Coupling of phytoplankton community structure to nutrients, ciliates and copepods in the Gulf of Gabès (south Ionian Sea, Tunisia)

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The summer spatial distribution of the phytoplankton community in the Gulf of Gabès (Tunisia, eastern Mediterranean Sea), together with environmental factors, were studied during a preliminary study conducted in July 2005 aboard the RV 'Hannibal'. The phytoplankton community, which showed a decrease in concentration along a coastal–open sea gradient, was dominated by Dictyochophyceae (41%) followed by Dinophyceae (25%), Bacillariophyceae (16%), Cyanobacteriae (17%) and Euglenophyceae (1%). The phytoplankton found along the coast was dominated by opportunistic species (e.g. Dictyocha fibula) associated with high nutrient availability. In the open sea, phytoplankton development seemed influenced by Atlantic hydrodynamics. In addition, the Gulf of Gabès is characterized by an oligotrophic status with a summer stratification that impacted on species composition especially in off-shore areas. The coupling of phytoplankton dynamics to nutrients, ciliates and copepods showed the potential role played by ciliates not only as predators of phytoplankton but also as prey for filter-feeding copepods accounting for the increased fisheries productivity of the Gulf of Gabès.

INTRODUCTION

The Gulf of Gabès (Southern Tunisia, 35°N and 33°N) has experienced a substantial decrease in fish resources over the last two decades, and studies suggest that such a decrease might have resulted from industrial and urban activities (Hamza-Chaffai *et al.*, 1995, 1996, 1997; Zairi & Rouis, 1999). This degradation of water quality has also been reported along the Mediterranean coastline (Duarte *et al.*, 2000; Verlecar *et al.*, 2006) in which phytoplankton communities are believed to be phosphate limited (Krom *et al.*, 1991; Thingstad *et al.*, 1998). Despite the fact that Gulf of Gabès harbours diverse algal species, field investigations of the change in the phytoplankton community structure along the coast and in the open sea are very scarce. Only the plankton-pigment signatures (Bel Hassen *et al.*, 2009a, b) and the spring ciliate distribution (Hannachi *et al.*, 2009) in this area have been the subject of investigations. On the other hand, numerous studies have shown that the phytoplankton abundance and species composition is governed by factors such as light, temperature, nutrients, grazers and water movements, in systems ranging from freshwater to man-made

coastal solar salterns (Aleya, 1991; Reynolds, 1997; Danilov & Ekelund, 2001; Paerl *et al.*, 2003; Oren, 2005; Abid *et al.*, 2008; Ayadi *et al.*, 2008). We therefore investigated the abundance and species composition of phytoplankton assemblages along the coast and in the open sea of the Gulf of Gabès in relation to the physical and chemical factors as well as the abundance of ciliates and copepods. We hypothesized that phytoplankton species should exhibit interspecific differences in relation to both the environmental variability and potential planktonic predators such as ciliates and copepods. To test these hypotheses, we explored the summer phytoplankton structure and biomass and their relationships with environmental factors together with ciliates as potential consumers, and copepods as potential competitors with ciliates upon phytoplankton prey. We used common statistical methods and both cluster and canonical correspondence analysis (CCA) to analyse the samples from 33 coast-to-offshore stations along 10 transects during a summer cruise in the Gulf of Gabès.

MATERIALS AND METHODS

Study area

This preliminary study was carried out in the Gulf of Gabès whose climate is dry (average precipitation: 210 mm) and

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sunny with strong easterly winds. The Gulf of Gabès (between $35°N$ and $33°N$) extends from 'Ras kapoudia' at the $35°N$ parallel level to the Tunisian–Libyan border (Figure 1) and includes various islands (Kerkennah and Djerba) and lagoons (Bougrara and El Bibane). Along the Tunisian coast, and during the cold period (winter–spring), the Atlantic water is characterized by low salinity very close to the surface. Conversely, during the other periods, higher salt content and more pronounced local circulation patterns within the water column suggest an enhancement of mixing and a weakening of the advection of the Atlantic water eastward. Semidiurnal tide characterized the Gulf of Gabès with a maximum range of about 2 m.

Sampling

Samples (N = 120) were collected in July 2005 in 33 coast-to-offshore stations on one cruise (Figure 1) with a conductivity–temperature–depth profiler (CTD: SBE 9, Sea-Bird Electronics, USA) equipped with a 12 Niskin bottle rosette sampler lowered from the surface to nearly the bottom. Water samples for physico-chemical (120 ml) phytoplankton and ciliate examination (1 l) were collected from 3 various depths (surface, middle of water column and bottom) in coastal stations between 20 m and <50 m deep; and from 5 various depths (surface, −10 m, −20 m, thermocline and bottom) in deeper stations >50 m in deep.

Physico-chemical factors

In each station, measurements of temperature, salinity and sigma-t (sigma-t = water density − 1000 kg. m^{-3}) were collected with the CTD profiler; pH was measured immediately after sampling using a Met Röhm® type pH meter. Samples for nutrient analysis were frozen immediately upon collection (−20°C, in the dark). Nutrients (NO_2^-, NO_3^-, NH_4^+, PO_4^{3-} and $Si(OH)_4$) and total-nitrogen (T-N) and total-phosphate (T-P) (after transformation into NH_4^+ and PO_4^{3-}, with potassium persulphate at 120°C, respectively) were analysed with a BRAN and LUEBBE type 3 autoanalyser and concentrations were determined colorimetrically using a UV-visible (6400/6405) spectrophotometer (APHA, 1992). We calculated also the N/P:DIN (DIN = NO_2^- + NO_3^- + NH_4^+) to DIP (DIP = PO_4^{3-}) and Si/Ni/Pi:silicate/DIN/DIP ratios. The concentration of the suspended matter was determined by measuring the dry weight of the residue after filtration of 1 l onto Whatman GF/C membrane.

For phytoplankton and ciliate enumerations, aliquots of discrete depth samples were preserved with Lugol's fixative (4% final concentration). Zooplankton were collected using a cylindro-conical net (30 cm aperture, 100 cm height and 100 μm mesh size) equipped with a flow meter. The net was towed obliquely from a depth near the bottom to the surface in each station during day and at night at a mean speed of 1 m s^{-1} for 10 minutes. After collection, zooplankton samples were rapidly preserved in 2% buffered formaldehyde solution (Drira et al., 2009).

Phytoplankton, ciliate and copepods enumeration

Sub-samples (50 ml) were counted under an inverted microscope after fixation with a Lugol (4%) iodine solution (Bourrelly, 1985) and settling for 24 to 48 hours using the Utermöhl method (1958) for phytoplankton and ciliate enumeration. Identification of algal taxa was achieved according to various keys (Tregouboff & Rose, 1957; Huber-Pestalozzi, 1968; Dodge, 1985; Balech, 1988; Tomas et al., 1996). Ciliate identifications were carried out according to Kofoid & Campbell (1929, 1939) and Balech (1959). Cell numbers were expressed as cells l^{-1} and biovolumes were calculated from cell dimensions (Lohman, 1908; Hillebrand et al., 1999), were converted to carbon biomass with the conversion factors proposed by Menden-Deuer & Lessard (2000): 1 μm^3 = 0.216 × 10^{-6} μgC, for all phytoplankton taxa except diatoms, and 1 μm^3 = 0.288×10^{-6} μgC, for diatoms. Samples for chlorophyll-a analysis (2 l), were filtered by vacuum filtration onto a 0.7 μm pore size and 47 mm-diameter glass fibre filter Whatman GF/F. Filters were then immediately stored at −20°C until analysis. Pigment analysis was performed by high performance liquid chromatography (HPLC) according to Pinckney et al. (2001).

