *Blanchot and Rodier* [1996] and *Partensky et al.* [1996].

[16] Fixed and frozen samples were stained after thawing with SYBR Green I (Molecular Probes Inc., USA) and analyzed using flow cytometry according to *Marie et al.* [1997] to assess heterotrophic bacteria concentrations.

[17] Samples for microscopic determination of phytoplankton community from the three reference stations (7, 20, and 29) were taken at the surface and the DCM, fixed with 2% neutralized formalin and analyzed using an inverted microscope (IM35, Zeiss, Germany) after sedimentation for at least 48 hours [*Utermöhl*, 1958; *Hasle*, 1978].

[18] Cell concentrations were converted to biomass estimates using the conversion factors indicated by *Campbell et al.* [1994] and *Li et al.* [1992]. These are 20 fg C cell⁻¹ for heterotrophic bacteria, 53 fg C cell⁻¹ per *Prochlorococcus*, 250 fg C cell⁻¹ per *Synechococcus*, and 2100 fg C cell⁻¹

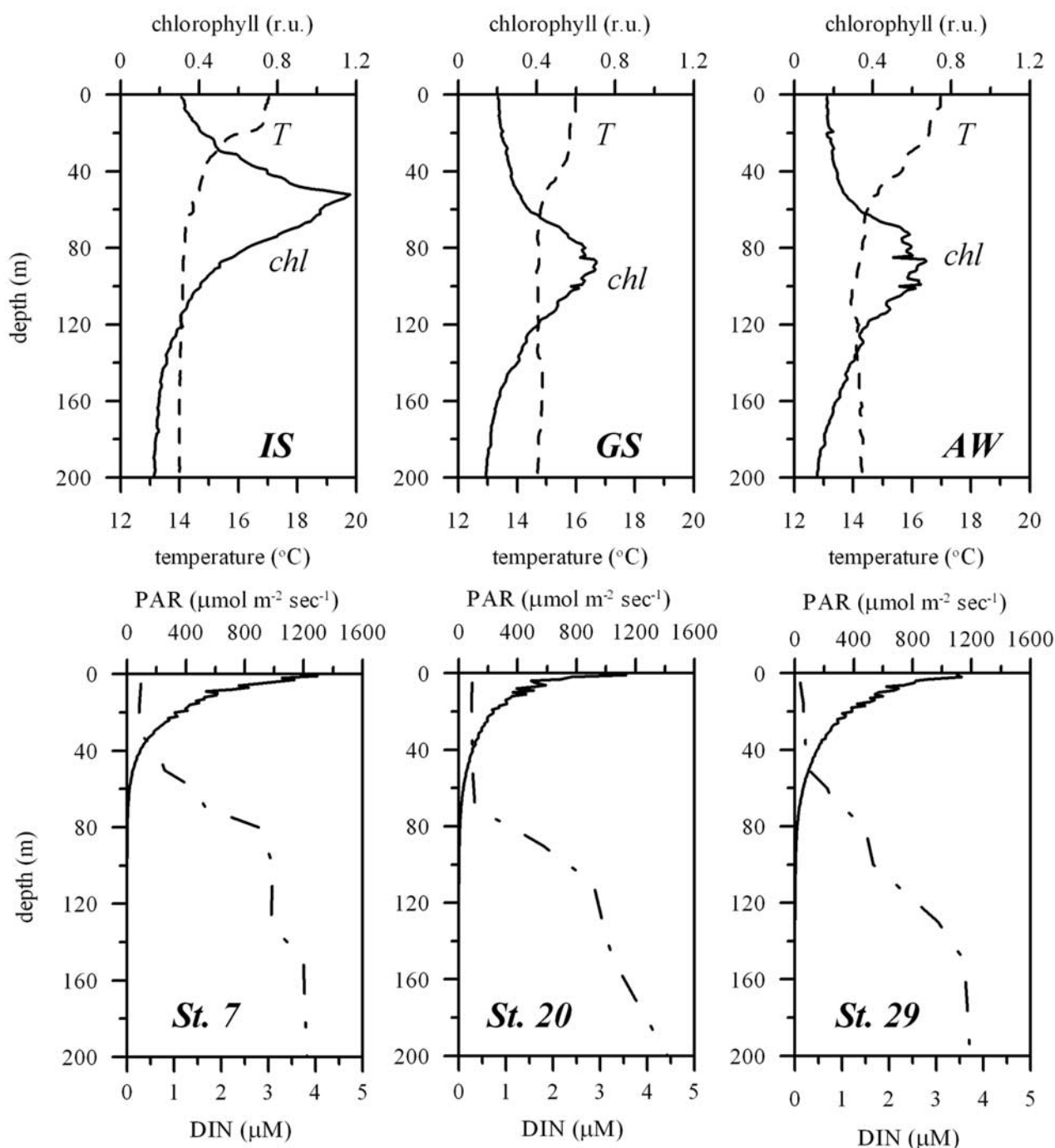


Figure 3. Ionian Sea. (top) Average profiles of temperature (T , °C, dashed line) and chlorophyll fluorescence (relative units, solid line) for the three areas identified in the study area, as measured by the CTD (IS, $n = 8$; GS, $n = 12$; AW, $n = 12$). (bottom) Dissolved Inorganic Nitrogen (DIN) concentrations (μM , dashed line) and PAR ($\mu\text{mol m}^{-2} \text{sec}^{-1}$, solid line) from station 7 (IS), station 20 (GS), and station 29 (AW).

per picoeukaryote. For total autotrophic biomass, a conversion factor of 50 for carbon to chl a was used [Fuhrman *et al.*, 1989].

2.4. Dilution Experiments

[19] At stations 7, 20, and 29, estimates of instantaneous growth rates (μ , d^{-1}) and grazing losses (g , d^{-1}) of ultra-

phytoplankton at 10 m depth and at the depth corresponding to the DCM (60, 75, and 70 m, respectively) were carried out using the dilution method of Landry and Hassett [1982] and its modifications [Campbell and Carpenter, 1986]. The samples from 10 m depth have been assumed to represent surface populations, as they lay inside the upper mixed layer of the euphotic zone.

[20] Each experiment was set up in 18 polycarbonate bottles of 250 mL volume, previously acid-cleaned [Fitzwater *et al.*, 1982]. Water for the dilution experiments was collected in 2 L Teflon bottles and filtered through 0.2 μm sterile inline filters (Millipore Inc., Bedford, USA), using tissue culture hoses and low pressure. Filtration was done immediately before setup of the experiments. Target concentrations for the dilution series were triplicates of 0, 33, 50, 67, and 100% undiluted seawater. Undiluted seawater was screened through a 200 μm net to exclude mesozooplankton.

[21] All experimental bottles were tightly capped after filling and incubated for 24 hours in temperature-controlled shipboard seawater incubators. These were wrapped with plastic neutral filters in order to mimic the light intensity at which samples were taken: 70% of surface light intensity on average for the 10 m samples and between 1 and 4% of surface light intensity for the DCM samples, as estimated from the SPMR. Incubations were begun at dusk and samples were collected at time 0 and after 24 hours and analyzed flow cytometrically without fixation as outlined above.

2.5. Primary Production

[22] Carbon assimilation rates were estimated at stations 7, 20, and 26 (chosen as representative of the IS, the GS, and the AW, respectively) using the ^{14}C method with in situ incubation for 3 hours, around noon. Samples were taken at 6 depths through the water column: at the surface, at the DCM, and at four additional depths chosen based on the fluorescence profile (generally 2–3 depths above and below the DCM). Each sample (300 mL) was inoculated with 1 mL (7.4×10^5 Bq) of $\text{NaH}^{14}\text{CO}_3$. After incubation, samples were filtered in dim light and radioactive content was measured using a Tri-Carb liquid scintillation counter (2100TR, Packard inc., USA), with 10 mL of Aquasol II scintillation cocktail. Production rates are means of three measurements and were calculated by normalizing the carbon uptake by the integrated PAR over the same time interval. Daily primary production rates were calculated by scaling the results to the daily integrated PAR.

3 Results

3.1. Hydrology

[23] Water mass distribution in the surface layer (0–200 m) and physical features are detailed in a related paper [Manca *et al.*, this section]. Briefly, the AW, which in the late 1980s–early 1990s circulated anticyclonically in the northwestern Ionian Sea [Malanotte-Rizzoli *et al.*, 1997, 1999], only occupied the southern part of the basin while flowing toward the Levantine Basin during the cruise (Figure 1, AW). A large-scale cyclonic circulation occupied the remaining part of the Ionian Sea. The main consequences were the absence of the AW in the northern Ionian Sea and a slight doming of the isolines of the intermediate water masses in the central part of the basin (not shown) [Manca *et al.*, 2003].