Community structure was assessed by H′ diversity index of Shannon & Weaver (1949). We also calculated the evenness (J) proposed by Pielou (1975) to prevent weighting of H′ index by rare species; it is expressed as:
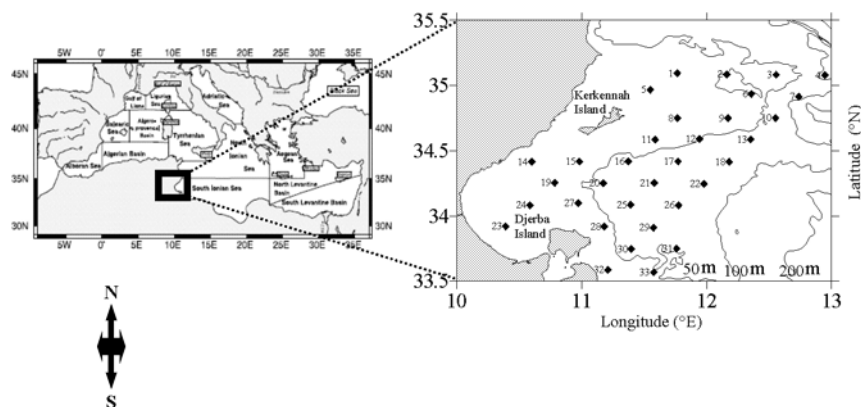
$$J = H' / \log_2 S,$$

Fig. 1. Map of the sampling stations in the Gulf of Gabès.

Table 1. Physical, chemical and biological parameters in neritic and deeper areas of the Gulf of Gabès in summer 2005.

| Biological and physico-chemical parameters	Neritic area			Deeper area		
	Minimum	Maximum	(Mean ± SD)	Minimum	Maximum	(Mean ± SD)
Physical parameters:						
Temperature (°C)	20.27	26.82	24.35 ± 1.99	21.65	24.75	22.79 ± 0.91
pH	8.34	8.471	8.40 ± 0.03	8.36	8.42	8.41 ± 0.03
Salinity (‰)	37.28	38.51	37.64 ± 0.37	37.10	37.81	37.33 ± 0.71
Sigma-t (kg m^{-3})	24.90	26.43	25.5 ± 0.42	25.60	26.26	25.92 ± 0.18
Suspended matter (mg l^{-1})	6.33	94.15	18.87 ± 22.40	6.88	36.5	14.66 ± 8.66
Wind speed (m s^{-1})	0.00	17.00	9.23 ± 4.00	4.00	17.00	9.69 ± 4.36
Chemical parameters:						
NO$_2$-N (μmol l^{-1})	0.20	0.56	0.37 ± 0.11	0.25	0.43	0.33 ± 0.06
NO$_3$-N (μmol l^{-1})	0.98	1.69	1.45 ± 0.21	0.95	1.75	1.36 ± 0.23
NH$_4$-N (μmol l^{-1})	0.26	0.90	0.62 ± 0.16	0.21	0.77	0.57 ± 0.16
PO$_4$-P (μmol l^{-1})	0.03	0.13	0.06 ± 0.02	0.04	0.18	0.07 ± 0.03
Total-N (μmol l^{-1})	11.24	14.51	12.91 ± 1.22	10.90	13.50	12.34 ± 0.61
Total-P (μmol l^{-1})	1.38	1.68	1.52 ± 0.08	1.51	1.75	1.61 ± 0.08
Silicate (μmol l^{-1})	0.25	4.56	1.77 ± 1.33	0.25	4.79	2.15 ± 1.20
N/P ratio	20.20	84.43	47.03 ± 17.64	14.06	53.03	38.66 ± 9.80
Si/Ni/Pi ratio	0.02	0.05	0.03 ± 0.01	0.03	0.09	0.05 ± 0.02
Biological parameters:						
Chlorophyll-a concentration (μg l^{-1})	0.04	0.26	0.05 ± 0.05	0.00	0.14	0.03 ± 0.04
Total phytoplankton density (cells l^{-1})	2.40×10^3	23.05×10^4	$2.88 \times 10^4 \pm 5.37 \times 10^4$	2.10×10^3	4.22×10^4	$1.60 \times 10^4 \pm 1.19 \times 10^4$
Dictyochophyceae density (cells l^{-1})	0	11.26×10^4	$8.08 \times 10^3 \pm 3.01 \times 10^4$	0	20	1.42 ± 5.34
Dinophyceae density (cells l^{-1})	6×10^2	3.86×10^3	$1.72 \times 10^3 \pm 0.86 \times 10^3$	5.33×10^2	3.80×10^3	$1.87 \times 10^3 \pm 0.89 \times 10^3$
Cyanobacteriae density (cells l^{-1})	0	6.05×10^3	$0.86 \times 10^3 \pm 1.50 \times 10^3$	33.33	7.84×10^3	$1.39 \times 10^3 \pm 2.03 \times 10^3$
Bacillariophyceae density (cells l^{-1})	2.33×10^2	72.30×10^3	$5.78 \times 10^3 \pm 1.91 \times 10^4$	25	7.75×10^3	$2.26 \times 10^3 \pm 2.40 \times 10^3$
Euglenophyceae density (cells l^{-1})	0	6.00×10^2	$0.83 \times 10^2 \pm 1.67 \times 10^2$	0	1.4×10^2	$0.17 \times 10^2 \pm 0.38 \times 10^2$
Total phytoplankton biomass (μgC l^{-1})	9.07	7.87×10^2	$1.32 \times 10^2 \pm 2.29 \times 10^2$	6.23	9.10×10^2	$2.89 \times 10^2 \pm 2.59 \times 10^2$
Dictyochophyceae biomass (μgC l^{-1})	0	48.4×10^{-3}	$1.42 \times 10^{-3} \pm 2.29 \times 10^{-3}$	0	0.98×10^2	$0.26 \times 10^2 \pm 0.07 \times 10^2$
Dinophyceae biomass (μgC l^{-1})	1.63	1.65×10^2	22.27 ± 41.04	3.28	25.46	9.29 ± 5.48
Cyanobacteriae biomass (μgC l^{-1})	0	21.72	5.41 ± 6.57	0	2.14×10^2	25.74 ± 56.82
Bacillariophyceae biomass (μgC l^{-1})	1.01	7.65×10^2	$1.04 \times 10^2 \pm 2.06 \times 10^2$	0	8.74×10^2	$2.47 \times 10^2 \pm 2.27 \times 10^2$
Euglenophyceae biomass (μgC l^{-1})	0	67.39×10^{-3}	$3.74 \times 10^{-3} \pm 15.88 \times 10^{-3}$	0	76.82×10^{-2}	$15.81 \times 10^{-2} \pm 22.01 \times 10^{-2}$
Total ciliates density (cells l^{-1})	0	733.33	95 ± 166	0	133.33	44.87 ± 44.67
Total copepods density (ind m^{-3})	1.14×10^2	3.37×10^4	$5.78 \times 10^3 \pm 9.12 \times 10^3$	1.57×10^2	4.25×10^3	$1.07 \times 10^3 \pm 1.10 \times 10^3$
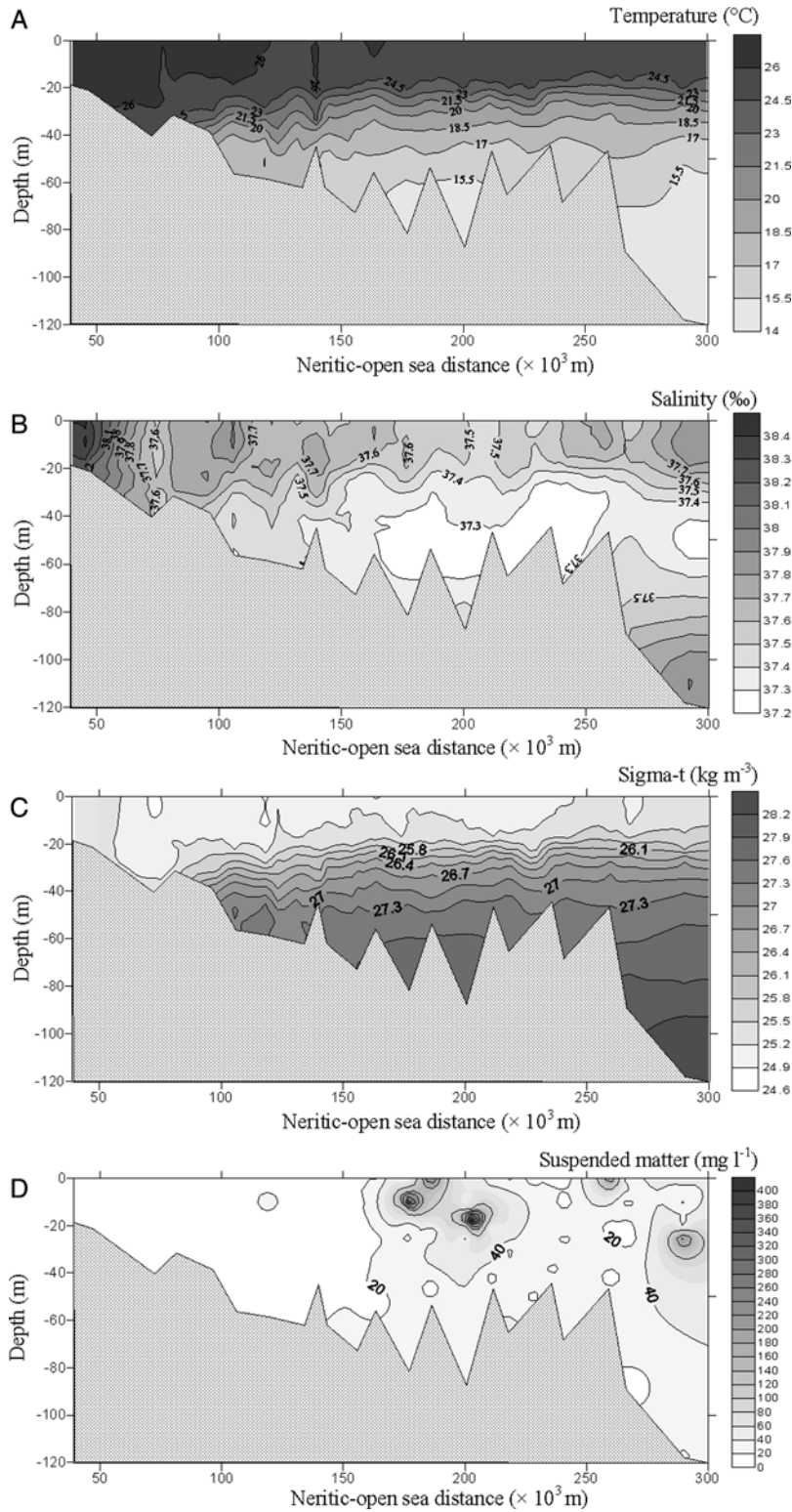
Fig. 2. Contour plots of temperature (A), salinity (B), sigma-t (C) and suspended matter (D) along a longitudinal gradient in the 0–120 m layer.