[24] Along the northernmost transect the intrusion of less salty and slightly colder water (Figure 2e), also relatively richer in chlorophyll (Figure 2d), was observed at station 3 in the first 50 m. This water mass was identified as Adriatic

Surface Water (ASW). Although the presence of the ASW was clearly observed only at station 3, its interaction with resident water masses through cyclonic circulation processes, generated water of mixed characteristics. This mixed water was situated close to the Italian coast and its thermocline was shallower with respect to the other areas present at the time of sampling (Figure 3). We called this the “Italian Side” (IS, Figure 1).

[25] At the opposite side of the basin, close to the western coast of Greece, a water mass of Levantine origin, with a deeper thermocline and nutricline (Figure 3) was observed (“Greek Side,” or GS, Figure 1).

[26] As a consequence of the direction of the AW, the general circulation inside the Ionian Sea was cyclonic, but no consequent nutrient enrichment of the upper water column was evident, probably due to the low concentrations involved. Model simulations [D’Ortenzio *et al.*, this section] showed that the upwelling of intermediate waters might be limited to depths deeper than the mixed layer, without strongly enriching the surface layer.

[27] Average profiles of temperature and DIN concentrations ($\mu\text{mol dm}^{-3}$) from stations 7, 20, and 29, are shown in Figure 3 (below). Depth-integrated total DIN concentration in the first 50 m was $0.400 \mu\text{mol dm}^{-3}$ in the IS (station 7), $0.285 \mu\text{mol dm}^{-3}$ in the GS (station 20), and $0.199 \mu\text{mol dm}^{-3}$ in the AW (station 29). Phosphates were homogeneously distributed through the water column with average values in the first 50 m of $0.040 \mu\text{mol dm}^{-3}$ at station 7 (IS), $0.027 \mu\text{mol dm}^{-3}$ at station 20 (GS), and $0.040 \mu\text{mol dm}^{-3}$ at station 29 (AW). Average nutrient values in GS were significantly lower when compared with the other two areas ($p < 0.05$ for DIN and $p < 0.001$ for phosphate). Surface, DCM, and integrated values (0–130 m) of DIN and phosphates are reported in Table 1.

3.2. Chlorophyll and Phytoplankton Pigments

[28] Chlorophyll concentrations ranged from 0.03 to $1.13 \mu\text{g dm}^{-3}$, with a deep chlorophyll maximum (DCM) always present from 55 to 100 m depth (60 m in the IS and 80 m in the other areas, on average). Integrated (0–130 m) values were higher in the IS and lowest in the AW (Table 1).

[29] The depth of the DCM matched the depth of the subsurface fluorescence maximum (DFM) revealed by the submersible fluorometer attached to the rosette sampler. The DFM was deeper and less intense in GS and AW than in IS (Figure 2).

[30] Eighty-two percent of phytoplankton biomass was made up of cells smaller than 10 μm , and more than 50% (56–61% on average for the three areas) of the total chlorophyll biomass passed through 2 μm mesh-size filters [picophytoplankton in the sense of Sieburth, 1979]. The proportion of picophytoplankton at the surface was higher in GS (60% $\text{SD} \pm 12\%$) than in IS (38% $\text{SD} \pm 5\%$), while in the DCM around 80% of chl *a* was represented by picophytoplankton in both areas. The fewer data available from AW confirm a dominance of $<2 \mu\text{m}$ cells.

[31] Relative percentage contributions of different taxonomic groups to the total chl *a* biomass were estimated from phytoplankton marker pigments analyzed by HPLC. Results for the different water masses are reported in Table 2.

[32] At the surface, prokaryotes (*Synechococcus* and *Prochlorococcus*, from zeaxanthin pigment marker) accounted

Table 1. Average Properties (\pm Standard Deviation) Measured in the Different Areas of the Ionian Sea^a

	IS	GS	AW
Surface chlorophyll, mg m ⁻³	0.26 (\pm 0.35)	0.06 (\pm 0.01)	0.04 (\pm 0.01)
Surface <i>Synechococcus</i> , 10 ⁴ cell cm ⁻³	1.62 (\pm 1.00)	1.29 (\pm 0.42)	1.72 (\pm 1.56)
Surface <i>Prochlorococcus</i> , 10 ³ cell cm ⁻³	7.37 (\pm 7.88)	2.92 (\pm 2.26)	8.52 (\pm 7.51)
Surface picoeukaryotes, 10 ³ cell cm ⁻³	3.10 (\pm 1.82)	2.16 (\pm 1.08)	0.97 (\pm 0.63)
Surface bacteria, 10 ⁵ cell cm ⁻³	3.11 (\pm 1.80)	1.57 (\pm 0.88)	2.74 (\pm 0.88)
Surface PP, ^b mg C m ⁻³ h ⁻¹	0.40	0.25	0.17
Surface <i>P/B</i> , ^b mg C mg chl ⁻¹ h ⁻¹	1.54	4.17	5.67
Surface DIN, ^b μ mol dm ⁻³	0.30	0.29	0.11
Surface phosphate, ^b μ mol dm ⁻³	0.04	0.03	0.04
DCM chlorophyll, mg m ⁻³	0.79 (\pm 0.30)	0.45 (\pm 0.08)	0.36 (\pm 0.07)
DCM <i>Synechococcus</i> , 10 ⁴ cell cm ⁻³	4.52 (\pm 2.29)	1.23 (\pm 1.02)	1.28 (\pm 1.74)
DCM <i>Prochlorococcus</i> , 10 ³ cell cm ⁻³	38.85 (\pm 25.69)	44.22 (\pm 25.85)	44.41 (\pm 23.70)
DCM picoeukaryotes, 10 ³ cell cm ⁻³	3.32 (\pm 3.35)	0.27 (\pm 0.30)	1.14 (\pm 1.70)
DCM bacteria, 10 ⁵ cell cm ⁻³	4.31 (\pm 3.40)	2.13 (\pm 1.76)	2.43 (\pm 1.61)
DCM PP, ^b mg C m ⁻³ h ⁻¹	0.78	0.61	0.31
DCM <i>P/B</i> , ^b mg C mg chl ⁻¹ h ⁻¹	1.30	1.65	0.79
DCM DIN, ^b μ mol dm ⁻³	1.43	1.79	1.48
DCM phosphate, ^b μ mol dm ⁻³	0.05	0.02	0.05
Integrated chlorophyll, mg m ⁻²	28.61 (\pm 11.82)	24.59 (\pm 4.95)	17.42 (\pm 6.63)
Integrated <i>Synechococcus</i> , 10 ⁶ cell cm ⁻²	2.5 (\pm 0.70)	1.9 (\pm 1.2)	2.6 (\pm 1.8)
Integrated <i>Prochlorococcus</i> , 10 ⁶ cell cm ⁻²	2.0 (\pm 1.00)	2.8 (\pm 1.2)	3.6 (\pm 1.1)
Integrated picoeukaryotes, 10 ³ cell cm ⁻²	2.6 (\pm 2.70)	1.1 (\pm 0.5)	1.1 (\pm 0.8)
Integrated bacteria, 10 ⁷ cell cm ⁻³	4.10 (\pm 2.96)	2.30 (\pm 1.76)	3.32 (\pm 1.03)
Integrated PP, ^b mg C m ⁻² /d ⁻¹	324.5	312.6	208.0
Integrated <i>P/B</i> , ^b mg C mg chl ⁻¹ h ⁻¹	11.40	20.47	8.57
Integrated DIN, ^b μ mol dm ⁻²	475.12	402.22	385.65
Integrated phosphate, ^b μ mol dm ⁻²	12.99	7.41	11.97
Vertical velocities, cm s ⁻¹	0.13	0.04	0.10

^aValues are given in volumetric units for surface or DCM samples, and in areal units for samples integrated through the upper water column (0–130 or 0–100 m for PP). DCM, deep chlorophyll maximum; PP, primary production (¹⁴C incorporation rates); and *P/B*, assimilation rate.

^bEstimated from the three reference stations: 7 (IS), 20 (GS), and 29 (AW).

for 18–41% of total chlorophyll biomass, and were the main taxonomic group both in the GS and the AW, while prymnesiophytes dominated in the IS (36%), followed by prokaryotes (18%). It is noteworthy that the very low prokaryote contribution at station 3 was coincident with the highest contribution of diatoms (*Rhizosolenia* sp.) This was probably related to the strong differences of the ASW with respect to the resident water masses of the Ionian Sea, suggesting a relationship with the late stages of the South Adriatic phytoplankton bloom, which developed earlier on (visible on Figures 2a–2d).

[33] In the DCM, the taxonomic composition was largely similar in the three water masses; chlorophytes and prymnesiophytes dominated chl_a biomass (28–41% and 21–29%, respectively). The assessment of chlorophyte contribution was biased by the fact that the HPLC method used did not allow discrimination between chl_b (marker pigment of chlorophytes) and divinyl-chl_b (present in *Prochlorococcus*). Therefore when picoeukaryote contribution was low and *Prochlorococcus* contribution high (as, for example, in the DCM of the GS, Table 1), a correct assessment of chlorophyte contribution to total chlorophyll biomass

Table 2. Pigment Markers, Conversion Factors, Contribution of Different Phytoplankton Groups to Total Chlorophyll (%) and F_p Ratio at the Surface (5 m) and in the DCM (60 m in the IS, 80 m in the GS and the AW)^a

	Diatoms	Dinoflagellates	Prymnesiophytes	Cryptophytes	Chlorophytes	Pelagophytes	Prokaryotes	F_p
Pigment marker	fucocanthin	peridinin	19 ^l HF	alloxanthin	Chl _b ^b	19 ^l BF	zeaxanthin	
Conversion factor	1.25	1.00	0.8	1.60	1.50	1.20	1.70	
<i>Surface</i>								
IS ($n = 6$)	13	4	36	2	15	11	18	0.205
GS ($n = 3$)	19	2	22	0	10	5	41	0.205
AW ($n = 3$)	6	17	18	0	12	8	39	0.215
St. 3	53	3	21	0	9	6	7	0.516
<i>DCM</i>								
IS ($n = 6$)	9	3	29	2	29	11	16	0.144
GS ($n = 3$)	7	4	22	2	41	10	13	0.108
AW ($n = 4$)	14	15	21	1	28	10	10	0.241
St. 3	51	3	17	2	14	9	3	0.513

^aConversion factors are from Casotti et al. [2000]. F_p is calculated according to Claustre [1994] as the ratio between the sum of the concentrations of the marker pigments of diatoms and dinoflagellates and the sum of all marker pigments. 19^lHF, 19^l hexanoyloxyfucoxanthin; 19^lBF, 19^l butanoyloxyfucoxanthin; IS, Italian Side; GS, Greek Side; AW, Atlantic Water; and n , number of stations considered.

^bIndicates a potential overestimation of chlorophyte contribution when many *Prochlorococcus* sp. were present (mainly in the DCM) due to the HPLC method used (see section 2).

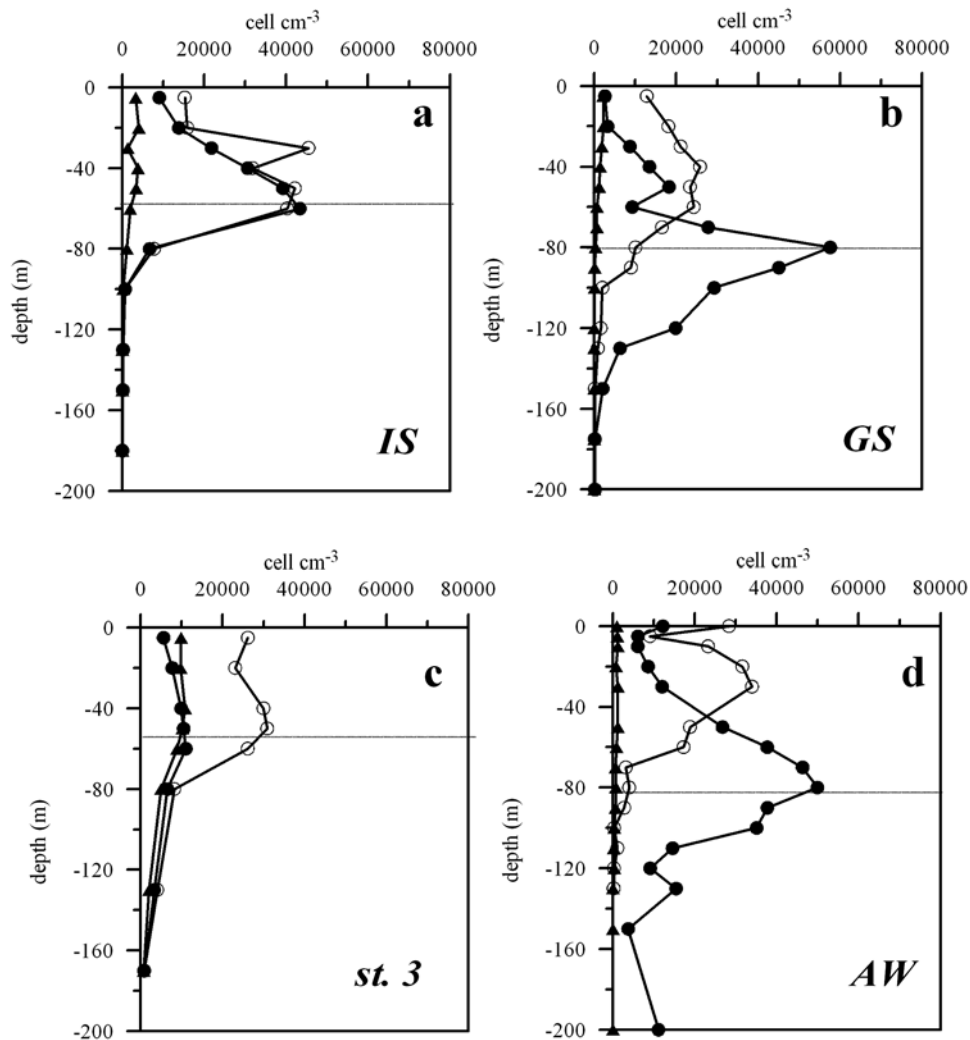


Figure 4. Ionian Sea. Average vertical profiles of abundance of *Prochlorococcus* (solid circles), *Synechococcus* (open circles), and picoeukaryotes (triangles), (a) in the IS ($n = 8$), (b) the GS ($n = 13$), (c) station 3, and (d) the AW ($n = 12$). Horizontal lines indicate the depth of the DCM. Error bars are not represented because of the confusion generated by their overlap.

was not possible. Prokaryotes were the third group in the IS and the GS (16 and 13%), while dinoflagellates were the third group in the AW (15%), similarly to the surface water.

[34] Microscopic counts at the three selected stations (7, 20, and 29, assumed to be representative of the three areas) matched HPLC data and confirmed the dominance of prymnesiophytes within the eukaryotes. These were mainly represented, at the three stations, by the coccolithophore *Emiliania huxleyi* both at the surface and in the DCM (3×10^4 cell dm^{-1} on average), except in the DCM of station 20 (in the GS), where it accounted for only 3% of total counts, and the prymnesiophytes detected by their pigment marker may have been represented by naked flagellated forms (possibly including *Phaeocystis* sp.). *E. huxleyi* was not visible by flow cytometry due to the small volume analyzed by this instrument (<1 mL). Microplanktonic diatoms accounted for 5×10^4 cell dm^{-1} at the surface of station 7 (IS), and 3×10^4 cell dm^{-1} both at stations 20 (AW) and 29

(GS), and were represented by different *Chaetoceros* species.

3.3. Ultraplankton

[35] Flow cytometry was used to identify different ultraplankton algae [$<3 \mu\text{m}$ in ESD, in the sense of Li, 1997], represented by phycoerythrin-containing cyanobacteria (*Synechococcus* sp.), prochlorophyte cyanobacteria (*Prochlorococcus* sp.), and picoeukaryotes, as usually encountered in oceanic waters. Average surface and DCM concentrations are indicated in Table 1, together with their integrated values (0–130 m). *Synechococcus* was the most abundant at the surface, with concentrations on the order of 10^4 cell dm^{-3} , one order of magnitude higher than *Prochlorococcus*. However, in the DCM *Prochlorococcus* was similarly (IS) or more abundant (4 times) than *Synechococcus*, being also one order of magnitude more concentrated (around 10^4 cell dm^{-3}) than at the surface. The relative vertical distribution of these three algal groups varied in the