where

$$H'_{\max} = \log_2 S$$

S: number of species of the community.

Copepods were stained with rose Bengal to identify their internal tissues and to facilitate the dissection of various appendices and of leg 5 of the different species. Copepods were identified according to Rose (1933) and Bradford-Grieve *et al.* (1999) and counted under a vertically mounted deep-focus dissecting microscope (Olympus TL 2). The zooplankton density was expressed as: $X = N/((\Pi r^2 s)/3)$, where N = number of individuals sampled, r = 15 cm: half of the diameter of the plankton net and s = turn numbers shown by the flowmeter (Drira *et al.*, 2009).
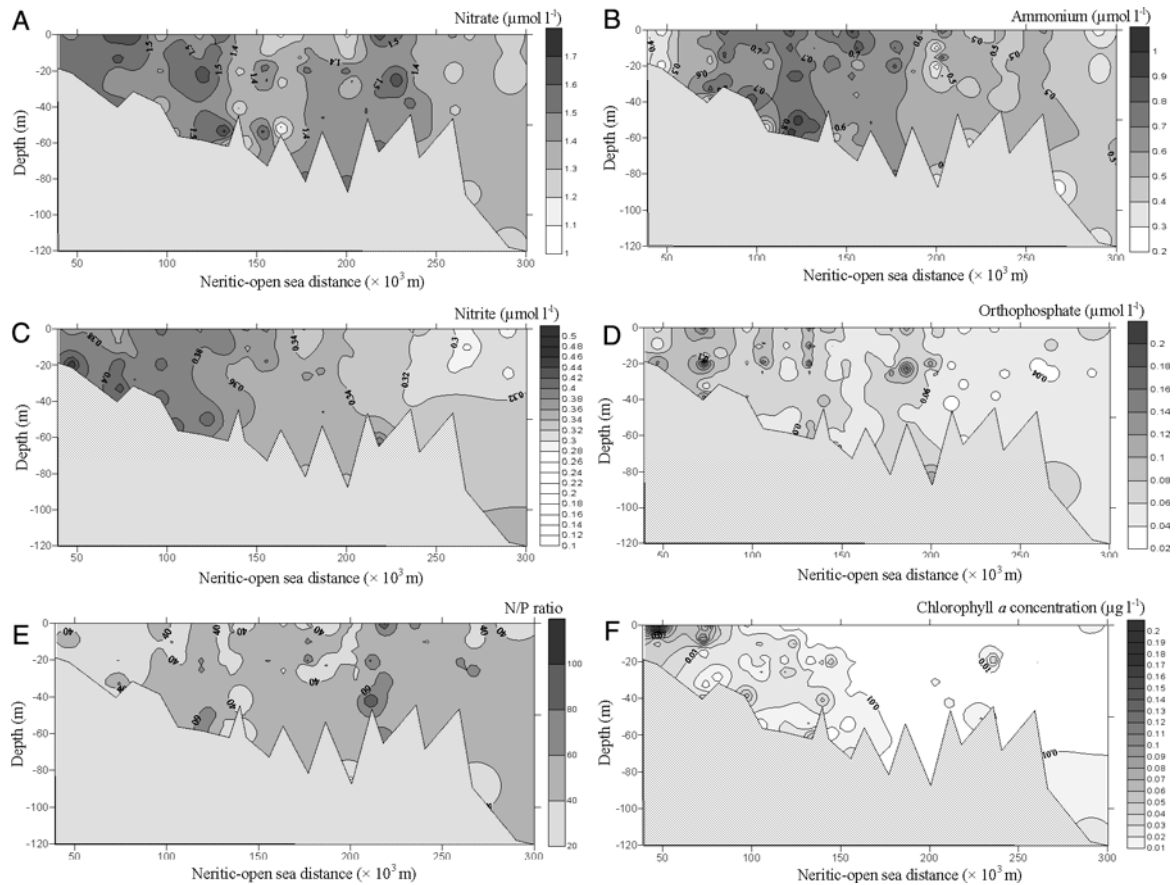
Fig. 3. Spatial distribution of nitrate (A), ammonium (B), nitrite (C), orthophosphate (D) concentrations and N/P ratios (E) and chlorophyll-*a* concentration (F) along a longitudinal gradient in the 0–120 m layer.

Statistical analysis

Mean and standard deviation (SD) are reported when appropriate. The potential relationships between variables were tested by Pearson's correlation coefficient using XL-stat software. Cluster analysis (CA) was performed using PRIMER v5.0 for Windows XP (Clarke & Gorley, 2001) to identify significant differences between study stations in the distribution of phytoplankton populations. CA was undertaken according to the Ward-algorithmic method. Results are illustrated in a dendrogram where steps in the hierarchical clustering solution and values of the squared Euclidean distances between clusters are shown.

A canonical correspondence analysis (CCA) was applied to physical (temperature, salinity and sigma-t), chemical (NO_3^-, NO_2^-, NH_4^+, PO_4^{3-}, T-N, T-P, N/P ratio, $Si(OH)_4$ and Si/Ni/Pi ratio) and biological parameters (chlorophyll-*a* concentration, total phytoplankton, Dictyochophyceae, Bacillariophyceae, Dinophyceae, Cyanobacteriae, Euglenophyceae and total ciliates, copepods densities) assessed by over 33 observations (33 stations) were considered (Ter-Braak, 1986).

Physico-chemical parameters

The physico-chemical characteristics of the study are summarized in Table 1. The temperature of coastal waters was

higher than that offshore and it decreased from surface to bottom (Table 1; Figure 2A). The pH was distributed homogeneously throughout all the monitoring stations (Table 1). The lowest salinity (37.20‰) was recorded in the deeper stations, in Station 2 at a mean depth of 52 m; whereas the highest was in coastal waters (38.51‰), in Station 24 at a mean depth of 33 m (Table 1; Figure 2B). The salinity minima are generally considered as characteristics of the Modified Atlantic Water (MAW) (Astraldi *et al.*, 2002). Moreover, the isohaline of 37.5‰ has been used to define the interface between Atlantic and Mediterranean waters (Rodriguez *et al.*, 1998). Sigma-t, mainly driven by the temperature, was homogeneously distributed both along the coast and in the open sea (Table 1; Figure 2C). It exhibited a high gradient from the surface to the bottom. The stratified layer corresponding to the sigma-t level between 25.5 and 26.7 kg m^{-3} is situated roughly at 25 m deep. This causes the confinement of the cool MAW in the deep water layers, which corroborated with the description of the MAW circulation in the Ionian Sea made by Béranger *et al.* (2004). At 50 m depth, high sigma-t coincided with both low salinity (r = −0.242, $P < 0.05$, df = 119) and temperature (r = − 0.816, $P < 0.001$, df = 119) (Figure 2A–C). However, the coast is characterized by a low sigma-t and a high salinity (r = −242, $P < 0.05$, df = 119) probably as a result of water evaporation. Concentrations of suspended matter in neritic stations were higher than in the open sea (Table 1). Nitrate, which was the dominant nitrogen form, was concentrated chiefly in coastal waters. Orthophosphate concentrations
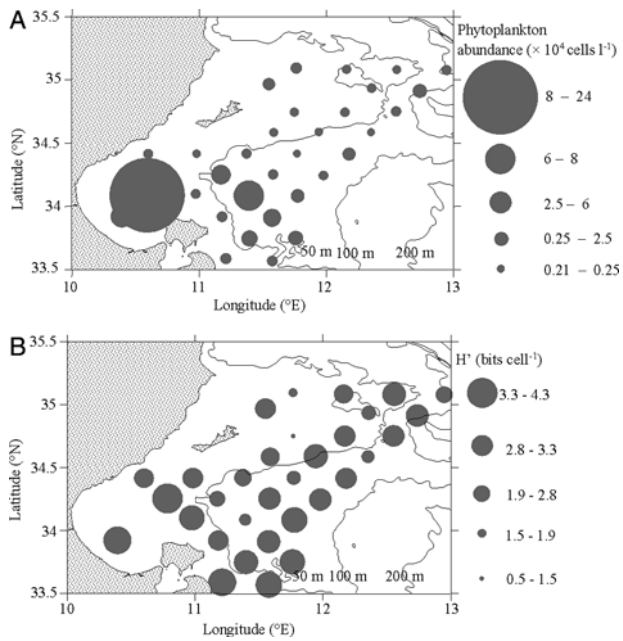
Fig. 4. The spatial distribution of total phytoplankton abundance (A) and the diversity index (B) in the Gulf of Gabès in July 2005.

were rather low and did not exceed 0.2 µmol l^{-1}; highest concentrations were recorded in the coastal area, whereas in the offshore area concentrations were below the limit of 0.06 µmol l^{-1}. Total nitrogen and total phosphate were homogeneously distributed throughout the neritic and deeper areas (Table 1). However, N/P: DIN (DIN $=$ NO$_2^-$ $+$ NO$_3^-$ $+$ NH$_4^+$) to DIP (DIP $=$ PO$_4^{3-}$) ratio was generally greater than the Redfield ratio (16) which suggests potential P limitation. N/P ratio of coastal waters (mean $\pm$ SD $=$ 47.03 $\pm$ 17.64) was higher than deeper waters (mean $\pm$ SD $=$ 38.66 $\pm$ 9.80) (Table 1; Figure 3A–E). Silica concentrations were slightly more important in deeper stations (2.15 $\pm$ 1.20 µmol l^{-1}) than in neritic areas

(1.77 $\pm$ 1.33 µmol l^{-1}) (Table 1) contributing to a higher Si/Ni/Pi ratio in deeper stations (0.05 $\pm$ 0.02) than in coastal (0.03 $\pm$ 0.01) areas.