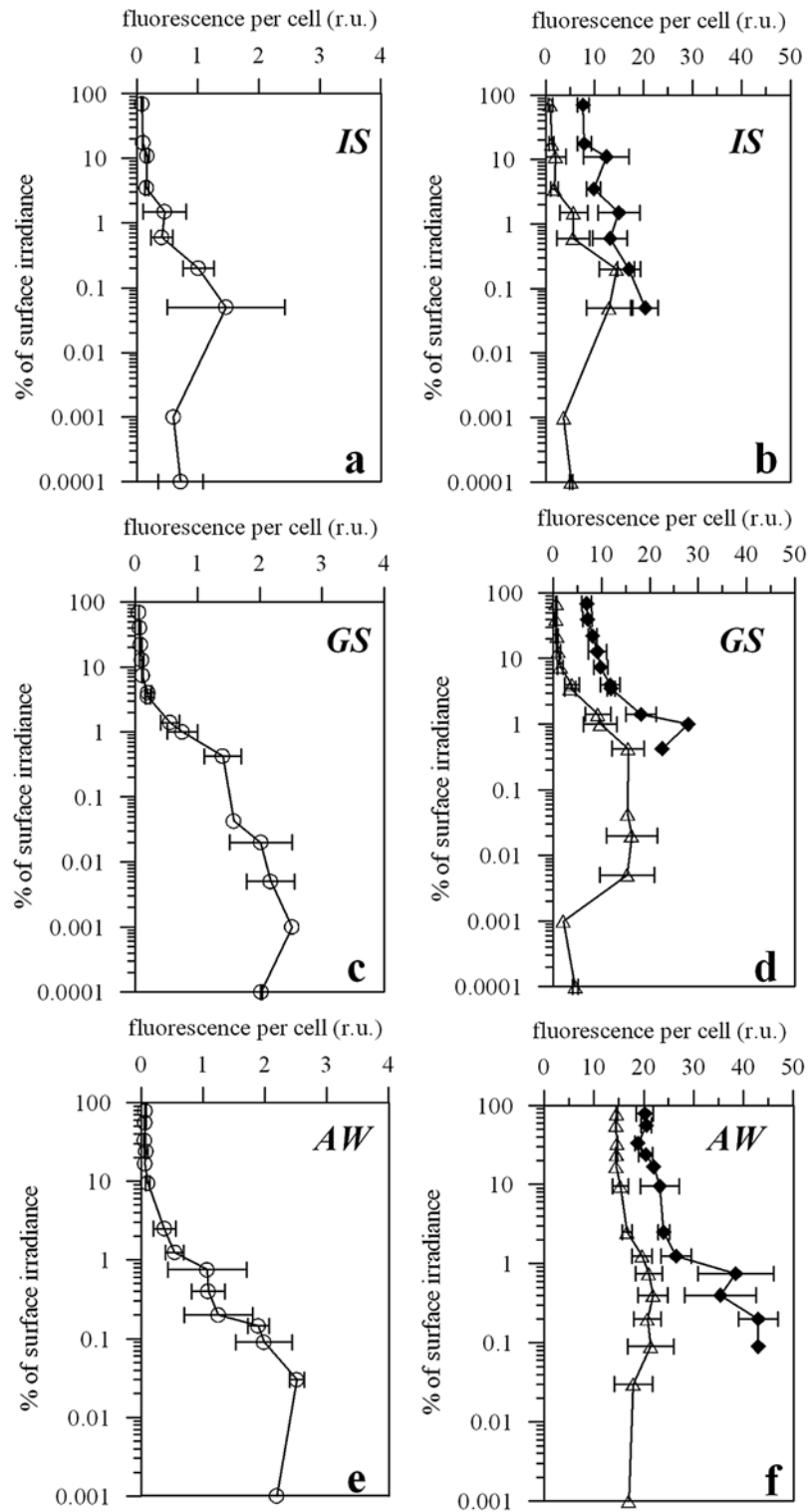


Figure 5. Ionian Sea. Vertical profiles of red fluorescence per cell of *Prochlorococcus* (circles), *Synechococcus* (squares), and picoeukaryotes (triangles) in the different water masses identified at the time of sampling: (a) and (b) IS, (b) and (d) GS, and (e) and (f) AW. Error bars are standard deviations. Data are presented as a function of percent surface irradiance in order to normalize the variations in depth of the euphotic zone.

different areas (Figure 4). *Synechococcus* and *Prochlorococcus* showed coincident vertical distribution in the IS, with a maximum coincident with the DCM, while in the GS *Synechococcus* dominated the upper water column and *Prochlorococcus* dominated at depth (in correspondence with the DCM).

[36] In the AW local conditions contributed to a higher diversity of patterns, but in general *Synechococcus* dominated in the surface layer (0–50 m), with higher abundance than in the GS, mainly at the surface and around 30 m depth. In this same area, *Prochlorococcus* showed a peak in coincidence with the DCM, around 80 m. Around the islands of Sicily and Malta (stations G and H), *Prochlorococcus* reached maximum observed abundance for the study in the area of the DCM, at 80 m (10^5 cells cm^{-3}).

[37] The highest concentrations of picoeukaryotes were measured at station 3 (10^4 cells cm^{-3}), where *Prochlorococcus* decreased by one order of magnitude in the first 50 m (10^3 cells cm^{-3}), and showed no deep peak (Figure 4c). *Synechococcus*, however, showed a relatively homogeneous profile with high abundance (3×10^4 cells cm^{-3}) until 50 m and then sharply decreased (Figure 4c).

[38] Mean chlorophyll red fluorescence per ultraphytoplankton cell was significantly different in the three areas and was highest in the IS, lowest in the AW (Student *t*-test, $p < 0.01$ at least). Comparisons were made considering only fresh samples (from stations 1 to 29), since cellular fluorescence is affected by fixation (stations A to H). The higher fluorescence in the IS probably resulted from a lower light penetration due to higher chlorophyll and particulate matter concentrations, as well as to the higher proportion of larger phytoplankton. The ratio of red to orange fluorescence in *Synechococcus* did not show significant differences in the three areas ($p > 0.05$), and therefore the differences in mean fluorescence values appeared to be driven by the local light environment rather than by physiologically diverse populations, although, the presence of such populations of *Synechococcus* could not be excluded.

[39] The vertical profiles of red or orange fluorescence per cell showed a strong increase with depth (and consequently light) for the ultraphytoplankton groups, as a result of photoacclimation (Figure 5). The light scattering of *Synechococcus* and *Prochlorococcus* did not increase with depth (not shown), and therefore the increase of *chl a* per cell with depth could be entirely attributed to photoacclimation, in agreement with Goericke and Welschmeyer [1998] and Du Rand et al. [2001]. The maximum relative increase for *Prochlorococcus* (44.8 times) was observed in the GS, while for *Synechococcus* and picoeukaryotes it was in the AW and the lowest in the IS. For the two latter groups it was lowest in the IS and highest in the AW (Table 3).

[40] “High-light” (HL)- and “Low-light” (LL)-adapted ecotypes of *Prochlorococcus* were identified based on the bimodal distribution of red fluorescence, similar to observations by other authors in the Mediterranean Sea [e.g., Casotti et al., 2000], HL having 30% (SD \pm 7%) less fluorescence than LL. The two ecotypes cooccurred only at depths where less than 2% of incident light penetrated (on average $22.55 \mu\text{mol m}^{-2} \text{s}^{-1}$), indicating that this is the higher threshold for the LL ecotype. The increase in fluorescence of HL with depth was more dramatic than the

Table 3. Maximum Relative Increase in Fluorescence (r.u.) of Ultraphytoplankton With Depth (Ratio Between the Highest and the Lowest Values, Taken From an Average Vertical Profile for the Different Areas (See Text and Figure 4))^a

	IS ($n = 6$)	GS ($n = 8$)	AW ($n = 15$)
Red fluorescence <i>Prochlorococcus</i>	17.5	44.8	39.5
Red fluorescence <i>Synechococcus</i>	14.9	29.0	44.7
Red fluorescence picoeukaryotes	2.7	4.0	6.4
Orange fluorescence <i>Synechococcus</i>	19.3	36.8	35.3

^a*n* is the number of stations considered for each area.

increase of LL (3–5 times higher), suggesting a higher photoadaptation capability of this ecotype.

[41] Red fluorescence of ultraphytoplankton was correlated to light intensity (PAR) with a significant exponential relationship, and the same was true for the orange fluorescence of *Synechococcus* (Figure 6). Exponents of equations expressing the relationships between light intensity (PAR) and fluorescence (red, orange, or red/orange) for the different groups of ultraphytoplankton in the different sampled areas are indicated in Table 4.

[42] Heterotrophic bacteria were more abundant at the surface than in the DCM, and in the IS than in the other areas. No correlation with *chl a* concentration was found ($p > 0.05$). Integrated values (0–130 m) were higher in the IS (4.10×10^7 cell m^{-2}) than in the other areas (2.30×10^7 cell m^{-2} in the GS and 3.33×10^7 cell m^{-2} in the AW, Table 1). Only rarely did vertical profiles show deep peaks, and in no case did these match peaks in chlorophyll. Often, two populations have been observed, mostly at depth, probably due to the presence of inactive bacteria, with relatively lower apparent DNA content, as already observed by Gasol and del Giorgio [2000], and no correlation has been found between the presence or concentration of these subpopulations and any measured parameter.

[43] Autotrophic carbon [estimated from chlorophyll *a*; Fuhrman et al., 1989] from all stations averaged 34% (SD 27%) of total POC, and values were always >60% in the DCM, indicating a dominance of the autotrophic components at these depths. The algal contribution always exceeded 50% of total carbon (bacteria plus phytoplankton), and therefore an inverted biomass pyramid was not observed, as contrary to other authors [Cho and Azam, 1990].

[44] Within the ultraplankton, *Synechococcus* dominated carbon biomass, accounting for 42% of total ultraplankton carbon (ultraphytoplankton plus bacteria).

3.4. Ultraphytoplankton Growth and Grazing Losses

[45] The serial dilution method [Landry and Hassett, 1982] was used to estimate growth and loss (grazing) rates of ultraphytoplankton at the surface (10 m) and in the DCM. Results are summarized in Table 5. At the surface, *Prochlorococcus* growth or grazing values were either negative or not significant, while *Synechococcus* growth values were significant only at the surface of IS, but very low (0.14 d^{-1}). Only half of its standing biomass was consumed there (0.07 d^{-1}). When significant, growth of picoeukaryotes was almost 0.