Phytoplankton community structure

The phytoplankton community consisted of Dictyochophyceae (represented by only one taxon *Dictyocha fibula*), Dinophyceae (78 taxa), Bacillariophyceae (33 taxa), Cyanobacteriae (5 taxa) and Euglenophyceae (one taxon, *Euglena acusformis*) which contributed 41, 25, 16, 17 and 1% of the total abundance, respectively. The diversity of the phytoplankton community was less pronounced on the coast of the gulf than in the open sea (Figure 4A, B; Table 2A, B). This was especially clear in Station 24 where *D. fibula* dominated (H′: 0.86, J: 0.20, Table 2A; Figure 4) reflecting presumably favourable growth conditions along the coast. This also applied to Stations 1 and 8 where the relative abundance of the cyanobacterium *Pseudoanabaena galeata*, resulted in a low diversity of the assemblage (Table 2A). The phytoplankton community was more abundant on the coast of the gulf than in the deeper areas (Table 1). Total density ranged from 2.1×10^3 to 2.3×10^5 cells l^{-1} (mean $\pm$ SD $=$ 2.3 10^4 $\pm$ 4.0×10^4 cells l^{-1}) (Figure 4A; Table 2A, B; Table 3). The phytoplankton community consisted of Dictyochophyceae (represented by only one taxon, *Dictyocha fibula*), Dinophyceae (78 taxa), Bacillariophyceae (33 taxa), Cyanobacteriae (5 taxa) and Euglenophyceae (one taxon, *Euglena acusformis*) which contributed 41, 25, 16, 17 and 1% of the total abundance, respectively (Figure 5). Diversity of the five groups was more pronounced on the coast of the gulf than on the open sea (Figure 4B). In terms of biomass, diatoms were the dominant group accounting for 45% of the total cell carbon (Figure 5). Dinophyceae abundance was significantly higher in both in-shore and off-shore areas (Table 1; Table 3; Figure 6), and so it was the case for diatoms. Dictyochophyceae were exclusively neritic (Table 1; Table 3; Figure 6). Cyanobacteriae were found throughout the water column and were more concentrated in the thermocline within the deeper

Table 2A. Quantitative and structural characteristics of the phytoplankton community sampled in neritic (A) and deeper (B) areas in the Gulf of Gabès during July 2005.

Stations	Phytoplankton abundance ($\times 10^4$ cells l^{-1})	Abundance of dominant species ($\times 10^4$ cells l^{-1})	Species number	Percentage of dominant species (%)	Diversity index (bits cell^{-1})	Evenness	Dominant species
1	1.43	0.87	13	61	1.83	0.43	*Pseudoanabaena galeata*
2	0.72	0.31	19	43	2.99	0.70	Dinocysts
3	0.53	0.22	22	41	3.48	0.82	*Pseudoanabaena galeata*
5	1.75	0.86	28	49	3.16	0.75	*Pseudoanabaena galeata*
6	0.81	0.74	18	91	2.45	0.58	Dinocysts
8	0.63	1.66	13	25	1.33	0.31	*Pseudoanabaena galeata*
9	0.79	0.42	26	53	3.20	0.76	Dinocysts
11	0.56	0.26	16	46	2.92	0.69	Dinocysts
14	0.98	0.29	17	30	3.03	0.71	*Biddulphia pulchella*
23	5.00	0.73	32	15	3.96	0.93	*Thalassionema nitzschoides*
24	23.05	20.80	51	90	0.86	0.20	*Dictyocha fibula*
25	7.87	3.78	37	48	2.18	0.51	*Trichodesmium erythraeum*
27	0.87	0.50	34	57	3.66	0.86	Dinocysts
28	1.20	0.78	28	65	3.11	0.73	*Ceratium furca*
30	3.03	0.62	32	20	3.53	0.83	*Trichodesmium erythraeum*
32	1.34	0.29	34	21	3.95	0.93	Dinocysts
33	1.16	0.29	25	25	3.79	0.89	Dinocysts

Table 2B.

Stations	Phytoplankton abundance ($\times 10^4$ cells l^{-1})	Abundance of dominant species ($\times 10^4$ cells l^{-1})	Species number	Percentage of dominant species (%)	Diversity index (bits cell^{-1})	Evenness	Dominant species
4	1.02	0.48	17	47	2.71	0.64	Dinocysts
7	2.31	0.36	28	16	3.37	0.79	Dinocysts
10	1.07	0.26	21	24	3.29	0.77	Dinocysts
12	0.40	0.10	18	25	3.55	0.84	Dinocysts
13	1.02	0.48	10	47	2.71	0.64	*Spirulina subsalsa*
15	0.40	0.35	22	87	3.14	0.74	Dinocysts
16	0.98	0.37	17	37	2.77	0.65	Dinocysts
17	0.21	0.51	10	52	2.28	0.53	Dinocysts
18	1.96	0.50	22	25	3.22	0.76	*Guinardia delicatula*
19	1.16	0.23	33	20	3.43	0.81	Dinocysts
20	4.22	1.67	30	40	2.59	0.61	*Biddulphia pulchella*
21	1.04	0.14	16	13	3.33	0.79	*Chaetoceros* sp.
22	0.79	0.31	18	39	3.34	0.79	Dinocysts
26	2.17	0.67	32	31	3.73	0.88	Dinocysts
29	3.69	1.37	35	37	4.22	1.00	*Guinardia delicatula*
31	2.58	0.65	33	25	3.67	0.87	Dinocysts

Table 3. The main phytoplankton taxa and their relative percentage in neritic and deeper areas of the Gulf of Gabès during July 2005.

	Abundance (%)	
	Neritic stations	Deeper stations
Total phytoplankton	68	32
Dictyochophyceae	100	0
Dictyocha fibula	100	0
Dinophyceae	65	35
Amphidinium sp.	2	1
Amphidinium ovoideum	–	2
Ceratium extensum	–	1
Ceratium furca	7	–
Dinocysts	42	59
Gyrodinium fusiforme	2	2
Hermesinium sp.	6	–
Karenia selliformis	6	8
Karenia papilionacea	1	3
Prorocentrum gracile	7	–
Prorocentrum lima	1	–
Protoperidinium depressum	–	1
Protoperidinium globulum	–	1
Protoperidinium sp.	5	4
Cyanobacteriae	81	19
Anabaena sp.	7	11
Microcystis sp.	–	3
Trichodesmium erythraeum	46	27
Pseudoanabaena galeata	47	58
Spirulina subsalsa	–	1
Bacillariophyceae	71	29
Biddulphia pulchella	8	17
Chaetoceros sp.	6	4
Coscinodiscus sp.	8	1
Ditylum brightwellii	3	2
Guinardia delicatula	9	26
Hemiaulus hauckii	24	17
Navicula sp.	11	16
Nitzschia sicula	5	3
Pleurosigma simonsenii	–	2
Rhizosolenia sp.	4	7
Thalassionema nitzschioides	10	–
Euglenophyceae	43	57
Euglena acusformis	100	100