[46] In the DCM ultraphytoplankton grew well only in the GS, where the fastest growth rates for picoeukaryotes

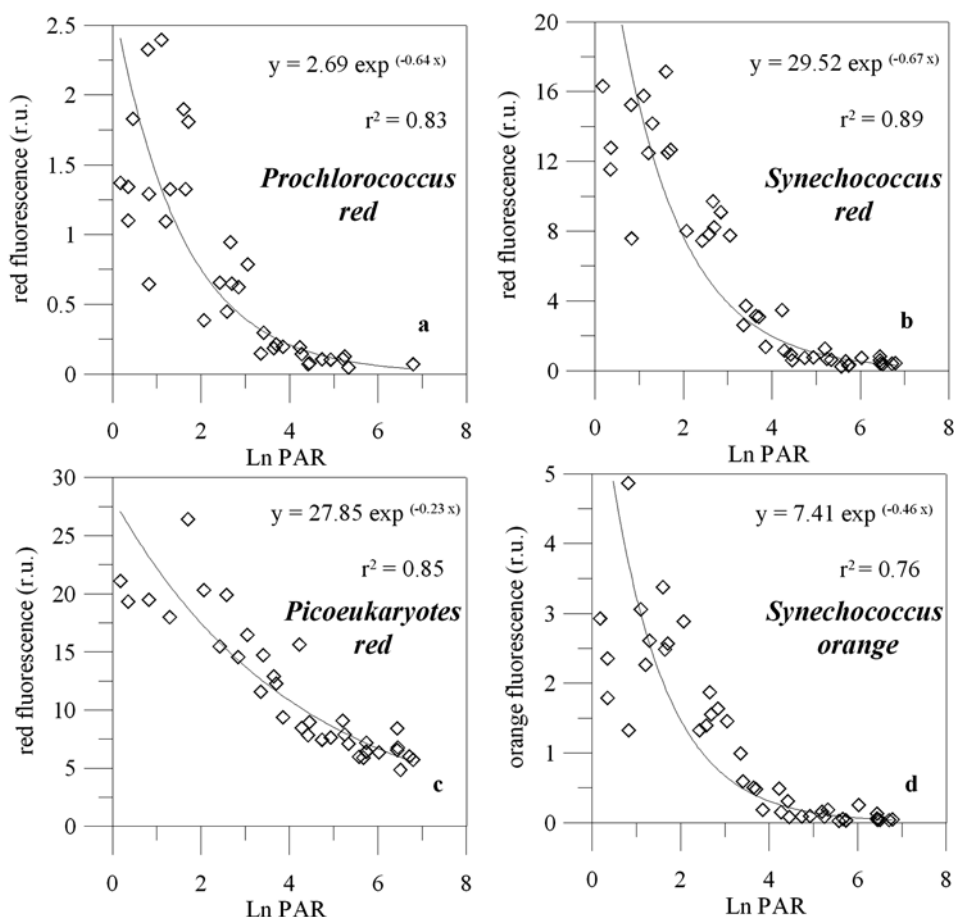


Figure 6. Ionian Sea. Total (all data) correlation between Ln of PAR (x , PAR) and mean red fluorescence per cell (y , relative units) from chlorophyll of (a) *Prochlorococcus* ($n = 39$), (b) *Synechococcus* ($n = 47$), (c) picoeukaryotes ($n = 39$), or (d) orange fluorescence from phycoerythrin of cyanobacteria ($n = 42$). n is number of data points used.

of 0.67 d^{-1} were measured. However, grazing of picoeukaryotes in the DCM was intense (0.80 d^{-1}), outstripping growth, so that picoeukaryotes did not accumulate at this depth. *Synechococcus* and *Prochlorococcus* grew more slowly (0.36 and 0.31 d^{-1} , respectively) than picoeukaryotes, and were grazed at the same rate. Under such conditions, newly produced cells were considered by other authors [Valoul *et al.*, 1995], to be preferentially consumed by grazers.

[47] In the DCM of the IS, picoeukaryote growth was not significant, while both prokaryotic groups grew very slowly

(0.22 – 0.24 d^{-1}), and only approximately 50% of the newly produced biomass was consumed by grazers.

[48] In the DCM of the AW *Synechococcus* did not grow well (n.s.), in contrast with picoeukaryotes (0.41 d^{-1}), which were also consumed at the same rate (0.40 d^{-1}). *Prochlorococcus* exhibited a slow growth rate (0.18 d^{-1}) and uncoupled consumption (0.07 d^{-1}). Their concentrations were positively correlated with heterotrophic ciliate abundance ($p < 0.001$), which represent their main consumers, while no correlation was found between total ciliate abundance and chlorophyll concentration (M. Modigh,

Table 4. Exponents of the Nonlinear Fit Between Photosynthetically Active Radiation (PAR) and Fluorescence (Red for all and Additionally Orange for Cyanobacteria) of Ultraphytoplankton in the Different Areas of the Ionian Sea^a

	Pro Red	Syn Red	Euks Red	Syn Orange	Syn Orange/Red
IS	-0.480 ($n = 8$, $r^2 = 0.95$)	-0.530 ($n = 9$, $r^2 = 0.94$)	-0.17 ($n = 9$, $r^2 = 0.84$)	-0.590 ($n = 9$, $r^2 = 0.92$)	-0.06 ($n = 9$, $r^2 = 0.64$)
GS	-0.770 ($n = 15$, $r^2 = 0.87$)	-0.730 ($n = 19$, $r^2 = 0.92$)	-0.26 ($n = 12$, $r^2 = 0.89$)	-0.810 ($n = 19$, $r^2 = 0.85$)	-0.08 ($n = 18$, $r^2 = 0.11$)
AW	-0.540 ($n = 7$, $r^2 = 0.84$)	-0.650 ($n = 11$, $r^2 = 0.87$)	-0.25 ($n = 10$, $r^2 = 0.92$)	-0.770 ($n = 11$, $r^2 = 0.89$)	-0.12 ($n = 11$, $r^2 = 0.91$)

^aEquation type is $y = a \exp^{(bx)}$, where y is fluorescence (relative units), x is Ln(PAR). Pro, *Prochlorococcus*; Syn, *Synechococcus*; euks, picoeukaryotes; red, red fluorescence from chlorophyll; orange, orange fluorescence from phycoerythrin. n is the number of data points considered. All r^2 values are significant at $p < 0.001$, except for Syn orange/red in the IS ($p < 0.01$), and in the GS (not significant).

Table 5. Values of Growth Rates (μ) and Grazing Losses (g) for the Three Groups of Ultraphytoplankton in the Three Areas of the Ionian Sea at the Surface (10 m) and at the DCM^a

Location	Depth, m	Pro μ , d ⁻¹	Pro g , d ⁻¹	Syn μ , d ⁻¹	Syn g , d ⁻¹	euk μ , d ⁻¹	euk g , d ⁻¹
<i>Surface</i>							
IS	10	-0.94	-0.70	0.14	0.07	0.03	-0.33
GS	10	-0.51	-0.15	-0.14	-0.40	-0.89	-0.97
AW	10	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
<i>DCM</i>							
IS	60	0.22	0.11	0.24	0.11	n.s.	n.s.
GS	80	0.31	0.37	0.36	0.40	0.67	0.80
AW	80	0.18	0.07	n.s.	n.s.	0.41	0.40

^aIS, st. 7; GS, st. 20; and AW, st. 29. Pro, *Prochlorococcus*; Syn, *Synechococcus*; and euk, picoeukaryotes. n.s., not significant ($p > 0.05$). Data are means of triplicates.

Stazione Zoologica di Napoli, personal communication, 2002).

3.5. Primary Production

[49] Integrated (0–100 m) production values for the three stations representative of the different areas are presented in Table 1. A peak was always present at the DCM, from 1.9 (in the IS and the AW) to 2.4 (GS) times higher with respect to the surface. Values at the surface were higher at station 7 (IS), than at station 20 (GS), but were closer in the DCM, while values at station 29 (AW) were the lowest both at the surface and at the DCM. The photosynthetic capacity, or assimilation rate [Morel, 2000; Psarra *et al.*, 2000] estimated by forming the ratio of the primary production to the average chlorophyll values from the three areas, showed that the GS had the most competent phytoplankton community, when compared to the richer IS or to the AW (Table 1).

[50] F_p ratio, indicator of the proportion of new producers' biomass, varied from 0.205 and 0.215 at the surface and from 0.108 and 0.241 in the DCM (Table 2), the only significant difference between the surface and the DCM being found in the IS ($p < 0.05$). At station 3, the F_p was the highest (0.510 approximately) both at the surface and in the DCM, due to a large abundance of diatoms (>50% of the total biomass). Values (except at station 3) were similar to those reported by *Claustre* [1994] for Mediterranean oligotrophic regimes.