zone (Table 1; Figure 6). This pattern is clearly illustrated by the dendrogram from the cluster analysis which shows 2 clusters at a linkage distance of 80%; cluster 1 segregates exclusively Cyanobacteriae and cluster 2 the remaining groups (Figure 7A). In addition, chlorophyll-*a* concentrations were higher along the coast than in offshore areas (Table 1; Figure 3F) and associated with the development of Dictyochophyceae (r = 0.775, $P < 0.0001$, df = 119), Dinophyceae (r = 0.760, $P < 0.0001$, df = 119), Bacillariophyceae (r = 0.829, $P < 0.0001$, df = 119) and Euglenophyceae (r = 0.780, $P < 0.0001$, df = 119) but no significant correlation was found with Cyanobacteriae (Table 4). The CCA allowed the discrimination of two groups around the F1 and F2 axes components (Figure 8) explaining 95.79% of the variance. These axes components selected positively the group G1 the biological parameters (chlorophyll-*a*, total phytoplankton, Dictyochophyceae, Bacillariophyceae, Dinophyceae, Euglenophyceae and total ciliates) with several physico-chemical (temperature, salinity, sigma-t, NO_2^-, PO_4^{3-}, T-N and T-P). F1 axis, which extracted 75.15% of the variability selected positively group G2 formed by copepods and NO_3^-, and group G3 composed of Cyanobacteriae and N/P ratio. This association confirms observations that phytoplankton abundance decreases with depth and is more concentrated in the coastal areas than in the open sea. In addition, the different
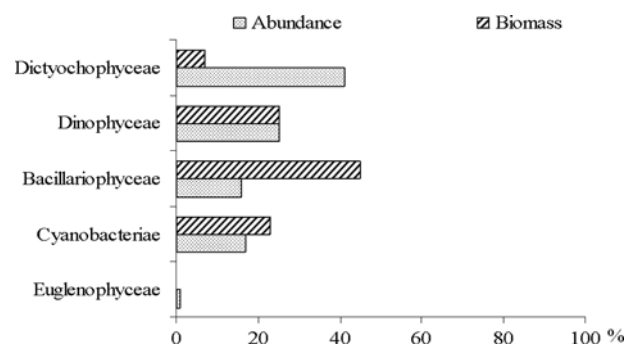

Fig. 5. Relative abundance and biomass of the different phytoplankton groups.
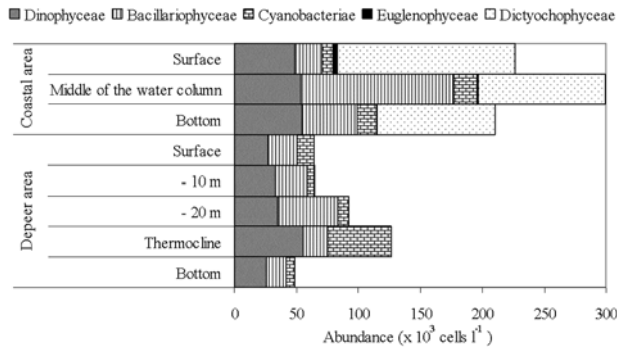
Fig. 6. Spatial and vertical distribution of the five phytoplankton groups along the water column in neritic and deeper areas of the Gulf of Gabès.

phytoplankton group depends on the nutrient availability (nitrate, nitrite, ammonium, orthophosphates, total-N and total-P) and especially on N/P ratios which seem to be the determining regulator of phytoplankton taxa. This association reflects the close links between the distribution of Dictyochophyceae and Dinophyceae ($r = 0.461$, $P < 0.05$, df = 119), between Dinophyceae and Bacillariophyceae ($r = 0.511$, $P < 0.05$, df = 119) and between Dinophyceae and Euglenophyceae ($r = 0.571$, $P < 0.05$, df = 119) (Table 4). We also found a significant correlation between nitrate concentrations and Dinophyceae abundance ($r = 0.539$, $P < 0.05$, df = 119), between Dictyochophyceae and total-N ($r = 0.368$, $P < 0.05$, df = 119) as well as between Euglenophyceae and total-N ($r = 0.457$, $P < 0.05$, df = 119) (Figure 7A; Table 4). These correlations confirm that the phytoplankton abundance was higher along the nutrient-rich coast than in the open sea. Clearly, there is a separation of nutrient-rich water masses with enhanced salinity along the coast (with high phytoplankton abundances) from poor-nutrient water masses with low salinity in the off-shore.

The spatial distribution of phytoplankton total abundance according to coastal–open sea gradient together with the prevailing potential predators (total ciliates and copepods) is illustrated in Figure 9. The abundance of phytoplankton (dominated by opportunistic *Dictyocha fibula*) and ciliates (dominated by the Tintinnid *Tintinnopsis* which accounted for 90% of total ciliate abundance) showed significant correlation for both groups ($r = 0.836$, $P < 0.0001$, df = 119). However, the abundance of phytoplankton did not correlate with that of copepods ($r = 0.023$, $P < 0.05$, df = 119) (Figure 9A–C). This was also confirmed by the CCA showing a linked ecological relationship between phytoplankton and ciliates while copepods seemed to be an independent planktonic group (Figure 7B).

DISCUSSION

The results indicate that the summer spatial distribution of phytoplankton assemblages along the coast and in the open sea was influenced by various environmental factors. On the whole, the phytoplankton community is more concentrated along the coast and especially near Djerba Island than in the deeper area. The striking finding is the strong proliferation in coastal samples of *D. fibula* (41% of the total phytoplankton abundance). Because of high surface to volume ratio, small cells like *D. fibula* take up nutrients, with low energy cost,
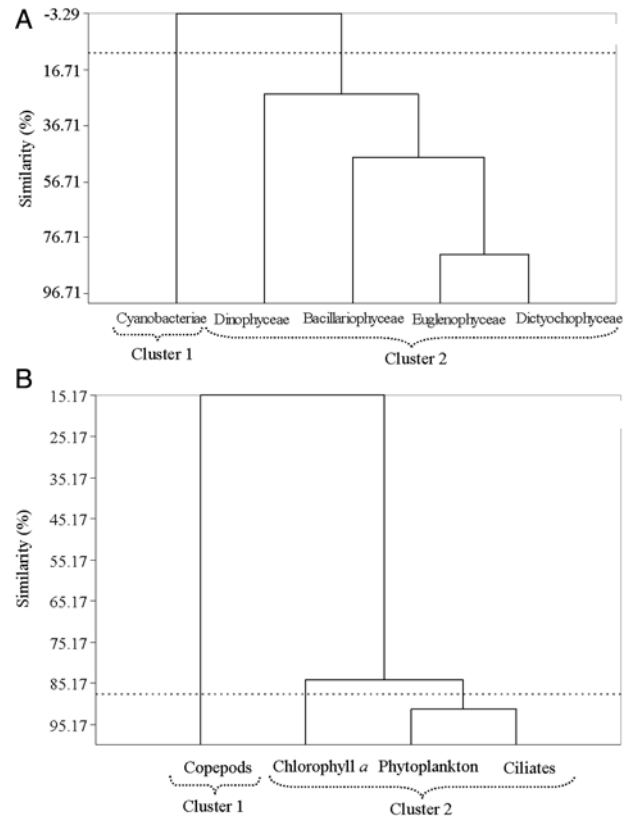