3.6. Vertical Displacement of Phytoplankton

[51] In order to estimate vertical velocities within the mixed layer and to confirm their effect over photoacclimation properties of phytoplankton, we performed a quantitative analysis of a photoreactive pigment, the Diadinoxanthin (Dd). This is a xanthophyll accessory pigment of Chromophyte algae involved in the photoprotection response at the cellular level.

[52] The average vertical profile of Dd/chla ratio in the three areas at the time of sampling showed an exponential decrease with depth, described by the equations:

$$\text{Dd/chla} = -0.004\text{Ln}(z) + 0.0466, \quad r^2 = 0.999, \quad (1)$$

$$\text{Dd/chla} = -0.013\text{Ln}(z) + 0.0298, \quad r^2 = 0.925, \quad (2)$$

$$\text{Dd/chla} = -0.0051\text{Ln}(z) + 0.0306, \quad r^2 = 0.986, \quad (3)$$

for the IS (1), the GS (2), and the AW (3), respectively, where z is depth.

[53] The trend showed that mixing occurred at timescales longer than the time it takes for the cells to adapt to the variations in the light regime. In the opposite case, the distribution of Dd/chla would be expected to be homogeneous through the upper layer of the water column.

[54] Previous data from incubation experiments of phytoplankton from the Gulf of Naples, Mediterranean Sea, submitted to shifts in light intensities, showed a change of 3.15% per hour in the ratio Dd/chla [Brunet *et al.*, 2003]. Although this value is dependent on the phytoplankton community, its physiological state and its recent past light history, we could reasonably assume that it should be at least of the same order of magnitude in our study area. When comparing average values of Dd/chla at the surface and at 35 m depth from average profiles for the different areas identified in the Ionian Sea, we found 23% difference in the IS, 77% in the GS, and 25% in the AW. From this, assuming that vertical displacement alone determined the differences, phytoplankton from the surface may have moved from 5 to 35 m depth in 7 h 18', 24 h 24', and 7 h 54', which translates into a vertical displacement of 0.13 cm s⁻¹ in the IS, 0.04 in the GS, and 0.10 in the AW (Table 1).

[55] The same photo-dependent parameter Dd/chla showed a strong correlation with Ln(PAR) in the three areas ($r^2 = 0.85, 0.92, \text{ and } 0.66$ for IS, GS, and AW, respectively). The significance of the correlation was strongly improved when values from the DCM were excluded, but only for IS and GS ($r^2 = 0.99$ for both). This implies that cells at the DCM of IS and AW were still carrying the memory of a past light history, when they were exposed to different light intensities. When considering the excluded values, it has been noted that they would best represent values observed at a lower depth for IS, and at a shallower depth for AW, indicating an upwelling movement in the first and a downwelling movement in the latter. The direction of the vertical movement was also confirmed when using flow cytometric data of ultraphytoplankton cell fluorescence to perform the same analysis. The initial good fit for GS data confirms the higher stability of this area (as suggested by the very low vertical velocities (Table 1)).

4. Discussion

4.1. General Biological Features and Mixing Estimates

[56] During the study period, the Ionian Sea appeared as a composite area, where different water masses and circulation patterns strongly influenced distribution and ecophysiology of plankton. General oligotrophy was reflected by low biomass and production rates [Morel, 2000], and reduced size of primary producers [e.g., Legendre and Rassoulzadegan, 1995; Fasham *et al.*, 1999]. Remote sensing showed that our sampling took place right after the spring bloom along the Italian coast [Calabrian bloom, D'Ortenzio *et al.*, this section], and also after the phytoplankton bloom of the South Adriatic Sea (Figure 2). These past events were still visible in the IS from the relatively higher proportion of larger eukaryotic cells, the relatively higher concentrations of diatoms at the surface, the higher

bacteria and POC concentrations (not shown), and the shallower DCM. The DCM lay well above the 1% surface irradiance level, and therefore light was not a limiting factor for the algae in it. Phytoplankton was not well adapted to this transitional and dynamic environment (high mixing), as reflected by the low assimilation rate, and also by the lower photo-dependent exponents reported in Table 4. Therefore the high *chl a* concentrations were likely to be due to local accumulation more than to active growth. As a matter of fact, growth rates of ultraphytoplankton were low in the IS and were not strictly coupled to grazing, indicating that transfers, at least within the microbial food web, were not as efficient.

[57] In contrast, the GS presented more stable oligotrophic characteristics in terms of biomass and production, with a better-adapted phytoplankton community, with higher assimilation rates and a deeper DCM. The relative increase of oligotrophy in this area was reflected in the dominance of ultraphytoplankton and might be related to the low availability of orthophosphate, which is known to be a key limiting factor in the eastern Mediterranean Sea [e.g., Thingstad and Rassoulzadegan, 1999; Siokou-Frangou et al., 2002]. Also the higher values of the exponents of the nonlinear fit of fluorescence versus PAR (Table 4), confirm that photoacclimation was stronger, at least for *Prochlorococcus* and *Synechococcus*. This is supported by the fact that there was also higher vertical stability, light levels having been constant for enough time to allow cells to adapt. The relative vertical distribution of prokaryotic autotrophs also reflected these features, with *Prochlorococcus* forming a maximum below *Synechococcus*. This distribution is more typical of other stable oligotrophic areas of the ocean [Bustillos-Guzman et al., 1995; Campbell et al., 1997], and it has been reported as being due to the relative ecophysiological optima for light and nutrients of these two cyanobacterial algae [e.g., Chisholm et al., 1988; Olson et al., 1990; Veldhuis and Kraay, 1993; Moore et al., 1995].

[58] The AW was the most oligotrophic area, with lowest nutrient (both DIN and phosphates) and *chl a* concentrations and assimilation rates. Vertical velocities within the mixed layer were comparable to the IS, with no influence of exogenous biomass accumulating (as from the ASW), or traces of a previous spring bloom (by remote sensing, not shown) being visible. The relatively higher presence of dinoflagellates (at the surface) or diatoms and dinoflagellates (in the DCM) suggest a relatively higher importance of new production, as also reflected by the high F_p values, but it may be due to local features rather than stable conditions. As a matter of fact, diatom presence has been suggested as a tracer of sporadic inputs of new nitrogen and consequently of a larger contribution to new production [Goldman, 1993]. Stations in this area were most probably influenced by local mesoscale features, which obviously contributed to the general variability of the sampled area, and were very important in determining biological patterns, in agreement with model simulation or experimental data in other areas [Campbell et al., 1998; Latasa and Bidigare, 1998; Casotti et al., 2000; Garçon et al., 2001; Rodriguez et al., 2001]. For example, the highest *Prochlorococcus* concentrations in the southwestern part of the sampled area may be due to the influence of a filament of cold deep water upwelled along

the Sicily coast [Bergamasco et al., 1993; Antoine et al., 1995; Casotti, 2000]. Also, local high *Synechococcus* concentrations observed in the vicinity of the Island of Crete may be due to its coastal inputs. Indeed, these algae have been shown to profit from local inputs of phosphates, due to their high affinity for these nutrients [Moutin et al., 2002]. In reality, a classification of this area appears artificial from the biological point of view, due to its intrinsic dynamical feature of flowing toward the Levantine Basin, with no intermediate boundaries.

[59] The estimates of vertical displacement based on the analysis of photo-reactive pigments lie in the range of values indicated by Falkowski [1983] and, apart from the absolute values, confirmed that the GS was a more stable area, when compared to the IS, where mesoscale dynamics, and general circulation trends contributed to the higher concentration but lower activity of the biological compartment. The higher stability of the GS led to a higher adaptation of the phytoplankton community, and consequently to a better utilization of local resources and photosynthetic performance. The estimates in the AW depicted an area of active mixing, but with stable characteristics with respect to cellular photoacclimation properties. This may reflect a real situation, maybe driven by the circulation patterns, although, the interpretation was biased by the high heterogeneity, distance between the stations and mesoscale patterns acting locally, making estimate generalization difficult.

[60] Mixing rate estimates, despite the general assumptions being made, represent a very valuable approach in using biological information to estimate a physical parameter, which is difficult to measure. Such measurements are important as they strongly affect aquatic productivity [Platt, 1975], and have relevance to the prediction of carbon fluxes in the world ocean. Indeed, they appear to be the most relevant parameter in determining the size structure of phytoplankton. In this respect, our data agree with the model of Rodriguez et al. [2001], since the relative proportion of larger algae increased with the magnitude of the upward velocity, as we observed in IS.