Fig. 7. Dendrogram of the Euclidean distance between the five phytoplankton algal groups recorded (A) and between planktonic communities (total phytoplankton, ciliates and copepods) and chlorophyll-a (B) in the Gulf of Gabès in summer 2005.

reaching numerous assimilation surface points (Aleya, 1989; Agawin *et al.*, 2000) and thus outperform large cells (Raven, 1998; Sin & Wetzel, 2000). High concentrations of *D. fibula* have also been observed in the French bay of Villefranche (Gomez & Gorsky, 2003) and in Mersin Bay (Eker & Kideys, 2000). However, these authors reported a decrease in the Dictyochophyceae abundance with increasing temperature, contrasting with our results which showed a warmer ($24.35 \pm 1.99°C$) water column along the coast than in the open sea ($22.79 \pm 0.91°C$), but conforming with those reported in the Gulf of Trieste (northern Adriatic) where *D. fibula* developed with a temperature optimum $>20°C$ (Fanuko, 1989). Other marine environments harbour the genus *Dictyocha*, especially the Mexican Pacific coasts (Hernandez-Becerril & Brovo-Sierra, 2001) and the North Pacific (Onodera & Takahashi, 2005) where *D. fibula and D. californica* remarkably dominated the phytoplankton community.

Nitrogen, which is the most common element limiting phytoplankton growth in most marine ecosystems (Vitousek & Howarth, 1991; Livingston, 2001), was found at substantial amounts along the coast of the Gulf of Gabès, while orthophosphate concentrations were low and N/P was higher than the Redfield ratio (16). This suggests that phosphate is more likely than nitrogen might be to limiting yields and to attainable growth rates. Furthermore, chlorophyll-a concentration (mean $\pm$ SD = 0.05 ± 0.05 µg l^{-1}) is found in the Gulf of Gabès, a trend largely reported in the Mediterranean Sea: (0.40 µg l^{-1}) on the Israeli coast
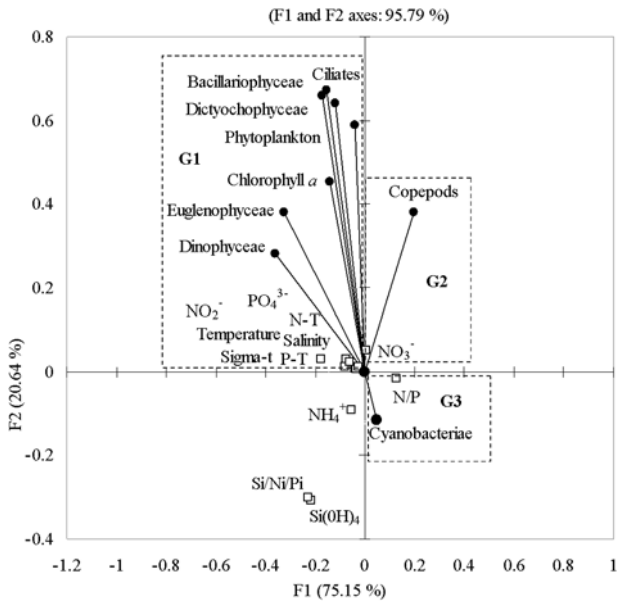
Fig. 8. Results of canonical correspondence analysis (CCA) of biological parameters (chlorophyll-*a* concentration, total and phytoplankton groups, ciliates and copepods) and selected environmental variables in the Gulf of Gabès during July.

Fig. 9. Spatial distribution of total phytoplankton (A), copepods (B) and ciliate densities (C) along neritic open-sea distance.

(eastern Mediterranean Sea) (Gitelson *et al.*, 1996); in the Alboran Sea (Corsini *et al.*, 2002; D'Ortenzio *et al.*, 2002); in the Gulf of Lions (0.06–0.10 μg l^{-1}) (Bosc *et al.*, 2004) and in the coastal north-western Mediterranean Sea (0.50 μg l^{-1}) (Bustillos-Guzman *et al.*, 1995). In the off shore of the Gulf of Gabès, low chlorophyll-*a* concentration together with an N/P ratio higher than the Redfield ratio indicate that this ecosystem is oligotrophic (OECD, 1982; Vollenweider *et al.*, 1992), confirming the observations reported from the off shore of the eastern Mediterranean basin (Krom *et al.*, 1991; Heurt *et al.*, 2005). However, the coastal area is showing signs of progressive eutrophication (Smaoui-Damak *et al.*, 2003, 2006). This difference in the trophic status between the coastal and open sea areas is also illustrated by the difference in the size of the sampled dinoflagellates, with larger taxa, such as *Ceratium* (mean size $\pm$ SD = $2.16 \times 10^2 \pm 2 \times 10^2$ μm), dominating in coastal waters; whereas smaller cells such as *Protoperidinium* (mean $\pm$ SD = 41.26 ± 18.56 μm), were exclusively oceanic ($>$100 km). Overall, the offshore eastern Mediterranean basin is oligotrophic (Krom *et al.*, 1991; Heurt *et al.*, 2005; Thingstad *et al.*, 2005) characterized by the dominance of dinoflagellates. A similar phytoplankton community size-structure was found in the oligotrophic Levantine Basin of the eastern Mediterranean (Kress *et al.*, 2005) and in the Strait of Gibraltar (Gomez *et al.*, 2000). Moreover, because of the lack of deep mixing along the coast due to stratification, which gives an advantage to motile cells over non-motile ones (e.g. diatoms) (Paerl, 1997), dinoflagellates thrived along the coastal sea. Similar observations were reported in the Bay of Villefranche in the north-western Mediterranean Sea (Gomez & Gorsky, 2003) and in the hypertrophic costal waters of Tokyo Bay (Matsuoka *et al.*, 2003). The Bacillariophyceae density in the Gulf of Gabès was significantly correlated with N/P (r = 0.473, *P* < 0.05, df = 119) and NO$_3^-$ (r = 0.494, *P* < 0.05, df = 119), concurring with previous results showing the well-known opportunistic
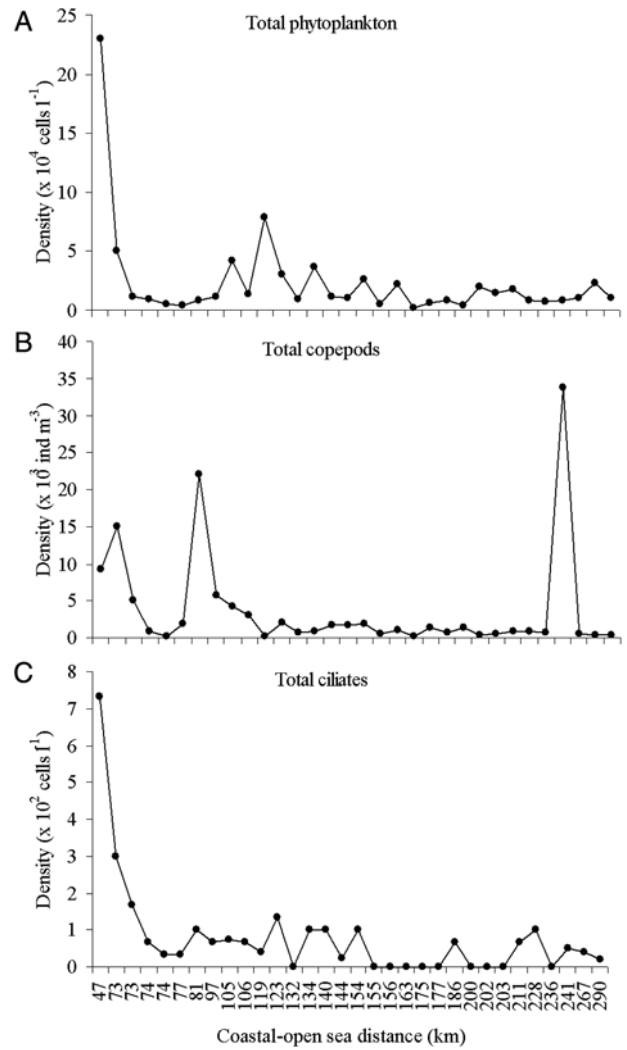
strategy of this group as far as taking advantage of the nutrient availability is concerned (Fogg, 1991; Aleya, 1992). Despite having an obligatory requirement for silica, the diatoms in the Gulf of Gabès were weakly correlated with silicate concentrations, probably due to excess of silica compared to the other nutrients.

Cyanobacteriae developed throughout the whole water column with a high density recorded in the thermocline and associated with *Trichodesmium erythraeum* and *Pseudoanabaena galeata* which contributed 41 and 50% of the total cyanobacterial abundance, respectively. In these layers, Cyanobacteriae abundances were correlated with both NO$_3^-$ (r = 0.343, *P* < 0.05, df = 119) and NH$_4^+$ (r = 0.344, *P* < 0.05, df = 119), and a significant correlation was recorded between Cyanobacteriae and N/P (r = 0.566, *P* < 0.05, df = 119). This indicates that the cyanobacterial growth was probably induced by the nitrate replenishment of the upper stratified layers after release by the thermocline.

The spatial distribution of the abundance of phytoplankton, ciliates (dominated by the genus *Tintinnopsis*) and copepods (dominated by two species *Oithona nana* and *Acartia clausi*; Drira *et al.*, 2009) suggests that the community of ciliates were consuming larger numbers of phytoplankton, especially

Table 4. Correlation matrix (Pearson test) made with Xl-stat for physical, chemical and biological variables under study in the Gulf of Gabès during summer 2005 (*$P < 0.05$; ***$P < 0.0001$; number of parameters $= 18$ and number of analysed samples: N $= 120$).

	Salinity	Temperature	δ^t	Chl-a	NO$_2^-$	NO$_3^-$	NH$_4^+$	PO$_4^{3-}$	T-N	T-P	Silicate	N/P	Si/Ni/Pi	Dictyochohyceae	Dinophyceae	Cyanobacteriae	Bacillariophyceae	Euglenophyceae	Phytoplankton	Copepods	Ciliates
Salinity	1																				
Temperature	0.236	1																			
Sigma-t	−0.242	***−0.816	1																		
Chlorophyll a	*0.461	*0.400	−0.156	1																	
NO$_2^-$	0.286	*0.391	−0.345	0.329	1																
NO$_3^-$	0.041	0.019	0.059	0.158	*0.437	1															
NH$_4^+$	0.325	0.193	*−0.435	−0.032	0.197	−0.026	1														
PO$_4^{3-}$	0.185	*0.415	−0.25	0.063	0.264	0.228	0.063	1													
T-N	0.325	*0.394	*−0.511	0.335	0.087	0.047	0.12	0.154	1												
T-P	*−0.376	*−0.491	*0.442	−0.137	−0.114	0.181	−0.104	−0.005	−0.273	1											
Silicate	0.029	0.029	−0.057	−0.144	−0.128	*−0.623	0.185	−0.044	−0.193	−0.102	1										
N/P	−0.114	−0.438	0.236	−0.079	0.056	0.339	−0.003	***−0.760	−0.102	0.113	−0.318	1									
Si/Ni/Pi	−0.035	−0.036	0.015	−0.201	−0.275	***−0.724	0.053	−0.099	−0.208	−0.088	***0.975	−0.338	1								
Dictyochphyceae	0.353	0.326	−0.108	***0.775	0.245	0.382	−0.382	0.106	*0.368	0.01	−0.258	−0.126	−0.238	1							
Dinophyceae	0.365	*0.499	−0.281	***0.760	0.325	0.539	0.116	0.204	0.332	−0.174	0.006	−0.184	−0.067	*0.461	1						
Cyanobacteriae	0.043	0.139	−0.227	0.183	−0.039	0.343	0.334	−0.112	−0.009	−0.275	0.053	0.566	0.03	−0.047	0.149	1					
Bacillariophyceae	0.351	0.346	−0.128	***0.829	0.266	0.494	−0.346	0.094	0.367	0.003	−0.266	0.473	−0.254	***0.990	*0.511	0.008	1				
Euglenophyceae	*0.449	*0.476	−0.262	***0.780	*0.415	0.022	−0.206	0.161	*0.457	−0.073	−0.06	−0.166	−0.086	***0.870	*0.571	−0.074	***0.881	1			
Phytoplankton	0.107	0.105	0.014	*0.744	0.068	0.019	0.072	0.002	0.110	0.000	0.065	0.002	0.064	***0.868	0.325	0.044	***0.930	***0.696	1		
Copepods	0.032	0.110	0.008	0.043	0.000	0.047	0.000	0.004	0.009	0.028	0.048	0.012	0.057	0.024	0.048	0.023	0.019	0.028	0.010	1	
Ciliates	0.195	0.120	0.021	0.681	0.102	0.034	0.080	0.014	0.152	0.000	0.063	0.008	0.069	***0.908	0.339	0.001	***0.917	***0.767	***0.836	0.023	1

Dictyocha fibula (r = 0.836, P < 0.0001, df = 119). In addition, there was a significant trend of increasing abundance in copepods coinciding with decreases in ciliate abundances. Although we did not conduct grazing experiments, these related patterns suggest that a competition between ciliates and copepods might have occurred for phytoplankton prey. Our assumption may be supported by the results reported from other aquatic environments where a substantial amount of the ciliate biomass was cleared by filter-feeding copepods (Lampert *et al.*, 1986; Atkinson, 1996; Pérez *et al.*, 1997) as well as in laboratory conditions (Hartmann *et al.*, 1993).

CONCLUSION

The phytoplankton community structure in the Gulf of Gabès showed clear variations along a coastal–open sea transect during a summer preliminary study achieved in July 2005. The phytoplankton community found along the coast was dominated by opportunistic small-sized species (e.g. *D. fibula*) that thrived as favoured by the nutrient-rich coast. The Gulf of Gabès is characterized by a summer stratification which impacts on phytoplankton development chiefly in the off-shore area, and the assemblage of different water masses; namely the Mediterranean water and the MAW could be determining factors of phytoplankton dynamics. On the other hand, trophic interplay between phytoplankton, ciliates and copepods suggests that factors other than hydrographic conditions and nutrients were also implicated in the environmental forcing of the summer phytoplankton dynamics in the Gulf of Gabès. In addition, phytoplankton may serve as a substantial food link between ciliates and copepods towards higher trophic levels of this area.

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