[61] The most evident mesoscale instability observed during our sampling was represented by the intrusion of surface water from the Adriatic Sea through the northern transect (station 3, Figure 2). The effects of the Adriatic water, with its own phytoplankton community, rich in diatoms, as a residual of the late-winter/spring bloom, were also strongly marked by the lack of *Prochlorococcus* and the high abundance of picoeukaryotes when compared to nearby stations. Inputs from the Adriatic Sea are variable from year to year, as shown by satellite imagery (F. D'Ortenzio, Stazione Zoologica of Naples, Italy, personal communication, 2002), and have strong climatological determinants [Marasović et al., 1989; Civitarese and Gacic, 2001]. This variability, together with general circulation patterns in the Northwestern area of the Ionian Sea, induced a local pattern, but did not affect the general oligotrophy of the Ionian Sea. At the basin scale, oligotrophy was also maintained by the depth of the mixed layer, which was never deep enough to enable nutrient injection from the intermediate waters into the euphotic zone [Stratford and Haines, 2002; D'Ortenzio et al., this section]. As a matter of fact, the resiliency of food webs to environ-

mental perturbation has been observed in other oligotrophic or nutrient-limited areas [e.g., Landry *et al.*, 2000].

4.2. Phytoplankton

[62] In terms of chlorophyll biomass, prokaryotes dominated the GS and the AW, accounting for 40% of total chl_a, while eukaryotes were the major group in the IS, with prymnesiophytes dominating at the surface (36%), or at the DCM (29%). No large differences were observed at the DCM of the three areas, where eukaryotes dominated with prymnesiophytes and pelagophytes and/or chlorophytes. Even though chlorophyte contribution cannot be accurately assessed due to the HPLC method used (see section 2), it is reasonable to assume that they were contributing to the picoeukaryote diversity significantly, at least in the DCM of the IS, where picoeukaryotes were relatively more abundant. Prymnesiophytes confirm their ubiquity and also their flexibility, in this case, due to presence of different groups, coccolithophorids at the surface and naked forms at depth. Although we cannot exclude the latter being represented by *Phaeocystis*, microscopical examinations of samples from the three reference stations do not reveal so. Abundance of pelagophytes and chlorophytes in oligotrophic areas confirms other reports [e.g., Hooks *et al.*, 1988], their success at depth being probably due to their peculiar pigment composition, very efficient at using the blue part of the irradiance spectrum [Glover *et al.*, 1986]. Research on light and nutrient requirement of deepwater flagellates is still in its infancy, yet the higher proportion of eukaryotes at depth suggests a nutrient control of their distribution [Claustre and Marty, 1995]. Diatoms were dominating phytoplankton biomass only at station 3, and could be considered as biomarkers of the Adriatic Water. Also, the dominance of large *Rhizosolenia* species has to be attributed to these enriched waters, which have even been shown to bring features of the Po River [Socal *et al.*, 1999] from the very northern Adriatic Sea.

[63] Numerically, phytoplankton was dominated by organisms of smaller size (<10 μm), whose proportion increased with depth and from West to East. This finding was confirmed by flow cytometric data and was in agreement with data from Boldrin *et al.* [2002] from the same area and from Yacobi *et al.* [1995] from the eastern Mediterranean in late summer. Our data also confirmed the occurrence and numerical dominance of *Prochlorococcus*, *Synechococcus*, and eukaryotic ultraplankton in the oligotrophic waters of the Mediterranean Sea [e.g., Raimbault *et al.*, 1988; Vaultot *et al.*, 1990; Li *et al.*, 1993; Martin, 1997; Denis *et al.*, 2000; Vidussi *et al.*, 2001].

[64] Within the ultraphytoplankton compartment, a transition to more oligotrophic conditions was associated with increasing *Prochlorococcus* abundance and decreases in other phytoplankton groups, as also observed by other authors [Agawin *et al.*, 2000a; Shalapyonok *et al.*, 2001]. The opposite was also true, as evident at station 3, where the dominance of large diatoms was coupled to the lack in *Prochlorococcus*. This also confirms that *Prochlorococcus* is a true open ocean species, mainly thriving in oligotrophic, warm waters [e.g., Lindell and Post, 1995]. *Synechococcus*, instead, showed less marked differences in the different areas, with little variations in abundance even at station 3,

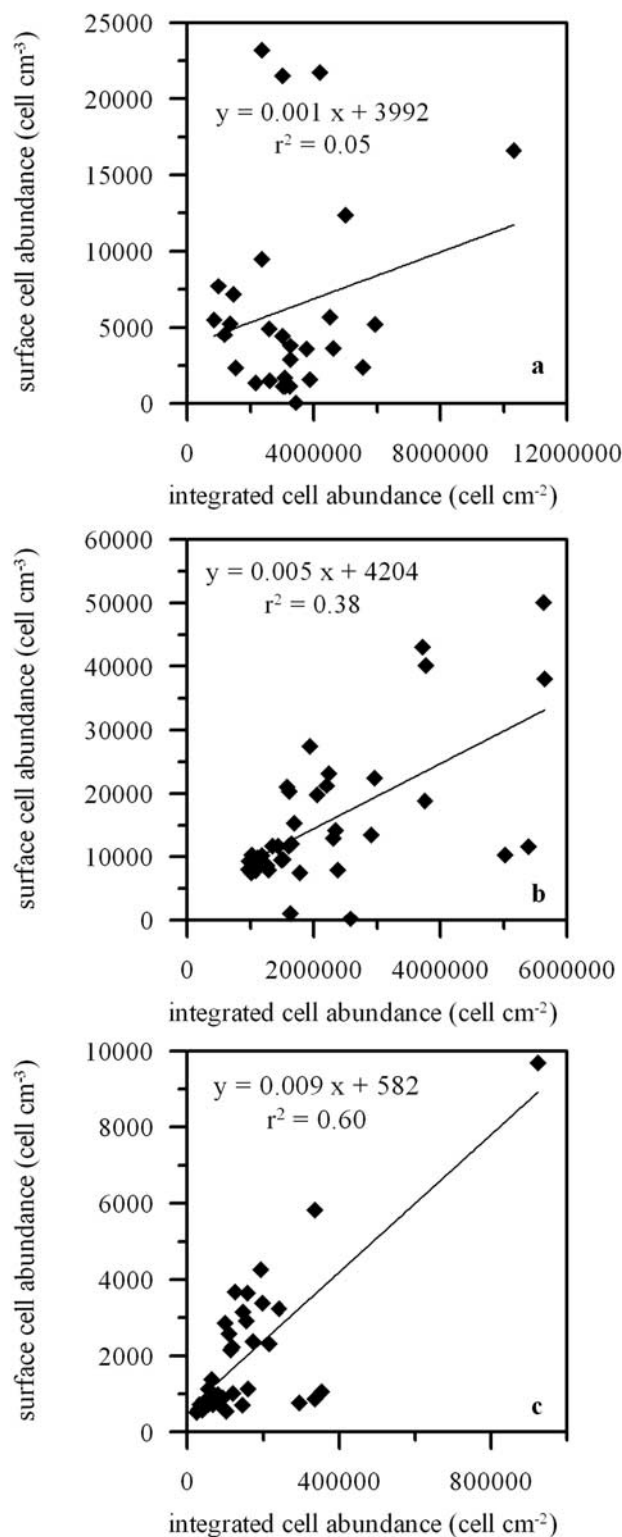


Figure 7. Ionian Sea. Comparison of integrated (0–130 m) cell numbers of (a) *Prochlorococcus* ($n = 28$), (b) *Synechococcus* ($n = 37$), and (c) picoeukaryotes ($n = 37$) with cell numbers at the surface (5 m). Line is the fit of linear regression. The relation was significant ($p < 0.001$) only for picoeukaryotes (Figure 7c).

suggesting a higher tolerance for wider nutrient conditions, as suggested by *Moutin et al.* [2002].

[65] A complementary vertical distribution of the two cyanobacteria groups was observed in GS and AW, with *Synechococcus* in the surface layer and *Prochlorococcus* at depth, similarly to observations made in other oligotrophic areas [*Campbell et al.*, 1998; *Blanchot and Rodier*, 1996; *Zubkov et al.*, 1998]. Depth-integrated abundance of ultraphytoplankton was highly correlated to surface concentrations only for picoeukaryotes (Figure 7), indicating that there was little variation in the relative depth distribution all over the area for these algae. This is consistent with their vertical distribution, since no peaks were observed. As a matter of fact, at least for the DCM of the GS and the AW, data indicate that growth of picoeukaryotes was strictly coupled to grazing losses, therefore masking a potential peak in abundance, and suggesting a steady state within the microbial community for this group of algae.

4.3. DCM

[66] The distribution of phytoplankton biomass was characterized by the presence of a deep *chl a* fluorescence maximum at all stations, matching the biomass maximum (DCM). The DCM closely followed the nutricline, its concentration declining as the nutricline deepened in an eastward direction, and was located at a depth receiving, on average, 4% in the IS and $\leq 1\%$ of the irradiance incident on the surface in the other areas. We can classify the DCMs observed as Typical Tropical Structure (TTS), following classification of *Cullen* [1982], in which the nutricline can be assumed to be the boundary between the nutrient-depleted surface layer and deeper water in which light limits phytoplankton growth [*Dugdale*, 1967].

[67] The localization of the DCM close to the nutricline has often been observed [*Fasham et al.*, 1985, and references therein] and it suggests that its dynamics were mainly ruled by biological factors. Physical determinants may have been important, for example at the beginning of spring stratification [*Agusti and Duarte*, 1999], but do not emerge from our observations, maybe also masked by spatial heterogeneity at the time of our sampling. On the other hand, DCM dynamics are known to depend on multiple physical and biological processes [*McCarthy and Goldman*, 1979; *Rodriguez et al.*, 2001], and a univocal view of its formation and maintenance has not been reached yet [*Claustre and Marty*, 1995; *Wiggert et al.*, 1999].

[68] The deepening and decrease in magnitude of the DCM has been reported in other areas when the water evolves to summer oligotrophic conditions [*Fasham et al.*, 1985], and also when comparing eutrophic and oligotrophic areas at the same time [*Herbland and Voituriez*, 1979; *Macedo et al.*, 2000]. This process has been attributed to differences in nitrate concentrations at the beginning of the spring bloom and, would also induce a deeper 1% light level [*Fasham et al.*, 1985], as observed in our case. This was also consistent with the model of *Kiefer and Kremer* [1981], predicting that a decrease in nitrate concentrations at the start of the spring bloom causes the depth of the DCM to increase. Other parameters, such as grazing, vertical stability, and light limitation can also contribute to the differences observed in DCM

depth and magnitude. As a matter of fact, grazing appears to have strictly controlled ultraphytoplankton growth in the GS, and may have been the cause of its lower intensity. Unfortunately, we have no data on grazing of larger phytoplankton.

[69] In the Ionian Sea, *Boldrin et al.* [2002] reported a deepening of the DCM from 40 to 70 m from March to August for the same station as our station 7, and *Rabitti et al.* [1994] a depth of 87 m (± 12.5 m) in October at different stations comparable to our AW and GS. Indeed, if this could be considered a continuous process (at least for the IS), it would occur at a rate of 6–7 m per month, not far from the values (7.5–10 m), indicated by *Strass and Woods* [1991] for the oligotrophic North Atlantic Ocean. Considering 40 and 100 m as the upper and lower limits, respectively, of this process, we may conclude that the IS at the time of our sampling was at the beginning of its evolution toward summer oligotrophy, maybe switching its phytoplankton toward a picophytoplankton-dominated community. The presence itself of a DCM in this area is considered a summer feature [*Turchetto et al.*, 2000], and, together with the coincident distribution of *Prochlorococcus* and *Synechococcus* through the water column, indicate a transition from a less stable water column to more stratified and oligotrophic summer conditions, as observed in other areas [*Bustillos-Guzman et al.*, 1995; *Campbell et al.*, 1997]. This dynamic feature was also reflected in a lower efficiency of phytoplankton, in terms of *P/B* and ultraphytoplankton growth (Tables 1 and 5). This also suggests that the DCM here is a relic of the past spring bloom, consistent with the model of *Kiefer and Kremer* [1981] for the generation of the DCM and with data of *Wiggert et al.* [1999] on the seasonal evolution of the DCM. At this stage, the structure of the water column, its dynamics (vertical motion) and perhaps light conditions, are not (yet) promoting rapid ultraphytoplankton growth or associated close-coupled grazing, as observed in GS.

[70] The depth of the DCM in GS has never been reported to be shallower than 80 m [*Rabitti et al.*, 1994], suggesting that in this area this is a more constant and stable feature. It also suggests low seasonality characterized by marked oligotrophy, which, in turn leads to a more efficient phytoplankton community, a higher proportion of picophytoplankton, and close-coupling of growth and grazing losses. The higher proportion of smaller phytoplankton cells is most probably due to their higher tolerance to phosphate limitation [e.g., *Parpais et al.*, 1996]. In these conditions phytoplankton growth would be dependent on regenerated nutrients [*Eppley and Peterson*, 1979].

[71] Despite similarities with the GS in terms of depth and intensity, the DCM of the AW was the least efficient, in terms of *P/B*. The highest proportion of diatoms and dinoflagellates were also found here, together with relatively high growth and grazing rates of picoeukaryotes (Tables 2 and 5). These data reflect a different structure and functioning of the phytoplankton community, with a higher proportion of eukaryotes sustaining a production based on new forms of nitrogen (F_p , Table 2), maybe induced by local mesoscale patterns (the filament of upwelled water in the western area), high mixing, or the vicinity to coastal areas,

which would also account for the shallower and more intense peak in *Synechococcus* abundance (see section 4.1).

4.4. Ultraphytoplankton Growth and Grazing

[72] Adaptation of phytoplankton to the physical environment strongly reflects on its performance, which, in turn, controls the fluxes of matter and energy within the ecosystem. Ultraphytoplankton growth rates were low, and extremely low at the surface at the three stations examined (mainly 0, except for low estimates for *Synechococcus* in the IS). We cannot exclude experimental failure for the samples from 10 m depth, due to empoisoning of algae in the vessel used for the incubations. Although, since manipulations and general experimental procedures were absolutely identical for all sets of dilution, one may also interpret this result as an indication of the presence of different (and more stressed and fragile) strains at the surface in comparison to the DCM, at least for *Synechococcus* and *Prochlorococcus*. The low growth rates reflect the low abundance of these algae in the surface layer, as related to unsuitable environmental conditions. Similar low subsurface rates have also been reported by Landry *et al.* [1995] and Vaulot *et al.* [1995] for the Equatorial Pacific, and interpreted as due to excess light or UV inhibition of photosynthesis. In our case, temperature might also be responsible for the estimated slow growth rates, since both *Synechococcus* and *Prochlorococcus* abundances have been shown to be directly related to temperature [Li, 1998, 2002], with a threshold of 14°–16°C approximately [Li, 1998; Jiao *et al.*, 2002], which is the range of temperatures measured in the first 200 m during our sampling (Figure 3). Other factors have also been reported as limiting ultraphytoplankton growth in oligotrophic areas, as for example cobalt for *Prochlorococcus* [Saito *et al.*, 2002], but no data are available on the concentrations of these elements in the Mediterranean Sea.

[73] Only *Synechococcus* in the IS showed positive (although slow) growth, maybe related to its higher tolerance for nutrient limitation [Agawin *et al.*, 2000b; Moutin *et al.*, 2002], or to the presence of ecotypes better fit to surface conditions.

[74] Ultraphytoplankton in the DCM also exhibited low growth rates, but different in the three areas. Only in GS did growth rates exceed 0.30 d⁻¹ for the three groups, with removal by consumers occurring at the same rate, indicating a rapid recycling within the microbial food web [Goldman and Caron, 1985; Reckermann and Veldhuis, 1997]. These data are consistent with efficient recycling of carbon and nutrients within a complex microbial food web [Goldman and Caron, 1985], and reflect in the smaller mesozooplankton size in GS [M.G. Mazzocchi *et al.*, this section].

[75] Considering that we observed an accumulation of *Prochlorococcus* in the DCM, maybe these estimates were biased by the presence of strains with different growth characteristics, as observed also by Reckermann and Veldhuis [1997] in the Arabian Sea. Also, these peaks may have been formed during a preceding period of higher growth, without grazers being able to consume them yet. Grazing-mediated removal of picoeukaryotes exceeded their growth and may instead explain the lack of a deep peak of these algae. Within the prokaryotes (*Synechococcus* and *Prochlorococcus*), the equivalent of 50% of the newly produced cells was removed daily in the IS and the AW, resulting in a net accumulation in

the DCM. The grazing pressure was therefore not severe, suggesting that their biomass was not recycled within the pelagic food web, and therefore that the system was at least partially sustained by new production, as suggested also by the F_p values (Table 2).

[76] Our observations are relevant to the estimation of productivity and phytoplankton dynamics by means of the biogeochemical provinces approach, in conjunction with remote sensing measurements of phytoplankton pigments [Longhurst *et al.*, 1995]. We suggest that more effort should be devoted to regional functions, based on experimental data relevant to phytoplankton production. In this context, the Ionian Sea is a crucial area, well suited to investigate the response of phytoplankton to subbasin scale dynamics as a response to climatic fluctuations.

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- C. Brunet, R. Casotti, F. D’Ortenzio, and M. Ribera D’Alcalá, Stazione Zoologica “A. Dohrn,” Villa Comunale, 80121 Naples, Italy. (raffa@szn.it)
- M. Denis, Laboratoire d’Océanographie et de Biogéochimie, 163 avenue de Luminy, Case 901, 13288 Marseille cedex 09, France.
- A. Landolfi, School of Earth and Ocean Science, University of Southampton, Southampton Oceanography Centre, European Way, Southampton SO14 3ZH, UK. (alan@mail.soc.soton.ac.uk)
- O. Mangoni, University of Naples “Federico II”, Dipartimento di Zoologia, Via Mezzocannone 8, 80134 Napoli, Italy. (olga.mangoni@unina.it)